# Training differentially affects feeding on live prey in two marine Mediterranean fish species reared for restocking

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**Abstract :**

Restocking initiatives have the potential to help conserve populations of threatened species, and there is a growing interest in applying this approach to marine fish. Sciaena umbra and Dentex dentex are two coastal fish species that inhabit the Mediterranean Sea and are categorized as 'Vulnerable' according to the IUCN Red List. This study investigated the performance of S. umbra and D. dentex hatchery-reared juveniles feeding on live prey. We evaluated whether 6 days of training and body size had an impact on feeding performance and behaviour. In both species, we found that training had a positive effect on fish feeding performance by (1) significantly increasing mean number of prey eaten, (2) decreasing the latencies before first attack and first ingestion and (3) increasing attack efficiency. In addition, there was a significant increase in the number of S. umbra individuals that ingested at least one prey item over the 6 training days. The percentage of fish that ingested at least one prey item did not, however, increase significantly for D. dentex individuals over this period; instead juveniles either (1) attempted to eat novel prey, succeeded and displayed an improvement of their feeding efficiency through training, or (2) did not forage or eat over the 6 training days. The high number of individuals exhibiting the second response could be linked to several factors, including fear, personality or the type of prey used in this study. In S. umbra, individuals from the [50–60[ mm total length size class outperformed other size classes. Our findings highlight differences in feeding behaviour between the two species and the positive impacts of training on feeding performance. Our results should be taken into account when developing release protocols for potential restocking programmes.

**Highlights**

► Training had a positive effect on feeding performance of both species. ► Nearly all *Sciaena umbra* juveniles ate at least one prey after 6 days of training. ► A majority of *Dentex dentex* juveniles did not eat prey during all tests. ► *S. umbra* from the [50–60[ mm size class exhibited better feeding performance.

## Introduction

For many years, marine biodiversity has been threatened by overexploitation of stocks, pollution and other anthropogenic pressures (Belim Imtiyaz et al., 2011; Crain et al., 2009). One way to replenish threatened marine stocks is to release hatchery-reared juveniles, in a process called 'restocking' (Bell et al., 2006). This conservation approach has been developed over the past several decades, and is being met with increasing interest. However, it has also been criticized due to the recurring low success of some restocking programs, linked to poor fish survival rate after their release in the wild (*e.g.* Brown & Laland, 2001; Suboski & Templeton, 1989). Several authors have suggested that, in addition to be in good health, released fish should also display behavioural responses necessary for survival in the natural environment (*e.g.* Olla et al., 1998; Salvanes & Braithwaite, 2006) and *in fine* for contributing to population dynamics (through spawning).

After being released in the wild, two factors are key for hatchery-reared fish survival: avoiding predation and feeding adequately (Olla et al., 1998). Feeding in the natural environment can however constitute one of the major difficulties encountered by hatchery-reared juveniles released for population restoration. Indeed, classical rearing methods often involve feeding strategies that do little to mimic prey availability in the natural environment, for example *ad libitum* feeding with dry pellets. Thus, hatchery-reared juveniles could present post-release behavioural deficits making them less capable and less efficient at feeding than their wild counterparts (*e.g.* Ellis et al., 2002; Ibrahim & Huntingford, 1992; Olla et al., 1998). Studies suggest that this unfortunate outcome can be avoided with training, which improved hatchery-reared juveniles feeding success with new and live food in *Micropterus salmoides* (Diana et al., 2018), *Epinephelus marginatus* (Donadelli et al., 2015), *Scophthalmus maximus* (Ellis et al., 2002), *Oncorhynchus gorbuscha* (Godin, 1978), *Gasterosteus aculeatus* (Ibrahim & Huntingford, 1992), and *Oncorhynchus kisutch* (Paszkowski & Olla, 1985). Thus, training before the release of hatchery-reared juveniles could potentially enhance their feeding efficiency and directly influence their survival in the wild.

The brown meagre (*Sciaena umbra*, Linnaeus 1758) and the common Dentex (*Dentex dentex*, Linnaeus 1758) are two coastal fish species that live in the Mediterranean Sea where they are considered 'Vulnerable' (IUCN Red List; Bizsel, Kara, et al., 2011; Bizsel, Yokes, et al., 2011). Both species are subject to severe fishing pressure (Bousquet et al., 2022; Garcia et al., 2022; Harmelin-Vivien et al., 2015; Marengo et al., 2015) because of their commercial value. Moreover, *S. umbra* and *D. dentex* are long-lived fish species (Baudouin et al., 2016; Grau et al., 2009; Marengo et al., 2014) which makes their populations all the more vulnerable to overexploitation. In addition to their economic and cultural importance, *S. umbra* and *D. dentex* are ecologically important, maintaining a key position in the food web as carnivorous species and apex predators (Engin & Seyhan, 2009; Marengo et al., 2014). Studies on both species production and rearing in captivity have flourished in recent years (*e.g.* Chatzifotis et al., 2006; Hamzaçebi & Can, 2021; Koumoundouros et al., 2004; Millot et al., 2022; Rueda & Martınez, 2001), highlighting the potential that these species hold for aquaculture, and therefore, also, the feasibility of restocking efforts.

Restocking programs require consideration of various factors to minimize the potential negative impact on wild populations (*e.g.* diseases, parasites, genetics) and maximize the survival rate of the released organisms. Care must be taken when selecting the release site (*e.g.* abundance of food and predators) and the released individuals' characteristics (*e.g.* age, size, health, behaviour) (Esquivel-Muelbert et al., 2018). The latter, as previously mentioned, include considering the behavioural capacities of the fish, but also their health (*e.g.* absence of pathogens, parasites, malformations) and other individual features that might impact the success rate of a restocking effort. For instance, body size have already been shown to influence dispersal (*e.g.* Lee et al., 2015), boldness (*e.g.* Brown & Braithwaite, 2004; Grant & Noakes, 1987), swimming performance, sensitivity to stress (*e.g.* Ducos et al., 2022) and survival (*e.g.* Leber, 1995). Body size and age may also impact the feeding efficiency of hatchery-reared juveniles (*e.g.* Donadelli et al., 2015; Godin, 1978; Meyer, 1988), which suggests that size-at-release could affect the feeding capacities of hatchery-reared juveniles in the wild.

The aim of this study was to assess *i)* if *S. umbra* and *D. dentex* hatchery-reared juveniles are capable of predating on novel live prey (*i.e.* never encountered before), *ii)* if body size influences predation behaviour towards novel live prey and *iii)* if training improves feeding performances towards novel live prey.

To this end, hatchery-reared juveniles of *S. umbra* and *D. dentex* of three size classes per species were tested over six consecutive days in the presence of live prey (*i.e.* mysis stage, larvae, of a crustacean species). Several variables allowing assessing individual feeding performance were measured in each experimental test (*e.g.* the number of successful attacks, the efficiency of attacks, latencies before the first attack and before the first ingestion, the percentage of fish that were taking prey).

Comparisons between species were undertaken since understanding species-specific performance is fundamental for developing species-specific adaptations and management strategies to maximize post-release survival.

## Materials & Methods

### Fish rearing procedures

Broodstocks were composed of 17 *S. umbra* (12:5; male:female) and 12 *D. dentex* (5:7; male:female) adult individuals held at the STELLA MARE research facility (stellamare.universita.corsica/). For *S. umbra*, the juveniles studied here were obtained from the same batch of eggs spawned on 27/03/2021. *Dentex dentex* were obtained from a mix of two egg batches, produced by the same broodstock, spawned on 30/01/2021 and 31/01/2021.

Before transferring juveniles to the experimental room, larvae from both species were reared in 2.29 $m^3$ cylindrical-conical tanks with several parameters recorded daily (salinity = 38 psu; water temperature = 17-22°C; oxygen saturation = 70-95%; pH = 7.7 ± 0.25). *Sciaena umbra* larvae were fed with *Artemia salina* nauplii from 7 to 22 days post hatch (DPH) and metanauplii from 19 to 50 DPH. *Dentex dentex* larvae were fed with rotifers from 3 to 20 DPH and *A. salina* nauplii from 12 to 25 DPH and metanauplii from 18 to 50 DPH. From 50 DPH onwards, both species were only fed with dry food (Gemma micro, Gemma Wean; Skretting, Stavanger, Norway).

### Experimental protocol

In order to evaluate the effect of body size on feeding performance, 3 size classes of juveniles were investigated for both species: [40-50[ mm (corresponding to 69-76 DPH), [50-60[ mm (corresponding to 77-83 DPH), [60-70[ mm (corresponding to 102-108 DPH) total length (TL) for *S. umbra* and [50-60[ mm (corresponding to 97-103 DPH), [60-70[ mm (corresponding to 104-110 DPH) and [70-80[ mm TL (corresponding to 114-124 DPH) for *D. dentex*. All these size classes are half-open intervals so that they do not overlap. The size classes investigated for *S. umbra* correspond to intermediate size classes that were previously studied in relation to exploratory, boldness and escape behaviours in *S. umbra* juveniles (Ducos et al., in prep). These previous experiments were part of the same project assessing individual performances and behaviours of juvenile fish for restocking purposes. This present experiment would thus allow to provide additional results and knowledge regarding *S. umbra*

hatchery-reared juveniles' behaviour for those three size classes, which mirror a range of potential size-at-release for this species.

For *D. dentex*, juveniles of TL below 32 mm are known to be delicate to handle: for example in Koumoundouros et al. (2004) some hatchery-reared individuals that were touched with a net soon died. Moreover, previous behavioural observations made in STELLA MARE facility have led us to believe that *D. dentex* juveniles smaller than approximately 50 mm TL were highly sensitive to stress (*e.g.* handling, light, sounds) (Ducos, pers. obs.). Based on those two observations, three size classes above 50 mm TL were studied here in order to minimize the harm and investigate size classes with an optimal survival rate after release in the wild.

To measure the effect of training on feeding performance of both species, individuals were tested once a day during six consecutive days, where the first day of experimentation (day 1) corresponds to the first encounter (*i.e.* naïve individuals) with new live prey. Naïve individuals were used for day 1 of each size class (number of naïve individuals tested corresponding to 'Training day 1' in Table 1). The live prey used in this experiment were the mysis stage of *Palaemon varians* (decapod crustacean). Crustaceans are known to be part of *S. umbra* and *D. dentex* diets in the wild, although the specific diet of Young of the Year juveniles for both species is not described in the literature. *Dentex dentex* is a largely piscivorous species (Marengo et al., 2014) that is also reported to feed on crustaceans (9%, Chemmam-Abdelkader, 2004; 35%, El-Fergani & El-Mor, 2014). Concerning *S. umbra*, the Decapoda order constitutes the major component of this species' diet (Chakroun & Ktari, 1981; Fabi et al., 1998). The prey used in this study measured between 0.64 and 2.09 cm TL and represented on average (± standard error, SE) 23.69 ± 0.13% (range: 10.51-37.76%) and 23.09 ± 0.11% (range: 11.86-39.77%) of *D. dentex* and *S. umbra* individual TLs, respectively.

To facilitate individual identification of each juvenile tested, and thus longitudinal traceability of performance throughout the six days of experimental tests, each fish was marked under the skin with fluorescent VI-alpha tags (1.2 mm x 2.7 mm; Northwest Marine Technology, Inc.). Before this tag

injection, all fish were individually anaesthetized (Benzocaïne in sea water, 150 ppm) and measured (TL, mm). The tags were coloured and individually numbered, with the identification numbers visible to the naked eye. Tagging took place ten days before the beginning of the first experimental day and the scar induced by the needle of the tag injector was healed before the first trial. Following the tagging session, fish were randomly distributed between six rearing tanks (240 L; cylindrical-conical) organized in duplicate (three batches x two replicates). The three batches corresponded to the three size classes tested for each species. The total number of marked fish corresponded to the number of fish tested on first training days (*i.e.* 77 *S. umbra* individuals and 76 *D. dentex* individuals; Table 1).

Temperature and oxygen concentration were monitored daily in each rearing tanks and maintained during the entire rearing period at the optimal value for the species ($O_2$ saturation in the range 80-100% and 82.1-100% for *S. umbra* and *D. dentex*, respectively; water temperature range: 18.2-20.3 °C and 18.1-19.9 °C for *S. umbra* and *D. dentex*, respectively). As *D. dentex* hatched before *S. umbra* individuals, the behavioural trials were first carried out on *D. dentex* and then on *S. umbra;* rearing tanks and the experimental room were thus used for one species at a time.

To account for potential high variability of behaviour upon first encounter with new live prey, an increased sample size was considered for day 1 to increase statistical power: 24 to 29 naïve fish were tested on the first day. Among these individuals, 11 to 15 fish were randomly subsampled and tested daily during the five following days. In total, 77 juveniles of *S. umbra* and 76 juveniles of *D. dentex* were individually tested, corresponding to 272 and 271 behavioural trials for *S. umbra* and *D. dentex*, respectively (Table 1).

Before the beginning of each trial, a fasted (from at least 14h) fish was individually transferred to the experimental tank (35 x 35 cm, water depth of approximately 7 cm). The prey (*N*=5) were introduced shortly before the fish but separated in a translucent container. Thus, during 10 min of acclimatization, the fish could observe the prey (as in Donadelli et al., 2015). After this time, the container was remotely removed, marking the start of the trial during which prey were available for the fish during 20 min (as

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in Godin, 1978). During this period, the experimental tank was video recorded at 25 frames per s (as in Steingrund & Fernö, 1997). At the end of each trial, all remaining prey were removed and counted. Water in the experimental tank was vigorously stirred and aerated between each fish, and changed every five fish. In order to represent conditions that the fish could face after being released, no food supply (besides prey available during the trials) was offered during the six consecutive days of experimental trials (as in Donadelli et al., 2015; Ellis et al., 2002). A photoperiod of 10L:14D was used both for the rearing and the experimental tanks. Luminosity was set on 30 Lux at the surface of the experimental and rearing tanks. At the end of the sixth day, each fish was anesthetized (Benzocaine; 150 ppm), weighed (g) and measured with a graduated calliper (total length, in mm).

### Data collection and analysis

Videos from each trial were analysed using EthoVision XT tracking software (version 16, Noldus, The Netherlands). In each 20-min video, the number of attacks on live prey was counted. An attack was considered to begin when a fish starts propelling itself (in a noticeable acceleration) towards prey, and could end in one of two ways: either the targeted prey disappeared between the fish's jaws and was ingested, corresponding to a successful attack (*i.e.* ingestion), or the fish abandoned (after none, one or several captures), corresponding to an unsuccessful attack. A capture was defined as prey being temporarily seized (entirely or a part of its body) between the fish's jaws (Paszkowski & Olla, 1985), before being released (the prey is not ingested).

The number of successful attacks (*i.e.* number of preys ingested) and the number of unsuccessful attacks were quantified for each trial. The efficiency of attacks was assessed for each trial by dividing the number of ingestions by the total number of attacks (*i.e.* number of successful and unsuccessful attacks). The latency before the first attack and before the first ingestion were assessed in each trial (for which fish displayed at least one attack and/or one ingestion) by calculating the time between the beginning of the trial and the beginning of the first attack and/or the time the prey disappeared inside the fish's mouth (before being ingested). During each successful attack, maximum swimming speed

and maximum acceleration were calculated by EthoVision (two black rectangles taped to the bottom of the experimental tank, measuring 20 cm in length, were used as calibration scales) and standardised by body length (by dividing the maximum swimming speed value or maximum acceleration value by the corresponding fish TL; leading to BL/s or BL/s$^2$ units). These relative values were averaged for each 20 min trial.

The percentage of fish that were taking prey were calculated as the percentage of fish that ingested at least one prey over the total number of fish tested for this particular size class and training day. In order to investigate if the percentage of fish that took prey displayed significant differences between days and between size classes, Fisher's exact tests were used. This test is recommended when samples sizes are small and when expected frequencies in the contingency tables are below 5 (Zar, 1984), which was the case in this study. Multiple comparisons after a significant Fisher's exact test were performed with the 'fisher.multcomp' function (pairwise comparisons using Bonferroni correction for p-values adjustment) of the *RVAideMemoire* R package (Hervé, 2022), in order to highlight significant increases in feeding fish compared to day 1.

The main effects of species, size class and training (*i.e.* time in experimental days, considered as a continuous variable) on:

- Number of successful and unsuccessful attacks were evaluated through the use of negative binomial generalized linear mixed models (GLMMs), relevant when investigating count data, with the 'glmmTMB' function (*glmmTMB* R package; Brooks et al., 2017) where family='nbinom1' was specified;

- Efficiency of attacks were evaluated through the use of a binomial GLMM (with the 'glmer' function of the *lme4* R package; Bates et al., 2022) as this family of model is recommended for proportional data (Crawley, 2013);

- Latency before the first attack, on latency before the first ingestion, on mean maximum swimming speed during successful attacks and on mean maximum acceleration during

successful attacks were evaluated with 4 different linear mixed models (LMMs; Gaussian family) with the 'lmer' function of the *lmerTest* R package (Kuznetsova et al., 2017).

Within each species, the main effects of size class and training as well as their interaction (*i.e.* X ~ SizeClass*Training, contrasts=list(SizeClass=contr.sum)) on the previously mentioned variables (*i.e.* on the number of successful and unsuccessful attacks, the efficiency of attacks, the latency before the first attack, the latency before the first ingestion, the mean maximal swimming speed and the mean maximal acceleration) were investigated through the same methods (*i.e.* negative binomial GLMM, binomial GLMM or LMM). Type III Analyses of Variance were performed (Wald *F* tests for Gaussian family models and Wald Chi² tests for the other models) on all models containing an interaction term, as this is the type of sums of squares (SS) that is generally recommended for unbalanced designs (as is the case in this study) when there is a presence of an interaction (Landsheer & Wittenboer, 2015). If an interaction effect was not found significant in the ANOVA outputs, the interaction term was removed from the model (*i.e.* leading to X ~ SizeClass+Training) and the statistical significance of the two models' main factors were investigated with type II Analyses of Variance (Wald *F* tests for Gaussian family models and Wald Chi² tests for the other models). Indeed, type II SS should be preferably used with unbalanced design when there is no significant interaction, as it is more powerful than type III SS in this context (Landsheer & Wittenboer, 2015; Langsrud, 2003). Therefore, in this study, type II Analyses of Variance were performed on all models where only main effects were incorporated. All ANOVA outputs studied were generated by the 'Anova' function of the *car* R package. Whenever a significant effect of size class or of the interaction term (*i.e.* SizeClass*Training) was assessed, post hoc pairwise comparisons were performed with the 'emmeans' function (*emmeans* package; Lenth et al., 2022) in order to investigate significant differences between size classes or within the interaction term.

For each model, model residuals were graphically checked to perform residual diagnostics (through 'residuals' function from the *stats* R package for lmer models in order to investigate homoscedasticity and normal distribution, and 'simulatedResiduals' function from the *DHARMa* R package (Hartig, 2020) for the other types of models). Both latency variables were log-transformed

(*e.g.* as used in Roesch et al., 2013) in order to meet the normality and homoscedasticity model assumptions. The mean maximal swimming speed values were square root transformed for the same reason. All models included identification number (ID) as a random effect in order to consider that each fish might have an individual intercept (*i.e.* (1|ID)) (Bates et al., 2015). Statistical analyses were performed on the totality of the tested individuals, not only the fish that were studied on all the six days of experimental trials.

All statistical analyses were performed on the R software (version 4.1.1) and were interpreted with a significance threshold of 5%.

### Ethical Note

All procedures performed in this study involving animals followed European Directive 2010/63 UE. All the practical research activities performed within this study were approved under the reference APAFIS #23731-2020012211568209 v6 by the French National Ethics Committee in Animal Experimentation (CNREEA).

All individuals tested in this present study were individually tagged with fluorescent VI-alpha tags (1.2 mm x 2.7 mm; Northwest Marine Technology, Inc.). Before this tag injection, all fish were individually anaesthetized in order to minimize stress and enhance their welfare. The tagging procedure did not last more than approximately 30 seconds and fish were then directly placed into a strongly stirred clear sea water container for them to quickly wake up. Post-tagging recovery was visually assessed during 10 days by examining fish behaviours, colouring, food intake as well as the healing of the scar (without taking them out of the water in order to minimize stress).

Transfers between the rearing tanks and the experimental tanks were gently performed with a hand net, in less than 30 seconds in order to minimize the duration of handling and, thus, stress. In addition to feeding and controlling water parameter in rearing tanks, behaviours (*e.g.* swimming, social interactions, motivation to feed) and fish coloration were inspected at least 3 times per day in order to best ensure individual fish welfare. In order to minimise adverse impacts on the welfare of subjects

or to enhance their welfare, some procedures were also taken for the live prey used in this experiment. Indeed, water parameters were controlled daily (*e.g.* oxygen saturation, water temperature), body colouring and behaviours (*e.g.* feeding, exploration) were observed.

## Results

Out of 543 experimental trials carried out in this study (*N*=272 on *S. umbra* and *N*=271 on *D. dentex*), 44.0% contained at least one attack (*N*=171 and *N*=69 for *S. umbra* and *D. dentex*, respectively). Most experimental trials containing at least one attack resulted in at least one ingestion (88.3% performed by *S. umbra* and 76.8% performed by *D. dentex*). Only a few individuals were capable of recognising and ingesting live preys at the first encounter (day 1; Figure 1a and 1b). However, the majority of *S. umbra* juveniles ingested at least one prey after 6 days of training (Figure 1a). Therefore, the percentage of *S. umbra* that ingested at least one prey increased through training (Figure 1a). This increase was significant, in comparison with day 1, from day 4 for both [40-60[ mm and [60-70[ mm size classes and from day 3 for the [50-60[ mm size class (Post hoc pairwise comparisons using Fisher's exact tests, $P < 0.05$). For *S. umbra* only day 3 displayed a significant difference between size classes (Fisher's exact test, $P < 0.05$) with the [50-60[ mm size class showing a significantly higher percentage of fish that were taking prey than the other two (92% versus 46-50%; Post hoc pairwise comparisons using Fisher's exact test, $P < 0.05$). Among *D. dentex* juveniles there were no significant differences among size classes in the percentage of fish that were taking prey for each day (Fisher's exact tests, $P > 0.05$). Moreover, even though 31%, 27% and 27% of *D. dentex* individuals (for ([50-60[ mm, [60-70[ mm and [70-80[ mm size classes, respectively) ingested at least one prey on day 6 (Figure 1b), training did not have a significant effect on the day to day percentage of *D. dentex* juveniles that were taking prey of the three size classes (Fisher's exact tests, $P > 0.05$). Finally, it should be noted that the *D. dentex* individuals that fed on live prey at any one point proceeded to eat at least one prey on the final day of training (day 6) (Appendix 1). Additionally, percentages of fish that were taking prey across species (Figure 1a and 1b) was investigated for all size classes combined, with *S. umbra* juveniles overall

displaying significantly higher values than *D. dentex* juveniles from day 3 onwards (Fisher's exact tests, $P < 0.01$).

The number of ingestions significantly increased over the course of training for *D. dentex* (Figure 1d; GLMM, Chisq = 35.6, $P < 0.001$) and *S. umbra* (Figure 1c; GLMM, Chisq = 27.9, $P < 0.001$). However, the number of ingestions was significantly higher for *S. umbra* than for *D. dentex* juveniles (GLMM, Chisq = 23.6, $P < 0.001$). *Sciaena umbra* individuals from the [50-60[ mm size class displayed significantly higher number of ingestions than *S. umbra* individuals from the other two size classes (Figure 1c; GLMM followed by post hoc pairwise comparisons, $P < 0.05$). For trials that displayed at least one attack, latency before the first attack was significantly reduced through training for *D. dentex* (Figure 2b; GLMM, F = 57.7, $P < 0.001$), for *S. umbra* (Figure 2a; GLMM, F = 59.3, $P < 0.001$), and did not display significant differences between size classes (GLMMs, F = 1.1 for *D. dentex* and F = 2.1 for *S. umbra, $P > 0.05$*) and between species (GLMM, F = 0.2, $P > 0.05$). For trials that displayed at least one successful attack, the latency before the first ingestion was also significantly reduced through training for *D. dentex* (Figure 2d; GLMM, F = 43.4, $P < 0.001$) and for *S. umbra* (Figure 2c, GLMM, F = 40.6, $P < 0.001$), with individuals ingesting sooner with more training days, and did not differ between size classes (GLMMs, F = 0.6 for *D. dentex* and F = 1.4 for *S. umbra*, $P > 0.05$) and between species (GLMM, F = 1.3, $P > 0.05$). In *S. umbra*, the interaction term of both size class and training variables (*i.e.* SizeClass*Training) was significant (GLMM, F = 4.7, $P < 0.05$; Figure 2c): training had a significantly stronger negative effect on the latency before the first ingestion in [50-60[ mm TL individuals (GLMM followed by post hoc pairwise comparisons; Appendix 2).

In addition to the increase in the number of ingestions, the number of unsuccessful attacks also significantly increased through time for *S. umbra* (GLMM, Chisq = 40.0, $P < 0.001$) and for *D. dentex* (GLMM, Chisq = 9.1, $P < 0.01$). A significantly higher mean number of unsuccessful attacks was recorded for *S. umbra* juveniles than for *D. dentex* juveniles (GLMM, Chisq = 7.0, $P < 0.01$). Despite this, *S. umbra* displayed higher efficiency of attacks than did *D. dentex* (Table 2; GLMM, Chisq = 6.4, $P <$

0.05) with a mean value (± SE) of 0.57 ± 0.03 versus 0.49 ± 0.04 over the entire training period. The efficiency of attacks was also significantly improved by training for *D. dentex* (Table 2; GLMM, Chisq = 7.1, *P* < 0.01) and for *S. umbra* (Table 2; GLMM, Chisq = 17.0, *P* < 0.001), with size class as a significant factor for both species. Indeed, among *S. umbra* juveniles, individuals from the [50-60[ mm size class displayed significantly higher attack efficiencies than individuals from the two other size classes (GLMM followed by post hoc pairwise comparisons, *P* < 0.01). Among *D. dentex* juveniles, individuals from the [70-80[ mm size class displayed significantly higher attack efficiencies than individuals from the [50-60[ mm size class (GLMM followed by post hoc pairwise comparisons, *P* < 0.05).

Training and body size did not have any significant effect on the mean maximum relative swimming speed during successful attacks for either species (GLMMs, *P* > 0.05). *Dentex dentex* mean maximum relative acceleration during successful attacks decreased through training (GLMM, F = 4.8, *P* < 0.05) with no significant differences between size classes (GLMM, F = 0.2, *P* > 0.05). Despite this apparent decrease over time, *D. dentex* juveniles displayed higher mean maximal relative swimming speed (GLMM, F = 75.1, *P* < 0.001) and mean maximal relative acceleration values (GLMM, F = 24.1, *P* < 0.001) during their successful attacks than did *S. umbra* juveniles. Indeed, during their successful attacks, mean maximal velocities observed (± SE) were 3.18 ± 0.11 BL/s and 5.38 ± 0.20 BL/s and mean maximal acceleration values were 59.62 ± 2.47 BL/s$^2$ and 90.92 ± 3.75 BL/s$^2$ for *S. umbra* and *D. dentex*, respectively.

## Discussion

Hatchery-reared fish are commonly fed dried food in captivity; their ability to adapt to feeding on live prey in the wild is a key challenge on which restocking success depends. This study investigated the feeding performance of hatchery-reared juveniles of *S. umbra* and *D. dentex*, both candidates for restocking efforts, in order to evaluate the value of feeding training prior to release and to estimate an optimal size-at-release.

***Training as a tool to improve feeding efficiency of hatchery-reared fish juveniles***

In the present study, we observed that training had a positive influence on feeding performance on live prey for *S. umbra and D. dentex* hatchery-reared juveniles illustrated by *i)* an increase in the mean number of prey eaten, *ii)* a decrease in the latencies before the first attack and ingestion and *iii)* an increase in attack efficiency.

Several studies showed that hatchery-reared fish were capable of ingesting novel and unknown live preys rapidly after their first contact with them (within 1 hour; *e.g.* Donadelli et al., 2015; Paszkowski & Olla, 1985). These results suggest that recognizing and feeding on natural preys are innate capacities in fish. However, this interpretation seems to be more nuanced and species-dependent. Indeed, other experiments (Brown et al., 2003; Donadelli et al., 2015; Ellis et al., 2002; Jackson et al., 2013) led the authors to hypothesize that, in these species, feeding efficiency on an unknown live organism is a learnt, rather than innate, mechanism revealed by the improvement through training of the number of prey ingested or of the feeding latency.

***Interspecies differences in feeding efficiency***

The results of our study showed that *S. umbra* and *D. dentex* hatchery-reared juveniles responded differently to experience. Concerning *D. dentex*, the average number of prey eaten significantly increased over the training days whereas this species did not display a significant increase in the percentage of fish that were taking prey. This shows that the individuals which did eat did so in larger quantities as training progressed. In addition, all the *D. dentex* juveniles which fed on live prey at some

point also ate at least one prey on the sixth experimental day. This suggests that once a fish initially succeeds in ingesting a prey item, it will continue to successfully feed in the following days hereby showing behavioural consistency and learning. We surmise that the tested *D. dentex* individuals displayed two divergent behavioural responses: both motivation and feeding success on novel live preys, or no attacks and hence no feeding for the entire training. This is in line with the findings of Thomas et al. (2010). They emphasized in *G. aculeatus* the presence of certain fish that, once their initial wariness had been overcome, dare eating a novel prey whereas other fish firmly refused to eat novel prey. A study on *S. maximus* juveniles showed that one third of the tested hatchery-reared individuals (mean TL ~ 90 mm) did not ingest an available live prey during the entire experimental period (*i.e.* nine days) while, as in our study, they were not given any other food supply (Ellis et al., 2002). Within this scenario, a lack of feeding motivation concerning *S. maximus* as well as *D. dentex* and *S. umbra* is unlikely. As previously showed in birds and reptiles, this refusal to eat could lead to starvation, and eventually death (Curio, 1976).

Reluctance to eat has sometimes been explained by fear (Curio, 1976), or personality (*e.g.* Ferrari et al., 2015; Øverli et al., 2007). In our study, the important percentage of *D. dentex* juveniles that do not eat a single prey could potentially be linked to stress (Olla et al., 1998). Indeed, *D. dentex* juveniles are known to be very sensitive to handling, which can even lead to death (Ducos et al., 2022; Koumoundouros et al., 2004). Therefore, handling (*i.e.* between the rearing tank and the experimental tank) could have induced fear, hence stress, which can have been reinforced by isolation. Isolation has already been shown to be a stressor in *Dicentrarchus labrax* juveniles (Ferrari et al., 2015), that are known to be rather gregarious, unlike adult individuals, which display solitary behaviour (as for *D. dentex* ; Marengo et al., 2014). Some factors, such as environmental enrichment for example, could be considered for reducing stress. For example, plants and structures were shown to significantly decrease *Sebastes schlegelii* basal stress level (Zhang et al., 2021).

Prey size could also explain the high percentage of *D. dentex* juveniles that did not eat. Indeed, prey size can directly be linked to fish feeding motivation as prey items that are too small provide low energy

return whereas too large items could provoke fear or lead to handling difficulties (Gill, 2003; Hart, 1986). In this study, the relative mean sizes of the given preys (23.2 and 23.7% for *S. umbra* and *D. dentex*, respectively) are values commonly found in the literature and could thus be considered appropriate for the individuals tested. Indeed, Scharf et al., (2000) highlighted that marine fish predators mainly consume prey measuring between 10 and 40% of their length. Moreover, experimental studies on feeding behaviour commonly used preys around 20% of predators' total length (25% in *S. maximus*, Ellis et al., 2002; between 28 and 41% in *M. salmoides* juveniles, Diana et al., 2018; up to approximately 20% in *G. aculeatus*, Ibrahim & Huntingford, 1992; between 17 and 35% in *E. marginatus*, Donadelli et al., 2015). However, *S. umbra* and *D. dentex* larvae and juveniles display a morphological difference that could have influenced live prey consumption: *D. dentex* juveniles have a smaller mouth size than *S. umbra* juveniles (Ducos, pers. obs.). In this study, only one capture was recorded within all *S. umbra* attacks whereas eight captures were recorded within five different trials of *D. dentex*. It therefore seems that some *D. dentex* individuals might display lower handling efficiency than *S. umbra* fish, which could be linked to their difference in mouth size. A link between differences in mouth gap and feeding performance has previously been highlighted in two freshwater fish species, *Perca flavescens* and *Sander vitreus*, where the species with a larger mouth size displayed higher capture efficiency (Graeb et al., 2005). However, in our study, prey provided to the largest *D. dentex* size class represented 19.11 ± 0.17% of TL vs 27.61 ± 0.14% for the smallest one. Aside from efficiency of attack, with significantly higher values in the [70-80[ than in [50-60[ mm size class, this did not lead to significantly different feeding performance between size. Therefore, prey size is probably not the main reason for the high proportion of *D. dentex* juveniles that did not eat after 6 experimental days. Although *D. dentex* individuals have been recorded feeding on crustaceans in the wild (Chemmam-Abdelkader, 2004; El-Fergani & El-Mor, 2014), this species is considered mainly piscivorous, feeding essentially on preys located in the water column (Marengo et al., 2014; Morales-Nin & Moranta, 1997), whereas *S. umbra* feeds mainly along the benthos. Thus, *D. dentex* juveniles potentially have innate feeding preferences directed to mobile fish prey rather than to crustaceans. However, several days of

fasting could have led to opportunistic feeding behaviour on the available crustacean larvae. Nevertheless, we believe that the type of prey used in this experiment might be an additional factor contributing to *D. dentex* refusal to feed.

Feeding preference of *D. dentex* for fish, and more generally for more mobile prey than *S. umbra*, may have been reflected in the different strategies employed resulting in successful attacks. *Dentex dentex* juveniles ingested their prey by reaching significantly higher maximal swimming speed and maximal acceleration values than *S. umbra* juveniles. The fact that *D. dentex* individuals were reported to mainly feed on fish (84% in Chemmam-Abdelkader, 2004; 19% in El-Fergani & El-Mor, 2014; 74% in Morales-Nin & Moranta, 1997) and cephalopods (5% in Chemmam-Abdelkader, 2004; 21% in El-Fergani & El-Mor, 2014; 26% Morales-Nin & Moranta, 1997) means that this species is generally feeding on highly mobile that might be hard to capture (Wainwright & Bellwood, 2002). Predators of this kind are presumed to use high-velocity propulsion and high acceleration during their attacks (Higham, 2007; Wainwright & Bellwood, 2002) and are usually considered to use a "ram feeding" strategy (Norton, 1995). In this study, *D. dentex* juveniles were indeed often observed pausing for a short moment after prey recognition, motionless, before explosively lunging towards the larvae. *Sciaena umbra* juveniles, by contrast, seemed to perform less explosive attacks. Given their natural diet mainly composed of benthic species, most Sciaenids are generally presumed to use a "suction feeding" strategy (Wainwright & Bellwood, 2002). In this study, *S. umbra* juveniles used lower swimming speed attacks than *D. dentex* for their crustacean larvae prey, which resulted, however, in higher attack efficiency.

### *Feeding behaviour and performance in relation to body size*

Among *S. umbra* juveniles, individuals from the [50-60[ mm size class displayed a higher number of ingestions, a higher attack efficiency as well as a stronger effect of training on reducing the latency before the first ingestion. In our study, the maximum differences between younger and older fish were 39 days in *S. umbra* and 27 days in *D. dentex* such that time in captivity should have scarcely any effect on fish behaviours across size classes. Differences in feeding behaviour and performance in relation to body size could be linked to ontogenetic behavioural or morphological changes. Both of these causes

have been hypothesized in a cichlid fish species, where age and size were shown to have a positive influence on the total number of attacks and the number of attacks performed during the first 30 s of a trial (Meyer, 1988). Juveniles of *S. umbra* have previously been shown to display changes in exploratory behaviour and boldness between 30 mm TL and 80 mm TL, with smaller individuals being bolder and more explorative than larger individuals (Ducos et al., in prep). These behavioural traits could also shape the feeding responses at live prey in a novel environment.

***Restocking perspectives, considerations and conclusions***

In this study, we showed that a majority (85-100%) of *S. umbra* juveniles and a minority (27-38%) of *D. dentex* juveniles learnt to feed on live prey after 6 days of training. For *D. dentex* this was due to the high proportion of individuals refusing to feed on novel live prey; a response that could be related to fear and/or personality and the type of prey offered in the experiment. To survive in the wild it is necessary that hatchery-reared fish be bold enough to explore and feed on new live preys, but should wary enough to avoid potential injuries, poisoning or predators (Thomas et al., 2010).

This study contributes to the literature by highlighting how training can be used as a tool to enhance feeding performance of hatchery-reared fish on live prey, and contribute to restocking success. Results from *S. umbra* support these previous recommendations whereas results on *D. dentex* suggest a more nuanced picture. Our results highlighted that the *D. dentex* juveniles which fed were positively affected by training; leading to the same reduction in latency (*i.e.* to first attack and to first ingestion) as measured for *S. umbra* juveniles. The *D. dentex* individuals which were feeding were likely less affected by stress, hence feeding activity could be seen as a proxy for acclimation to the natural environment. It would be valuable to investigate additional factors (and their interactions) that could help *D. dentex* hatchery-reared juveniles feed more efficiently on novel live prey. Such factors could include environmental enrichment, such as including shelters and/or plants, during fish rearing. For example, in a study with hatchery-reared *S. salar*, enrichment coupled with a prior exposure to live prey improved feeding performance (Brown et al., 2003). Enrichment has also been linked to basal stress reduction in *S. schlegelii* (Zhang et al., 2021) and has shown a positive effect on boldness and the ability

on feeding on live prey in *Salvelinus confluentus* (Brignon et al., 2018). It may also be important to consider social environment during feeding training, as fish from several species were shown to be more effective in feeding when they were part of shoals instead of in isolation (Brown & Laland, 2003). Additionally, it would be interesting to investigate the feeding behaviour of hatchery-reared *D. dentex* juveniles when trained on other prey species, such as fish larvae.

Studying the aforementioned factors would help deepen and extend the findings obtained in the present study, contributing to optimal protocols for a restocking purpose on *D. dentex* and *S. umbra*. We suggest that providing training with live prey to hatchery-reared individuals of *D. dentex* and *S. umbra* could help to maximize post-release feeding effectiveness. In addition, we suggest using *S. umbra* juveniles of [50-60[ mm TL for restocking purposes as these hatchery-reared individuals exhibited better feeding performance than the other size classes tested.

## ACKNOWLEDGEMENTS

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**Table 1:** Number of *Sciaena umbra* and *Dentex dentex* individuals tested for each size class and training day

| Size class (mm TL) | Training day | N *Sciaena umbra* tested | N *Dentex dentex* tested |
|---|---|---|---|
| [40-50[ | 1 | 29 | 0 |
| | 2 | 14 | 0 |
| | 3 | 14 | 0 |
| | 4 | 14 | 0 |
| | 5 | 14 | 0 |
| | 6 | 14 | 0 |
| [50-60[ | 1 | 25 | 25 |
| | 2 | 12 | 13 |
| | 3 | 12 | 13 |
| | 4 | 12 | 13 |
| | 5 | 12 | 13 |
| | 6 | 12 | 13 |
| [60-70[ | 1 | 23 | 27 |
| | 2 | 13 | 15 |
| | 3 | 13 | 15 |
| | 4 | 13 | 15 |
| | 5 | 13 | 15 |
| | 6 | 13 | 15 |
| [70-80[ | 1 | 0 | 24 |
| | 2 | 0 | 11 |
| | 3 | 0 | 11 |
| | 4 | 0 | 11 |
| | 5 | 0 | 11 |
| | 6 | 0 | 11 |

**Table 2:** Efficiency of attacks of *Sciaena umbra* and *Dentex dentex* juveniles averaged (mean ± Standard Error, SE) for each experimental day and each size class of interest

| | *Sciaena umbra* | | | *Dentex dentex* | | |
|---|---|---|---|---|---|---|
| | [40-50[ mm | [50-60[ mm | [60-70[ mm | [50-60[ mm | [60-70[ mm | [70-80[ mm |
| D1 | 0.308 ± 0.123 (*N*=8) | 0.240 ± 0.124 (*N*=5) | 0.375 ± 0.239 (*N*=4) | 0.700 ± 0.300 (*N*=2) | 0.377 ± 0.132 (*N*=6) | 0.333 ± 0.333 (*N*=2) |

| | | | | | | |
|---|---|---|---|---|---|---|
| D2 | 0.359 ± 0.138 (*N*=8) | 0.516 ± 0.105 (*N*=8) | 0.272 ± 0.159 (*N*=6) | 0.267 ± 0.194 (*N*=5) | 0.417 ± 0.083 (*N*=3) | 1.000 ± 0.000 (*N*=2) |
| D3 | 0.528 ± 0.132 (*N*=9) | 0.727 ± 0.068 (*N*=11) | 0.437 ± 0.128 (*N*=8) | 0.209 ± 0.108 (*N*=6) | 0.533 ± 0.148 (*N*=3) | 0.667 ± 0.167 (*N*=3) |
| D4 | 0.556 ± 0.096 (*N*=10) | 0.771 ± 0.088 (*N*=12) | 0.629 ± 0.090 (*N*=12) | 0.227 ± 0.133 (*N*=6) | 0.611 ± 0.187 (*N*=4) | 0.347 ± 0.193 (*N*=3) |
| D5 | 0.484 ± 0.077 (*N*=11) | 0.723 ± 0.071 (*N*=12) | 0.605 ± 0.073 (*N*=12) | 0.425 ± 0.125 (*N*=5) | 0.515 ± 0.057 (*N*=4) | 0.750 ± 0.250 (*N*=2) |
| D6 | 0.624 ± 0.075 (*N*=12) | 0.815 ± 0.064 (*N*=12) | 0.658 ± 0.106 (*N*=11) | 0.443 ± 0.159 (*N*=5) | 0.651 ± 0.152 (*N*=4) | 1.000 ± 0.000 (*N*=3) |

The number (*N*) in brackets refers to the number of individuals used for calculating this variable (i.e. the number of individuals displaying at least one attack during the trial) for each size class and day (from day 1, D1, to day 6) combination.

**Appendix 2:** Outputs from post hoc pairwise comparisons ('emmeans' function from the *emmeans* R package) on the interaction term "SizeClass*Training"

| | Estimate | SE | Df | t.ratio | *P* |
|---|---|---|---|---|---|
| Training[40-50[ - Training[50-60[ | 0.459 | 0.183 | 30.2 | 2.507 | *P* < 0.05 |
| Training[40-50[ - Training[60-70[ | -0.003 | 0.192 | 332.8 | -0.015 | *P* > 0.05 |
| Training[50-60[ - Training[60-70[ | -0.462 | 0.186 | 34.5 | -2.490 | *P* < 0.05 |

This test followed the identification of a significant effect of this interaction term in the GLMM evaluating the latency before the first ingestion in *Sciaena umbra* juveniles

**Appendix 3:** ANOVA (using 'Anova' function of the *car* R package) outputs performed on GLMMs

| Explained variable | Dataframe content | Explanatory variable | F | Chisq | Df | Df.res | *P* |
|---|---|---|---|---|---|---|---|
| Latency before the first attack (log-transformed) | Both species | Time (days) | 109.0713 | | 1 | 211.398 | <2e-16 |
| | | Species | 0.1899 | | 1 | 55.851 | 0.665 |
| | | Size classes | 0.9877 | | 3 | 55.405 | 0.405 |
| | *Dentex dentex* | Time (days) | 57.6676 | | 1 | 56.2 | 3.54E-10 |
| | | Size classes | 1.0719 | | 2 | 15.482 | 0.367 |

| Response | Species | Factor | | | df | | p |
|---|---|---|---|---|---|---|---|
| | *Sciaena umbra* | Time (days) | 59.3397 | | 1 | 152.943 | 1.55E-12 |
| | | Size classes | 2.1446 | | 2 | 37.333 | 0.131 |
| Latency before the first ingestion (log-transformed) | Both species | Time (days) | 81.3691 | | 1 | 181.836 | 2.62E-16 |
| | | Species | 1.2674 | | 1 | 44.59 | 0.266 |
| | | Size classes | 1.3367 | | 3 | 45.419 | 0.274 |
| | *Dentex dentex* | Time (days) | 43.3637 | | 1 | 45.845 | 3.88E-08 |
| | | Size classes | 0.5805 | | 2 | 10.672 | 0.576 |
| | *Sciaena umbra* | (Intercept) | 1126.195 | | 1 | 139.9 | <2.2e-16 |
| | | Time (days) | 40.611 | | 1 | 134.12 | 2.76E-09 |
| | | Size classes | 1.4494 | | 2 | 139.45 | 0.238 |
| | | Time (days)×Size classes | 4.655 | | 2 | 133.94 | 0.011 |
| Number of ingestions | Both species | Time (days) | | 51.0242 | 1 | | 9.12E-13 |
| | | Species | | 23.6002 | 1 | | 1.19E-06 |
| | | Size classes | | 3.2821 | 3 | | 0.350 |
| | *Dentex dentex* | Time (days) | | 35.5613 | 1 | | 2.47E-09 |
| | | Size classes | | 0.0972 | 2 | | 0.953 |
| | *Sciaena umbra* | Time (days) | | 27.934 | 1 | | 1.26E-07 |
| | | Size classes | | 8.0192 | 2 | | 0.018 |
| Number of unsuccessful attacks | Both species | Time (days) | | 45.6544 | 1 | | 1.41E-11 |
| | | Species | | 7.0176 | 1 | | 0.008 |
| | | Size classes | | 4.0125 | 3 | | 2.60E-01 |
| | *Dentex dentex* | Time (days) | | 9.0897 | 1 | | 0.003 |
| | | Size classes | | 1.4245 | 2 | | 4.91E-01 |
| | *Sciaena umbra* | Time (days) | | 39.9604 | 1 | | 2.59E-10 |
| | | Size classes | | 1.0188 | 2 | | 0.601 |
| Efficiency of attacks | Both species | Time (days) | | 22.2184 | 1 | | 2.43E-06 |
| | | Species | | 6.3796 | 1 | | 0.012 |
| | | Size classes | | 11.2412 | 3 | | 1.05E-02 |
| | *Dentex dentex* | Time (days) | | 7.1477 | 1 | | 0.008 |
| | | Size classes | | 7.1857 | 2 | | 2.75E-02 |
| | *Sciaena umbra* | Time (days) | | 17.047 | 1 | | 3.65E-05 |
| | | Size classes | | 13.314 | 2 | | 0.001 |
| Maximal swimming speed during successful attacks (square root transformed) | Both species | Time (days) | 0.1264 | | 1 | 176.063 | 0.7226 |
| | | Species | 75.0928 | | 1 | 38.267 | 1.47e-10 |
| | | Size classes | 1.8448 | | 3 | 39.161 | 0.1550 |
| | *Dentex dentex* | Time (days) | 2.9151 | | 1 | 46.75 | 0.09423 |
| | | Size classes | 0.0802 | | 2 | 10.212 | 0.92359 |
| | *Sciaena umbra* | Time (days) | 0.4886 | | 1 | 125.962 | 0.4858 |
| | | Size classes | 2.4832 | | 2 | 29.997 | 0.1005 |
| Maximal acceleration value during successful attacks | Both species | Time (days) | 0.7800 | | 1 | 173.757 | 0.3784 |
| | | Species | 24.0999 | | 1 | 41.420 | 1.47e-05 |
| | | Size classes | 0.7804 | | 3 | 41.778 | 0.5116 |
| | *Dentex dentex* | Time (days) | 4.8165 | | 1 | 46.75 | 0.033 |
| | | Size classes | 0.1548 | | 2 | 10.212 | 8.59E-01 |
| | *Sciaena umbra* | Time (days) | 0.0443 | | 1 | 125.640 | 0.8336 |

|            |        |   |        |        |
|------------|--------|---|--------|--------|
| Size classes | 1.2907 | 2 | 30.204 | 0.2898 |

| Explained variable | Dataframe content | Random effects | Variance | Standard deviation | Fixed effects | Estimate | Standard error | df | t value | z value | P |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Latency before the first attack (log-transformed) | Both species | ID | 0.2227 | 0.4719 | | | | | | | |
| | | *Residual* | 0.6323 | 0.7952 | | | | | | | |
| | | | | | (Intercept) | 7.00411 | 0.20743 | 109.21558 | 33.766 | | <2e-16 |
| | | | | | Time (days) | -0.35864 | 0.03422 | 211.2827 | -10.479 | | <2e-16 |
| | | | | | Species_DentexDentex | -0.09257 | 0.21174 | 55.49884 | -0.437 | | 0.664 |
| | | | | | Size classes_[50-60[ | -0.29984 | 0.2268 | 51.53041 | -1.322 | | 0.192 |
| | | | | | Size classes_[60-70[ | -0.25505 | 0.22824 | 53.15678 | -1.117 | | 0.269 |
| | | | | | Size classes_[70-80[ | 0.09527 | 0.41137 | 58.0682 | 0.232 | | 0.818 |
| | *Dentex dentex* | ID | 0.5023 | 0.7088 | | | | | | | |
| | | *Residual* | 0.6357 | 0.7973 | | | | | | | |
| | | | | | (Intercept) | 7.42424 | 0.39879 | 29.66893 | 18.617 | | <2e-16 |
| | | | | | Time (days) | -0.50285 | 0.06518 | 56.52868 | -7.715 | | 2.15E-10 |
| | | | | | Size classes_[60-70[ | -0.57188 | 0.4545 | 16.09492 | -1.258 | | 0.226 |
| | | | | | Size classes_[70-80[ | 0.06884 | 0.51045 | 15.98077 | 0.135 | | 0.894 |
| | *Sciaena umbra* | ID | 0.114 | 0.3376 | | | | | | | |
| | | *Residual* | 0.6059 | 0.7784 | | | | | | | |
| | | | | | (Intercept) | 6.79116 | 0.19969 | 106.90109 | 34.008 | | <2e-16 |
| | | | | | Time (days) | -0.30437 | 0.03934 | 152.01388 | -7.736 | | 1.32E-12 |
| | | | | | Size classes_[50-60[ | -0.40154 | 0.19692 | 33.55767 | -2.039 | | 0.049 |
| | | | | | Size classes_[60-70[ | -0.13465 | 0.19981 | 35.67373 | -0.674 | | 0.505 |
| Latency before the first ingestion (log-transformed) | Both species | ID | 0.1647 | 0.4058 | | | | | | | |
| | | *Residual* | 0.6226 | 0.7891 | | | | | | | |
| | | | | | (Intercept) | 7.06892 | 0.22662 | 98.52198 | 31.192 | | <2e-16 |
| | | | | | Time (days) | -0.34172 | 0.03773 | 180.91466 | -9.057 | | <2e-16 |
| | | | | | Species_DentexDentex | -0.24471 | 0.21663 | 41.96482 | -1.13 | | 0.265 |
| | | | | | Size classes_[50-60[ | -0.34486 | 0.22126 | 40.46654 | -1.559 | | 0.127 |
| | | | | | Size classes_[60-70[ | -0.06816 | 0.22734 | 41.76777 | -0.3 | | 0.766 |
| | | | | | Size classes_[70-80[ | 0.14479 | 0.41469 | 43.77618 | 0.349 | | 0.729 |
| | *Dentex dentex* | ID | 0.4757 | 0.6897 | | | | | | | |
| | | *Residual* | 0.6247 | 0.7904 | | | | | | | |
| | | | | | (Intercept) | 7.40146 | 0.49138 | 18.6827 | 15.063 | | 6.69E-12 |
| | | | | | Time (days) | -0.47448 | 0.07072 | 45.87731 | -6.709 | | 2.52E-08 |
| | | | | | Size classes_[60-70[ | -0.45224 | 0.51907 | 10.32163 | -0.871 | | 0.403 |
| | | | | | Size classes_[70-80[ | 0.05685 | 0.58283 | 10.38486 | 0.098 | | 0.924 |
| | *Sciaena umbra* | ID | 0.05959 | 0.2441 | | | | | | | |
| | | *Residual* | 0.58001 | 0.7616 | | | | | | | |
| | | | | | (Intercept) | 6.64257 | 0.19627 | 139.75006 | 33.845 | | <2e-16 |
| | | | | | Time (days) | -0.28057 | 0.04373 | 133.24616 | -6.416 | | 2.25E-09 |
| | | | | | Size classes_n1 | -0.06969 | 0.26683 | 136.76541 | -0.261 | | 0.794 |
| | | | | | Size classes_n2 | 0.4424 | 0.26441 | 140.89244 | 1.673 | | 0.097 |

| | | | | | | Estimate | Std. Error | df | t value | | p value |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Time (days):Size classes_n1 | 0.05425 | 0.05974 | 133.23102 | 0.908 | | 0.365 |
| | | | | | Time (days):Size classes_n2 | -0.18331 | 0.06015 | 131.73576 | -3.048 | | 0.003 |
| Number of ingestions | Both species | ID | 2.7 | 1.643 | | | | | | | |
| | | | | | (Intercept) | -1.15931 | 0.48278 | | | -2.401 | 0.016 |
| | | | | | Time (days) | 0.23748 | 0.03325 | | | 7.143 | 9.12E-13 |
| | | | | | Species_DentexDentex | -2.51196 | 0.51708 | | | -4.858 | 1.19E-06 |
| | | | | | Size classes_[50-60[ | 1.06181 | 0.59313 | | | 1.79 | 0.073 |
| | | | | | Size classes_[60-70[ | 0.73549 | 0.60219 | | | 1.221 | 0.222 |
| | | | | | Size classes_[70-80[ | 0.6949 | 0.89634 | | | 0.775 | 0.438 |
| | Dentex dentex | ID | 46.15 | 6.793 | | | | | | | |
| | | | | | (Intercept) | -8.08419 | 1.86558 | | | -4.333 | 1.47E-05 |
| | | | | | Time (days) | 0.29005 | 0.04864 | | | 5.963 | 2.47E-09 |
| | | | | | Size classes_[60-70[ | 0.43006 | 1.819 | | | 0.236 | 0.813 |
| | | | | | Size classes_[70-80[ | -0.08773 | 1.96054 | | | -0.045 | 0.964 |
| | Sciaena umbra | ID | 0.3572 | 0.5976 | | | | | | | |
| | | | | | (Intercept) | -0.42641 | 0.28492 | | | -1.497 | 0.135 |
| | | | | | Time (days) | 0.22839 | 0.04321 | | | 5.285 | 1.26E-07 |
| | | | | | Size classes_[50-60[ | 0.69393 | 0.27248 | | | 2.547 | 0.011 |
| | | | | | Size classes_[60-70[ | 0.056 | 0.27347 | | | 0.205 | 0.838 |
| Number of unsuccessful attacks | Both species | ID | 1.203 | 1.097 | | | | | | | |
| | | | | | (Intercept) | -0.81142 | 0.32881 | | | -2.468 | 0.014 |
| | | | | | Time (days) | 0.26 | 0.03848 | | | 6.757 | 1.41E-11 |
| | | | | | Species_DentexDentex | -0.89608 | 0.33826 | | | -2.649 | 0.008 |
| | | | | | Size classes_[50-60[ | -0.04752 | 0.39361 | | | -0.121 | 0.904 |
| | | | | | Size classes_[60-70[ | -0.18647 | 0.394 | | | -0.473 | 0.636 |
| | | | | | Size classes_[70-80[ | -1.16241 | 0.64913 | | | -1.791 | 0.073 |
| | Dentex dentex | ID | 4.871 | 2.207 | | | | | | | |
| | | | | | (Intercept) | -2.46488 | 0.85127 | | | -2.896 | 0.004 |
| | | | | | Time (days) | 0.21072 | 0.06989 | | | 3.015 | 0.003 |
| | | | | | Size classes_[60-70[ | -0.21041 | 0.83961 | | | -0.251 | 0.802 |
| | | | | | Size classes_[70-80[ | -1.07754 | 0.93592 | | | -1.151 | 0.250 |
| | Sciaena umbra | ID | 0.2789 | 0.5281 | | | | | | | |
| | | | | | (Intercept) | -0.6187 | 0.25955 | | | -2.384 | 0.017 |
| | | | | | Time (days) | 0.28687 | 0.04538 | | | 6.321 | 2.59E-10 |
| | | | | | Size classes_[50-60[ | -0.24643 | 0.273 | | | -0.903 | 0.367 |
| | | | | | Size classes_[60-70[ | -0.21445 | 0.2659 | | | -0.806 | 0.42 |
| Efficiency of attacks | Both species | ID | 0.4063 | 0.6374 | | | | | | | |
| | | | | | (Intercept) | -1.01806 | 0.27957 | | | -3.641 | 0.0003 |
| | | | | | Time (days) | 0.198 | 0.04201 | | | 4.714 | 2.43E-06 |
| | | | | | Species_DentexDentex | -0.70266 | 0.27819 | | | -2.526 | 0.012 |
| | | | | | Size classes_[50-60[ | 0.73859 | 0.29521 | | | 2.502 | 0.012 |
| | | | | | Size classes_[60-70[ | 0.46892 | 0.30457 | | | 1.54 | 0.124 |
| | | | | | Size classes_[70-80[ | 1.71894 | 0.56927 | | | 3.02 | 0.003 |

| Response variable | Group | Parameter | Estimate / Variance | Std.Error / SD | df | t / z value | p value |
|---|---|---|---|---|---|---|---|
| | | ID | 0.4676 | 0.6838 | | | |
| | *Dentex dentex* | (Intercept) | -1.58919 | 0.50246 | | -3.163 | 0.002 |
| | | Time (days) | 0.20275 | 0.07584 | | 2.674 | 0.008 |
| | | Size classes_[60-70[ | 0.85604 | 0.51496 | | 1.662 | 0.096 |
| | | Size classes_[70-80[ | 1.57069 | 0.59493 | | 2.64 | 0.008 |
| | | ID | 0.2985 | 0.5464 | | | |
| | *Sciaena umbra* | (Intercept) | -1.04608 | 0.28741 | | -3.64 | 0.0003 |
| | | Time (days) | 0.20869 | 0.05054 | | 4.129 | 3.65E-05 |
| | | Size classes_[50-60[ | 0.96157 | 0.27974 | | 3.437 | 0.001 |
| | | Size classes_[60-70[ | 0.17129 | 0.2888 | | 0.593 | 0.553 |
| Maximal swimming speed during succesful attacks (square root transformed) | | ID | 0.007313 | 0.08551 | | | |
| | | Residual | 0.101467 | 0.31854 | | | |
| | Both species | (Intercept) | 1.859056 | 0.081318 | 66.704603 | 22.862 | <2e-16 |
| | | Time (days) | -0.005337 | 0.014943 | 167.905715 | -0.357 | 0.721 |
| | | Species_DentexDentex | 0.607459 | 0.069699 | 20.22513 | 8.716 | 2.76E-08 |
| | | Size classes_[50-60[ | -0.109856 | 0.07371 | 19.028375 | -1.49 | 0.153 |
| | | Size classes_[60-70[ | -0.17502 | 0.074073 | 20.372455 | -2.363 | 0.028 |
| | | Size classes_[70-80[ | -0.153116 | 0.134012 | 21.174847 | -1.143 | 0.266 |
| | | ID | 0.01068 | 0.1034 | | | |
| | | Residual | 0.08509 | 0.2917 | | | |
| | *Dentex dentex* | (Intercept) | 2.48474 | 0.13153 | 21.83816 | 18.891 | 5.12E-15 |
| | | Time (days) | -0.0426 | 0.02451 | 47.71228 | -1.738 | 0.089 |
| | | Size classes_[60-70[ | -0.04759 | 0.11695 | 7.39463 | -0.407 | 0.696 |
| | | Size classes_[70-80[ | -0.03125 | 0.13224 | 7.85888 | -0.236 | 0.819 |
| | | ID | 0.01509 | 0.1229 | | | |
| | | Residual | 0.10058 | 0.3171 | | | |
| | *Sciaena umbra* | (Intercept) | 1.7818 | 0.09637 | 46.41055 | 18.489 | <2e-16 |
| | | Time (days) | 0.01295 | 0.01841 | 110.70578 | 0.704 | 0.483 |
| | | Size classes_[50-60[ | -0.09196 | 0.08531 | 9.23411 | -1.078 | 0.308 |
| | | Size classes_[60-70[ | -0.19166 | 0.08568 | 10.06519 | -2.237 | 0.049 |
| Maximal swimming speed during succesful attacks | | ID | 155.2 | 12.46 | | | |
| | | Residual | 717.6 | 26.79 | | | |
| | Both species | (Intercept) | 69.872 | 7.663 | 64.325 | 9.118 | 3.37E-13 |
| | | Time (days) | -1.142 | 1.287 | 165.133 | -0.887 | 0.376 |
| | | Species_DentexDentex | 34.848 | 7.07 | 23.983 | 4.929 | 4.98E-05 |
| | | Size classes_[50-60[ | -5.068 | 7.516 | 22.502 | -0.674 | 0.507 |
| | | Size classes_[60-70[ | -11.199 | 7.518 | 23.483 | -1.49 | 0.15 |
| | | Size classes_[70-80[ | -9.854 | 13.547 | 24.921 | -0.727 | 0.474 |
| | | ID | 265.3 | 16.29 | | | |
| | | Residual | 548.3 | 23.42 | | | |
| | *Dentex dentex* | (Intercept) | 113.187 | 13.041 | 19.851 | 8.679 | 3.44E-08 |
| | | Time (days) | -4.599 | 2.056 | 46.708 | -2.237 | 0.030 |
| | | Size classes_[60-70[ | -7.258 | 13.164 | 9.553 | -0.551 | 0.594 |
| | | Size classes_[70-80[ | -5.596 | 14.794 | 9.733 | -0.378 | 0.713 |
| | | ID | 131.8 | 11.48 | | | |

|  | | | | | | |
|---|---|---|---|---|---|---|
| | *Residual* | 769.9 | 27.75 | | | |
| *Sciaena umbra* | (Intercept) | 64.015 | 8.5476 | 53.9704 | 7.489 | 6.64E-10 |
| | Time (days) | 0.3424 | 1.6157 | 114.4819 | 0.212 | 0.833 |
| | Size classes_[50-60[ | -4.7745 | 7.6647 | 11.9448 | -0.623 | 0.545 |
| | Size classes_[60-70[ | -12.2753 | 7.6905 | 12.9275 | -1.596 | 0.135 |

(Intercept) 64.015 35

Size classes_[50-60[ -4.7745 7.6647 11.9448 -0.623 0.545

Size classes_[60-70[ -12.2753 7.6905 12.9275 -1.596
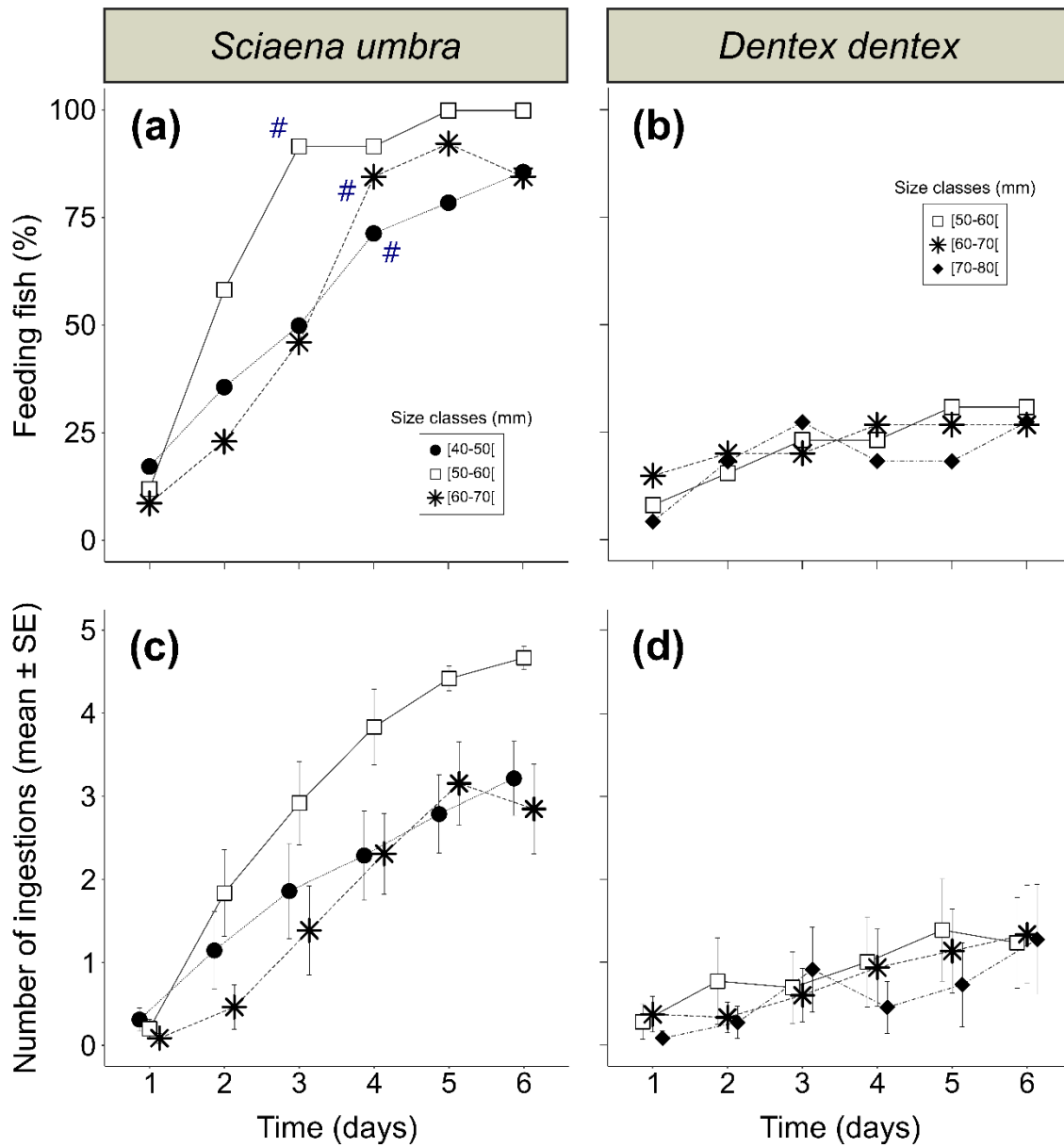
**Figure 1:** Effect of time (in days) on the percentage of eating fish (**a** and **b**) and the mean number of ingestions (**c** and **d**) in three size classes of *Sciaena umbra* (**a** and **c**) and *Dentex dentex* juveniles (**b** and **c**). The numbers of fish used in this figure correspond to the totality of fish tested and are summarized in Table 1. (Panel **(a)**: # indicates first significant increase compared to day 1; *Post hoc pairwise comparisons using Fisher's exact tests, P < 0.05*)
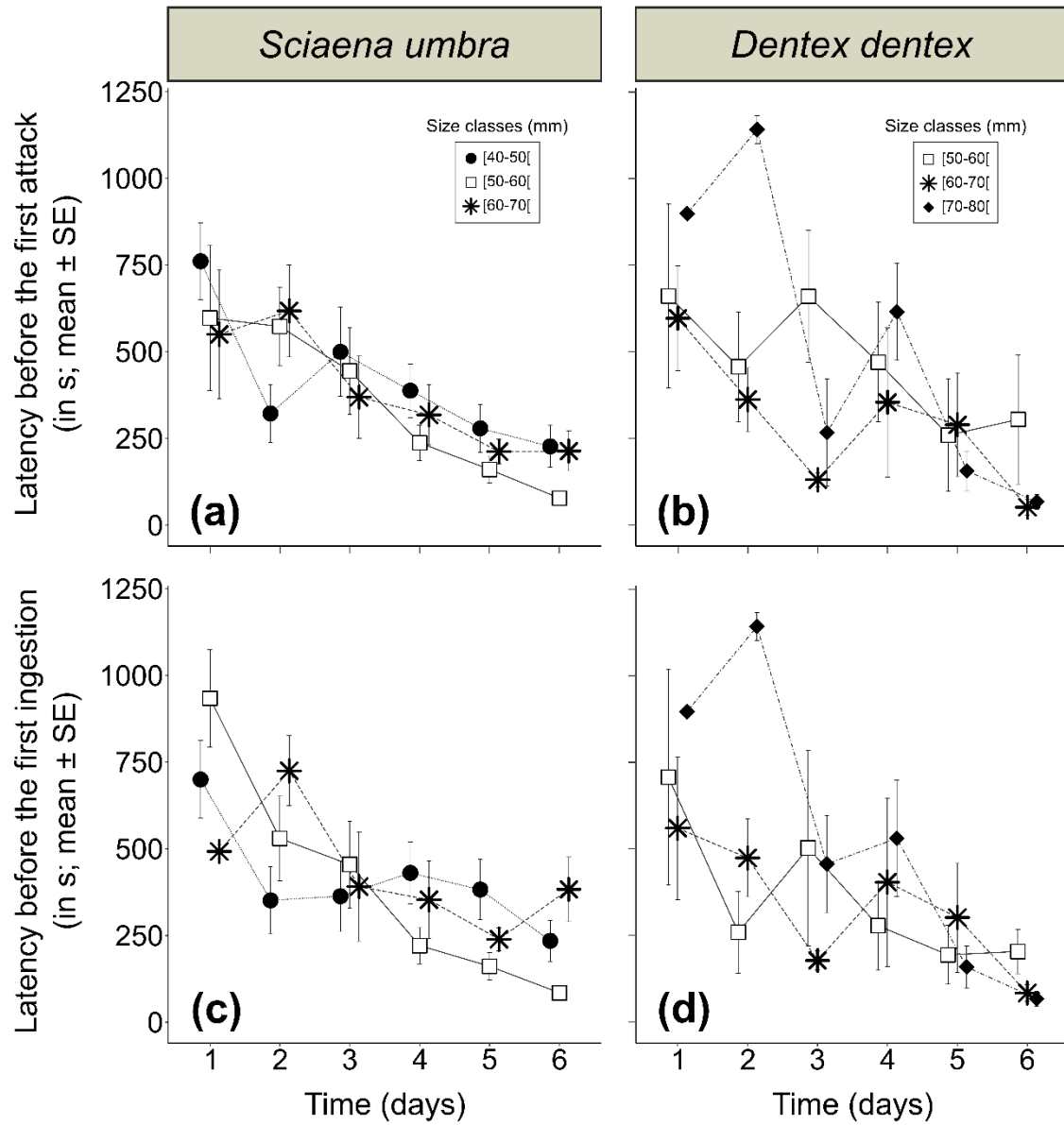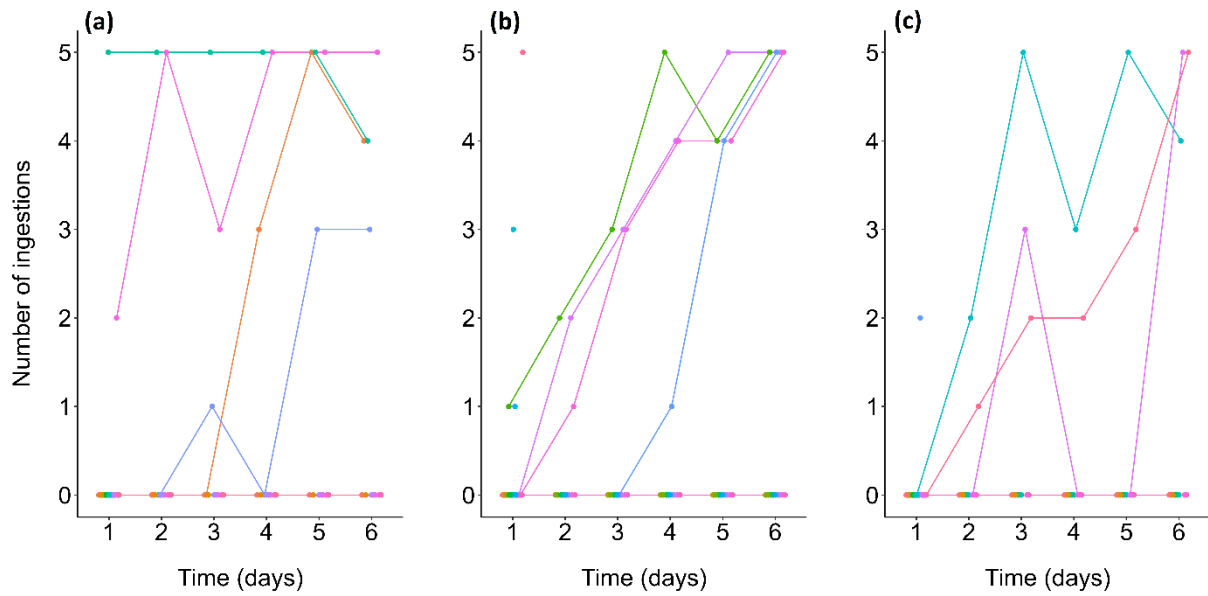
**Figure 2:** Effect of time (in days) on the mean latency (in s) before the first attack (**a** and **b**) and before the first ingestion (**c** and **d**) in three size classes of *Sciaena umbra* (**a** and **c**) and *Dentex dentex* juveniles (**b** and **c**). The numbers of fish used in this figure range between 4 and 12 (in **a**), 2 and 6 (in **b**), 2 and 12 (in **c**), 1 and 5 (in **d**); variation according to day × size class

**Appendix 1:** Effect of time (in days) on the number of ingestions for the (**a**) [50-60[, (**b**) [60-70[ and (**c**) [70-80[ mm TL size classes of *Dentex dentex* juveniles. Within each plot (either **a**, **b** or **c**) colours are specific to one individual (and the same individual was joined by a continuous line between time points). Individuals were only tested within one size class.