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Ducos Salomé (Orcid ID: 0000-0002-5661-6598)

# Ontogeny of swimming performance of hatchery-reared post-larvae and juvenile fish: a case of two threatened Mediterranean species

Ducos Salomé<sup>1, 2</sup>, Pugliese Sally<sup>1</sup>, Demolliens Mikaël<sup>1</sup>, Beraud Louisa<sup>1</sup>, Boussard Alizée<sup>1</sup>, Delmas Alban<sup>1</sup>, Agostini Sylvia<sup>1, 2</sup>, Garcia Jessica<sup>1</sup>, Aiello Antoine<sup>1</sup>, Durieux Eric D. H.<sup>1, 2</sup>

<sup>1</sup> Università di Corsica Pasquale Paoli, UMS CNRS 3514 Plateforme marine STELLA MARE, 20620 Biguglia, France

<sup>2</sup> Università di Corsica Pasquale Paoli, UMR CNRS 6134 Sciences pour l'Environnement, 20250 Corte, France

## Corresponding authors:

Salomé Ducos

Email: [ducos\\_s@univ-corse.fr](mailto:ducos_s@univ-corse.fr)

Postal address: UMS CNRS 3514 STELLA MARE, Lieu-dit U Casone, Lido de la Marana, 20620 Biguglia, France

Eric Durieux

Email: [durieux@univ-corse.fr](mailto:durieux@univ-corse.fr)

Postal address: UMS CNRS 3514 STELLA MARE, Lieu-dit U Casone, Lido de la Marana, 20620 Biguglia, France

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## **ABSTRACT**

Swimming performance is a well-established key physiological parameter of fish that is highly linked to their fitness in the wild. In the context of fish restocking or restoration purposes, it therefore appears crucial to study this specific behaviour. Here, we investigated intra and interspecies differences in the swimming performance of hatchery-reared post-larvae and juveniles belonging to two Mediterranean candidate threatened species, the common dentex, *Dentex dentex* (Sparidae), and the brown meagre, *Sciaena umbra* (Sciaenidae), with body sizes ranging from 8 to 37 mm TL (from 24 to 58 days post-hatch). The swimming abilities were estimated through the calculation of their critical swimming speed ( $U_{crit}$ ), their relative  $U_{crit}$  and their Reynolds number ( $Re$ ). Two different patterns were observed between *D. dentex* and *S. umbra*, showing a different effect of ontogeny on the performance of both species. The relative  $U_{crit}$  of *S. umbra* decreased linearly through ontogeny, whereas the relative  $U_{crit}$  and  $U_{crit}$  of *D. dentex* increased linearly through the range of sizes tested. The ontogenetic change in  $U_{crit}$  of *S. umbra* occurred in two stages: a first stage of sharp improvement and a second stage of a slow decrease in performance. Both stages were separated by a breakpoint that coincided with the appearance of a refusal to swim behaviour that occurred shortly after the end of metamorphosis and can potentially be associated with the establishment of this species' sedentary behaviour. The swimming performance of both species showed ontogenetic differences. *Sciaena umbra* had the highest relative performance when its body sizes were the smallest, whereas *D. dentex* showed the highest relative performance as its largest body sizes. These results will be linked to future research on both of these species concerning their escape, exploratory and predatory behaviours, and for restocking purposes to draw a more realistic overview of hatchery-reared juvenile performance. Knowledge of both species' behavioural and swimming performance through ontogeny is important to consider when

using hatchery-reared fish juveniles for restocking, as size-at-release can have a large impact on fish survival and thus on restocking success.

**KEYWORDS**

critical swimming speed, *Dentex dentex*, restocking, Reynolds number, *Sciaena umbra*

## 1. Introduction

In relation to the decrease in marine stocks and biodiversity, *ex situ* conservation is currently a tool receiving much attention in relation to threatened species whose reproduction and juvenile production have been mastered in captivity (J. D. Bell et al., 2008). Such a method has been used for several years on fish species used for exploitation purposes (e.g. salmonids), called “sea ranching”, or for biodiversity conservation purposes (e.g. sturgeon), called “restocking”. Even though restocking is now considered an important tool for fish species conservation, only recent studies have started to focus on fish behaviour and performance as key points to consider for restocking purposes (e.g. D’Anna et al., 2012; Du et al., 2014).

The swimming performance of teleost fishes corresponds to the link between endurance and swimming velocity (Plaut, 2001; Wolter & Arlinghaus, 2003). Thus, knowing the individual swimming speed of a fish and its capacity to maintain this effort over time are essential variables for determining swimming ability (Gui et al., 2014). Swimming performance is important to consider when determining the probability an organism will survive in the natural environment. Indeed, individual swimming performance directly affects the dispersal, predation efficiency and escape performance of an organism, thus establishing a close link between swimming ability and survival (Stobutzki & Bellwood, 1997; Wolter & Arlinghaus, 2003). In addition to survival, habitat colonization is a mechanism linked to swimming performance and must be considered when estimating the success of a restocking program (Esquivel-Muelbert et al., 2018). Therefore, the swimming performance of targeted species is key and should not be ignored.

Critical swimming speed ( $U_{crit}$ ) is a category of prolonged swimming speed and is thus a measurement allowing the assessment, over a short duration, of maximum swimming performance of a fish (Gui *et al.*, 2014; Plaut, 2001). This is a measurement commonly reported in the literature, and it makes comparisons between species, ontogenetic stages and environments possible (*e.g.* Allen *et al.*, 2006; Faria *et al.*, 2009; ; A. Rossi *et al.*, 2019). Many studies exploring fish swimming performance have focused on larval or juvenile stages because it is necessary to better understand survival, dispersal, settlement and recruitment in terms of population dynamics and connectivity (*e.g.* Clark *et al.*, 2005; Stobutzki & Bellwood, 1997).

The Mediterranean Sea is a precious environment containing rich biodiversity and emblematic species (Coll *et al.*, 2010). However, some of the latter are considered threatened in the Mediterranean region by the IUCN Red List. Such is the case for the brown meagre *Sciaena umbra* Linnaeus, 1758 (Sciaenidae) and the common dentex *Dentex dentex* Linnaeus, 1758 (Sparidae), both of which are listed as “Vulnerable” in the Mediterranean region (Bizsel, Yokes, *et al.*, 2011; Bizsel, Kara, *et al.*, 2011, respectively). They both are fish species of great importance for local small-scale fisheries and are targeted by recreational fisheries. Additionally, both species have a long life span (longer than 15 years for *S. umbra* (Grau *et al.*, 2009) and 20 years for *D. dentex* (Marengo *et al.*, 2014)), which makes them increasingly vulnerable to fisheries activities. In the wild, those two coastal species spawn in the spring, are gonochoristic (Grau *et al.*, 2009; Marengo *et al.*, 2014) and are referred to as demersal species, as, unlike their pelagic larval phase, they live close to the substrate during their juvenile and adult stages. *Sciaena umbra* and *D. dentex* juveniles are found at shallow depths, notably on rocky substrates and in *Posidonia oceanica* meadows (Dulčić *et al.*, 2002; Grau *et al.*, 2009; Marengo *et al.*, 2014), which are threatened by anthropogenic pressures. Juvenile

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individuals, especially young-of-the-year, of both species are rarely observed *in situ* (Dulčić *et al.*, 2002), which does not allow for a detailed knowledge of their ecology and behaviour. However, the ecological and behavioural characteristics of adult individuals are better known (e.g. for *D. dentex*: Aspillaga *et al.*, 2017; Marengo *et al.*, 2014; and for *S. umbra*: Alós & Cabanellas-Reboredo, 2012; Brazo *et al.*, 2021). Adult *D. dentex* individuals are mostly seen swimming solitarily in open water, above *P. oceanica* or rocky bottoms (Marengo *et al.*, 2014; Morales-Nin & Moranta, 1997). Adults of *S. umbra* are often observed in groups of several individuals relatively close to the bottom or hiding in rocky substrate (e.g. caves, rocks, rocky crevasse) during the daytime (Harmelin & Marinopoulos, 1993). This ecological behaviour of *S. umbra* was related to the demonstration of this species' sedentary behaviour, *i.e.* they have narrow home ranges and high site fidelity (Alós & Cabanellas-Reboredo, 2012).

Although *D. dentex* and *S. umbra* are two species that have been receiving increasing attention in the last 20 years concerning their rearing (e.g. Chatzifotis *et al.*, 2006; Koumoundouros *et al.*, 2004), no studies, to our knowledge, have studied the swimming behaviours or performances of hatchery-reared individuals of both species.

In the present study, we aimed to assess the swimming performance of hatchery-reared *D. dentex* and *S. umbra* late-stage larvae and juveniles to determine how the critical swimming speeds of both species are influenced by ontogeny. This main goal was directly connected to the necessity of obtaining a better understanding of both species to benefit restocking and conservation purposes. Indeed, this study could have implications in selecting each species size-at-release to maximize the survival of hatchery-reared individuals after their release in the wild for restocking purposes.

## 2. Materials & Methods

The care and use of experimental fish in this study complied with French animal welfare laws, guidelines and policies as approved by the French National Ethics Committee in Animal Experimentation (CNREEA).

### 2.1. Fish rearing procedures

All the fish used in this experiment were produced using *D. dentex* and *S. umbra* captive broodstocks. Breeders were fished in the Corsican littoral waters (Mediterranean Sea) between 2015 and 2020. The broodstock used to produce the batch of *S. umbra* eggs that provided the fish of the study was composed of 17 wild individuals. *Dentex dentex* individuals came from the same egg batch produced by a broodstock of 12 wild individuals. Spawning occurred through shifted natural photoperiod and temperature manipulations to advance the spawning period a few months backwards and was never induced through hormone injections.

*Sciaena umbra* post-larvae and juveniles were raised with controlled parameters (water salinity: 38 psu; water temperature: 19-21 °C; oxygen saturation: 75-100% and pH: 6.9-7.3) in a 200 l black cylindrical-conical tank. Reared individuals were fed *Artemia salina* nauplii, metanaplii, *Tigriopus spp* and dry food (Gemma micro & Gemma wean, SKRETTING; 75 to 800 µm diameter size) until 40 days post-hatch (DPH) and then only with dry food afterwards.

The rearing period of *D. dentex* post-larvae and juveniles was made in a 2290 l black cylindrical-conical tank and parameters were monitored daily (water salinity: 38 psu; water temperature range: 17-21 °C; oxygen saturation range: 75-100% and pH: 6.9-7.3). The rearing tank was enriched with *Tisochrysis lutea* and *Nannochloropsis oculata* (from hatching to 20 DPH; 100 000 cell/ml). The alimentation was composed of dry food (Gemma micro & Gemma

wean, SKRETTING; 75 to 800  $\mu\text{m}$  diameter size) and supplemented with living prey: rotifers (from 3 to 20 DPH) and *A. salina* (from 12 to 50 DPH).

## 2.2. Experimental protocol

Experimental tests for *S. umbra* took place from May to June 2020 (17 days; from 24 to 58 DPH;  $n = 120$ ). Experimental tests for *D. dentex* took place from February to March 2021 (22 days; from 26 to 57 DPH;  $n = 163$ ). A higher number of *D. dentex* was used due to the high mortality rate of the smallest size classes observed during the experiment.

Experiments were performed between 09.00 and 13.00 hours. Tested fish were not fed since the previous evening, meaning that they had all fasted for approximately 12 hours. All fish were tested only once in order to exclude any training effect. The temperature of the experimental tank water was maintained at  $20.9 \pm 0.5$  °C (range = 20-21.8 °C) for both species, and  $\text{O}_2$  saturation was kept around  $90.2 \pm 6.3\%$  (range = 80-100%).

The trial started with the transfer of one individual inside the swimming chamber (170 ml cylindrical chamber) of a Loligo Systems swimming tunnel (model name: SW10000). A two minute acclimatization time was given to each individual before the beginning of the trial. After this time, the same swimming protocol was applied to all the fish tested with the aim of calculating the individual critical swimming speed,  $U_{crit}$ , which is commonly described as the maximum swimming velocity at which the fish is no longer capable of retaining its position in the water flow (Brett, 1964). The measurement of  $U_{crit}$  is based on imposed water speed increments: the flow speed was gradually increased every 2 minutes with a speed increment ( $U_i$  in the latter formula) corresponding to approximately 0.6 body length (BL).  $U_{crit}$  calculations were acquired using Brett's equation (Brett, 1964):  $U_{crit} = U + [U_i \times (\frac{t}{t_i})]$ , where  $U$  is the last flow speed at which the fish was able to retain its position in the water flow during the entire 2

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minute interval ( $\text{cm}\cdot\text{s}^{-1}$ ),  $U_i$  is the speed increment ( $\text{cm}\cdot\text{s}^{-1}$ ),  $t$  is the duration (s) during which the fish maintain its position in the water flow at the last 2 minute interval, and  $t_i$  is the time between two speed increments (120 s). As the studied individuals displayed a wide range of body sizes, relative  $U_{\text{crit}}$  measurements were used and were calculated by dividing the  $U_{\text{crit}}$  values by the individual's total lengths.

Inside the swimming chamber, the flow speed ( $\text{cm}\cdot\text{s}^{-1}$ ) was modified through the use of a controller by varying the turbine rotational speed. The incoming voltage of the turbine was given by a voltmeter wired to the controller and was linked to the flow speed through this calibration equation:  $y = 2.4439x - 1.1107$  ( $R^2 = 0.9931$ ), where  $x$  is the incoming voltage (V) and  $y$  represents the flow speed ( $\text{cm}\cdot\text{s}^{-1}$ ).

For each single fish, the Reynolds number ( $Re$ ) was calculated *via* the following equation (Webb & Weihs, 1986):  $Re = U_{\text{crit}} \times SL / \nu$  (where  $U_{\text{crit}}$  is expressed in  $\text{m}\cdot\text{s}^{-1}$ ,  $SL$  is the individual fish standard length, in m, and  $\nu = 1.03 \times 10^{-6} \text{ m}^2\cdot\text{s}^{-1}$  and corresponds to seawater kinematic viscosity). This variable indicates the type of fluid forces the fish is undergoing and is often used as an index of fish swimming capacity: the lowest values of  $Re$  ( $< 300$ ) seem to indicate a viscous fluid regime or, in other words, inefficient swimming, whereas  $Re$  values above 1000 seem to be linked to fully effective swimming (Leis, 2006). The range of values between 300 and 1000 is considered an intermediate interval where both inertial and viscous regimes take place. Therefore, viscous losses are considered smaller for fish swimming with a higher  $Re$  value and vice versa.

After each trial, fish were anaesthetized (Benzocaine in sea water; 100 ppm), measured (total length, standard length, body height; in mm) and weighed (in g). This means that fish total length (TL) was measured after each trial and was thus visually estimated before each experiment in order to choose the appropriate  $U_i$  value (0.6, 0.9, 1.2, 1.5, 1.8 or 2.1  $\text{cm}\cdot\text{s}^{-1}$  in

relation to the body size class observed). Only fish with a TL that corresponded to the increment applied  $\pm 0.25$  cm were kept for the next analysis (same method as Koumoundouros *et al.*, 2002).

During each trial, several behaviours were observed and identified. For instance, fish laying temporarily or permanently their entire body or their caudal fin on the swimming chamber grid with no sign of swimming against the water flow and unrelated to swimming exhaustion were characterized as displaying a refusal to swim. Mortality induced by extreme stress was also quantified with the number of individuals dying before the beginning of the trial (mainly observed during the transfer, *via* a beaker, between the rearing tank and the swimming chamber).

*Sciaena umbra* and *D. dentex* larval metamorphosis were visually assessed. For *S. umbra*, the end of this transformation from the larval form to the juvenile form was estimated in our study when pigmentation started on the caudal fin and when caudal peduncle was fully pigmented. This approach was consistent with the study of Millot *et al.* (submitted) that assessed larval metamorphosis in hatchery-reared *S. umbra*. For *D. dentex*, the end of metamorphosis was estimated when the caudal peduncle was fully pigmented and when the pigmentation of the fish body was nearly completed (Crec'hriou *et al.*, 2015).

### **2.3. Data analysis**

To evaluate the relationships between individual body length and  $U_{crit}$ , or relative  $U_{crit}$ , for both species, regression models were implemented.

Linear regressions were computed for the relative  $U_{crit}$  and TL relationships for both species and for the  $U_{crit}$  and TL relationships for *D. dentex*. As all of these data presented a normal distribution as well as homogeneous variances, Pearson correlation and linear regression models were used.

The relationship between  $U_{crit}$  and individual TL of *S. umbra* was computed through a piecewise (segmented) regression model because a classic linear regression was not adequate for those data and a piecewise (segmented) regression was proven to significantly improve the accuracy of the model compared to a linear regression (ANOVA,  $P < 0.001$ ). This method highlights the presence of one or several breakpoints in the relationship between two variables, and the continuous intervals on both sides of the breakpoints are modelled with linear regressions. This regression model was used with the help of the *segmented* R library. To estimate differences in relative swimming performance ( $U_{crit}/TL$ ) between both species, the 95% confidence intervals for the intercept and slopes of both linear regressions ( $y = ax + b$  where  $a$  is the slope and  $b$  the intercept) were calculated.

As the increments ( $U_i$  values, in  $cm.s^{-1}$ ) were directly linked to fish body length, six different size classes were investigated: 10, 15, 20, 25, 30 and 35 mm ( $\pm 2.5$  mm). Significant differences for the  $U_{crit}$  and relative  $U_{crit}$  mean values between size classes were investigated for both species separately using Kruskal-Wallis tests, followed by a Dunn's test when a significant difference was found. Significant differences for  $U_{crit}$  and relative  $U_{crit}$  mean values between both species were conducted for each size class separately using Student's  $t$ -tests.

The effect of size classes on different observed behaviours was examined using  $G$ -tests, as the contingency tables displayed one or several expected frequencies beneath 5 (Zar, 1984).

All statistical analyses were performed *via* R software (version 4.1.1).

### 3. Results

A total of 90 common dentex and 94 brown meagre individuals were used with the correct size increment and were therefore included in the analyses (Table 1).

In this study, the *D. dentex* larval metamorphosis stage occurred between 23 and 38 DPH, which was consistent with previous studies on this species in the literature (e.g. Santamaria, 2001), indicating that swimming measurements were collected from post-larvae and juveniles. The end of the transformation to the juvenile stage corresponded to a mean TL of  $18.2 \pm 0.3$  mm in *D. dentex*.

At 25 DPH, *S. umbra* started metamorphosis from the larval to juvenile stage, which ended for all individuals at approximately 37 DPH at an approximate TL of 15 mm. This was consistent with the study of Millot *et al.* (submitted), where the metamorphosis of *S. umbra* was estimated to occur between 25 and 35 DPH, with an average TL of  $16.450 \pm 1.012$  mm marking the end of metamorphosis. Afterwards, morphological changes continue to occur in this species especially concerning the size of the first dorsal and pectoral fins becoming extremely large and disproportionate (Crec'hriou *et al.*, 2015).

#### Swimming performance

*Dentex dentex* swimming performance ( $U_{crit}$ ) strongly increased linearly with body size for the interval of sizes tested (from 8.8 to 36.6 mm TL;  $U_{crit} = -1.895 + 0.713 \times TL$ ,  $R^2 = 0.80$ ,  $P < 0.001$ ; Figure 1a) and showed increasing relative swimming performance even if the variation range was quite wide, inducing a weak correlation coefficient (relative  $U_{crit} = 5.090 + 0.048 \times TL$ ,  $R^2 = 0.07$ ,  $P < 0.01$ ; Figure 1c).

When looking at *S. umbra* individuals, the piecewise regression model showed that the relationship between *S. umbra* body size (range: 8 to 37.3 mm TL) and critical swimming speed differed between the smallest and the largest individuals tested ( $U_{crit} = 3.368 + 0.516 \times TL -$

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0.704 x (TL - 22.857) x (TL > 22.857),  $R^2 = 0.31$ ,  $P < 0.001$ ; Figure 1b), inducing a nonlinear relationship between these two variables. This segmented regression supported the presence of a breakpoint in the data (pseudo score test,  $P < 0.001$ ) at TL = 22.857 mm (95% C.I.: 18.783 to 26.931 mm). The slope of the segment representing the smallest fish was 0.516 (95% C.I.: 0.297 to 0.736). The slope for the second segment was -0.188 (95% C.I.: -0.416 to 0.040). Regarding the relative  $U_{crit}$  values of *S. umbra* individuals, its representation with TL showed a linear relationship with a negative slope (relative  $U_{crit} = 10.587 - 0.195 \times TL$ ,  $R^2 = 0.53$ ,  $P < 0.001$ ; Figure 1d), *i.e.*, relative swimming performance decreased with an increase in body length. Relative critical swimming speed linear regressions were found to be significantly different between both species (*S. umbra*:  $a = -0.195$  with 95% C.I.: -0.233 to -0.158;  $b = 10.587$  with 95% C.I.: 9.687 to 11.487; and *D. dentex*:  $a = 0.046$  with 95% C.I.: 0.011 to 0.803;  $b = 5.148$  with 95% C.I.: 4.343 to 5.953) (Figures 1c and 1d).

Therefore, individual TL appeared to be a strong predictor of the  $U_{crit}$  and relative  $U_{crit}$  values in both species ( $P < 0.001$  or 0.01; Figure 1).

For the range of sizes tested, the *D. dentex*  $U_{crit}$  values were between 3.3 and 27.8  $\text{cm}\cdot\text{s}^{-1}$ . Both of these extreme values corresponded to the bounds of the relative  $U_{crit}$  values interval, *i.e.* 3 and 9.3  $\text{BL}\cdot\text{s}^{-1}$ , respectively. Concerning *S. umbra* performances, the  $U_{crit}$  values were between 5.5 and 22.7  $\text{cm}\cdot\text{s}^{-1}$ , and the relative  $U_{crit}$  values were between 1.9 and 14.2  $\text{BL}\cdot\text{s}^{-1}$ .

When investigating the effect of the predefined size classes (*i.e.*  $10 \pm 2.5$ ,  $15 \pm 2.5$ ,  $20 \pm 2.5$ ,  $25 \pm 2.5$ ,  $30 \pm 2.5$  and  $35 \pm 2.5$  mm TL) on *S. umbra* and *D. dentex* swimming performance, the *D. dentex* relative  $U_{crit}$  values were not affected by body size class (Kruskal-Wallis test,  $P = 0.082$ ; Figure 2b). However, the *S. umbra* mean  $U_{crit}$  values (Kruskal-Wallis test,  $P < 0.001$ ; Figure 2a) and the relative  $U_{crit}$  values (Kruskal-Wallis test,  $P < 0.001$ ; Figure 2b), and the *D. dentex* mean

$U_{crit}$  values (Kruskal-Wallis test,  $P < 0.001$ ; Figure 2a) were found to be significantly different between at least two size classes.

Moreover, significant differences in the mean  $U_{crit}$  and relative  $U_{crit}$  values were found between both species (Figure 2). *Sciaena umbra* and *D. dentex* juveniles presented significantly different mean  $U_{crit}$  values for the 10, 20, 30 and 35 mm TL size classes (Figure 2a), as well as significantly different mean relative  $U_{crit}$  values for the 10, 15, 30 and 35 mm TL size classes (Figure 2b). In brief, the *S. umbra*  $U_{crit}$  and relative  $U_{crit}$  values were significantly higher than the *D. dentex* values for the smallest size classes and significantly smaller for the largest size classes.

The  $R_e$  calculation for each fish showed that none of the *S. umbra* juveniles and only one *D. dentex* individual (TL = 11.02 mm, DPH = 27) displayed a value reflecting swimming that was very energetically costly (values beneath 300; Leis, 2006). Moreover, the juveniles tested showed Reynolds numbers above 1000 as soon as they measured approximately 14.5 mm TL for *D. dentex* and 12.5 mm TL for *S. umbra* (Figure 3).

#### *Swimming behaviours*

For *S. umbra* individuals, a new behaviour, which was never noticed before, was observed from 43 DPH (included in size class  $20 \pm 2.5$  mm TL) and characterized by individuals who temporarily or permanently refused to swim. These individuals rested on the bottom of the swimming chamber and made no effort to swim against the flow either temporarily (before being motivated to swim by a visual stimulation) or permanently (marking the end of the trial). A significant difference in the presence of this behaviour was detected between size classes ( $G$ -test,  $P < 0.001$ ; Table 2). Indeed, the first two size classes (10 and 15 mm TL) were

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significantly different from the last four ones (20, 25, 30 and 35 mm TL) from which this behaviour first occurred (Table 2).

The experiments carried out on *D. dentex* post-larvae and juveniles highlighted that the small individuals were sensitive to manipulation, leading to extreme stress-induced behaviours and even death. The individuals were removed from the rearing tank and placed in the swimming chamber through the use of a 500 mL glass beaker to avoid manipulating them with a net, as it has already been shown to induce 100 % mortality in individuals between 11 and 32 mm TL (Koumoundouros *et al.*, 2004). However, in our study, some of the studied individuals between 10 and 25 mm TL ( $\pm 2.5$  mm) died during the transfer between the rearing tank and the swimming tunnel (Table 2). The frequency of this consequence of manipulation appeared to be significantly different between size classes (*G*-test,  $P < 0.001$ ; Table 2). Higher frequencies of mortality were found for the 15 and 20 mm TL size classes and were significantly different from the low frequencies found in the 25, 30 and 35 mm TL size classes. No mortality was recorded in *S. umbra* fish.

#### 4. Discussion

The measurement of individual critical swimming speeds is a widespread tool often used to evaluate fish swimming ability. Indeed, it is considered an easy method (Plaut, 2001) that offers the advantage of being used for intraspecific comparisons (Leis, 2006).

This work represents the first study highlighting *S. umbra* and *D. dentex* hatchery-reared post-larvae and juvenile swimming performance for restocking purposes.

Our laboratory study did not directly measure the *in situ* swimming velocity of individuals but is still considered realistic as this measure can be approximated as half of the  $U_{crit}$  and that the use of relative  $U_{crit}$  allows comparisons between species and body sizes (Leis, 2006). Indeed, this study allowed the comparison of the swimming performance of two fish species, *S. umbra* and *D. dentex*, assessed as “Vulnerable” in the Mediterranean region (Bizzel, Kara, et al., 2011; Bizzel, Yokes, et al., 2011). Moreover, this study also allowed comparisons between body sizes. Our results showed that individual body size was a good predictor of critical swimming speed, which was consistent with previous studies highlighting as well a strong relationship between both variables (e.g. Clark et al., 2005; Faria et al., 2009).

In this study, the range of critical swimming speed values found for both species was consistent with the values found in the literature for other fish species, notably in coastal Mediterranean species (from 6.3 to 32.9  $\text{cm}\cdot\text{s}^{-1}$  for TL between 14 and 30 mm in 14 species such as *Apogon imberbis*, *Chromis chromis*, *Diplodus sargus* and *Sparus aurata*; A. Rossi et al., 2019).

It would be valuable to compare our results to the swimming performance of wild *S. umbra* and *D. dentex* juveniles to estimate if hatchery-reared individuals could display naturalistic swimming abilities and behaviours after they are released into the natural environment.

However, this experiment would probably be difficult to set up, as juveniles of both species

are rarely observed *in situ* (Dulčić et al., 2002). Several studies comparing the swimming performance of wild and hatchery-reared individuals have been conducted, but have shown contradictory results between studies (e.g. Basaran et al., 2007; Faria et al., 2009). Indeed, it is often supposed that the swimming ability and behaviour of hatchery-reared fish might differ from those of wild fish (e.g. Basaran et al., 2007). However, for *Sciaenops ocellatus* larvae, Faria et al. (2009) showed that wild and hatchery-reared individuals displayed similar  $U_{crit}$  values and thus suggested that this measurement, made on reared fish, could fully represent the swimming performance of wild individuals.

*Changes in behaviour and swimming performance trajectories through ontogeny in S. umbra*

For brown meagre, *S. umbra*, the  $U_{crit}$  measurements through the range of tested sizes showed two phases that were separated at approximately TL = 22.9 mm (95% C.I.: 18.8 to 26.9 mm), and this change in the absolute swimming performance patterns seemed to follow the end of the post-larval stage (at approximately 15 mm TL). Thus, the size interval presenting the strongly positive increase in absolute swimming performance corresponded to the late-stage larvae (*i.e.* before the end of the metamorphosis between the larval and the juvenile shape) and was followed by a later phase of a slow post-metamorphosis decrease in performance: the early-juvenile stage. Changes in swimming performance trajectory through ontogeny have already been observed in several species, such as *Myoxocephalus scorpius* (Guan et al., 2008), *Lates calcarifer* (T. Rossi et al., 2015), and a Sciaenidae: *S. ocellatus* (Faria et al., 2009). These modifications were observed after the end of metamorphosis for the first two species and at the settlement stage for the last one. These three studies submitted the hypothesis that this ontogenetic decline in swimming ability was directly due to settlement, which causes a shift in habitat and therefore a change in behaviour. It has also been shown that spontaneous swimming activity could drastically decrease after settlement, reflecting a

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transition between an exploratory behaviour characteristic of the period of habitat colonization and the well-established sedentary behaviour of 0-group juveniles in coastal habitats (Durieux *et al.*, 2010). Therefore, we hypothesize in our study that the decline in swimming performance through *S. umbra* ontogeny highlighted by the  $U_{crit}$  measurements could be linked to settlement and to the changes in habitat and behaviour that are induced by it. The linear decrease in critical swimming speed scaled to body size in *S. umbra* was also consistent with this hypothesis, as pre-settlement individuals leave the pelagic environment and settle in a sustainable habitat, thus inducing higher relative swimming speeds in pre-settlement individuals than in juveniles (Bellwood & Fisher, 2001; Leis, 2006).

Moreover, the sharp decrease in swimming performance after the end of larval metamorphosis in our study coincided with the first observations of refusal to swim behaviours (*i.e.* at 43 DPH), highlighting a strong connection between swimming performance and behavioural modifications through ontogeny. Both ontogenetic changes might therefore reflect the establishment of sedentary behaviour, which is characteristic of this species (Alós & Cabanellas-Reboredo, 2012; La Mesa *et al.*, 2008).

#### *Increase in swimming performance through ontogeny in D. dentex*

Concerning the range of values obtained for *D. dentex*, a previous study on Mediterranean fish larvae measured the  $U_{crit}$  of one *D. dentex* individual (15 < TL < 20 mm), producing a value of 17.8 cm.s<sup>-1</sup> (Faillettaz *et al.*, 2018). For this size range, our study showed a mean  $U_{crit}$  value of approximately 10 cm.s<sup>-1</sup>, with values ranging between 6.1 and 15.4 cm.s<sup>-1</sup>. It is known (and observed in our study) that inter-individual variability in swimming performance can be quite important and, thus, our values could be considered close to the  $U_{crit}$  measurement previously found for *D. dentex* (Faillettaz *et al.*, 2018).

Throughout the entire range of sizes tested in our study, there was no distinct modification of the swimming ability trajectory of *D. dentex*: speed measurements showed the same linear relationship in post-larvae and early juveniles. The  $U_{crit}$  values strongly increased with body size, while the relationship between relative swimming speeds and body size was less obvious. The relative critical swimming speeds significantly increased with body size even if no significant difference was found in the mean relative  $U_{crit}$  between the size classes.

Absolute swimming speed has been shown to increase with body size in other fish species (e.g. Fisher *et al.*, 2000). This can certainly be explained by two different mechanisms, which are based on the facts that *i)* for the same number of tail-beats, the distance covered by a fish is proportional to its body size (Bruslé & Quignard, 2004) and *ii)* this swimming performance is presumably linked to the development of several morpho-anatomical and physiological characteristics that are linked to locomotion (e.g. muscles, energy reserves) (Fisher *et al.*, 2000).

Concerning the low handling tolerance of *D. dentex*, the abrupt and significant difference in the percentage of mortality between the size classes above 20 mm TL and the size classes less than or equal to 20 mm might be linked to the larval metamorphosis of the species. Metamorphosis is a phase during which fish undergo many morphological (on which we based our identification of the transition between the larval and juvenile stages), physiological, behavioural and metabolic modifications (McMenamin & Parichy, 2013). These modifications are known to be driven, in part, by hormonal (e.g. cortisol, thyroid hormones) and chemical (e.g. nucleic acids, amino acids) alterations (Ishibashi *et al.*, 2005). It has been shown in another Sparidae species (*Pagrus major*) that these alterations induce an increase in vulnerability to environmental stressors (e.g. temperature, salinity, oxygen level) during

metamorphosis (Ishibashi et al., 2005). Thus, late-stage larvae are less able to deal with stressful situations, such as handling, than are juvenile fish.

#### *Species swimming performance comparison*

Previous studies have already highlighted that even ecologically similar (as for *S. umbra* and *D. dentex*) or phylogenetically closely related species can display large differences in swimming performance (e.g. A. Rossi et al., 2019) and the associated link with body size. In our study, interspecific comparisons showed that *S. umbra* had better relative swimming abilities than *D. dentex* for the smallest body sizes tested before both species entered an inertial regime ( $R_e = 1000$ ). However, both species were equally efficient swimmers when starting their juvenile life, as relative swimming performance was equivalent after the end of metamorphosis (i.e. the 20 and 25 mm TL size classes were the first size classes corresponding to both species in the post-metamorphosis stage). Finally, at body sizes greater than 30 mm TL, the opposite pattern was observed with *D. dentex* being more efficient swimmers than *S. umbra* during the early-juvenile stage. This early-juvenile stage performances pattern could be seen as reflecting adult swimming and ability of both species. Indeed, as adult *S. umbra* displays sedentary behaviour (previously mentioned), are predators of benthic prey (Fabi et al., 1998) and are gregarious and slow-swimming individuals, it could be considered that the adults of this fish species do not need high swimming abilities. Adults *D. dentex*, in contrast, are much more mobile and are predators of demersal as well as pelagic prey (e.g. Morales-Nin & Moranta, 1997), leading them to have much higher swimming abilities than those of adult *S. umbra*.

The different swimming performance patterns found in both species support the idea that swimming abilities are species dependent, notably due to their difference in morphologies (e.g. A. Rossi et al., 2019), fin shape, ecological behaviour and swimming mode (Wolter &

Arlinghaus, 2003). However, when considering both species' swimming capacities through the use of the Reynolds number, it appeared that most of the individuals of this experiment had small viscous losses and were thus actively moving in their environment.

#### *Perspectives in relation to restocking purposes and conclusion*

Considering that swimming ability might be closely connected to survival, notably through escape and predation performance, the two species presented two different patterns of survival maximization after potentially being released in the wild. As previously mentioned, *S. umbra* showed maximum relative swimming performance for the smallest body sizes tested, whereas *D. dentex* showed maximum relative swimming performance for the largest body sizes tested. This result would thus imply that, to maximize the escape and foraging abilities of hatchery-reared individuals for restocking purposes, the largest body sizes for *D. dentex* and the smallest body sizes for *S. umbra* could be considered as the ideal sizes-at-release. Moreover, *D. dentex* that were smaller than 25 mm TL have been shown to be sensitive to handling, which, for some of them, led to mortality. Thus, the use of a larger size-at-release for *D. dentex* juveniles would surely minimize mortality caused by handling stress. In addition, it is important to remember that fish with a larger size-at-release have been shown to present a higher survival rate than smaller fish (e.g. Willis *et al.*, 1995). This result could be linked to the fact that smaller individuals are more likely to be subjected to a higher predation pressure (A. M. Bell *et al.*, 2011). However, to maximize survival after releasing individuals in the wild, it is recommended to keep them in captivity for as little time as possible, as it affects their adaption capacity to the wild less (Philippart, 1995). Therefore, it induces the necessity of a trade-off between minimizing the effect of domestication by choosing a small size-at-release and minimizing the predation pressure by choosing a larger size-at-release.

This is the first study highlighting *S. umbra* and *D. dentex* hatchery-reared post-larvae and juvenile swimming performance for restocking purposes. Indeed, a better understanding of both species' swimming performances and behaviours seems necessary to consider when estimating, for example, the body size-at-release that is most appropriate for the release of hatchery-reared juveniles in relation to biodiversity conservation purposes.

Drawing a conclusion on the body size-at-release of interest for conservation strategies of both species might require further investigations, notably concerning other targeted behaviours. For instance, understanding the effect of ontogeny on the exploratory behaviours of both *D. dentex* and *S. umbra* hatchery-reared juveniles could provide us with more information for understanding dispersal (Poulsen *et al.*, 2012), and investigating the effect of ontogeny on escape and predatory behaviours might allow us to estimate survival more precisely.

This study is thus a first step towards estimating release protocols, rearing methods and sizes-at-release, which will help us maximize the post-release survival of hatchery-reared *S. umbra* and *D. dentex* individuals in a potential future restocking program.

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## **CONTRIBUTIONS**

Ducos S. conceived and designed the analysis, collected the data, performed the analysis of the data and wrote the paper.

Pugliese S. collected the data, read and corrected the paper.

Demolliens M. designed the experimental plan, read and corrected the paper.

Beraud L. collected the data, read and corrected the paper.

Boussard A. reared the individuals used in this study, read and corrected the paper.

Delmas A. reared the individuals used in this study, read and corrected the paper.

Agostini S. read and corrected the paper.

Garcia J. edited, read and corrected the paper.

Aiello A. coordinated the study, read and corrected the paper.

Durieux E.D.H. coordinated the study, edited, read and corrected the paper.

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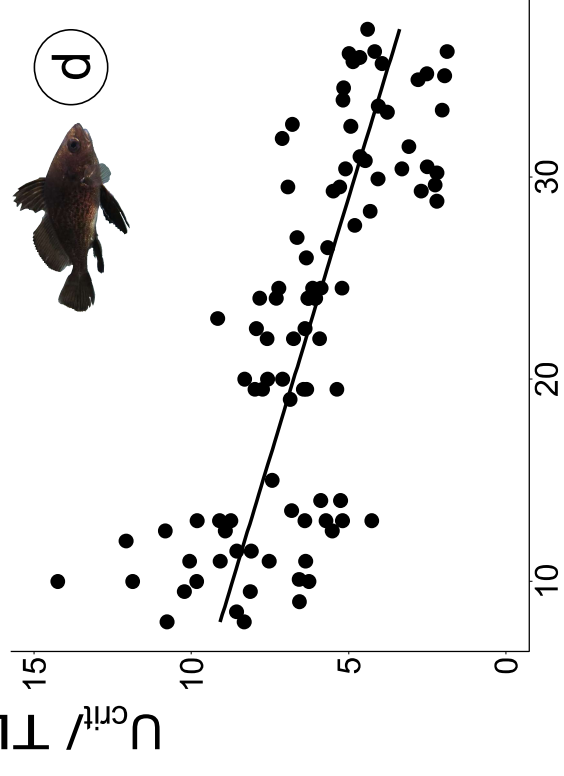
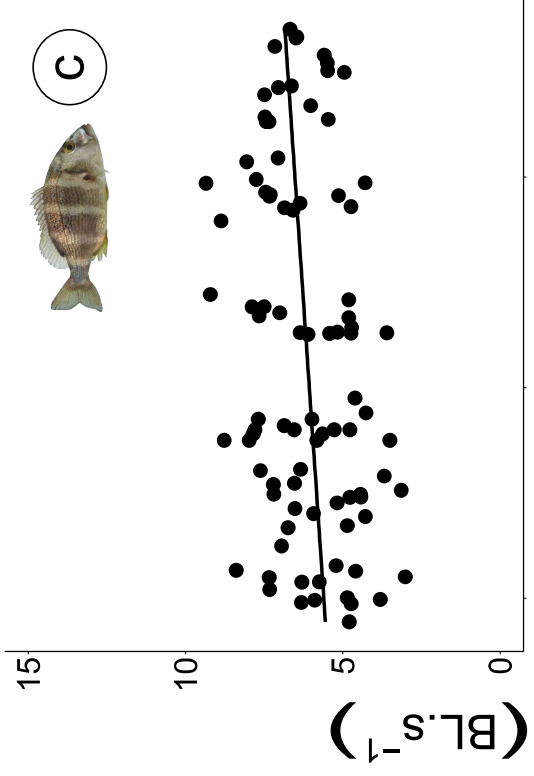
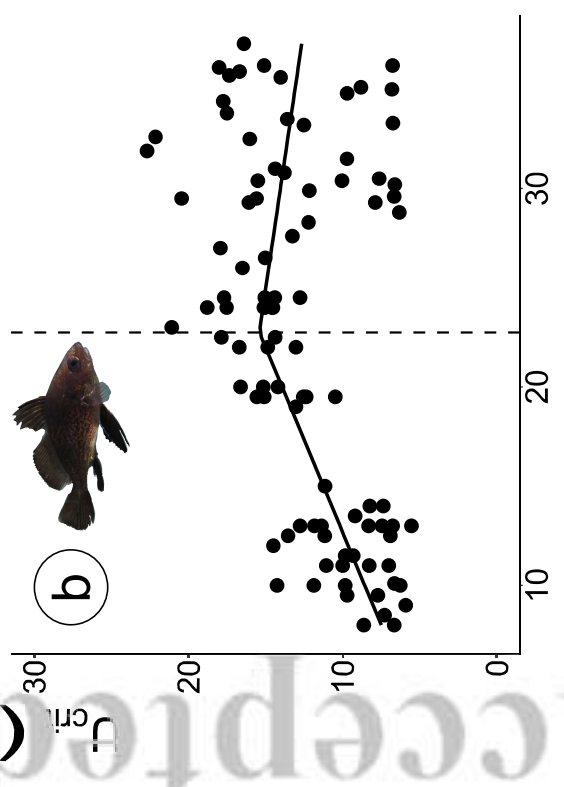
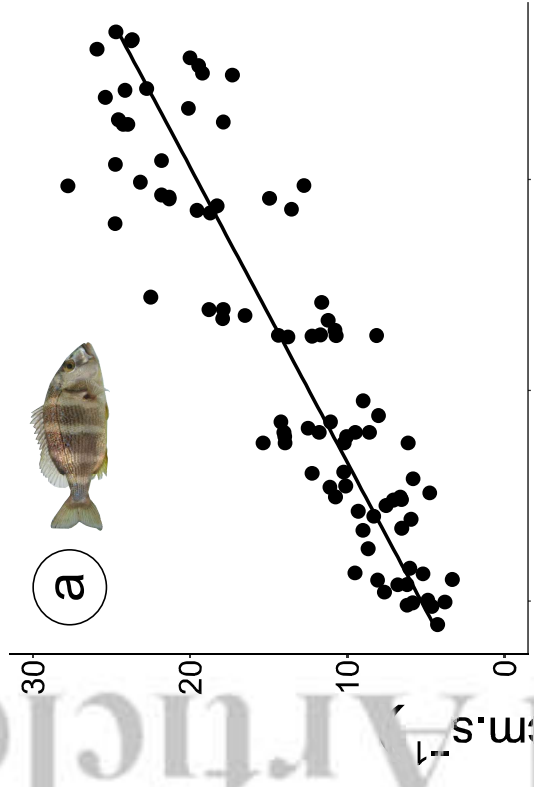
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**FIGURE 1:** Ontogeny of critical (*left side*) or relative critical swimming speed (*right side*) for **(a)** **(c)** *Dentex dentex* and **(b)** **(d)** *Sciaena umbra* post-larvae and juveniles. Black lines represent the regressions lines and the dotted line (in **(b)**) represents the breakpoint in the relationship at TL = 22.857 mm. Regression lines: **(a)**  $y = -1.895 + 0.713 \times TL$ ,  $R^2 = 0.80$ ,  $P < 0.001$ ; **(b)**  $y = 3.368 + 0.516 \times TL - 0.704 \times (TL - 22.857) \times (TL > 22.857)$ ,  $R^2 = 0.31$ ,  $P < 0.001$ ; **(c)**  $y = 5.090 + 0.048 \times TL$ ,  $R^2 = 0.07$ ,  $P < 0.01$ ; **(d)**  $y = 10.587 - 0.195 \times TL$ ,  $R^2 = 0.53$ ,  $P < 0.001$ ).

**FIGURE 2:** Effect of body length (TL), represented by 6 size classes (body size class  $\pm 2.5$  mm), on **(a)**  $U_{crit}$  ( $\text{cm.s}^{-1}$ ) and **(b)** relative  $U_{crit}$  (in  $\text{BL.s}^{-1}$ ) for both species (white boxplots: *Sciaena umbra*; grey boxplots: *Dentex dentex*). The horizontal black line inside each boxplot represents mean values of  $U_{crit}$  or  $U_{crit}/TL$  for each size class. Above boxplots, lower case letters represent the results of Dunn's tests (where similar letters show non-significant differences of mean values between size classes) for *S. umbra* juveniles. Capital letters represent the results of Dunn's tests between size classes for *D. dentex*. No letters were added on *D. dentex*  $U_{crit}/TL$  boxplots **(b)** because relative  $U_{crit}$  values were not significantly different between body size classes (Kruskal-Wallis test,  $P > 0.05$ ). Stars highlight significant differences ( $P < 0.001$ : \*\*\*;  $P < 0.01$ : \*\*;  $P < 0.05$ : \*) between both species mean values for each size classes (1-way ANOVAs).

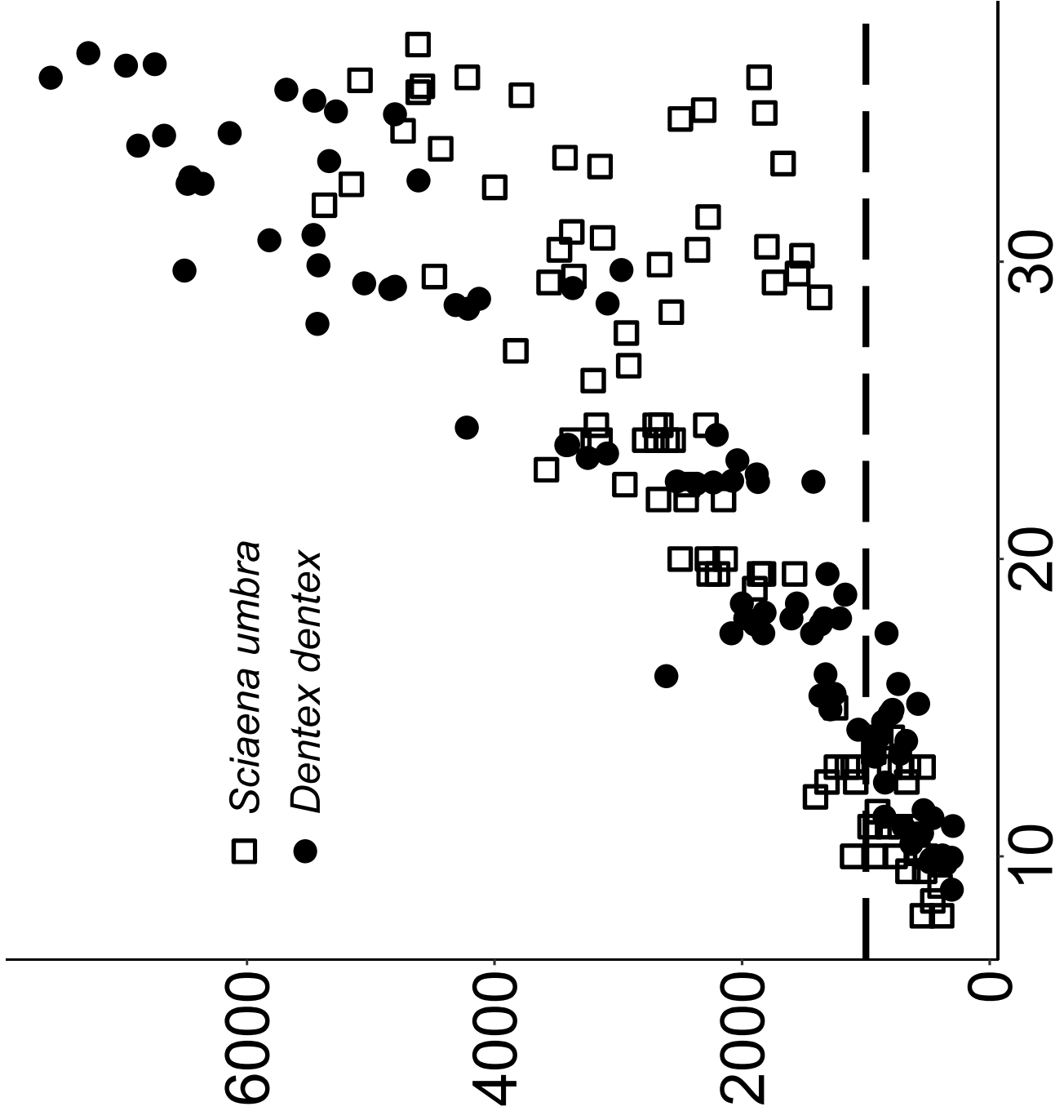
**FIGURE 3:** Reynolds number ( $Re$ ) of *Dentex dentex* (black dots) and *Sciaena umbra* (white squares) fish versus total length. The dotted line ( $Re = 1000$ ) represents the transition in a fully effective inertial environment (*above*).



Total length (mm)

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**TABLE 1:** Number of *Dentex dentex* and *Sciaena umbra* fish used for  $U_{crit}$  calculations in each size class ( $\pm 2.5$  mm)

Size class (mm)	<i>D. dentex</i>	<i>S. umbra</i>
10	15	18
15	15	14
20	15	13
25	15	15
30	15	17
35	15	17

**TABLE 2:** Observed swimming behaviours of *Dentex dentex* and *Sciaena umbra* fish tested for each size class ( $\pm 2.5$  mm). The percentages of fish dying during the transfer between the rearing tank and the swimming tunnel were given for *D. dentex* fish and the percentages of fish that displayed refusal to swim behaviour were given for *S. umbra* fish. The results of *G*-tests used to study the effect of size class on both behaviours were showed in the associated columns, where a difference in letters between size classes highlights a significant difference in frequencies.

Size class (mm)	<i>D. dentex</i>		<i>S. umbra</i>	
	Mortality following transfer (%)	<i>G</i> -test	Refusal to swim behaviour (%)	<i>G</i> -test
10	19	ac	0	a
15	25	ab	0	a
20	44	b	44	b
25	6	cd	28	b
30	0	d	35	b
35	0	d	57	b

Assessment of fish swimming behaviour and performance is crucial to estimate the survival of hatchery-reared individuals in the wild. Studying *Dentex dentex* and *Sciaena umbra* post-larvae and juvenile stages swimming performance allowed to highlight interspecies and ontogenetic differences in hatchery-reared individuals. Moreover, the sizes characterizing metamorphoses were found to be linked to behavioural and performance modifications for those species. This study is the first step for maximizing the efficiency of both species potential restocking strategy.