

RESEARCH ARTICLE

Behavioural and kinematic components of the fast-start escape response in fish: individual variation and temporal repeatability

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SUMMARY

Inter-individual variation in physiological performance traits, which is stable over time, can be of potential ecological and evolutionary significance. The fish escape response is interesting in this regard because it is a performance trait for which inter-individual variation may determine individual survival. The temporal stability of such variation is, however, largely unexplored. We quantified individual variation of various components of the escape response in a population of European sea bass (*Dicentrarchus labrax*), considering both non-locomotor (responsiveness and latency) and locomotor (speed, acceleration, turning rate, turning angle and distance travelled in a fixed time, D_{esc}) variables. We assessed whether variation in performance was temporally stable and we searched for any trade-offs among the components of the response that might explain why the variation persisted in the population. The coefficient of variation was high for all components, from 23% for turning rate to 41% for D_{esc} , highlighting the non-stereotypic nature of the response. Individual performance for all variables was significantly repeatable over five sequential responses at 30 min intervals, and also repeatable after a 30 day interval for most of the components. This indicates that the variation is intrinsic to the individuals, but there was no evidence for trade-offs amongst the components of the response, suggesting that, if trade-offs exist, they must be against other ecologically important behavioural or performance traits.

Key words: fast start, individual variation, repeatability, sea bass, fish, swimming performance, escape response, anaerobic performance, stereotype.

INTRODUCTION

The fast-start escape response is the main locomotor behaviour that fish use to evade predators. It consists of a contraction of the axial muscle that very rapidly propels the fish in a direction away from the threat (Weihs, 1973; Webb, 1978; Domenici and Blake, 1997). The response is usually controlled by the Mauthner cells, a pair of large reticulospinal neurons that receive various sensory inputs, in particular visual and mechanoacoustic elements (Eaton et al., 2001). The response integrates a complex combination of behavioural and kinematic components. Behavioural components include responsiveness and response latency. Kinematic components include escape speed and acceleration, as well as manoeuvrability variables such as turning rate (Domenici et al., 2007a). Given the fundamental importance of the fast start for predator avoidance (Walker et al., 2005), it has often been assumed to be a stereotypic response, with performance maximized by natural selection and little variation among individuals of a given species (Webb, 1986; Reznick et al., 2004; Facchin et al., 2009). Other work has found, however, that there may in fact be significant variation in various components of the response (Eaton et al., 2001; Tytell and Lauder, 2002) (for review, see Domenici, 2009).

There is a growing interest in investigating phenotypic variation in quantitative performance traits such as the escape response (Oufiero and Garland, 2009; Jones and Godin, 2010) because this may provide insight into their ecological or evolutionary significance. To have such significance, it is essential to demonstrate that individual variation in the trait is temporally stable and therefore an intrinsic, potentially life-long, characteristic of the individual (Oufiero and Garland, 2009), and thus subject to natural selection (Arnold, 1983). The existence of standing variation is essential for the trait to evolve in response to future environmental change (Hayes and Jenkins, 1997; Bolnick et al., 2003; Sears et al., 2009), and it may be indicative of underlying physiological or behavioural trade-offs within or amongst traits such that no single phenotype is best under all circumstances (Mangel and Stamps, 2001; Stamps, 2007).

In fish, wide temporally stable individual variation has been demonstrated for a number of swimming performance traits over an interval of minutes/hours (short term), days/weeks (medium term) and months/years (long term). This is true for measures of swimming ability that reflect aerobic cardiorespiratory performance, such as critical swimming speed (Randall et al., 1987; Kolok and Farrell, 1994; Claireaux et al., 2007; McKenzie et al., 2007; Oufiero and Garland, 2009) and maximum aerobic swimming speed (Marras et

al., 2010). It also appears to be the case for some forms of anaerobic swimming performance, such as maximum sprinting speed (Reidy et al., 2000; Nelson et al., 2002; Nelson and Claireaux, 2005; Nelson et al., 2008).

The escape response is a performance trait for which inter-individual variation has been linked to differential success in predator avoidance and therefore survival (Walker et al., 2005). There is evidence that individual maximum escape speed is quite variable (see Domenici, 2009) and that this variation is repeatable over the short and long term (Gibson and Johnston, 1995; Langerhans et al., 2004; Oufiero and Garland, 2009). Overall escape success is likely, however, to be influenced by factors other than such purely kinematic components of the response (Fuiman and Cowan, 2003; Walker et al., 2005; Domenici et al., 2007a). For example, Scharf and colleagues exposed four fish species to a fish predator, and found that the most successful in evading predation was not the species with the highest escape speed but the one with the shortest reaction distance (Scharf et al., 2003). This suggests that overall escape success can also be affected by non-locomotor components. Therefore, it is likely that escape success is the result of a combination of all of the non-locomotor and locomotor components of the response. It is also possible that variation in overall escape performance is maintained in a population because of trade-offs amongst the individual components of the response (Turesson et al., 2009).

In this study, we investigated inter-individual variation and its temporal stability in a suite of behavioural and kinematic components of the escape response in juvenile European sea bass. This species is a temperate perciform that, during its juvenile stages, inhabits shallow coastal waters where it can be subject to significant predation pressure by other fish and birds (Quignard, 1984; Dufour et al., 2009). It is, therefore, an appropriate model on which to investigate the components of the escape performance.

We examined three main hypotheses: (1) that the degree of variation in the components of the escape response is too great for it to be considered 'stereotypic' in sea bass (Wainwright et al., 2008; Domenici, 2009); (2) that this variation is repeatable over the short term (30 min) and medium term (30 days) and, hence, probably intrinsic to the individuals; and (3) that trade-offs in performance exist amongst the various different non-locomotor and locomotor components of the escape response, which allow intrinsic variation in performance to persist within a population.

MATERIALS AND METHODS

Animals

Juvenile European sea bass *Dicentrarchus labrax* (Linnaeus 1758) derived from wild western Mediterranean broodstock, were obtained from a local fish farm (Salses le Chateau, France; 42°49'N, 2°57'E) in February 2008. On arrival at the laboratory, fish were transferred to a square holding tank (0.8 m²) with re-circulating, filtered natural seawater. Sea bass were kept at constant temperature (20±0.3°C) and salinity (35.1±0.2‰) under the prevailing natural photoperiod, for at least 4 weeks before the beginning of the experiments. Fish were fed four times a week with commercial pellets (Aphytec, Mèze, France) but individuals were fasted for at least 24 h before use in experiments.

Experimental set-up and protocol

Experiments were performed in a circular tank (100 cm diameter, 80 cm depth and 25 cm water depth), supplied with re-circulating seawater at 20°C. The escape response was induced by mechanical stimulation. A PVC cylinder with a tapered point and an iron bolt

at the opposite end (10 cm height, 2 cm diameter, weighing 35 g) was released by an electromagnet from a height of 150 cm above the water surface. To prevent visual stimulation before contact with the water, the stimulus fell within a vertical PVC tube (15 cm diameter) positioned 0.5 cm above the surface. A mirror inclined at 45 deg was attached to the end of the vertical tube to video record the time of contact between the stimulus and the water surface (Dadda et al., 2010). Floodlighting was supplied by two 250 W spotlights and the arena was covered by a black tarpaulin to screen the fish from visual disturbance. A high speed camera (Redlake Motion Scope, DEL Imaging Systems LLC, Cheshire, CT, USA) was positioned above the experimental tank. The camera was connected to a PC by a Pinnacle analog-to-digital conversion system (Avid Technology Inc., New York, NY, USA) and recorded the escape response at 250 Hz. The camera was triggered to capture video from 1 s before the stimulation to 3 s after.

Individual fish were transferred to the experimental tank and left undisturbed for 60 min. To assess short-term repeatability of performance, a fish was stimulated five times at ~30 min intervals (i.e. five repetitions in trial 1). To avoid differences in relative performance between repetitions due to different orientation and distance from the stimulus, the fish was stimulated only within a range of angles between 80 and 100 deg relative to the stimulus, and at a relatively fixed distance from the stimulus of between 20 and 25 cm. A gentle circular flow (~3 cm s⁻¹) was created in the experimental tank using the inflow from the re-circulating filter system. This elicited positive rheotaxis, which induced the fish to keep a relatively unchanging position for the duration of the experiment, so that it was possible to deliver the stimulus at set intervals of between 30 and 35 min. After the 5th stimulation, the fish was removed from the tank, anaesthetized (2-phenoxyethanol; 0.3 ml l⁻¹) and measured for length and mass. The fish was then tagged with a Visual Implant AlphaTag (Northwest Marine Technology, Shaw Island, WA, USA) beneath the transparent periocular tissue, for individual identification. Fish were subsequently returned to their stock tank and left undisturbed for 30 days. After this interval, the same protocol of five sequential stimulations (i.e. five repetitions in trial 2) was performed, to assess medium-term repeatability of performance. A total of 38 sea bass were tested.

Escape response measurements

Escape sequences were analysed using Redlake MotionScope PCI (ver. 2.21.1). Two-dimensional *X*-, *Y*-coordinates of the fish's centre of mass (CoM) and tip of the head were plotted every 4 ms from 20 ms before to 160 ms after the stimulus onset (45 frames in total).

The following variables were analysed according to Lefrançois and Domenici (Lefrançois and Domenici, 2006): (1) responsiveness, i.e. the percentage of fish, of the total analysed, that responded to the stimulation with an escape response; (2) latency, defined as the time interval between when the stimulus broke the water surface and the first detectable escape movement of the fish; (3) distance–time variables, evaluated within a fixed time (58 ms) (Dadda et al., 2010), which approximately corresponded to the mean duration of stage 1 and 2 of all fish considered for all tests (mean escape duration), including cumulative distance (*D*), maximum escape speed (*U*_{max}) and maximum acceleration (*A*_{max}); (4) *D*_{esc}, a measure of the distance covered by the fish within 88 ms of being stimulated (this time interval was the sum of the mean latency and the mean escape duration for each trial); (5) stage 1 turning angle, calculated as the angle between the segment joining CoM and the tip of the head, at the beginning and end of stage 1; and (6) stage 1 turning rate, calculated as the angle between the segment joining

CoM and the tip of the head, at the beginning and end of stage 1, divided by the stage duration. A polynomial regression procedure with five smoothed moving points was then applied for each derivative procedure (i.e. speed and acceleration) as described by Lanczos (Lanczos, 1956).

Data analysis and statistics

The mass (M) and fork length (FL) of each fish were used to calculate condition factor (K_f , $100M/FL^3$), as an index of the relative stoutness of each individual, to compare quantitatively within the population. For each individual and for each trial, the best value for each escape variable (B_v) was identified, wherever this occurred during the five stimulus repetitions. Paired t -tests were used to compare individual differences in FL, M , K_f and in the B_v of each escape variable, between trial 1 and trial 2. Multiple linear regressions, with the escape response variables as the dependent variable and fish FL, M and K_f as independent variables, were used to investigate whether size affected performance variables within trials. In order to evaluate whether the relative changes in size had an effect on the relative change in ranking, further multiple linear regressions were performed, with the relative rank difference measured as $\Delta R = \text{rank } B_v \text{ trial 2} - \text{rank } B_v \text{ trial 1}$ as the dependent variable, for each performance variable, and the percentage size difference between trials 1 and 2 measured as $\Delta FL = FL \text{ trial 2} - FL \text{ trial 1}$, $\Delta M = \text{mass trial 2} - \text{mass trial 1}$ and $\Delta K_f = K_f \text{ trial 2} - K_f \text{ trial 1}$ as independent variables. The effects of subsequent escape tests on responsiveness were assessed using a χ^2 test. A two-way repeated measures ANOVA with fish as the subject, repetition as the repeated factor, and trial as the second factor was used to analyse differences in escape latencies, distance–time variables, D_{esc} , stage 1 turning rates and stage 1 turning angles. Short-term repeatability was tested by comparing the best *versus* the second best value of performance (for the five stimulations performed) for each individual. Two different procedures were used to assess the short-term repeatability: (1) Pearson's product-moment correlation coefficient (i.e. a parametric test); and (2) the intraclass correlation coefficient (ICC) (Shrout and Fleiss, 1979). This coefficient is the ratio of variance among individuals to the total (among + within) variance and is calculated from the mean square terms of the ANOVA (Becker, 1984; Lessells and Boag, 1987). The intraclass correlation coefficient ranges from 0, when all individuals have the same mean, to 1, when all individuals have a different mean and all measurements on the same individual are identical (i.e. perfect repeatability). Medium-term repeatability was tested by comparing the best value achieved in trial 1 with the best value achieved in trial 2, 30 days later. In this case, Pearson's correlation was the only method used to assess repeatability. As animals increased in M during the 30 days between the two tests (and the mean M between the repeated measures shifted), intraclass correlation was not reliable for this kind of analysis (Hayes and Jenkins, 1997). The coefficients of variation ($CV = s.d./\text{mean}$) were used to assess the extent of variation in the escape components. CV should be inversely related to stereotypy, i.e. components with a high CV show low stereotypy. Relationships between variables, in particular, those indicative of performance trade-offs, were tested using linear regressions. Statistical analyses were performed using SigmaPlot Version 11.0 (Systat Software Inc., www.systat.com). A probability less than 5% ($P < 0.05$) was taken as the limit for statistical significance.

RESULTS

Size and habituation effects

Fish FL, M and K_f increased significantly from trial 1 to trial 2 (FL from 10.6 ± 0.8 cm to 12.1 ± 1 cm, mean \pm s.d.; paired t -test; $P < 0.05$;

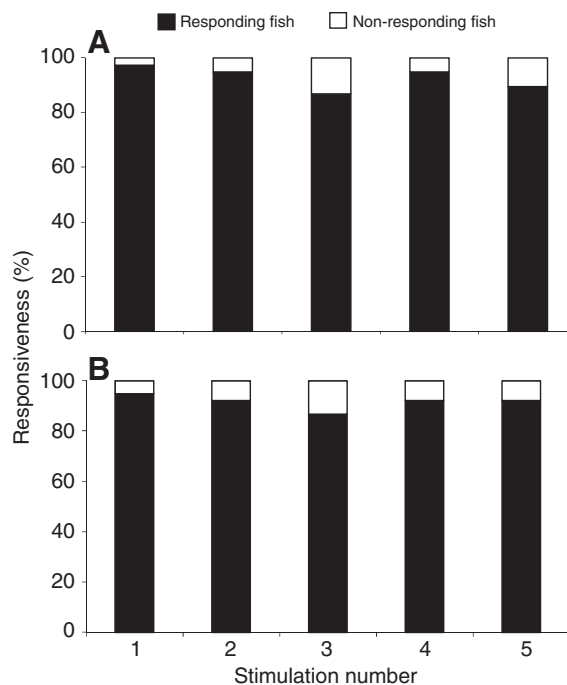


Fig. 1. Responsiveness (% of total) in sea bass over five sequential stimulations in trial 1 (A) and trial 2 (B).

M from 13.4 ± 3.5 to 21.3 ± 6.7 g; paired t -test; $P < 0.01$; K_f from 0.89 to 1.01; paired t -test; $P < 0.01$). B_v values did not, however, differ between trials (paired t -test; for all variables $P > 0.05$). Fish FL, M and K_f had no effect on the B_v values of either trial (multiple linear regression; trial 1, all $P > 0.05$; trial 2, all $P > 0.05$). Individual differences in fish FL, M and K_f between trials did not influence the ranking differences (ΔR) of any of the escape response variables (multiple linear regression; for all escape variables, $P > 0.05$). Animal orientation and distance to the stimulus at the time of stimulation (88 ± 5 deg and 21.5 ± 2.1 cm, respectively) did not influence any of the components of the escape response (multiple linear regression; $P > 0.05$).

Fish showed no habituation effects across the five sequential tests at 30 min intervals, for all of the escape performance components. A χ^2 test showed that responsiveness did not vary across the five stimulations, in either of the two trials ($P > 0.05$; Fig. 1). The ANOVA revealed a similar result for all other components across the sequential stimulations in both trials.

Variation

The inter-individual CVs of all escape performance components are shown in Fig. 2 and given in Table 1. Among the components of the response, escape latency and D_{esc} were most variable, with a CV of 37.5% in trial 1, and 35.3 and 40.7%, respectively, in trial 2. The least variable component was turning rate, in both trial 1 and 2 (CV of 23.5 and 23.2%, respectively).

Repeatability

All of the components of the fast-start escape response were repeatable over the short term, within each trial ($P < 0.001$; Table 1; Figs 3–6). Only 5 of the 7 measured performance components were, however, repeatable over the medium term; namely, D ($P = 0.03$), U_{max} ($P = 0.01$), turning rate ($P = 0.04$), turning angle ($P = 0.03$) and D_{esc} ($P < 0.01$) (Table 1; Figs 7 and 8). Latency ($P = 0.21$) and

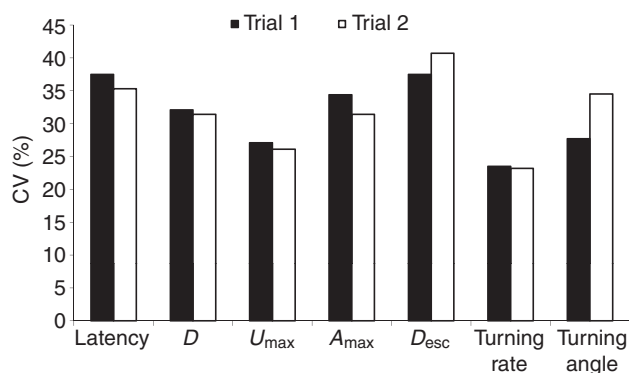


Fig. 2. Coefficients of variation (CV) of the seven performance variables measured. *D*, cumulative escape distance; *U*_{max}, maximum escape speed; *A*_{max}, maximum escape acceleration; *D*_{esc}, escape distance covered in 88 ms.

*A*_{max} ($P=0.22$) were not repeatable over the medium term (Table 1; Fig. 9).

Correlations between the escape components

We found no evidence of trade-offs (i.e. negative correlations) between the components of the escape response. On the contrary, we found some positive correlations. Distance–time variables were all correlated with each other (*D* and *U*_{max}, $P<0.01$; *D* and *A*_{max}, $P<0.05$; *U*_{max} and *A*_{max}, $P<0.05$). Turning rate was positively correlated with *D* ($P<0.05$), *U*_{max} ($P<0.05$) and *D*_{esc} ($P<0.05$), but not with latency ($P>0.05$) and *A*_{max} ($P>0.05$). Turning angle was positively correlated with stage 1 *D* ($P<0.05$), but not with the other variables. *D*_{esc} was positively correlated with latency ($P<0.01$) and *D* ($P<0.05$) but this was expected as *D*_{esc} is a composite variable derived from *D* and latency.

DISCUSSION

Our results reveal a large degree of standing inter-individual variation in the behavioural and kinematic components of the escape response in this population of juvenile European sea bass. The results also demonstrate that relative individual performance of all components of the response was repeatable over short-term intervals of minutes/hours. That is, although each individual varied in their sequential responses, when the two highest performance trials were plotted against each other, there was a significant positive relationship within the overall population.

Some individual components were also repeatable over the medium-term interval of 30 days. There was no evidence that the standing variation reflected trade-offs in performance among components of the response.

Escape performance is not stereotypic

A recent review of the literature reveals that behaviours that are considered to be stereotypic have a CV that falls between 0 and 20% and, in most cases, is below 10% (Domenici, 2009). This was not the case for the escape response variables, which all exhibited CVs in excess of 20% (Domenici, 2009). The CVs for the escape variables in the present study were also relatively high, ranging from 23 to 41%. Wainwright and colleagues suggested that there is no absolute threshold CV that defines whether or not a specific behaviour should be considered to be stereotyped (Wainwright et al., 2008). Rather, a decision should be made within a comparative context. Therefore, a valid means to evaluate the stereotypy of escape response variables is by comparison against the CVs of other performance variables from the same species. The CVs of critical swimming speed, maximum sprint speed, maximum speed achieved with constant acceleration test and gait transition speed are all markedly lower (17, 17, 18 and 15%, respectively) (Nelson and Claireaux, 2005; Claireaux et al., 2007; Marras et al., 2010) than the CVs of the escape response variables in the sea bass. The most variable fast-start component was *D*_{esc}, with a CV of 41%. Because this component was measured considering latency and locomotor components, its variation receives a contribution from the variation in all of these components. Latency was, in fact, highly variable (CV of 37%). Latency is the temporal summation of three sequential events: (1) the time interval from the stimulus onset to Mauthner cell firing; (2) the interval between Mauthner cell firing and muscle activation; and (3) the time between muscle activation and the first detectable movement of the fish (Eaton et al., 2001; Hale, 2002; Turesson and Domenici, 2007). Individual variation in any or all of these events could contribute to the wide variation in latency. The locomotor distance–time variables also showed a high degree of variation, especially *A*_{max}. This may be because acceleration suffers from an accumulation of measurement errors as it is derived from *U*_{max}, which, in turn, is derived from *D* (Harper and Blake, 1989; Walker, 1998). With a CV of approximately 23%, maximum turning rate was the least variable component of the escape response. This performance trait is an indicator of maximum muscular output acting against body rigidity (Domenici, 2001). The relatively low variation among individuals (no significant differences in *K*_f) suggests that they were all in a similar physical condition with a similar muscle mass.

Table 1. Short- and medium-term repeatability and coefficients of variation of seven variables measured in European sea bass

Escape variable	Short-term repeatability						Medium-term repeatability Pearson correlation
	Trial 1			Trial 2			
	Intraclass correlation	Pearson correlation	CV (%)	Intraclass correlation	Pearson correlation	CV (%)	
Latency	0.66	$P<0.001$	37.5	0.82	$P<0.001$	35.3	$P=0.207$
<i>D</i>	0.81	$P<0.001$	32.1	0.92	$P<0.001$	31.4	$P=0.032$
<i>U</i> _{max}	0.83	$P<0.001$	27.1	0.88	$P<0.001$	26.1	$P=0.013$
<i>A</i> _{max}	0.80	$P<0.001$	34.4	0.67	$P<0.001$	31.4	$P=0.216$
<i>D</i> _{esc}	0.80	$P<0.001$	37.5	0.84	$P<0.001$	40.7	$P=0.001$
Turning rate	0.79	$P<0.001$	23.5	0.86	$P<0.001$	23.2	$P=0.040$
Turning angle	0.81	$P<0.001$	27.7	0.83	$P<0.001$	34.5	$P=0.026$

CV, coefficient of variation; *D*, cumulative escape distance; *U*_{max}, maximum escape speed; *A*_{max}, maximum escape acceleration; *D*_{esc}, escape distance covered in 88 ms.

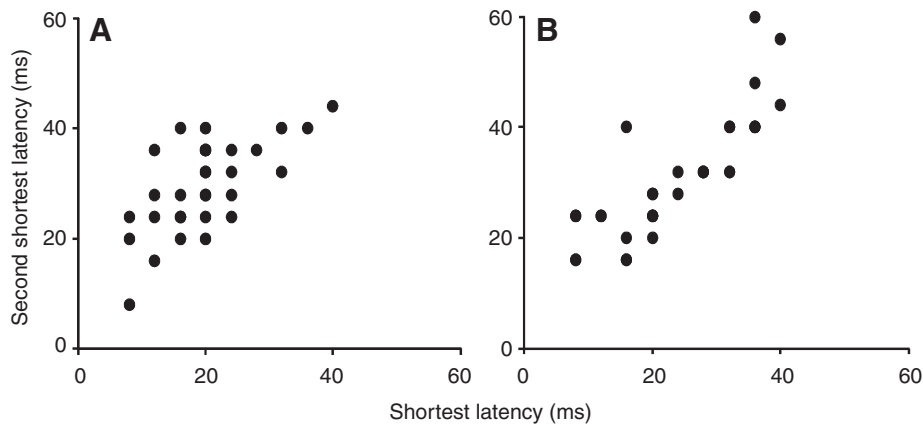


Fig. 3. Short-term repeatability of the latency in the escape response of European sea bass shown as the relationship between the shortest and the second shortest latency measured for each individual fish in trial 1 (A) and trial 2 (B; performed after an interval of 30 days).

Individual escape performance is repeatable

We developed a protocol where individual fish were tested over five sequential repetitions in each trial. This was done for three reasons: (1) to determine whether a decline in performance would occur over subsequent short-term tests; (2) to ensure that maximum performance was elicited in at least one repetition, to avoid any potential confounding effects from underestimating maximum performance (Adolph and Pickering, 2008); and (3) to permit assessment of short- and medium-term repeatability of maximum performance. We found no decline or habituation effect in any of the fast-start components. Responsiveness, a key component for the escape response (Fuiman and Cowan, 2003), was not affected by the short-term sequence of stimulations. In fact, although some animals did not respond in some repetitions, this was never the same individual but was a random effect amongst the 38 fish. Latency did not show habituation over the short-term repetitions (30min),

in accordance with previous neurobiological studies which indicate that, although the nerves enter the refractory phase and cannot fire again until ion gradients are restored, this takes only few seconds in the Mauthner system (Kohashi and Oda, 2008). Therefore, the 30min interval used between trials was certainly sufficient for response restoration. Distance–time variables did not decline over subsequent repetitions, presumably indicating that there was no accumulative muscle fatigue. The escape response uses anaerobic white muscle and the sudden acceleration comprises only a few powerful tail beats. This presumably did not exhaust the endogenous fuels that power this type of muscular work in fish (Richards et al., 2002) and there was recovery of muscle homeostasis within the 30min prior to the subsequent stimulus. Although size is known to have an effect on some of the variables we tested (reviewed in Domenici, 2010), we did not find any effect of size within trials and, despite a size increase over the 30 days between trials,

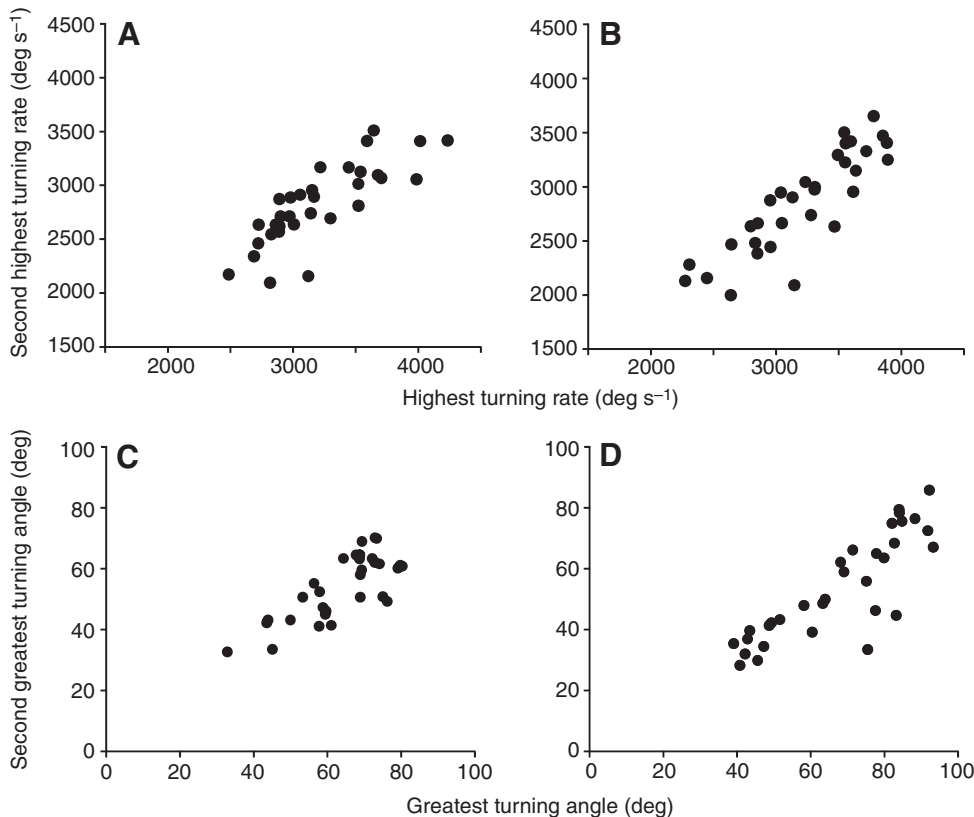


Fig. 4. Short-term repeatability of turning rate (A and B) and turning angle (C and D) in the escape response of European sea bass shown as the relationship between the highest and the second highest values of turning rate and turning angle measured for each individual fish in trial 1 (A and C) and trial 2 (B and D; performed after an interval of 30 days).

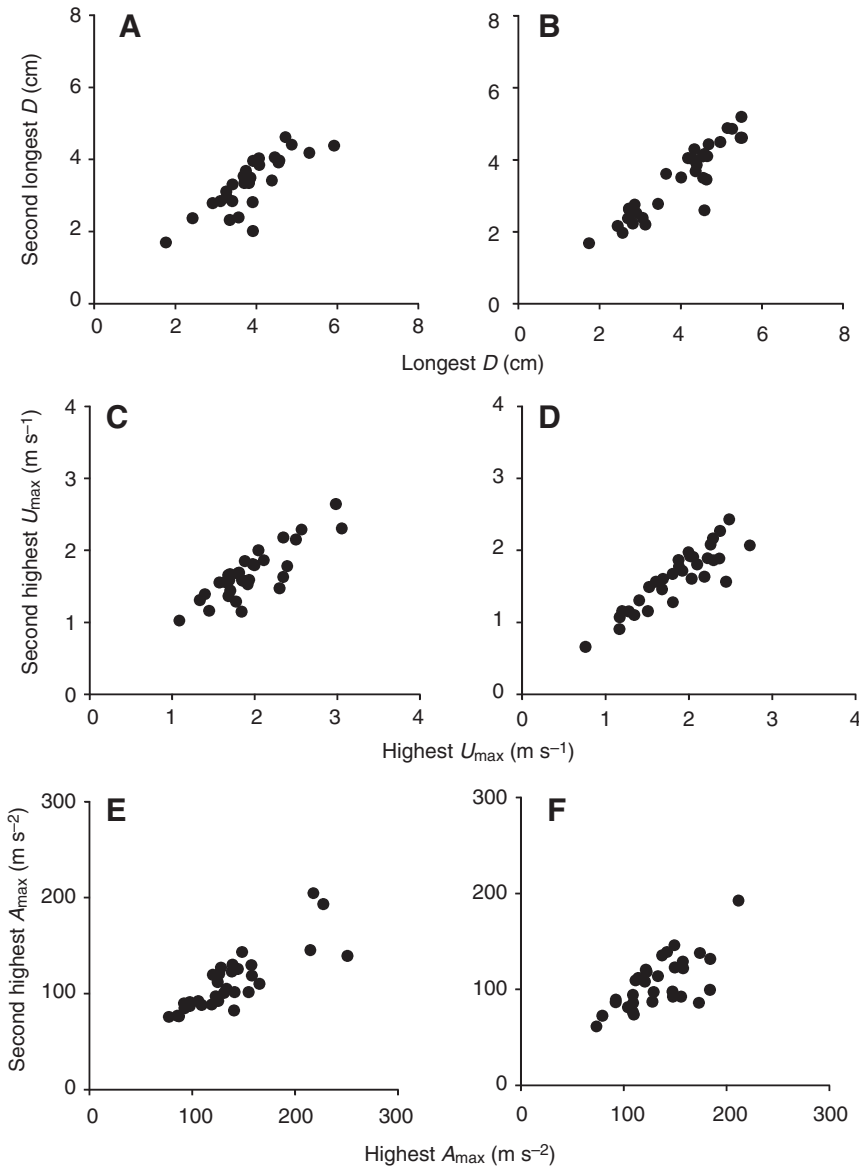


Fig. 5. Short-term repeatability of maximum D (A and B), highest U_{max} (C and D) and highest A_{max} (E and F) in the escape response of European sea bass shown as the relationship between the highest and the second-highest measurement of three components of the escape response measured in trial 1 (A, C and E) and trial 2 (B, D and F; performed after an interval of 30 days).

performance did not change significantly. This is perhaps due to the relatively short time interval between trial 1 and trial 2, which was associated with a relatively small (11%) increase in length. More importantly, the size increase between trials 1 and 2 did not affect the relative ranking of individual fish for any of the escape variables tested.

It has been demonstrated that individual variation in critical swimming speed, sprint speed and escape speed is temporally stable over periods of several months (up to 1 year) in various teleost species (Kolak, 1992; Nelson and Claireaux, 2005; Claireaux et al., 2007; Oufiero and Garland, 2009). Other components of the escape response such as responsiveness, latency to visual stimulus, distance

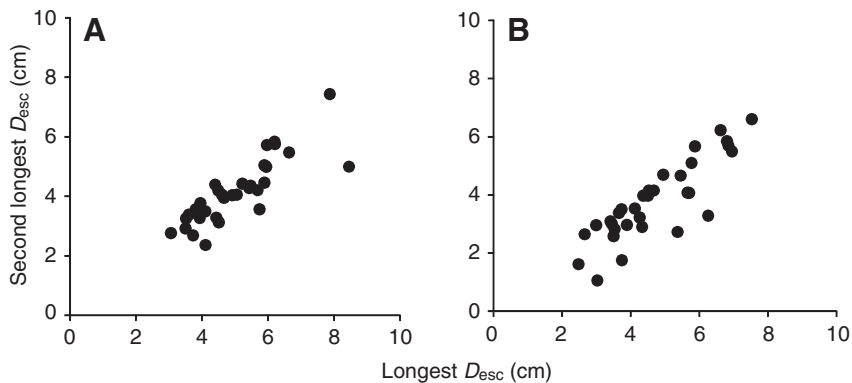


Fig. 6. Short-term repeatability of D_{esc} in the escape response of European sea bass shown as the relationship between the longest and the second longest D_{esc} measured for each individual fish in trial 1 (A) and trial 2 (B) performed at an interval of 30 days.

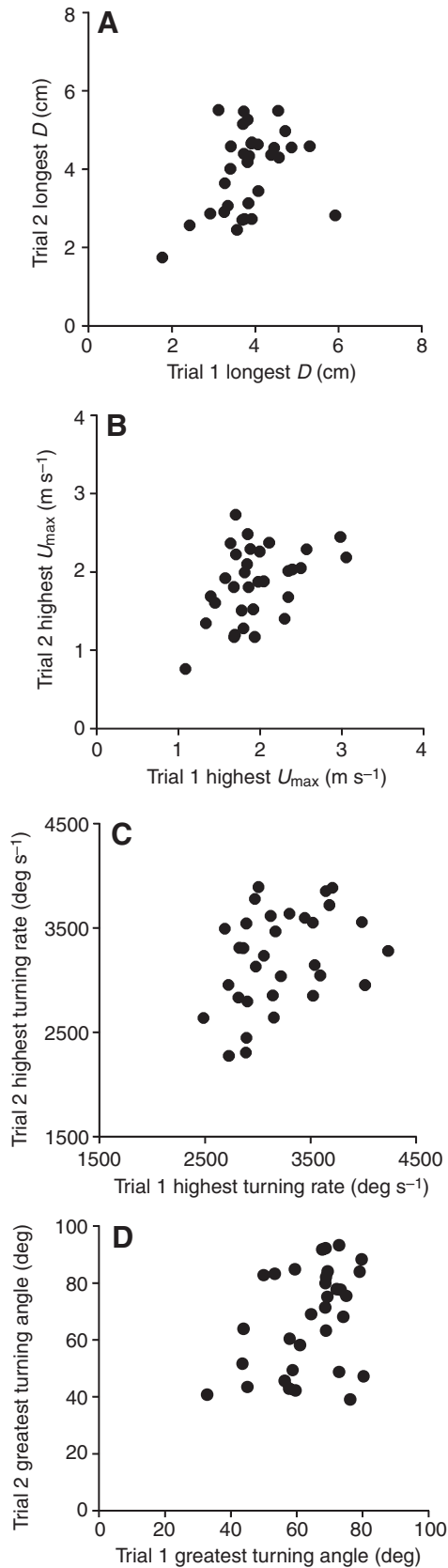


Fig. 7. Medium-term repeatability of maximum D (A), highest U_{\max} (B), highest turning rate (C) and greatest turning angle (D) in the escape response of European sea bass shown as the correlations among values for individual sea bass over an interval of 30 days.

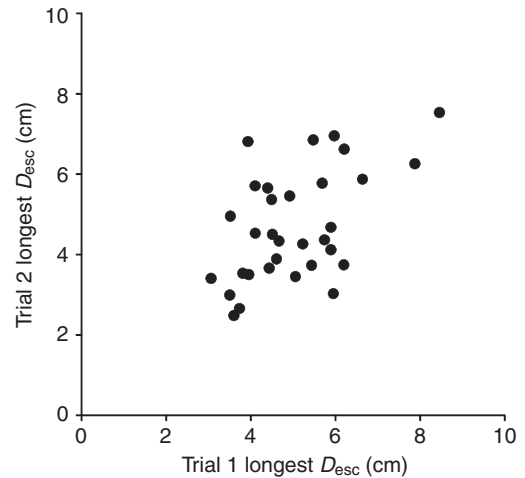


Fig. 8. Medium-term repeatability of D_{esc} shown as the relationship between values for individual sea bass over an interval of 30 days.

covered, response duration and speed were significantly repeatable in fish larvae over intervals of minutes to hours (Fuiman and Cowan, 2003). Here, we show that D , U_{\max} , turning rate, turning angle and D_{esc} were also repeatable after an interval of 30 days. This was not the case for A_{\max} , perhaps because of its high variation, which may be related to having calculated it by double differentiation. Latency was also not repeatable over the medium term. This suggests that neurobiological performance may be less conservative than muscular performance in escape responses, although further studies would be necessary to test this idea empirically. Nevertheless, although latency was not repeatable over the medium term, D_{esc} was, which is in part dependent upon latency. D_{esc} is probably the most ecologically relevant component as it represents the distance travelled by the fish after being attacked.

To understand fully the potential evolutionary significance of these variables, quantitative genetic studies would need to be performed to investigate whether the intrinsic variation that we measured in this study is heritable across generations. Without these studies we cannot exclude a role for phenotypic plasticity, or even factors such as variation in maternal provisioning, in creating variation in the measured traits.

The standing variation does not reflect trade-offs amongst the components of escape performance

Individual variation in performance in fish may determine individual survival (Walker et al., 2005), so if the fast start is important for escaping predators, it is surprising that selection has not maximized performance (Law and Blake, 1996). Thus, the existence of such standing variation in the sea bass suggests that there may be physiological and/or behavioural trade-offs within the response itself, or against other complex traits. For example, Turesson and colleagues found that accuracy in directionality may trade-off against reaction time in black gobies: individuals with longer latencies showed a higher proportion of escapes directed away from the stimulus (Turesson et al., 2009). In the current study, there was no evidence for trade-offs amongst the components of the response that we measured. This indicates that trade-offs, if they exist, must be against other ecologically important behavioural or performance traits. Behavioural ecology studies have revealed that particular components of the escape response in animals (e.g. reaction distance) may be modulated by alternative behavioural strategies, which

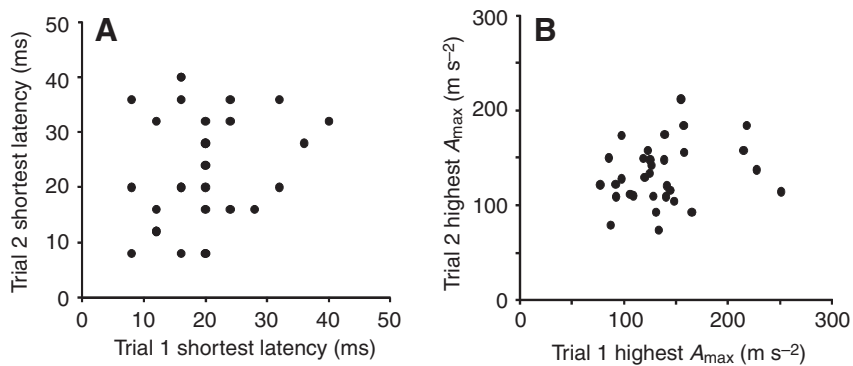


Fig. 9. Medium-term repeatability of latency (A) and A_{\max} (B) shown as the relationship between values for individual sea bass over an interval of 30 days.

depend upon the prevailing context (Ydenberg and Dill, 1986; Lima and Dill, 1990). Thus, the exact costs and benefits of having a rapid escape response may be highly context dependent (Domenici, 2010). Animals do not automatically escape as soon as the predator is detected, indicating that there are inherent trade-offs in escaping *versus* remaining in the vicinity. For example, the cost of remaining can be modulated by the presence of a refuge. As a result, prey that are attacked when close to a refuge exhibit a smaller reaction distance (Ydenberg and Dill, 1986). In fish, Jones and Godin described a trade-off between escape performance and exploratory foraging behaviour, where fast escape reactors were slower explorers and *vice versa* (Jones and Godin, 2010). Trade-offs may also exist between the burst performance used in the escape response and other types of swimming. They have been proposed to exist when comparing species, or morphs, specialized for different lifestyles and foraging strategies (Webb, 1984; Webb, 1998; Domenici et al., 2008; Langerhans, 2009). For example, Tiger musky (*Esox* sp.), an esociform accelerator that can achieve bursts at very high speed, shows low steady swimming performance, while cruising specialists (e.g. tuna) may swim steadily for long periods of time but have low burst swimming performance (Webb, 1988; Domenici, 2003).

A complex life cycle, such as that of sea bass, may also be a source of variation in performance. During its life, this species occupies diverse environments where the fish may be subjected to various types and degrees of predation pressure (Quignard, 1984; Dufour et al., 2009). In environments with many predators, it may be beneficial to possess physiological adaptations toward increased burst performance, heightened sensory capabilities and short latencies. These adaptations may, however, be unnecessary and costly in habitats with few predators (O'Steen et al., 2002; Langerhans et al., 2004). The possibility that a rapid fast-start response may be more beneficial in some environments than in others may explain the presence of multiple phenotypes within a given population, especially during the early life stages. In this regard, it would be interesting to compare the coefficients of variation for different quantitative traits of two populations exposed to different degrees of variation in predator pressure.

Conclusions and perspectives

The existence of temporally stable phenotypic variation in the escape performance suggests that it is an intrinsic characteristic of the individual and that this performance trait can be subject to natural selection (Arnold, 1983). This is particularly relevant within the context of global change. New environmental scenarios may have differential effects on populations of predators and prey (Domenici et al., 2007b), and therefore it is likely that the ability to escape predation will be of fundamental importance in determining future

changes in distribution and abundance. Indeed, the individuals that will survive in the future may not be those that were the most fit in past environments (Carey, 2005). A large degree of intrinsic variation in escape performance is therefore likely to be particularly advantageous in populations that may face changes in predator pressure as a result of new environmental situations.

Further studies, in particular comparative studies between populations that might be expected to differ, should consider the potential for extensive variation in the components of the escape response, because this may have consequences for the ability to find statistically significant population differences.

LIST OF SYMBOLS AND ABBREVIATIONS

A_{\max}	maximum escape acceleration
B_v	best value of each escape variable measured over the five stimulus repetitions, for each individual and for each trial
CoM	centre of mass
CV	coefficient of variation
D	cumulative escape distance
D_{esc}	escape distance covered in 88 ms
FL	fork length
ICC	intraclass correlation coefficient
K_f	condition factor
M	mass
s.d.	standard deviation
U_{\max}	maximum escape speed

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