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Repeatability and reliability of the provoked escape response test for estimating fish maximum swimming speeds

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ABSTRACT

In fish, burst swimming performance is essential for escaping predators, capturing prey, and overcoming velocity barriers. Forced swimming trials often underestimate performance, whereas volitional swimming tests provide more ecologically relevant data, but require costly infrastructure. A cost-effective alternative is the provoked escape response test, where an object is dropped near the fish to trigger an escape response, and maximum swimming speed is estimated over a pre-determined time-period. The robustness of this test has, however, been little investigated. Here we test its repeatability at both the individual and group levels by running two repeated trials on 118 individuals of the Padanian goby (*Padogobius bonelli*) on two consecutive days. The estimated maximum swimming speed was not repeatable at the individual fish level, suggesting that the test may be unreliable when individual fish performance measures are important. The testing protocol did consistently show that large fish outperform small fish and remains a useful, simple, and cheap method for estimating average swimming performance and for comparing the performance between groups. Lower performance in the second compared to the first test indicates that fish experience, such as habituation or stress, can influence estimated maximum swimming speeds, suggesting that absolute estimates should be used with caution.

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Introduction

Swimming performance is fundamental for the ecology of fish, governing movement, reproduction and predator-prey interactions (Tudorache et al. 2013; Castro-Santos et al. 2022). Based on the physiological mechanisms that drive the muscle activity, fish swimming is categorised into three modes – sustained, prolonged, and burst swimming (Videler 1993). Burst swimming uses white muscles powered by anaerobic metabolism, whereas sustained swimming is powered by red muscles through aerobic (oxygen-dependent) processes. Due to limited anaerobic energy reserves stored in white muscle, fish can only perform burst swimming for a short period of time (seconds) while they can, theoretically, swim in the sustained mode indefinitely. Prolonged swimming is an intermediate swimming mode that involves both red and white muscles, with fatigue occurring after seconds to hundreds of minutes depending on the effort required (Videler 1993; Hammer 1995). Sustained swimming constitutes continuous swimming, for example in relation to patrolling, food seeking, or long-distance movements, while burst swimming is fundamental for overcoming velocity barriers and for predator-prey interactions (Videler 1993; Katopodis et al. 2019). Burst swimming is also of particular interest for the design of fish passage solution (Castro-Santos 2005; Katopodis et al. 2019). It is, however, relatively rarely quantified (Katopodis and Gervais 2012).

Fish swimming capability is often assessed in forced swimming trials where fish are placed to swim against a known current velocity in a swim tunnel or a flume until fatigued (Tudorache et al. 2013). The critical velocity test involves a step-wise increment of the flow velocity at fixed time intervals to estimate critical swimming speed (U_{crit}) as an approximation of maximum sustained swimming speed (Tudorache et al. 2013). Using the same logic, burst swimming capacity, or maximum swimming speed, has been estimated by step-wise increases in velocity at very short time intervals (Starrs et al. 2011; Tan et al. 2021). Alternatively, fixed velocity tests involves a series of repeated trials at different, but constant, flow

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velocities against which time-to-fatigue is recorded. Data obtained from fixed velocity tests are then used to construct fatigue curves, as a descriptor of fish swimming performance (Katopodis and Gervais 2012; Ashraf et al. 2024c). Forced swimming trials have, however, proven to be sensitive to experimental conditions such as flume length (Tudorache et al. 2007; Deslauriers and Kieffer 2011; Ashraf et al. 2024b), the use of encouragement stimuli (Ashraf et al. 2024a), and station holding behaviour of the fish (Crawford et al. 2025). The short duration of burst events, also poses a problem for estimating burst speeds in forced swimming trials (Crawford et al. 2025). Indeed, forced swimming trials often underestimate the swimming capacity of fish (Peake 2008; Castro-Santos et al. 2013).

Recently, volitional swimming tests have emerged as a method to estimate burst swimming speeds. Here, fish are released in a downstream pool and voluntary choose to swim upstream against a known flow velocity while the time and distance of ascent is recorded using video or PIT-telemetry (Castro-Santos 2004; Peake 2008; Castro-Santos et al. 2013). These volitional swimming tests ensure that the tested fish is motivated to swim, and, from an applied perspective, also connect directly to potential fish passage related swimming behaviour (Castro-Santos 2005; Castro-Santos et al. 2013). Unfortunately, volitional swimming trials require relatively costly testing facilities, which limits their application. As a compromise, quasi-volitional bursts have been used to quantify burst performance of fish within forced swimming trials. This is done by measuring the velocity and duration of their upstream transitions within a flume (Schiavon et al. 2023). Another methodological approach is to provoke an escape response (a sudden burst to escape perceived danger) in a fish at rest and quantify the velocity of its escape over a predetermined time from the onset of the escape (Domenici and Blake 1997; Nelson et al. 2002; Tudorache et al. 2008). As provoked escape response tests elicits a natural and volitional behaviour, the measured performance relates directly to predator avoidance in nature (Domenici and Blake 1997).

In a special case of the provoked escape response test, an escape response is incited by dropping an object in the vicinity of the fish mimicking a potential predator attack (Tudorache et al. 2008; Nyqvist et al. 2023). This method has been used to estimate maximum swimming speed (a burst swimming performance) for a range of small-sized fish species, including perch, roach, riffle dace, barbel, brown trout, gudgeon, spiny loaches, bullhead, and gobies (Knaepkens et al. 2007; Tudorache et al. 2008; Nyqvist et al. 2023, 2024a, 2024b, 2024c). For applied purposes, the method has been used to evaluate tagging effects (Knaepkens et al. 2007; Nyqvist et al. 2023, 2024b, 2024c), compare the performance of native and non-native fish (Nyqvist et al. 2024a), and to inform fish passage design (Emadi et al. 2024). Although this type of escape response tests (dropping an object in the vicinity of the fish) are inexpensive and easy to perform, their robustness for estimating swimming performance is relatively underexplored.

The repeatability of swimming performance estimates, at both individual and group levels, provides insights into the reliability of fish swimming tests. Unless the capability of fish changes between trials, a reliable test should be repeatable. Fish swimming performance has been shown to be repeatable over time both in aerobic and anaerobic swimming modes for a range of fish species (Gregory and Wood 1998; Reidy et al. 2000; Oufiero and Garland Jr 2009). For burst swimming speed, repeatable individual performance has been achieved in fixed velocity swim chamber tests for rainbow trout and in a French press exercise system for medaka (Gregory and Wood 1998; Hechter and Hasler 2019). In laser diode-photocell raceways, where fish movement in the raceway is tracked following a physical tap, Atlantic cod and sea bass have shown repeatable performances at the individual level (Reidy et al. 2000; Claireaux et al. 2007). Tapping the tank to produce an escape response has produced repeatable measures of burst speeds over short time interval (20–160 ms) in swordtail (Royle et al. 2006), guppy (Chappell and Odell 2004), and sticklebacks (Garenc et al. 1999). Similarly, individual burst speeds over 30 ms were repeatable in mosquito fish startled by the downward thrust of a cylinder in the vicinity of the fish (Langerhans et al. 2004). The repeatability of the provoked escape response tests by dropping an object in the vicinity of the fish has, to our knowledge, not yet been tested.

Here we test the repeatability of this latter version of provoked escape response test at both the individual and group levels. This by running two repeated tests on the same individual of the benthic, intermittently swimming Padanian goby (*Padogobius bonelli)* on two consecutive days. We test for the correlation in individual performance between the first and second test, and assess group level effects by comparing large and small fish performance across both tests. We hypothesise individual burst speed to be repeatable, no difference in group performance between the first and second test, and the estimated performance to be consistently higher among large compared to small fish.

Material and methods

Using wading electrofishing (direct current; ELT60 IIGI, Scubla, Italy), Padanian goby were caught in the Lemme River (Italy) on 19 March 2024 (UTM 478725E, 4952707 N, zone 32 T). The fish were brought to the Alessandria Province Hatchery (Predosa, Italy), where the experiment was conducted. Upon arrival fish were left to recuperate overnight, and tagged the following day. Fish smaller than 50 mm were tagged with 8 mm (8.4 mm × 1.4 mm, 0.03 g) passive integrated transponders (PIT-tags; Biomark, USA), while fish larger than 50 mm were tagged with either 8 mm or 12 mm tags (12 mm × 2.1 mm; 0.10 g). A separate study showed no effect of tagging on survival or swimming performance in Padanian gobies of similar sizes and length to tag ratios (Nyqvist et al. 2024b). Before tagging, fish were anaesthetised in clove oil (Aromalabs, USA; approximately 0.2 ml clove oil/L water). A 2–3 mm incision was made on the ventral side of the fish, anterior to the pelvic fins, and slightly offset from the centre. The tag was pushed into and forward in the abdominal cavity of the fish to align with the body, and the incision was left to close itself (Schiavon et al. 2023; Nyqvist et al. 2024b).

Fish were held in a spring-fed flow-through tank (length × width × depth = 200 cm × 200 cm × 60 cm) equipped with shelters (perforated bricks and shingles) for 28 days before the swimming performance experiments. They were fed wild caught macroinvertebrates and cultured *Daphnia magna* regularly, and kept under stable temperatures (14 ± 0.5 °C; mean ± SD) under a natural light cycle (ceiling lighting and windows in the hatchery).

On 17–18 April the swimming trials commenced. Fish were not fed during the 24 h preceding, nor during, the trial period. Individual fish were netted gently from the holding tank and inserted into the experimental arena (length × width × depth = 565 × 365 × 100 mm). The arena was illuminated from above by a LED-lamp distanced about 1 m from the water surface. Fish were left to habituate to the arena for approximately ten minutes (Ashraf et al. 2024a) before an escape response was provoked by dropping a spherical weight (5 g, ⌀15 mm), from a height of about 1 m, in the vicinity of the fish. Typically, fish showed an instant escape response followed by some time moving around in the arena. When a fish stopped moving, a second spherical weight was dropped near the fish to trigger another escape response. Overall, three escape responses were provoked (Knaepkens et al. 2007; Tudorache et al. 2008; Nyqvist et al, 2023). Four trials were conducted in parallel in opaque plastic tanks spatially separated to avoid conducting vibrations between the tanks. Water was changed regularly to maintain a stable temperature (measured in a separate, identical tank; 14.5 ± 0.3 °C) across all trials. After stopping for the third time, the fish was netted, anaesthetised, checked for tag ID, measured for weight and length before being placed in a flow through tank (110 × 120 × 40 cm) to recuperate. Fish were 51.6 ± 10 (mean ± SD) mm long and weighted 1.6 ± 1.0 g, and could be divided into 61 large fish (≥50 mm) and 57 small fish (< 50 mm). On 19 April, 14–48 h after the first trial, the swimming trials were repeated using the same experimental protocol but without anaesthetizing and measuring the fish after the test.

The experimental arena was recorded with an overhead video camera (Sony 4K, FDR-AX43, 50fps, Minato City, Tokyo, Japan). The fish escape responses were then manually tracked using a custom-made script (https://github.com/SilverFox275/manual-point-tracking) in MATLAB (R2021b; The Math-Works Inc., Natick, MA, USA). Fish were positioned every 100 ms and maximum swimming speed was estimated by extracting the fastest 400 ms during the provoked escape response (that is the fastest burst over the three induced escape responses). The 400 ms correspond to the time period used in applied research in the literature (Knaepkens et al. 2007; Tudorache et al. 2008). Known dimensions of the arena were used to transform distances in pixels to distances in meters.

Adjusted repeatability of maximum swimming speed between the first and second test was estimated using the rptR package in R (Stoffel et al. 2017). To control for difference in fish length, this variable was included as a fixed effect. Complementary, the correlation between the estimated maximum swimming speeds in the first and second trial was tested using a Pearson correlation test. The difference in swimming performance between the first and second test and between large and small fish was tested using a linear mixed effects model. The interaction between fish size group (large/small) and test number was included in the model. Fish ID was included as a random slope to take repeated measures from the same fish into account. As the time between the first and second test was relatively variable, a potential effect of this time on the percentual change in estimated maximum swimming speed from the first to second test was tested using a Spearman correlation test. Here, Spearman correlation was used as the data was not normally distributed. For the first set of trials, peak velocity and time swimming before standing still were quantified for the first, second, and third escape response. Differences between the first and the following escape responses within a trial were tested using t-tests.

Data management, statistical analysis, and plotting were performed in R. The linear mixed effect model was run with the lme4-package (Bates et al. 2015) and model assumptions were tested with the Dharma package (Hartig and Hartig 2021). Plots were constructed using ggplot (Wickham 2016).

The study was performed in agreement with the Ufficio Tecnico Faunistico e Ittiofauna (Wildlife and Ichthyofauna Office) of the Province of Alessandria (n. 9948 of 29 February 2024), pursuant to art. 2 of the National Decree n.26/2014 (implementation of Dir. 2010/63/EU).

Results

The average estimated maximum swimming speed for the 118 individual Padanian gobies was 0.62 ± 0.20 m/s (mean ± sd) for the first test, and 0.50 ± 0.17 m/s for the second test. This corresponds to relative swimming speeds of 12.2 ± 4 BL/s and 9.8 ± 3 BL/s for the two tests respectively. No significant repeatability (Adjusted repeatability, $R = 0$, $p = 0.5$), nor correlation, was found between individual maximum speed in the first and second test (Figure 1; Pearson correlation, $r = 0.13$, $p = 0.16$). Within trials, the first escape response was fastest in 48% of trials, the second in 34%, and the third in 18%. Mean duration between provoked escape responses (time swimming after the weight was dropped) was 1.8 s. On average, both the maximum swimming speed and time swimming were higher for the first escape response compared to the two following (t-test, $p < 0.05$).

Average maximum swimming speed was significantly reduced between the first and the second test, and in both tests large fish did consistently outperform small fish (Table 1, Figure 2). There was no correlation between time between tests and change in performance from the first to the second test (Spearman correlation, $p = 0.37$).

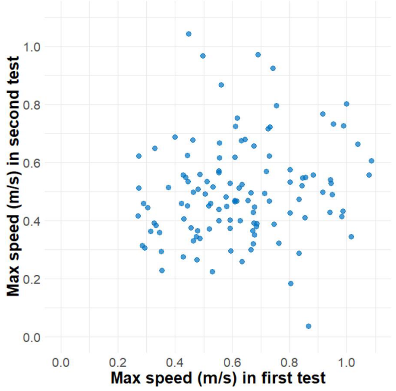

Figure 1. Estimated maximum swimming speed in first (*x*-axis) and second (*y*-axis) provoked escape response tests.

Discussion

An escape response was induced by dropping a weight in the vicinity of a fish at rest and the escape swimming velocity was quantified. The estimated maximum swimming speed from this special case of a provoked escape response test was not significantly repeatable at the individual fish level. Also, the estimated swimming performance declined between the first and second test. The test did, however, consistently show that large fish performed better than small fish. These results indicate that the provoked escape response test can be used to test for average difference in swimming performance between fish belonging to different groups of fish, while the estimate for the individual fish is not to be treated as a robust measurement. The results also seem to be influenced

Table 1. Output from the linear mixed-effects model.

	Estimate	Std. error	t value	p
Intercept	−0.42	0.05	−9.18	<0.001
Size	−0.22	0.07	−3.32	<0.001
Test	−0.25	0.07	−3.98	<0.001
Test*Size	0.05	0.09	0.51	0.6

The table includes estimate, standard error, t-value and p-value for the intercept, size group, test (first vs second), and their interaction.

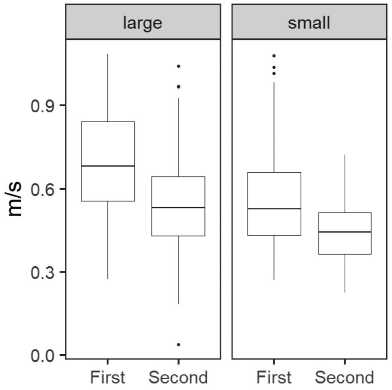

Figure 2. Estimated maximum swimming speed for large and small fish for the first and second provoked escape response test. Median value is marked with the solid black horizontal line inside the bounding box. The black dots represent the outliers, whereas the bounding box defines the interquartile range (IQR). The vertical solid black lines mark Q1–1.5·IQR (bottom end) and Q3 + 1.5·IQR (top end), where Q1 and Q3 are the 25th and 75th percentiles, respectively.

by the experience of fish, showing reduced performance in the second trial compared to the first.

Burst swimming speed has previously been shown to be repeatable in a range of fish species using several different methods (Garenc et al. 1999; Reidy et al. 2000; Chappell and Odell 2004; Langerhans et al. 2004; Royle et al. 2006). In this provoked escape response test, the weight was dropped manually from a height. This makes the relation between the fish and the impact point (e.g. distance and angle) different between drops. This variability may have resulted in different threat signals and hence variation in escape responses and burst velocities between escapes (Domenici 2010; Roche et al. 2023). In addition, the fish were not equally positioned in relation to the walls of the tank for every provoked escape response, potentially contributing to inter- and intra-individual variability (Roche et al. 2023). To account for these factors, three scaring events are used per test, and the fastest burst is used as the test output. The lack of repeatability, however, indicates that this might not be enough to compensate for the variability in test conditions between scaring events. The bulk of the previous studies showing repeatability in burst performance use a more standardizable approach, either forcing the fish in swim chambers (Gregory and Wood 1998), manually poking the fish (Claireaux et al. 2007), or inciting escape responses by striking the side of the tank (Garenc et al. 1999; Chappell and Odell 2004; Royle et al. 2006). Forced swimming tests, poking, and vibrations or sound from striking the side of the tank are more likely to cause similar (repeatable) experiences for the fish between trials compared to the dropping of the spherical weight in the tested provoked escape response test. Therefore, when the difference in individual performance is important, such a more repeatable protocol is advised.

The great advantage of the provoked escape response test is that it is relatively cheap, both in time and infrastructure, compared to flume or swimming chamber trials. This allows testing many fish with relatively limited resources. As evidenced by the intra-individual variability between trials, however, fish do not always perform their best. In addition, it is possible that the spatial constrains and artificial environment (the experimental arena) restricted the performance (Roche et al. 2023). This suggests that resulting estimates of maximum swimming speeds should be seen as conservative. Under more natural conditions, a more complete expression of their burst performance may be likely. This limitation is, however, shared by many, if not most swimming tests, especially the ones where fish are forced to swim. For example, fish may underperform in forced swimming test compared to volitional swimming trials where the individual fish decides to swim against the flow (Peake 2008; Castro-Santos et al. 2013). Encouragingly, the provoked escape response did consistently separate the average performance of fish belonging to two groups (large and small fish) across the two tests. In this case, inter-trial differences in individual performance were evened out when group averages were the estimated metric. This suggests that, while keeping the noise from individual variability in mind, the test can still be useful for testing differences between groups. This is also reflected in its use for testing effects of tagging (Nyqvist et al. 2023, 2024c) or difference in performance between species (Nyqvist et al. 2024a), and mirrors the usefulness of the critical swimming speed test (Tudorache et al. 2013).

An advantage of the provoked escape response test is that it evokes a natural, and volitional, behaviour and hence quantifies a performance directly relevant to the fish ecology (Nelson et al. 2002). Burst performance is relevant both for predator-prey interactions as well as for negotiating velocity barriers, and is an important consideration in the design and construction of fish passage solutions (Castro-Santos et al. 2022). Since the provoked escape response test evokes a natural and volitional behaviour, the resulting performance measures are directly transferable to predator avoidance in nature (Domenici and Blake 1997), and have also been used to inform fish passage design (Emadi et al. 2024). Here different research questions might be reflected in the use of different time-periods for integrating the maximum swimming speed, with tens of millisecond being relevant for predator avoidance while longer time periods are used to also inform on applied questions (Domenici and Blake 1997; Tudorache et al. 2008; Emadi et al. 2024). Importantly, how maximum swimming performance, quantified in provoked escape response tests, translates to performance in natural environments (or in fish passage solutions) remains to be tested.

Overall, lower performance in the second test compared to the first underlines the importance of fish experience when quantifying swimming performance. Even if 12 h recovery is deemed sufficient for fish to recover from burst exercise (García-Vega et al. 2023), it is possible that accumulation of stress in the hatchery environment (including handling and anaesthetics) may have reduced the recovery capacity of the fish and contributed to a reduced performance in the second trial (Jain et al. 1998; Wagner et al. 2005). An alternative explanation is that the fish habituated to the experimental protocol, and therefore showed a reduced response to the scaring stimuli (Boeger et al. 2006; Chanin et al. 2012). An inter-individual difference in both habituation and recovery may also have contributed to the lack of correlation in individual performance between the first and the second test (Martins et al. 2011).

Conclusions

A provoked escape response test, elicited by dropping a weight near the fish and estimating its maximum swimming velocity during the subsequent escape, did not produce repeatable performance estimates for individual fish between successive tests in the examined fish species. Therefore, the use of this method is discouraged when the performance of individual fish is important. The testing protocol may, however, remain a useful, simple and cheap method for estimating average swimming performance and for comparing different groups of fish. A lower performance in the second compared to the first test shows that fish experience (habituation or stress) can influence the estimated maximum swimming speed, highlighting that absolute estimates should be used with caution. In the applied realm, the relationship between the estimated maximum swimming speed and the performance over velocity barriers (e.g. fishways) needs to be further investigated.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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