



# Using Telemetry Sensors Mapping the Energetic Costs in European Sea Bass (*Dicentrarchus labrax*), as a Tool for Welfare Remote Monitoring in Aquaculture

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Physiological real-time monitoring could help to prevent health and welfare issues in farmed fishes. Among physiological features that can be of interest for such purposes, there is the metabolic rate. Its measurement remains, however, difficult to be implemented in the field. Thus, mapping the fish acceleration recorded by tag with the oxygen consumption rate ( $MO_2$ ) could be promising to counter those limitations and to be used as a proxy for energy expenditure in the aquaculture environments. In this study, we investigated the swimming performance ( $U_{crit}$ ) and the swimming efficiency ( $U_{opt}$ ,  $COT_{min}$ ), and we estimated the metabolic traits (standard and maximum metabolic rates, SMR and MMR, as well the absolute aerobic scope, AS) of European sea bass (*Dicentrarchus labrax*;  $n = 90$ ) in swimming tunnel. Among all tested fish, 40 fishes were implanted with an acoustic transmitter to correlate the acceleration recorded by the sensor with the  $MO_2$ . In this study, the mean SMR, MMR, and AS values displayed by sea bass were 89.8, 579.2, and 489.4  $mgO_2 kg^{-1} h^{-1}$ , respectively. The  $U_{opt}$  and  $COT_{min}$  estimated for sea bass were on average 1.94  $km h^{-1}$  and 113.91  $mgO_2 kg^{-1} h^{-1}$ , respectively. Overall, implantation of the sensor did not alter fish swimming performance or induced particular stress, able to increase  $MO_2$  or decrease swimming efficiency in tagged fish. Finally, acceleration recorded by tag has been successfully correlated with  $MO_2$  and fish mass using a sigmoid function ( $R^2 = 0.88$ ). Overall, such results would help for real-time monitoring of European sea bass health or welfare in the aquaculture environment in a framework of precision livestock farming.

**Keywords:** acoustic telemetry,  $MO_2$ , welfare, energy expenditure, aquaculture, sea bass (*Dicentrarchus labrax*) L

## INTRODUCTION

The real-time monitoring technologies to manage animal farming are gaining uses to improve production and to monitor the health and welfare of farmed animals (Føre et al., 2018; Halachmi et al., 2019; Brijs et al., 2021). One approach developed in a framework of precision livestock farming is to monitor a number of sentinel animals using sensors (Halachmi et al., 2019). Continuous real-time monitoring may allow early detection of health or welfare issues, also leading to an early response from producer, and so to increase the likelihood of response success

implemented. Overall, this would help to improve the lives of farmed animals by reducing suffering related to an impaired welfare state and enhance farm production. During the last decades, a wide range of sensors has been developed to remotely monitor animal behavior and physiology, including in fishes (Brijs et al., 2021). Among these, some sensors are measuring position, acceleration, internal temperature, muscle activity, metabolic rate, or heartbeat rate of fish (e.g., Brijs et al., 2019; Carbonara et al., 2020b; Gesto et al., 2020; Muñoz et al., 2020; Rosell-Moll et al., 2021). For instance, the fish acceleration measured by some sensors was found to be sensitive to acute stressors found in aquacultures, such as hypoxia or ammonia exposure (Gesto et al., 2020; Rosell-Moll et al., 2021), or chronic stressors, such as stocking density (Carbonara et al., 2019, 2020a). Therefore, the use of such sensors could represent a promising tool for health and welfare remote monitoring in aquaculture, fish welfare being of great concern for consumers, producers, and regulatory authorities (Ashley, 2007; European Food Safety Authority, 2009).

Among physiological features that can be of interest for fish health and welfare monitoring, there is the metabolic rate, which could be used as proxy of the energetic expenditure related to fish's daily activities (Chabot et al., 2016a; McKenzie et al., 2016; Norin and Clark, 2016). Briefly, the oxygen consumption rate ( $MO_2$ ) displayed by a fish is comprised between the standard metabolic rate (SMR), which represents the minimal amount of oxygen needed by a fish to support its aerobic metabolic rate, and the maximum metabolic rate (MMR) which refers to the maximum rate of aerobic metabolism that can be sustained by the animal (Chabot et al., 2016a; Norin and Clark, 2016). The numerical difference between MMR and SMR defines the absolute aerobic scope (AS), which quantifies the amount of oxygen that can be consumed to support all physiological and locomotive activities, such as migration, feeding, and reproduction (Fry, 1947; Brett, 1972). In rearing conditions, sustaining a high metabolic rate, close to the MMR, consumes energy, and this energy will be no more available for other life activities, or to be invested in growth or reproduction, leading to potential health and welfare issues for fish. The SMR and MMR of fish are typically measured in the laboratory during the critical swimming test ( $U_{crit}$ ) in swimming chamber. Briefly, the SMR and MMR can be estimated based on the relationship between the  $MO_2$  and swimming speed, by extrapolating the value of  $MO_2$  when the speed value is equal to zero for the SMR, while the MMR is overall measured at the  $U_{crit}$  value during the critical swimming test (Chabot et al., 2016a; McKenzie et al., 2016).

Although the  $MO_2$  is a good indicator of fish physiological state, its measurement is not easily applicable to fishes either in the wild or in aquaculture environments (McKenzie et al., 2016). Thus, mapping the acceleration recorded by a sensor with the  $MO_2$  during the  $U_{crit}$  test could be promising to later use the tag acceleration data as an estimation of  $MO_2$  in free-swimming fish, and so as proxy of energetic costs related to the environment (e.g., Wilson et al., 2013; Wright et al., 2014; Alfonso et al., 2021a,b; Carbonara et al., 2021; Zupa et al., 2021). However, it is important to first emphasize

that, as metabolic rate is known to be affected by different factors (e.g., size, species, temperature),  $MO_2$  estimate using accelerometer tags needs accurate specific species mapping, at a given size and temperature, prior to being used in aquaculture environments (Chabot et al., 2016a; Rubio-Gracia et al., 2020).

The aim of this study was (1) to investigate the swimming performance, metabolic traits, and swimming efficiency for tagged and untagged European sea bass (*Dicentrarchus labrax*), a key species for the European marine aquaculture (Vandeputte et al., 2019) and (2) to calibrate the acceleration recorded by tag with the  $MO_2$  of the fish to be later used as a proxy of its energy expenditure. To do so, we assessed first the swimming performance of sea bass in the swimming tunnel and estimated the metabolic traits and swimming efficiency in sea bass ranging from 212 to 998 g at 18°C. Among all fishes, a subsample was implanted with an accelerometer tag, and the acceleration recorded by the sensor was correlated with the  $MO_2$ . In addition, the metabolic traits, swimming performance, and swimming efficiency were compared between tagged and untagged fish to evaluate tagging effect on these variables. Overall, this work could later benefit to health and welfare of farmed fish by remote real-time monitoring of the European sea bass in the framework of precision livestock aquaculture farming.

## MATERIALS AND METHODS

All experiments were performed in accordance with EU recommendations (Directive 2010/63/EU) and the Italian National Legislation (D. lgs. 26/2014) on the fish welfare, with the authorization of Italian Health Ministry number code 838/2019-PR.

### Fish

European sea bass were provided by an aquaculture farm (Ittica Caldoli, Lesina, Italy) and then kept 6 weeks for acclimation in our facility at Coispa Tecnologia & Ricerca (Bari, Italy) before proceeding to experimental procedures described below. Fish were kept in 1.2-m<sup>3</sup> circular fiberglass tanks in a flow-through system with marine water input of 150 L h<sup>-1</sup> (35 PSU). Stocking density was ~12 kg.m<sup>-3</sup>, oxygen saturation was at ~80%, and temperature was maintained constant at 18 ± 1°C. The light regime was also maintained constant during the entire experimental period (12-h light:12-h dark). The fish were fed ~1% of the body mass using commercial food Marine 3P (Skretting, Vignetto, Italy).

### Critical Swimming Test ( $U_{crit}$ ) and Estimation of Metabolic Traits and Cost of Transport (COT)

Critical swimming tests were conducted using a swim tunnel respirometer Loligo Systems (Viborg, Denmark) of 30- or 90-L in accordance with the manufacturer's instruction depending on the fish size. In more detail, fish larger than 450 g

were challenged in the 90-L swim tunnel whereas other fish were tested in the 30-L swim tunnel. The trials were controlled using the DAQ-M device (no. AR12500, Loligo Systems, Viborg, Denmark). The speed of the water flow was calibrated by means of a flow-meter Flowtherm NT (Höntzsch, Germany), whereas the oxygen concentration was measured using a polymer optical fiber oxygen probe (POF; Loligo Systems) inserted in the swimming chamber. The oxygen probe was connected to the WITROX oxygen instrument 1 (no. OX11800; with a high-accuracy temperature sensor; Loligo Systems) to sample oxygen variations during the trials. Finally, the swimming chambers were housed in a buffer tank to maintain a constant temperature of  $18 \pm 1^\circ\text{C}$  during the trial.

About 24 h before introducing fish into the swimming tunnel for the trial, fish were starved to ensure a post-absorptive state (McFarlane et al., 2004) and were lightly anesthetized using  $30\text{ mg L}^{-1}$  hydroalcoholic solution of clove oil (bathed for  $\sim 1$  min in anesthetic) for taking morphometric measurements (Zupa et al., 2015). After the fish being introduced into the swimming chamber, the fish was left undisturbed for 30 min at least before induction of swimming velocity of  $0.1\text{ m s}^{-1}$ . Velocity has been maintained for 90 min at least, allowing fish acclimation before starting the trial. The swimming trial started when the oxygen consumption ( $\text{MO}_2$ ) reached a constant low plateau (Martos-Sitcha et al., 2018). During the trial, the swimming speed has been increased with a constant ramp of  $0.1\text{ m s}^{-1}$  at constant time intervals of 10 min until fatigue was reached (Carbonara et al., 2010). Each interval was constituted of 3 steps: a 5-min step of “flushing” 2-min step of “waiting,” and 3-min step of “ $\text{MO}_2$  measurement” (Alfonso et al., 2021a). During the  $\text{MO}_2$  measurement step, the oxygen concentration of the swim tunnel water was recorded every second.  $\text{MO}_2$  was automatically calculated by the software AutoResp v.2.3 (Loligo Systems) from linear decrease in the  $\text{O}_2$  concentration inside the chamber, using the appropriate constants for oxygen solubility in seawater (salinity, temperature, and barometric pressure).

The  $U_{\text{crit}}$  values were estimated according to Brett (1964) and corrected for solid blocking effects (Smit et al., 1971; Kline et al., 2015). Absolute  $U_{\text{crit}}$  ( $\text{m s}^{-1}$ ) was also accounted for size and displayed as relative  $U_{\text{crit}}$  ( $\text{BL s}^{-1}$ ). During the swimming trial, the  $\text{MO}_2$  was fitted as a function of swimming speed, and the model was used for estimating the values of the metabolic variables: SMR, MMR, and the absolute AS (refer to “Statistical Analyses”). The cost of transport (COT) was fitted as the function of swimming speed ( $U$ ,  $\text{km h}^{-1}$ ) according to the study by Zupa et al. (2015), and  $U_{\text{opt}}$  and  $\text{COT}_{\text{min}}$  were estimated based on the model (refer to “Statistical Analyses”).

In this study, 90 fish were challenged in the swimming chamber for the  $U_{\text{crit}}$  trial. Among the 90, 50 fish were will serve as a baseline of swimming performance and  $\text{MO}_2$  (named untagged fish), whereas 40 fish were implanted with accelerometer tag (named tagged fish) to correlate the acceleration recorded by tag with the  $\text{MO}_2$ . Morphometric data of fish used in the study are displayed in **Table 1** for both untagged and tagged fish.

**TABLE 1** | Morphometric measures (mass [g] and total length, TL [mm]) and sample size of European sea bass (*Dicentrarchus labrax*) tested in the swimming chamber for  $U_{\text{crit}}$  trials depending on condition (untagged and tagged fish).

Condition	n	Mass (g)	Total length (mm)
Untagged	50	$571.78 \pm 230.14$	$358.18 \pm 51.42$
Tagged	40	$589.94 \pm 232.09$	$362.43 \pm 49.95$
Total	90	$579.85 \pm 229.09$	$360.07 \pm 50.54$

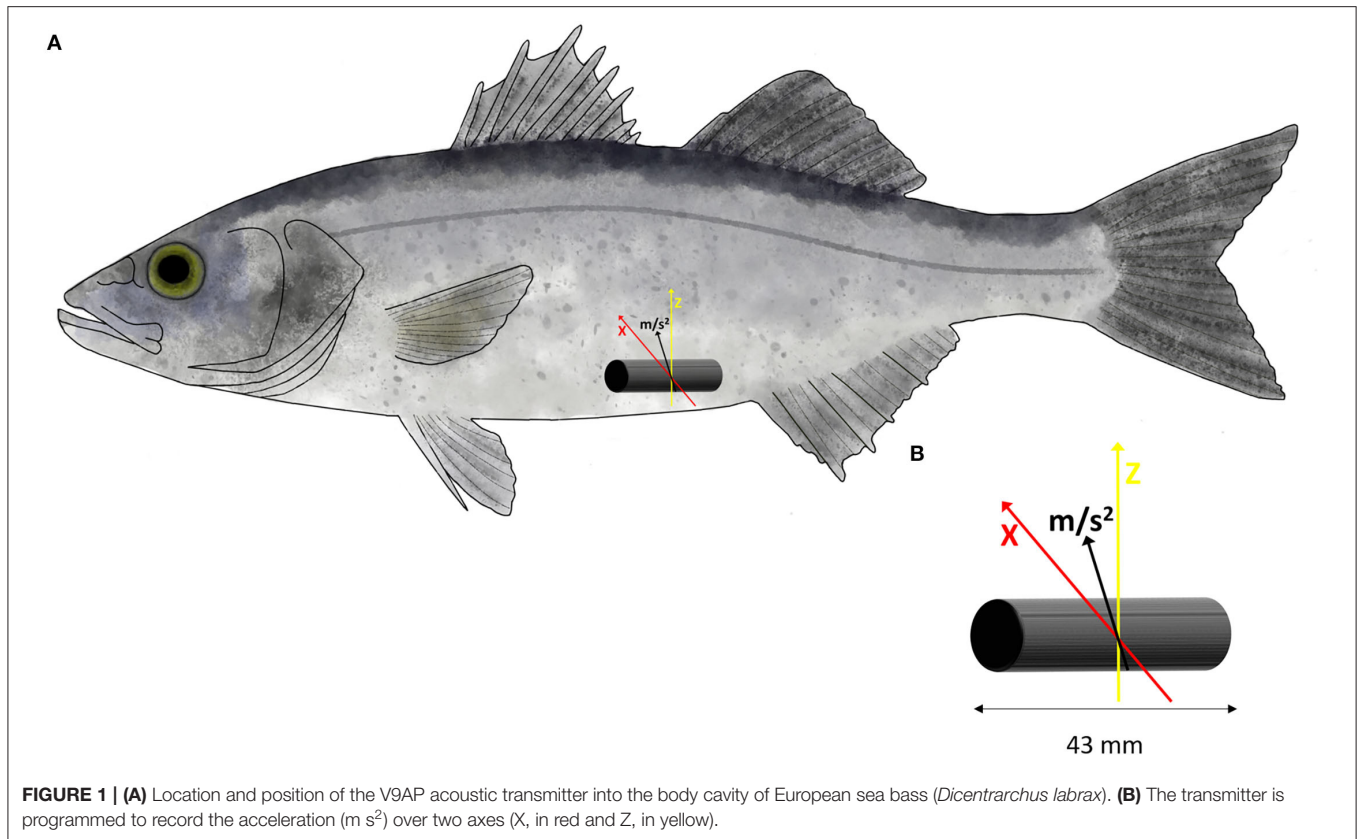
## Implantation of Accelerometer Tags and Calibration of Acceleration With $\text{MO}_2$ During $U_{\text{crit}}$ Trial

A total of 40 fish (**Table 1**) were randomly selected for mapping the swimming activity recorded by accelerometer tag with the  $\text{MO}_2$  during the  $U_{\text{crit}}$  trials. The fish was starved 24 h before the implantation of tag. Prior to proceeding to the surgery, fish was anesthetized using  $30\text{ mg L}^{-1}$  of hydroalcoholic clove oil solution for  $\sim 3$  min, and the gills of fish were continuously irrigated with the anesthetic bath during the surgical procedure. The acoustic transmitter VEMCO V9AP (AMIRIX Systems Inc., Nova Scotia, Canada) was implanted into the body cavity through a 1.5-cm incision and carefully sutured, as described in the study of Alfonso et al. (2021a) (**Figure 1**). After the surgery, fish was left undisturbed in a separate tank for 5 days of recovery before trial in a swimming tunnel as described above. Choice of 5 days of recovery was based on the preliminary work in sea bass (Carbonara et al., 2021). Daily observations following the surgery were carried out to ensure that fish did eat and behave normally before being tested.

For the  $U_{\text{crit}}$  trial, the accelerometer tag was programmed to record, with a sampling rate of 10 Hz, the acceleration over two axes (X and Z) (Brownscombe et al., 2018), excluding the y-axes of the backward or forward movements (**Figure 1**). The tag transmits the coded values that correspond to fish acceleration on average of every 30 s. The tag provided an 8-bit value which represents the root mean square (RMS) acceleration. The value ranges from 0 to 255 and displayed as an arbitrary unit (AU). Value can be converted in acceleration using the following equation ( $\text{acceleration (m s}^{-2}) = 0.01955(x)$ ), where x is the value given by tags) resulting from the contribution of two axes. The data were stored in acoustic receivers Vemco VR2W (AMIRIX Systems Inc., Nova Scotia, Canada) located near the swimming chamber until the end of trial. Then, the data were extracted from the receiver using the software VUE (AMIRIX Systems Inc., Nova Scotia, Canada), and the values retrieved from the tag were averaged for each step of swimming speed before processing to the mapping with  $\text{MO}_2$  recorded during the trial.

## Statistical Analysis

Statistical analyses were carried out using the R software version 4.0.4 (R Core Team, 2021) at the 95% level of significance. Data are presented as mean  $\pm$  SE except otherwise mentioned. For boxplot representation, the central line of the boxplot indicates the median whereas the boxes on either side represent the quartiles (whiskers covering 95% of the values). In boxplots,



**FIGURE 1 | (A)** Location and position of the V9AP acoustic transmitter into the body cavity of European sea bass (*Dicentrarchus labrax*). **(B)** The transmitter is programmed to record the acceleration ( $m/s^2$ ) over two axes (X, in red and Z, in yellow).

the values are represented by dots, and the outlier values are represented by bigger dots.

Concerning analyses, the swimming performance ( $U_{crit}$ ) was first compared using the  $t$ -test between the tagged and untagged sea bass. Subsequently, swimming performance ( $U_{crit}$ ) was evaluated using ANOVA as a function of two factors, the fish mass and tagging condition, and the interaction of both factors. Since tagging conditions, as well the interaction mass and tagging, were not significant (refer to **Supplementary Table S1**), they were both removed before running ANOVA, and so the swimming performance was analyzed only as a function of fish mass.

The  $MO_2$  of sea bass during the  $U_{crit}$  trials was fitted as a function of swimming speed ( $U$ ) using an exponential model for each fish using the following formula:

$$MO_2 = \alpha e^{\beta U}$$

where  $\alpha$  and  $\beta$  are constant. SMR was estimated by extrapolating the  $MO_2$  value when the swimming speed ( $U$ ) was equal to 0 (Chabot et al., 2016b), whereas the MMR value was estimated using the  $MO_2$  value at the  $U_{crit}$  value (i.e., when the swimming speed  $U = U_{crit}$ ) (Norin and Clark, 2016). The numerical difference between MMR and SMR indicates the absolute AS (Halsey et al., 2018). Linear regressions were carried out for all metabolic traits as the function of fish mass to evaluate the relation between mass and metabolic rates in

sea bass. Metabolic traits were compared between tagged and untagged fish using the  $t$ -test.

As briefly explained above, the COT ( $mgO_2 kg^{-1} km^{-1}$ ), which provides an index of overall swimming efficiency, was modeled as the function of swimming speed ( $U$ ,  $km h^{-1}$ ) following the following formula according to the study by Zupa et al. (2015):

$$COT = \frac{a e^{bU}}{U}$$

where  $a$  and  $b$  are constant. The COT function is characterized by a U-shaped (Claireaux et al., 2006) and has a minimum (minimum cost of transport,  $COT_{min}$ ), which corresponds to the optimal swimming speed  $U_{opt}$  (i.e., best swimming efficiency).  $U_{opt}$  was calculated as follows:

$$U_{opt} = \frac{1}{b}$$

Linear regressions were applied for  $U_{opt}$  and  $COT_{min}$  as the function of fish mass to evaluate the relationship between mass and swimming efficiency in sea bass. In addition, the  $U_{opt}$  and  $COT_{min}$  were compared using the  $t$ -test between tagged and untagged fish.

To calibrate the swimming activity measured by the tag with the  $MO_2$ , two modeling steps were performed as described in

the study by Alfonso et al. (2021a). Briefly, for the first step, the  $MO_2$  was modeled as a function of the swimming activity using self-starting non-linear least squares (NLS) logistic models (SSlogis) for each fish (**Supplementary Table S2**), based on the following formula:

$$y = \frac{A_{sym}}{1 + e^{\frac{x_{mid} - x}{scal}}}$$

where  $A_{sym}$  is a numeric parameter representing the asymptote;  $x_{mid}$  is a parameter representing the x value at the inflection point of the curve, when  $y = A_{sym}/2$ , and  $scal$ : is a scale parameter of the x-axis.

Parameters of the model (i.e.,  $A_{sym}$ ,  $x_{mid}$ , and  $scal$ ) for each fish were retrieved and were tested depending on fish mass using linear regression (**Supplementary Table S2**; **Supplementary Figure S2**). For the second step, one SSlogis model accounting for all fish has been fitted. In this model, the parameters have been adapted depending on the link between the parameter and fish mass (results from the first step). In more details, in the step 1, the  $A_{sym}$  was the unique parameter that was affected by the fish mass ( $A_{sym} = 633.8 - 0.21 * \text{Mass}$ ;  $p < 0.001$ ;  $R^2 = 0.36$ ; **Supplementary Figure S2**). So, in step 2, the  $A_{sym}$  parameter was modified from fixed to the equation displayed above accounting for fish mass, whereas the two other parameters were kept as constant (since no influenced by mass). These latter two parameters ( $x_{mid}$  and  $scal$ ) were estimated using the classic iteration method.

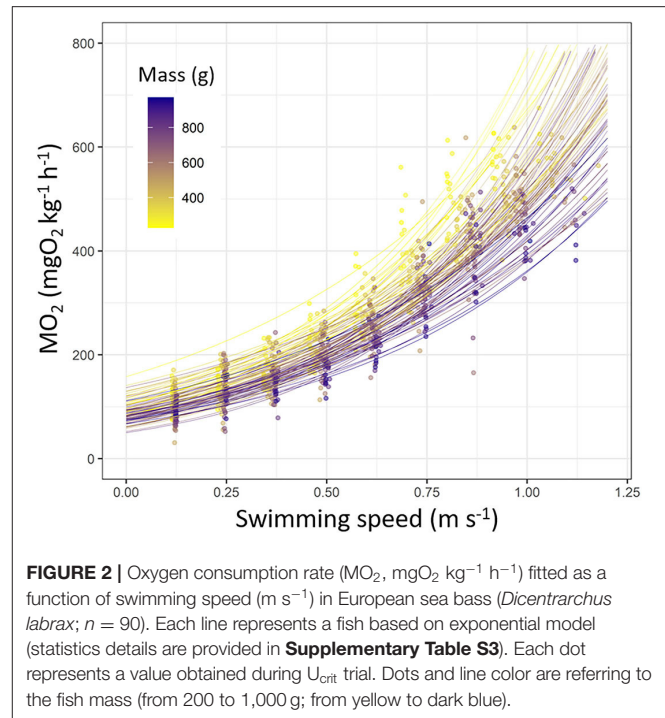
## RESULTS

### Critical Swimming Speed ( $U_{crit}$ ), Estimation of Metabolic Traits, and COT

Overall, the absolute  $U_{crit}$  values ranged from 0.86 to 1.26  $m\ s^{-1}$  with an average of  $1.05 \pm 0.07\ m\ s^{-1}$ . The relative  $U_{crit}$  values ranged from 2.06 to 4.19 with on average of  $2.98 \pm 0.45\ BL\ s^{-1}$ . The implantation of tag did not influence the fish swimming performance, whatever was measured as absolute or relative  $U_{crit}$  (**Supplementary Figure S3**; **Supplementary Table S1**). The absolute  $U_{crit}$  resulted to be not correlated to the fish mass ( $p > 0.05$ ; **Supplementary Figure S3A**) whereas the relative  $U_{crit}$  decreased as a function of fish mass ( $p < 0.001$ ;  $R^2 = 0.75$ ; **Supplementary Figure S3B**).

The  $MO_2$  increased following an exponential pattern in sea bass during the  $U_{crit}$  trial (**Figure 2**). Exponential models fitted did explain well the  $MO_2$  during  $U_{crit}$  ( $p < 0.001$  for all fish;  $R^2 > 0.7$ ; refer to **Supplementary Table S3** for statistics details). The parameter  $\beta$  of the exponential model did not vary according to fish mass ( $p > 0.05$ ) whereas the parameter  $\alpha$  decreased with the increase of fish mass ( $R^2 = 0.14$ ;  $p < 0.01$ ; **Supplementary Table S3**).

For each fish, the SMR value has been retrieved from the  $MO_2$  when swimming speed = 0 based on the exponential model, and MMR was extrapolated from the  $MO_2$  value at the  $U_{crit}$  trial. The estimated SMR, MMR, and absolute AS values estimated by the models were  $89.77 \pm 20.35$ ,  $579.21 \pm$



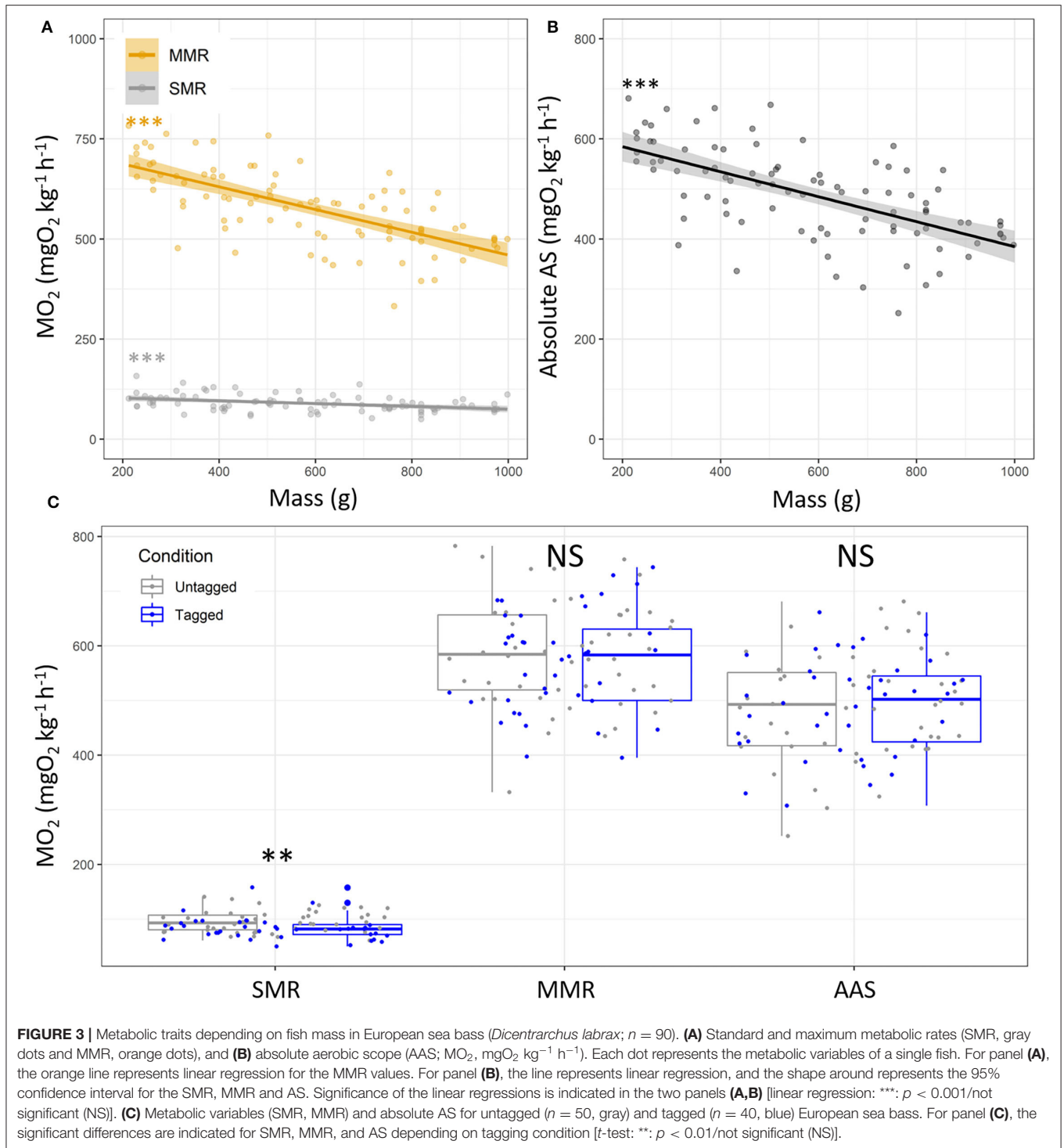
**FIGURE 2** | Oxygen consumption rate ( $MO_2$ ,  $mgO_2\ kg^{-1}\ h^{-1}$ ) fitted as a function of swimming speed ( $m\ s^{-1}$ ) in European sea bass (*Dicentrarchus labrax*;  $n = 90$ ). Each line represents a fish based on exponential model (statistics details are provided in **Supplementary Table S3**). Each dot represents a value obtained during  $U_{crit}$  trial. Dots and line color are referring to the fish mass (from 200 to 1,000 g; from yellow to dark blue).

$94.89$ , and  $489.44 \pm 92.37\ mgO_2\ kg^{-1}\ h^{-1}$ , respectively, with higher variability for MMR and the absolute AS than SMR (**Supplementary Table S3**). The SMR and MMR were negatively correlated with the fish mass (SMR,  $y = 109.88 - 0.03 * x$ ;  $p < 0.001$ ;  $R^2 = 0.14$ ; MMR,  $y = 744.06 - 0.28 * x$ ;  $p < 0.001$ ;  $R^2 = 0.47$ ; **Figures 3A,B**). This resulted into lower absolute aerobic scope for larger fish ( $y = 634.18 - 0.25 * x$ ;  $p < 0.001$ ;  $R^2 = 0.38$ ; **Figure 3B**). The estimated SMR values were lower in tagged fish than untagged fish ( $82.79 \pm 20.06\ mgO_2\ kg^{-1}\ h^{-1}$  vs.  $95.35 \pm 18.98\ mgO_2\ kg^{-1}\ h^{-1}$ ;  $p < 0.01$ ), whereas the MMR and absolute AS were similar between conditions ( $p > 0.05$ ; **Figure 3C**).

The estimated  $U_{opt}$  and  $COT_{min}$  by the models were  $1.94 \pm 0.33\ km\ h^{-1}$  and  $113.91 \pm 17.54\ mgO_2\ kg^{-1}\ km^{-1}$  in sea bass (**Figure 4A**; refer to **Supplementary Table S4** for statistics details). The  $U_{opt}$  was not affected by the fish mass (**Supplementary Table S4**;  $p > 0.05$ ), whereas the  $COT_{min}$  decreased with the increase in fish mass (**Figure 4B**;  $y = 141.45 - 0.05x$ ;  $p < 0.001$ ;  $R^2 = 0.38$ ). Both the  $U_{opt}$  and  $COT_{min}$  were lower in tagged fish than untagged ones (**Figures 4C,D**;  $p < 0.01$  for both), i.e.,  $1.82 \pm 0.33$  vs.  $2.03 \pm 0.30\ km\ h^{-1}$  and  $107.39 \pm 16.20$  vs.  $119.11 \pm 16.97\ mgO_2\ kg^{-1}\ km^{-1}$ , respectively, for  $U_{opt}$  and  $COT_{min}$ .

### Mapping Fish Acceleration Measured by tag With the $MO_2$

During the  $U_{crit}$  trial, the swimming activity recorded by tag increased with the increase of swimming speed following an exponential pattern for all challenged fish ( $p < 0.05$  for all fish; **Figure 5**; refer to **Supplementary Table S5** for statistics details). The swimming activity pattern recorded by tag resulted to be

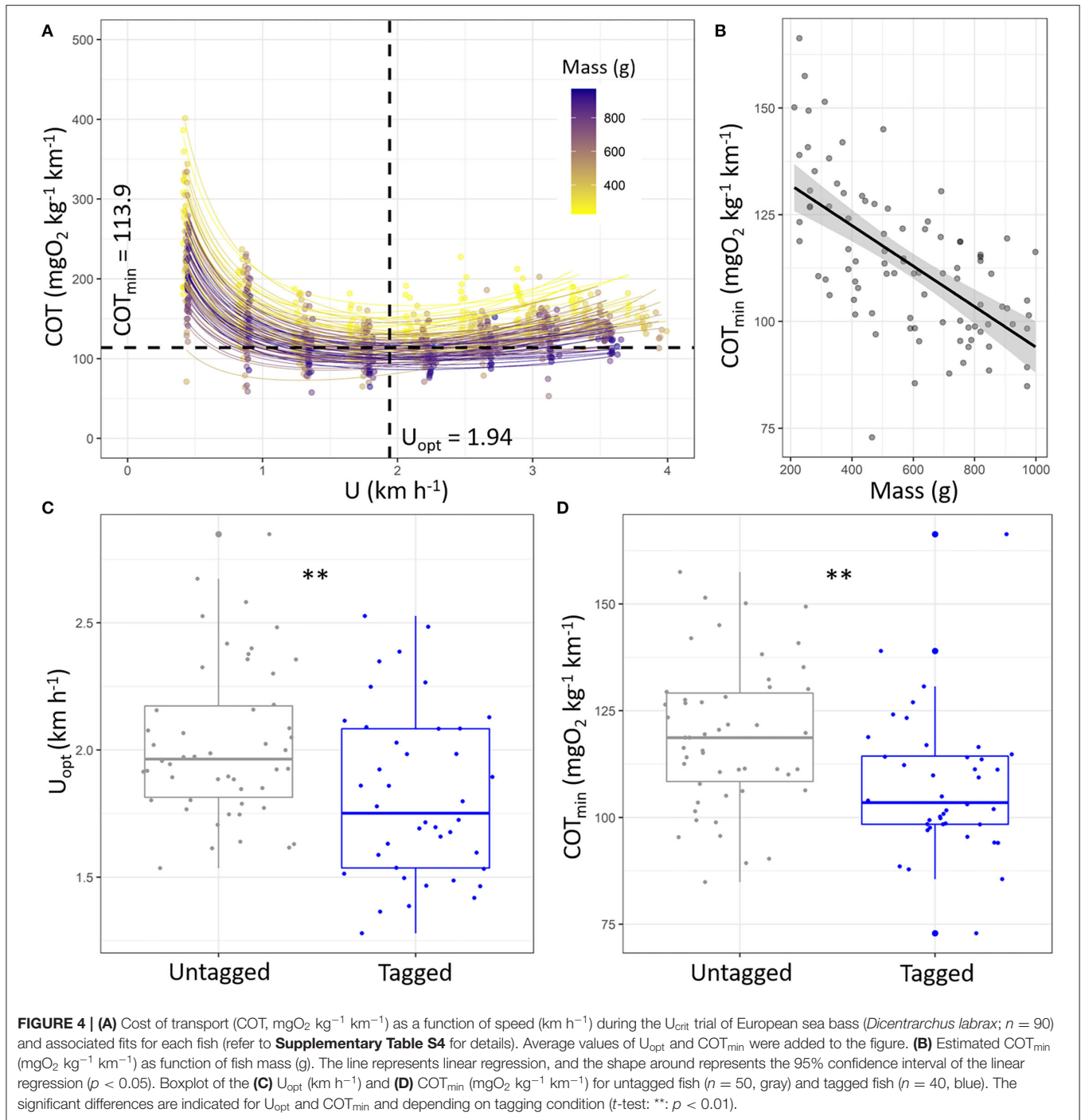


not different depending on the fish mass, since both parameters of the models ( $\alpha$  and  $\beta$ ) did not significantly change as the function of the fish mass (ANOVA,  $p > 0.05$  for both parameters; **Supplementary Table S5**).

Particularly, the  $\text{MO}_2$  has been fitted using the sigmoid model (**Table 2**;  $R^2 = 0.88$ ). In this model, the  $A_{\text{sym}}$  parameter was

replaced by the linear equation accounting for fish mass (refer to the section “statistical analyses” for details). According to the two modeling steps (**Table 2**), the  $\text{MO}_2$  can be estimated as follows:

$$\text{MO}_2 = \frac{633.8 - 0.21 * x_2}{1 + e^{\frac{x_{\text{mid}} - x_1}{\text{scal}}}}$$

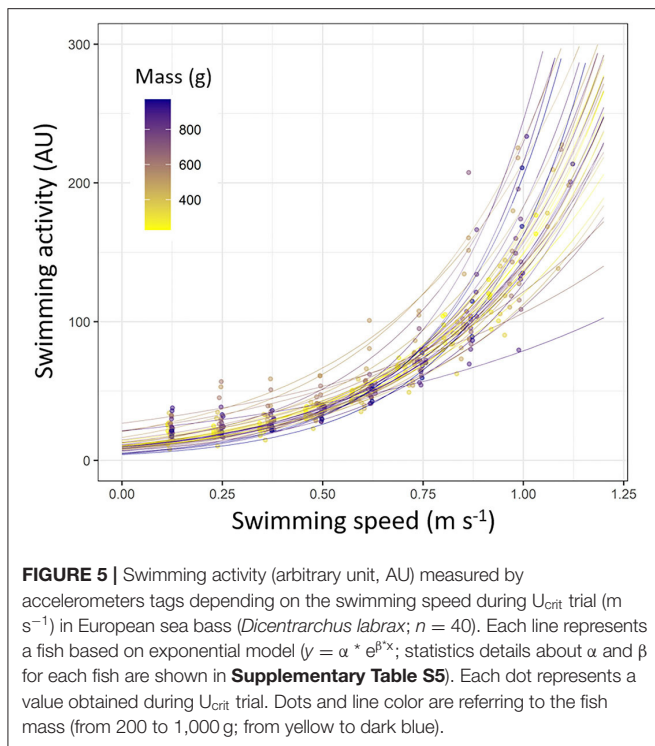


where  $x_1$  is the swimming activity measured by tag and  $x_2$  is the fish mass (g).  $x_{\text{mid}}$  and  $\text{scal}$  were  $52.3 \pm 0.8$  and  $25.7 \pm 0.9$ , respectively (Table 2).

Looking at the model predictions, for low acceleration values displayed by tag, the  $\text{MO}_2$  increases in all fish but the increase is faster in smaller sea bass than in larger ones. The  $\text{MO}_2$  asymptote ( $A_{\text{sym}}$ ) is reached sooner by larger fish than for smaller ones, i.e., the plateau phase of the  $\text{MO}_2$  is lower for larger fish than for smaller ones (Figure 6).

## DISCUSSION

Here, we measured the swimming performance and estimated the metabolic traits and swimming efficiency of European sea bass, which is a key species for the European marine aquaculture (Vandeputte et al., 2019), and we then evaluated the possible effects of accelerometer tag implantation on these parameters. Finally, we correlated the acceleration values recorded by the tag with  $\text{MO}_2$ , to be later used as a proxy of energy expenditure



in free-swimming sea bass in response to the environments, including in aquaculture environments (Alfonso et al., 2021b).

In this study, the absolute  $U_{crit}$  values ranged from 0.86 to 1.26  $m s^{-1}$  and relative  $U_{crit}$  values ranged from 2.06 to 4.19 BL  $s^{-1}$  and were consistent with values reported in the literature European for sea bass (Chatelier et al., 2006; Claireaux et al., 2006; Zupa et al., 2015; Carbonara et al., 2021). The absolute  $U_{crit}$  values did not vary according to fish mass contrary to what is expected, but the relative  $U_{crit}$  values decreased with the increase of fish mass, as already reported for this species (Zupa et al., 2015), and following overall classic pattern in fishes. Strong currents are known to affect the schooling structure, fish behavior, swimming speed, and so the energy expenditure (Oppedal et al., 2011; Hvas et al., 2021). Therefore, measuring  $U_{crit}$  and understanding the swimming capability in key aquaculture species are of primary importance to make a correct farming site selection while avoiding stress and/or high energetic costs due to high currents exposure (Oppedal et al., 2011; Remen et al., 2016; McKenzie et al., 2021). In addition, the implantation of the accelerometer tag in the fish body cavity has been found not to trigger any significant disruption of the swimming performance, suggesting low invasiveness for tag implantation, as previously shown in various studies (Alfonso et al., 2020, 2021a; Arechavala-Lopez et al., 2021; Føre et al., 2021), and so, the trust that the measures carried out in implanted fish can be expected to be similar to fish without, as long as a few conditions are met (Jepsen et al., 2005, 2011; Macaulay et al., 2021). In conclusion, the tagged fish can be considered as highly representative of the entire monitored fish population (i.e., both tagged and untagged) (Alfonso et al., 2020). This is of particular interest when using tagged sentinel

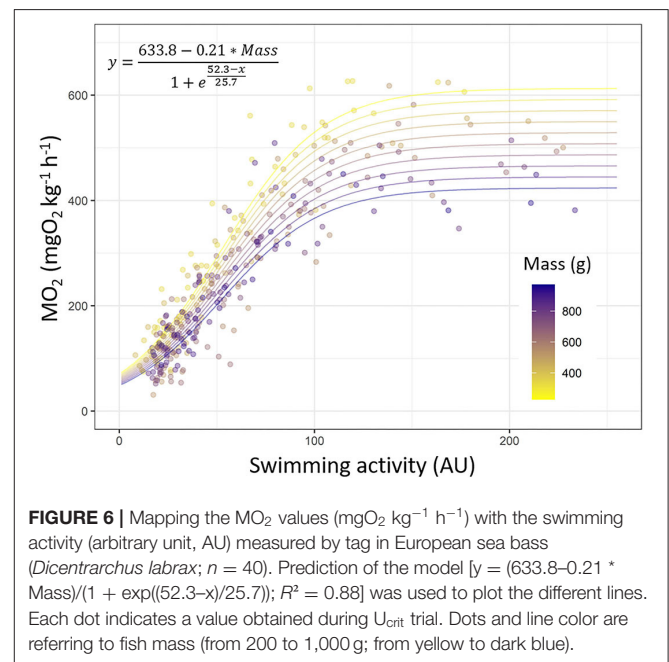
**TABLE 2 |** Outputs of the significant linear regression for the  $A_{sym}$  parameter ( $p < 0.001$ ;  $R^2 = 0.36$ ), and for the model mapping the  $MO_2$  depending on swimming activity measured by tag (SSlogis,  $p < 0.001$ ;  $R^2 = 0.88$ ) in European sea bass (*Dicentrarchus labrax*;  $n = 40$ ).

**$A_{sym}$  – linear regression**

Parameters	Estimate	Std. error	t-value	p-value
(intercept)	633.83	28.61	22.16	<0.001
Mass	-0.21	0.05	-4.74	<0.001

**Calibration model – SSlogis**

Parameters	Estimate	Std. error	t-value	p-value
$x_{mid}$	52.35	0.82	63.97	<0.001
scal	25.71	0.93	27.73	<0.001



fish for health or welfare monitoring of the whole population under aquaculture conditions (e.g., Føre et al., 2017; Alfonso et al., 2021b).

The  $MO_2$  of European sea bass during the  $U_{crit}$  test has been previously modeled depending on swimming speed using an exponential model (Claireaux et al., 2006). Overall, the estimated SMR, MMR, and absolute AS values by the models were  $89.77 \pm 20.35$ ,  $579.21 \pm 94.89$ , and  $489.44 \pm 92.37 mgO_2 kg^{-1} h^{-1}$ , respectively, with higher variability for the estimations of MMR and the absolute AS than SMR. The estimations carried out by the models are in the range of what can be expected for this species (Chatelier et al., 2006; Claireaux et al., 2006; Zupa et al., 2015). For similar temperature ( $18 \pm 1^\circ C$ ), in the study of Zupa et al. (2015), we estimated SMR at  $166 mgO_2 kg^{-1} h^{-1}$ , MMR at  $599 mgO_2 kg^{-1} h^{-1}$ , resulting in an absolute AS of  $483 mgO_2 kg^{-1} h^{-1}$  for sea bass of  $\sim 260 g$ , whereas higher values were found for sea bass of  $\sim 420 g$  with SMR estimated at 163, MMR at  $827 mgO_2 kg^{-1} h^{-1}$  and resulting absolute AS at



664 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>. Whereas Claireaux et al. (2006) estimated SMR at 92 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>, MMR at 338 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>, resulting in absolute AS of 246 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> for sea bass of ~150 g, for sea bass (~200 g) at 20°C. Chatelier et al. (2006) estimated SMR at 86, MMR at 509 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>, resulting in absolute AS of 423 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>. Even if SMR, MMR, and absolute AS values are in the expected range, SMR and AS are higher than those estimated by Chatelier et al. (2006) and Claireaux et al. (2006). Besides the size and/or temperature effects on metabolic variables, high variability of SMR and MMR values between individuals is generally observed (Burton et al., 2011; Norin and Clark, 2016), with higher variations observed for MMR. The observed variability may be mainly explained by the differences in experimental protocol to estimate metabolic traits (e.g., difference in the duration of time intervals of the trial, difference in the velocity increase between two velocity step intervals) (Chabot et al., 2016b; Norin and Clark, 2016). In this work, both SMR and MMR measured decreased with the increase of fish mass, resulting in lower absolute AS in larger sea bass. Therefore, smaller sea bass, overall having a higher absolute AS than larger ones, have a greater oxygen amount to be used for routine activities, to invest in biological processes or for stress coping. The SMR was found to be slightly lower in tagged sea bass than in untagged ones (82.79 ± 20.06 vs. 95.35 ± 18.98 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>), whereas both MMR and absolute AS were similar between untagged and tagged sea bass. This may appear a bit confusing but it could be explained by some stresses induced by handling and introduction in the swimming chamber for untagged sea bass, which translated into a slightly higher SMR; sea bass being highly stress responding fish (Fanouraki et al., 2011; Alfonso et al., 2019). On the contrary, this stress would not be perceived for tagged individuals which were already handled and implanted with tag 5 days before the swimming trial, reducing stress for further handling. Indeed, repeated exposures to the same stressor can desensitize fish and attenuate the neuroendocrine and metabolic responses to subsequent exposure to stressors (Reid et al., 1998; Barton, 2002). For instance, Barton et al. (1986) found in rainbow trout stressed several times that cortisol response was lower than the one measured in unstressed fish, indicating possible desensitization of the hypothalamic–pituitary–interrenal (HPI) axis to repeated disturbances. Further studies have investigated SMR values for tagged fish (vs. untagged) more days later tagging to validate this hypothesis. This may be also tested by handling untagged fish in a similar way than tagged ones although not tagging them. Nevertheless, the results of the study overall indicate that tagging did not induce particular stress to the species that could impact the MMR and reduce the AS, as already suggested by a previous study using other variables (e.g., growth performance, cortisol levels) (Jepsen et al., 2011; Wright et al., 2014; Alfonso et al., 2020).

In this study, the U<sub>opt</sub> and COT<sub>min</sub> estimated for sea bass were on average 1.94 ± 0.33 km h<sup>-1</sup> and 113.91 ± 17.54 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup>. Overall, these values are consistent with the literature concerning this species, ranged from 2.08 to 2.48 km h<sup>-1</sup> for U<sub>opt</sub> and ~85–200 mgO<sub>2</sub> kg<sup>-1</sup> h<sup>-1</sup> for COT<sub>min</sub> at 18°C (Claireaux et al., 2006; Zupa et al., 2015). The U<sub>opt</sub> was not affected by the

fish mass, as already observed, whereas the COT<sub>min</sub> decreased with the increase of fish mass despite what was observed for sea bass ranging from 200 to 450 g (Zupa et al., 2015). In this study, we investigated the relation between COT<sub>min</sub> and mass for sea bass ranging from 212 to 998 g with greater sampling size (i.e., *n* = 90 vs. *n* = 20), overall providing stronger results regarding that relationship in sea bass, which is also consistent with the literature in fishes (e.g., Oldham et al., 2019; Palstra et al., 2020). In addition, we found that the U<sub>opt</sub> and COT<sub>min</sub> were lower in tagged fish than untagged ones. Lower U<sub>opt</sub> and COT<sub>min</sub> for tagged sea bass have been already observed by other authors (Wright et al., 2014). It was probably due to the fact that fish in that study were challenged prior to and after the tag implantation, and thus, that fish were more acclimated to the swimming chamber (Wright et al., 2014). It was not the case in our experiment, but like for the observations of lower SMR in tagged fish, we would suggest that these results may be explained by a slight greater stress state following handling for untagged fish, less experienced in handling than tagged ones recently before the U<sub>crit</sub> test and by desensitization of the HPI-axis with a consequent lower hormonal, metabolic, and energy response (Barton, 2002). Nevertheless, as explained before, this hypothesis needs to be tested before being fully validated. Altogether, these results are supporting the use of accelerometer sensors in free-swimming sea bass, as a proxy of energy expenditure in response to aquaculture environments and practices.

Finally, for mapping the acceleration measured by tag with the MO<sub>2</sub> and mass of sea bass, we applied a sigmoid function which gives a very good fit with the data; this function accounts the initial exponential pattern of MO<sub>2</sub> and then the slowdowns near U<sub>crit</sub>, as well as the effects of mass. The asymptote of this model is reached after for smaller fish (i.e., with greater MO<sub>2</sub> values) than for larger ones, being consistent with size-related metabolic traits (Robinson et al., 1983). Further calibrations could also take into account for another parameter, such as temperature, to improve the accuracy of the MO<sub>2</sub> estimations (Wilson et al., 2013) or could be retrieved from the literature (Claireaux et al., 2006; Wright et al., 2014). The slowing down of the increase in MO<sub>2</sub> near U<sub>crit</sub> corresponds to the attainment of the MMR, and the fuel for sustaining swimming is provided by anaerobic metabolism through burst swimming or at high intensity (Mckenzie, 2011). This has been previously observed for sea bass using electromyogram analysis in red and white muscles (Lembo et al., 2007; Zupa et al., 2015), with the progressive start of aerobic metabolism located at ~65 % of the U<sub>crit</sub> (i.e., 0.69 m s<sup>-1</sup>). In addition, Claireaux et al. (2006) estimated the U<sub>max</sub> at ~0.9 m s<sup>-1</sup>, defined as the start of using the anaerobic metabolism by starting to display a burst swimming mode, and the MO<sub>2</sub> is usually leveled off or decreased slightly. Based on these three works, that corresponds to accelerometer values of ~70–125 AU (refer to **Figure 5**) and corresponds to the attainment of the asymptote of the MO<sub>2</sub> value (refer to **Figure 6**). Therefore, according to these studies, we suggest that the high swimming activity values recorded by tags (>70 AU) are also informing about the progressive contribution of anaerobic metabolism to sustain swimming. This needs to be acknowledged

when using acceleration recorded by tag as a proxy of energetic costs, in addition to anaerobic ones.

In conclusion, this study provides insights regarding swimming performance, swimming efficiency, and aerobic metabolism for a wide range of sizes (from 212 to 998 g) in tagged and untagged sea bass. In addition, we found that the implantation of an accelerometer tag does not induce particular swimming disruption, or stress triggering an increase in the oxygen consumption rate during swimming (5 days after the implantation), supporting the use of such sensors for remotely health or welfare monitoring in aquaculture. Finally, mapping the acceleration recorded by tag with the  $MO_2$  brings valuable insights about energetic costs, which can be used in free-swimming fish to assess the fish response to environmental variations and/or aquaculture practices.

## DATA AVAILABILITY STATEMENT

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request. Requests to access the datasets should be directed to SA, [salfonso@coispa.eu](mailto:salfonso@coispa.eu).

## ETHICS STATEMENT

The animal study was reviewed and approved by Italian Health Ministry (protocol 838/2019-PR approved on 17 December 2019).

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## AUTHOR CONTRIBUTIONS

MS, GL, and PC contributed to conceptualization, funding acquisition, and project administration. SA, WZ, MS, GL, and PC contributed to methodology, writing, reviewing, and editing the manuscript. SA and WZ contributed to formal analysis and data curation. MS and GL contributed to resources. SA contributed to writing the original draft. All authors contributed to the article and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fanim.2022.885850/full#supplementary-material>

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