# Combined effects of ocean acidification and temperature on larval and juvenile growth, development and swimming performance of European sea bass (Dicentrarchus labrax)

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# Combined effects of ocean acidification and temperature on larval and juvenile growth, development and swimming performance of European sea bass (*Dicentrarchus labrax*)

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## Abstract

Ocean acidification and ocean warming (OAW) are simultaneously occurring and could pose ecological challenges to marine life, particularly early life stages of fish that, although they are internal calcifiers, may have poorly developed acid-base regulation. This study assessed the effect of projected OAW on key fitness traits (growth, development and swimming ability) in European sea bass (*Dicentrarchus labrax*) larvae and juveniles. Starting at 2 days post-hatch (dph), larvae were exposed to one of three levels of $PCO_2$ (650, 1150, 1700 μatm; pH 8.0, 7.8, 7.6) at either a cold (15˚C) or warm (20˚C) temperature. Growth rate, development stage and critical swimming speed ($U_{crit}$) were repeatedly measured as sea bass grew from 0.6 to ~10.0 (cold) or ~14.0 (warm) cm body length. Exposure to different levels of $PCO_2$ had no significant effect on growth, development or $U_{crit}$ of larvae and juveniles. At the warmer temperature, larvae displayed faster growth and deeper bodies. Notochord flexion occurred at 0.8 and 1.2 cm and metamorphosis was completed at an age of ~45 and ~60 days post-hatch for sea bass in the warm and cold treatments, respectively. Swimming performance increased rapidly with larval development but better swimmers were observed in the cold treatment, reflecting a potential trade-off between fast grow and swimming ability. A comparison of the results of this and other studies on marine fish indicates that the effects of OAW on the growth, development and swimming ability of early life stages are species-specific and that generalizing the impacts of climate-driven warming or ocean acidification is not warranted.

## Introduction

Over the last 150 years, the burning of fossil fuels has contributed to an increase in atmospheric $CO_2$ from approximately 280 to 410 ppm and a further increase (730 to 1020 ppm) is

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anticipated by the end of 2100 [1,2]. This increased concentration of atmospheric $CO_2$ ($PCO_2$) has enhanced greenhouse warming around the globe at a rate of ~ 0.2˚C per decade in the past 30 years [3] and, after dissolving in the oceans, it is causing ocean acidification (OA). During the 20$^{th}$ century, the pH of ocean surface waters has decreased by 0.1 pH units and a further reduction of 0.3–0.5 pH units is expected to occur by the end of the present century [4]. These changes in $PCO_2$, pH and temperature of the oceans have impacted the distribution, physiological performance, morphology and behavior of marine organisms [5]. The effect of the interaction between OA and warming (OAW) on marine flora and fauna is difficult to predict, especially since impacts are often life stage- and species-specific, and ocean warming (OW) could either offset [6] or aggravate impacts of OA.

Gaining a mechanistic, physiologically-based understanding of how OAW affects marine flora and fauna is essential for reliable projections of future effects of climate change [7]. Studies examining the consequences of OA on marine organisms have mainly focused on calcifying invertebrates [8, 9] with far fewer studies conducted on fish [10]. In fish, accumulating bicarbonate is a classical response aimed at regulating acid-base balance when the internal milieu acidifies. The net increase of $HCO_3^-$ in plasma occurs in exchange for $Cl^-$, predominantly at the gills [11], but this $HCO_3^-$ / $Cl^-$ exchange eventually reaches a species-specific threshold beyond which acid-base regulation may occur at the expense of internal ionic/osmotic balance [12]. Juvenile and adult fish have efficient acid-base and osmo-ionic regulatory systems and are particularly tolerant to environmental hypercapnia and acidification [13]. Young larvae, however, have not yet developed full regulatory capacity and, consequently, they are expected to be more sensitive to changes in internal $PCO_2$ and pH [14, 15]. This appears to be the case as several studies have reported decreased survival and/or abnormal development in marine fish larva exposed to OA [16, 17, 18] and behavior can be impacted via impaired sensory abilities such as olfaction [19]. Within the thermal tolerance window, warming increases rates of biochemical reactions and, thus, overall energy requirements and oxygen demand. After a certain thermal threshold is exceeded, however, deterioration in cellular activities occurs, resulting in reduced tissue and organismal-level performance. Decrements in performance may be due to the limited capacity of the oxygen transport chain to sustain temperature-driven increases in ATP production by mitochondria [20, 21, 22]. It might also be explained by the 'multiple performances–multiple optima' (MPMO) hypothesis, which posits that each physiological activity has its own thermal optimum which can shift with life stage and the nature of the thermal challenge [23].

In early life stages of marine fish, growth and development lead to improvements in locomotor performance, a fundamental trait that influences food acquisition, predator avoidance and habitat connectivity (e.g. between spawning sites and larval nursery areas) [24]. Hence, locomotor performance is a key determinant of Darwinian fitness. Critical swimming speed ($U_{crit}$; [25]) is a popular measure of swimming performance, estimating the athleticism of fish. The $U_{crit}$ is also a well-established index to monitor the ontogeny of swimming performance in marine fish larvae, especially in tropical species [26]. Moreover, $U_{crit}$ has been frequently used to evaluate the effects of environmental factors (e.g. temperature, dissolved oxygen concentration, presence of toxins and pathogens) on the physiological performance of fish [27]. Therefore, when examining the effects of OA and/or OW on organismal-level performance, examining $U_{crit}$, along with growth and development, provides an integrated measure of physiological impact with clear ecological relevance.

The European sea bass (*Dicentrarchus labrax*) is one of the most important commercial and recreational fish species in the Northeast (NE) Atlantic and Mediterranean Sea, and potential sensitivity to stressors can negatively impact the productivity of this species and its fisheries [28]. Due to its importance as an aquaculture target, standard rearing protocols exist for

rearing sea bass early life stages, and swimming performance has been well measured, including inter-individual variability and repeatability [29, 30]. We examined the effects of OAW on the somatic growth, development and swimming capacity throughout the larval and early juvenile phase of sea bass reared at two temperatures (15˚C and 20˚C) and three $PCO_2$ levels (650, 1150, 1700 μatm; pH 8.0, 7.8, 7.6). We compared our results with previous studies conducted on sea bass and critically reviewed the literature published on the effects of OA, OW, and OAW on the swimming ability of marine fish early life stage.

## Materials and methods

The present work was performed within Ifremer-Centre de Bretagne facilities (agreement number: B29-212-05). Experiments were conducted according to the ethics and guideline of the French law and approved by the governmental ethics committee of the Brittany region (Comité d'Ethique Finistérien en Experimentation Animal, CEFEA, registering code C2EA-74) (Authorization APAFIS 4341.03).

### Animals and experimental conditions

**Water parameters.** The larvae and post-larval juveniles were incubated within 6 different OAW treatments. The acidification conditions included three different $CO_2$ partial pressures ($PCO_2$). For the control treatment, the targeted level of $CO_2$ was set to approximately 650 μatm, today's ambient situation in coastal waters of Brittany [31, 32], with an annual mean $PCO_2$ level of 603 μatm (range 284–888 μatm) in the Bay of Brest, in 2014 [33]. Climate projections indicate that the oceans will reach about 1000 μatm $PCO_2$ in the next 130 years [2, 4, 34]. A second treatment was based on the IPCC Representative Concentration Pathway (RCP) 8.5 scenario projecting a $\Delta PCO_2$ of ~500 μatm above current values (labelled Δ500, approx. 1150 μatm) [2]. Sea bass juveniles and adults are usually found in coastal waters and estuaries where the impact of $PCO_2$ might be exacerbated [35, 36]. Wallace et al., 2014 [37] reported $PCO_2$ values >2000 μatm in northeast US estuaries, while values up to 3000 μatm were recorded in coastal areas of the SW Baltic Sea [38]. Based on those data, and $PCO_2$ values of European estuaries provided by Frankignoulle et al., 1998 [39], a higher $CO_2$ treatment of Δ1000 μatm from ambient level (labelled Δ1000, approx. 1700 μatm) was applied representing $CO_2$ condition encountered occasionally by the adults and may become more common under future climate. Acidification conditions were crossed with two temperatures: a 'cold' (ambient condition) and a 'warm' (global warming) treatment. Under ambient condition, larvae were reared at 15˚C and juveniles experienced 15 to 18˚C (natural, seasonal differences reflecting ambient summer conditions in the Bay of Brest (see http://marc.ifremer.fr/en/results/temperature_and_salinity/mars3d_channel_bay_of_biscay_model/(typevisu)/map/(zoneid)/sudbzh#appTop) [40, 41]. In the warm treatment, larvae were reared at 20˚C and juveniles experienced 20 to 23˚C (5˚C warmer than the cold treatment). The 5˚C increase was based on the 'business-as-usual (RCP 8.5) scenario predicted by the general circulation models (GCMs) by the end of the century [42]. We applied constant temperatures for larvae and seasonally changing temperatures for juveniles to better depict thermal conditions experienced by these life stages in the wild. Due to relatively fast rates of growth and development, sea bass larvae experience less differences in temperature compared to juveniles. Larvae hatch offshore, and then juveniles enter estuaries in the late spring and grow in these waters through the summer months [43, 44].

The sea water was pumped from a depth of 20 m approximately 500 m from the coastline in the Bay of Brest, passed through a sand filter (~500 μm), heated (tungsten, Plate Heat Exchanger, Vicarb, Sweden), degassed using a column, filtered using a 2 μm membrane and

finally UV sterilized (PZ50, 75W, Ocene, France) assuring high water quality. Replicate treatment tanks (n = 3 for larval rearing and n = 2 for juvenile rearing) were supplied with sea water via header tanks where water $PCO_2$ was controlled using an IKS Aquastar system (IKS Computer Systeme GmbH, Germany). This design used interdependent treatment replicates which was corrected using tank as a random factor in the analysis [45]. The system continuously measured water pH and controlled a solenoid valve connected to a $CO_2$ cylinder. This valve controlled the amount of $CO_2$ injected into the header tank water, which supplied the fish rearing tank. Temperature and pH were checked daily with a WTW 3110 pH meter (Xylem Analytics Germany, Weilheim, Germany; with electrode: WTW Sentix 41, NBS scale) before feeding the fish. The pH meter as well as the IKS Aquastar system were calibrated daily with NBS certified WTW technical buffers pH 4.01 and pH 7.00 (Xylem Analytics Germany, Weilheim, Germany). Total alkalinity was measured once a week following the protocol of Anderson and Robinson, 1946 [46], and Strickland and Parsons, 1972 [47]: a 50 ml sample of filtered tank water (200 μm nylon mesh) was mixed with 15 ml HCl (0.01 M) and pH was measured immediately. Total alkalinity was then calculated with the following formula:

$$TA = \frac{V_{HCl} \cdot c_{HCl}}{V_{sample}} - \frac{(V_{HCl} + V_{sample})}{V_{sample}} \cdot \frac{\{H^+\}}{\gamma_{H^+}} \left[\frac{mol}{l}\right]$$

With: TA—total alkalinity [mol * $l^{-1}$], $V_{HCl}$—volume HCl [l], $c_{HCl}$—concentration HCl [mol * $l^{-1}$], $V_{sample}$—volume of sample [l], $H^+$—hydrogen activity ($10^{-pH}$), $\gamma^{H+}$—hydrogen activity coefficient (here $\gamma^{H+} = 0.758$).

The Microsoft Excel macro CO2sys [48] was used to calculate seawater carbonate chemistry, the constants after Mehrbach et al., 1973 [49] (as cited in CO2sys) refit by Dickson et al., 1987 [50] (as cited in CO2sys), were employed. Values of pH are presented on the free proton concentration scale ($pH_{free}$) [51]. Oxygen saturation (WTW Oxi 340, Xylem Analytics Germany, Weilheim, Germany) and salinity (WTW LF325, Xylem Analytics Germany, Weilheim, Germany) were measured once a week together with total alkalinity, from juvenile stage onwards (Table 1).

**Animals.** Larvae were obtained from an aquaculture facility (Aquastream, Ploemeur-Lorient, France) at 2 days post-hatch (dph) (20.01.2016). Brood stock fish were caught in the sea off Morbihan, France. Four females (mean weight 4.5 kg) were crossed with ten males (mean weight 2.4 kg) which spawned naturally using photothermal manipulation. Conditions in the aquaculture facility during breeding were as followed: 8h45 light and 15h15 darkness, 13˚C, 35 psu, pH 7.6. Spawning of eggs took place on 15.01.2016; larvae hatched on 18.01.2016 and were transported to our laboratory facilities on 20.01.2016.

Larval rearing was performed in a temperature-controlled room using black, 35-L tanks initially stocked with *ca.* 5000 larvae $tank^{-1}$ in order to accommodate our sampling design. Allocation among experimental tanks took place at 3 dph (21.01.2016). During the following three days, the temperature for the warm condition was increased 1˚C during the first day and 2˚C during each of the following days. The $PCO_2$ conditions were applied directly after fish allocation to the experimental treatments. Starting at 7 dph (mouth opening), larvae were fed with live brine shrimp (*Artemia salina)* nauplii, hatched from High HUFA Premium cysts (Catvis, AE's-Hertogenbosch, Netherlands). From 7 to 16 dph a concentration of ~120 nauplii per larva $day^{-1}$ was delivered, after 16 dph concentration was ~800 nauplii per larva $day^{-1}$. Until 33 dph, larvae were fed newly hatched (24-h old) nauplii. Older larvae were fed with nauplii enriched with cod liver oil and dry yeast for 24 h. The nauplii were transferred from their storage tanks (one per temperature condition) to the larval rearing tanks using peristaltic pumps at ad libitum feeding concentrations continuously during 6 hours. Larvae experienced a 15-h

**Table 1. Water parameters during the larval (L) and juvenile (J) rearing done in this study.** Larval period from 21.01.2016 (3 days post-hatch (dph)) until 04.03.2016 (46 dph) and 18.03.2016 (60 dph) for warm (W) and cold (C) life condition respectively; juvenile period until 24.10.2016 (280 dph) and 08.02.2017 (387 dph) for warm (W) and cold (C) life condition respectively. Values show mean ± SE overall replicate tanks per condition. Temperature (Temp.) and pH (free scale) were measured daily; salinity and total alkalinity (TA) and oxygen weekly; $PCO_2$ was calculated with CO2sys. Inflow sea water (SW) parameters were measured in 2017 and 2018 and annual average values are shown. A, Ambient $PCO_2$; Δ500, ambient + 500 μatm $CO_2$; Δ1000, ambient + 1000 μatm $CO_2$.

| Treatment | $pH_{Free}$ (-) | Temp. (˚C) | Salinity (psu) | O2 (% airsat.) | TA () | $PCO_2$ (μatm) |
|---|---|---|---|---|---|---|
| L C A | 7.95±0.01 | 15.3±0.0 | 33.0±0.1 | - | 2364±17 | 656±16 |
| L C Δ500 | 7.77±0.01 | 15.3±0.0 | 33.0±0.1 | - | 2382±19 | 1041±26 |
| L C Δ1000 | 7.58±0.00 | 15.3±0.0 | 33.0±0.1 | - | 2394±26 | 1682±26 |
| L W A | 7.88±0.01 | 20.0±0.1 | 33.1±0.1 | - | 2369±21 | 832±13 |
| L W Δ500 | 7.79±0.01 | 20.0±0.1 | 33.1±0.1 | - | 2383±22 | 1057±30 |
| L W Δ1000 | 7.60±0.01 | 20.0±0.1 | 33.1±0.1 | - | 2380±23 | 1672±33 |
| J C A | 7.97±0.01 | 16.0±0.2 | 34.2±0.1 | 90.9±0.5 | 2396±18 | 655±18 |
| J C Δ500 | 7.75±0.01 | 16.0±0.2 | 34.2±0.1 | 92.2±0.6 | 2404±19 | 1107±21 |
| J C Δ1000 | 7.55±0.01 | 16.1±0.2 | 34.2±0.1 | 90.9±0.6 | 2399±19 | 1841±40 |
| J W A | 7.92±0.01 | 21.9±0.2 | 35.0±0.2 | 90.2±0.9 | 2418±12 | 788±22 |
| J W Δ500 | 7.78±0.01 | 21.8±0.2 | 35.0±0.2 | 90.5±0.7 | 2420±15 | 1133±43 |
| J W Δ1000 | 7.59±0.01 | 21.9±0.2 | 35.0±0.2 | 91.3±0.6 | 2423±12 | 1808±65 |
| SW cold | 8.05±0.01 | 14.5±0.5 | 33.0±0.2 | 101.2±0.6 | 2434±21 | 522±18 |
| SW warm | 7.95±0.02 | 21.2±0.4 | 32.7±0.1 | 102.3±1.4 | 2433±28 | 723±33 |

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photoperiod (7:00 to 22:00), the light intensity progressively increased with larval age, from total darkness to 96 lux according to S1 Table. Median larval mortality (n = 18 tanks) was 30%, see S2 Table. Flow rate through the larval tanks was 0.18 L $min^{-1}$, corresponding to a water exchange of 30% per hour, and organic compounds were removed from the tanks using a protein skimmer.

Fish were moved from the larval to juvenile tanks at 50 dph and 65 dph for fish reared in the warm and cold life conditions, respectively. Fish were counted, and all individuals from replicate tanks at one condition (temperature x $PCO_2$) were pooled in the same tank for about three weeks and then randomly allocated to two 670-L treatment tanks (S1 Fig). Having only two replicates limited our ability to estimate variance but dividing the fish randomly removed any potential effect of larval rearing tank. Mortality of 24.8 to 43.4% occurred after loading to the juvenile tanks, likely due to handling stress (S3 Table). Juveniles were fed daily with commercial fish food (Neo Start) (Le Gouessant, Lamballe, France). Food was distributed ad libitum via automatic feeders. Size and amount was adjusted all through the juvenile rearing period, as recommended by the supplier. This amount was calculated according to the tank biomass, number of fish and temperature. Around 200 dph, for example, 90 g $tank^{-1}$ $day^{-1}$ and 160 g $tank^{-1}$ $day^{-1}$ of food pellets was distributed for the 15˚C-reared fish (mean biomass ~ 6.9 kg) and the 20˚C-reared fish (mean biomass ~ 4.2 kg), respectively. Photoperiod was adjusted each week to mimic natural conditions. Uneaten food and feces were siphoned from tanks each day (after pH measurements). Water flow rates maintained oxygen saturation levels above 90%.

## Swimming tests

**Larvae.** Swimming tests and morphological measurements were performed from 15 dph until the end of the larval stage i.e., when the caudal fin was completely formed. Swimming experiments were conducted on larvae from the six treatments ($PCO_2$ x T) conditions. In each swimming trial, 3 randomly selected larvae from each replicate tank (9 larvae per treatment)

**Table 2. Summary of the methodology used during the critical swimming trials with larval (L) and juvenile (J) European sea bass.** Abbreviations: BL, body length; C, cold treatment; W, warm treatment; A, Ambient $PCO_2$; Δ500, ambient + 500 μatm $CO_2$; Δ1000, ambient + 1000 μatm $CO_2$.

| Treatment | BL (mm) | Age (dph) | Total larvae tested (n) | Acclimation period | Water flow steps (cm $s^{-1}$) | Time steps (min) |
|---|---|---|---|---|---|---|
| L C A | 6.67–16.69 | 21–59 | 58 | 5 min at 0.8–1.6 cm $s^{-1}$ | 0.4–0.8 (0.5 Bls) | 3 |
| L C Δ500 | 7.45–16.83 | 21–58 | 51 | | | |
| L C Δ1000 | 7.82–17.97 | 22–58 | 59 | | | |
| L W A | 7.55–16.66 | 17–46 | 54 | 5 min at 0.8–1.6 cm $s^{-1}$ | 0.4–0.8 (0.5 Bls) | 3 |
| L W Δ500 | 7.61–17.41 | 18–45 | 55 | | | |
| L W Δ1000 | 6.35–17.35 | 18–45 | 54 | | | |
| J C A | 83.2±7.1 | 239–242 | 30 | 30 min at 7 cm $s^{-1}$ | 2.8 | 10 |
| J C Δ500 | | | 30 | | | |
| J W A | 119.9±9.3 | 233–238 | 30 | 30 min at 7 cm $s^{-1}$ | 5.6 | 10 |
| J W Δ500 | | | 30 | | | |

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were measured. Trials were conducted every 3 to 5 days, and 6 to 7 trials were conducted per treatment.

All measurements of $U_{crit}$ were performed on an individual larva swimming in one lane (24 x 3 x 2.5 cm) of a custom-made Brett-type flume [52]. Water was pumped (universal, EHEIM, Germany) from a header tank into the flume and velocity was adjusted using a valve calibrated to water flow rate. A laminar flow was made by passing the water through a honeycomb section (length = 10 cm) placed upstream and a mesh screen was located at the downstream end of the lane. Pilot trials with dye ensured that cross-sectional water velocity in the lane was homogenous. Treatment water conditions of the tested larva were maintained in the flume. Temperature was controlled using a cooling/heating system (Tr10, TECO, Italy) and $PCO_2$ was maintained by injecting $CO_2$ directly in the water of the header tank via a gas diffuser.

A larva was introduced into the swimming lane and was acclimated to the lowest water velocity for 5 min (Table 2). The water velocity was then increased at a rate of 0.5 BL $s^{-1}$ every 3 min until the larva was unable to swim against the flow and drifted to the downstream mesh screen. At the beginning of each trial, the average length of the fish in each replicate tank was determined so that a standard velocity increment could be established (among all trials). Larvae swam in the middle of the chamber suggesting minimal or no wall effects. Once the test was completed, the larva was euthanized with an overdose of anesthetic (Tricaine methanesulfonate MS222, PharmaQ Limited, Hampshire, United Kingdom, as prescribe by the European legislation to minimize fish stress), digitally photographed under a stereomicroscope (Leica MZ 16, Wetzlar, Germany) and stored in 4% formalin. Body length (BL), body height (BH) and tail flexion angle, were measured using ImageJ [53]. For preflexion larvae, BL was equal to the notochord length, which corresponded to the length from the tip of the snout to the end of the notochord. For flexion and postflexion larvae, BL was determined by measuring standard length, corresponding to the distance from the tip of the snout to the posterior end of the hypural plate. The notochord angle was also measured to estimate the size at which larvae reached the postflexion stage. Unfortunately, due to the small sample size of larvae $< 10$ mm in length (n = 45 for 15˚C and n = 54 for 20˚C), it was not possible to run a logistic regression to calculate the mean larval size at which 50% of the larvae completed flexion. Instead, we determined the size at which postflexion was first observed.

**Juveniles.** Juveniles from four treatments were tested: cold and warm temperatures at both ambient $PCO_2$ (650 μatm) and RCP8.5 (Δ1000; 1700 μatm). When tested, juveniles in the cold and warm treatments were 242 and 233 dph and had a mean (± s.e.m) BL of

83.2(0.8) and 119.9(1.2) mm, respectively. For each treatment, thirty individuals (~15 per replicate tank) were tested. For each run, fish were tested in groups of 8 or 5 individuals, for 15˚C and 20˚C- reared fish, swimming in a 46 x 14 x 14 cm chamber of the Loligo Systems swim tunnel (Denmark). A streamline and homogenous flow was maintained using honeycomb section (confirmed by dye tests). Fish were tested at their treatment water conditions (see section 2.2.1). Water velocity was calibrated with a vane-wheelflow meter (HFA, Höntzsch GmbH, Germany), and controlled by an AC motor [54]. Acclimation time was 30 min (Table 2).

Fish were considered to be exhausted when they were up against the downstream grid for 5 consecutive seconds. Without interrupting the flow, these individuals were then removed from the tunnel, via a hatch located above the grid, anesthetized, measured (BL) and transferred to a recovery tank before being returned to their rearing tank where they were maintained for future research. For juveniles, BL is equivalent to standard length. The corresponding time and water velocity was recorded. The test was completed when all 5 fish were removed from the swim chamber.

**$U_{crit}$ measurement.** The $U_{crit}$ (cm $s^{-1}$) was calculated using the equation provided by Brett, 1964 [25], which adds the velocity of the most recently completed increment to the product of the incremental increase in velocity and the proportion of the final increment completed before fatigue. No correction for the solid blocking effect of the fish was considered, as the total cross-sectional area of the fish did not exceed 5% of that of the swimming chamber [55] (Table 2). Larvae which did not orientate themselves to start swimming during the acclimation period were removed from the test and dataset.

## Statistical analysis

Differences in growth (in BL) across treatments were analyzed, in larvae, with a linear mixed model that included fixed effects (age, temperature, $PCO_2$) and random effects (tank). Similarly, differences in BH were also tested with a linear mixed model (BL, temperature and $PCO_2$ as fixed effects, tank as a random effect). When no effect of OA was observed, data were pooled across OA treatments and regressions were calculated on pooled data. In larvae, inter-individual variability in $U_{crit}$ was large and increased with body size, thus, we used quantile regression to estimate the maximum $U_{crit}$–at-size (i.e. maximum swimming capacity) across treatments [56]. A backward model selection procedure was used to identify variables (e.g. size, temperature, $PCO_2$) influencing maximum $U_{crit}$ starting with the most complex model (including all interactive effects among fixed factors) and ending with only significant factors. Models were fit to the upper 85 to 95% quantiles (in 1% steps) to ensure patterns were consistent, and treatment differences were tested with an ANOVA. Model residuals were tested for a potential effect of rearing tank with an ANOVA. All quantile regression analyses were done with the "quantreg" package in R. Normality and homoscedasticity of data were tested using Shapiro-Wilk and Levene tests, respectively. The effects of temperature and $PCO_2$ levels on the percentage (%) of larvae with the ability / choice to swim was tested using two-way ANOVAs after logit transformation of the data. Larvae not swimming already at acclimation speed were excluded from the other analysis. The effect of $PCO_2$ on juvenile $U_{crit}$ was tested using one-way ANOVA when assumption of normality (Shapiro-Wilk) and homoscedasticity (Levene test) were met (case for 20˚C-reared fish after log10 transformation). ANOVA included $PCO_2$ as a fixed effect and run as a random effects. When one or more of these assumptions was not met (for 15˚C-reared fish), a generalized linear mixed-effects model (GLMM) was performed, including fixed effect ($PCO_2$) and random effects (run). All statistical analyses were performed using R (version 3.4.1, R Core Team 2014).

## Results

### Larval growth and development

The mean (± SE) growth rate of sea bass larvae at ambient, Δ500, Δ1000 (650, 1150, 1700 μatm $PCO_2$; pH 8.0, 7.8 and 7.6) was, 0.17 (0.01), 0.17 (0.01) and 0.16 (0.01) mm $d^{-1}$, respectively, at 15˚C and 0.21 (0.02), 0.21 (0.02) and 0.28 (0.03) mm $d^{-1}$, respectively, at 20˚C. Larval growth rate was significantly higher at 20˚C compared to 15˚C ($p < 0.001$), but there was no significant effect of $PCO_2$ treatment ($p = 0.120$) (Fig 1). Larval BH increased linearly with BL (Fig 2) and this relationship was significantly impacted by temperature ($p< 0.001$) but not $PCO_2$ ($p = 0.805$). For example, 10-mm larvae at 20˚C had a 16% larger BH than those reared at 15˚C (mean BH of 1.63 and 1.37 mm, respectively). These morphological differences were related to a faster development at the warmer temperature. At 15˚C, notochord flexion was completed between 9.0(±0.3; mean±SE) and 10.8(±0.1), 8.7(±0.2) and 11.1(±0.5), and 9.8 (±0.2) and 11.4(±0.2) mm BL at ambient, Δ500, and Δ1000 $PCO_2$, respectively. At 20˚C, notochord flexion was completed between 7.8(±0.1) and 9.6(±0.3), 7.9(±0.1) and 8.9(±0.1), and 7.0 (±0.2) and 9.4(±0.1) mm BL in the ambient, Δ500 and Δ1000 $PCO_2$ treatments, respectively. Unfortunately, the sample size of <12 mm BL larvae was too small to conduct further analyses.

### Swimming capacity of larvae

The $U_{crit}$ and inter-individual differences in $U_{crit}$ of sea bass larvae increased with increasing BL (Fig 3). The final quantile regression model ($90^{th}$ percentile) reported significant effects of BL, temperature and their interaction (S4 Table), but no significant effect of $PCO_2$ (ANOVA;

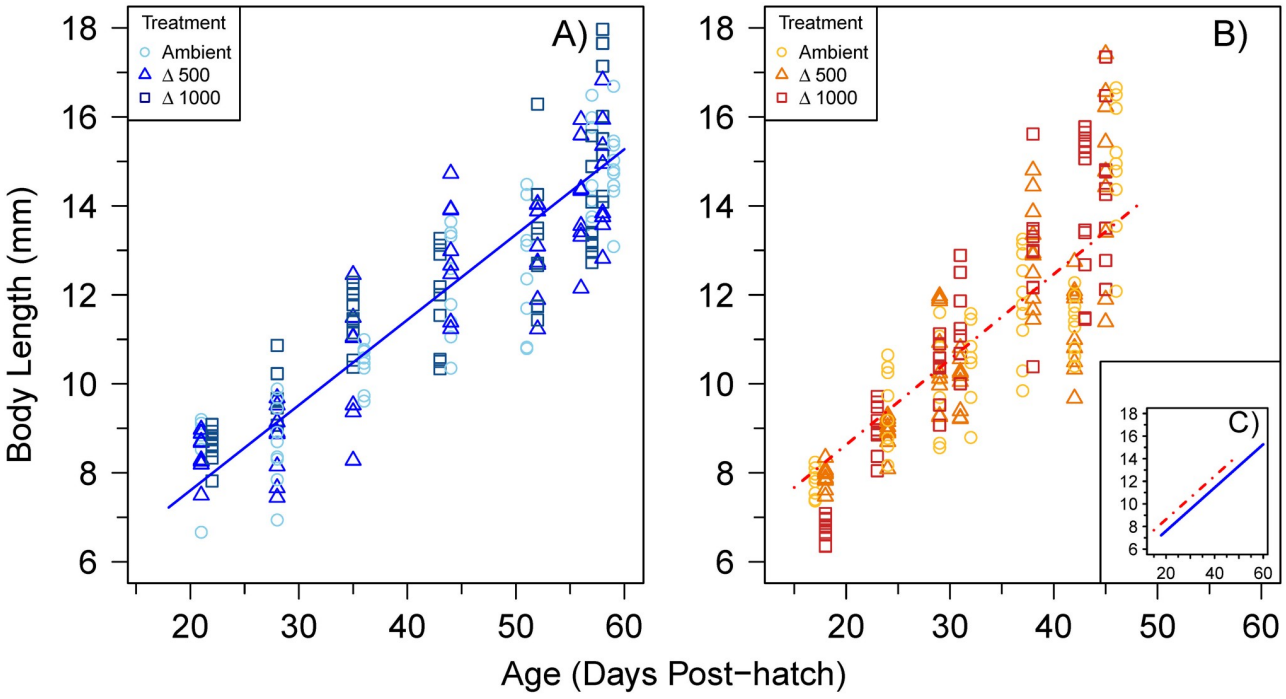


**Fig 1. Body length (BL) with age, in days post-hatch, of European sea bass larvae reared at A) cold condition (15˚C) and B) warm condition (20˚C).** Symbols and colors indicate the $PCO_2$ treatment (A, Ambient $PCO_2$; Δ500, ambient + 500 μatm $CO_2$; Δ1000, ambient + 1000 μatm $CO_2$). Regression (mean ± SE parameter estimates) are included: 15˚C, (n = 180) BL = 017(0.01)*Age + 4.62(0.28), $R^2 = 0.80$, $p < 0.001$; 20˚C (n = 190) BL = 0.23(0.01)*Age + 3.44(0.36), $R^2 = 0.73$, $p < 0.001$). For clarity, both regression lines are compared in subpanel **C**) (insert).

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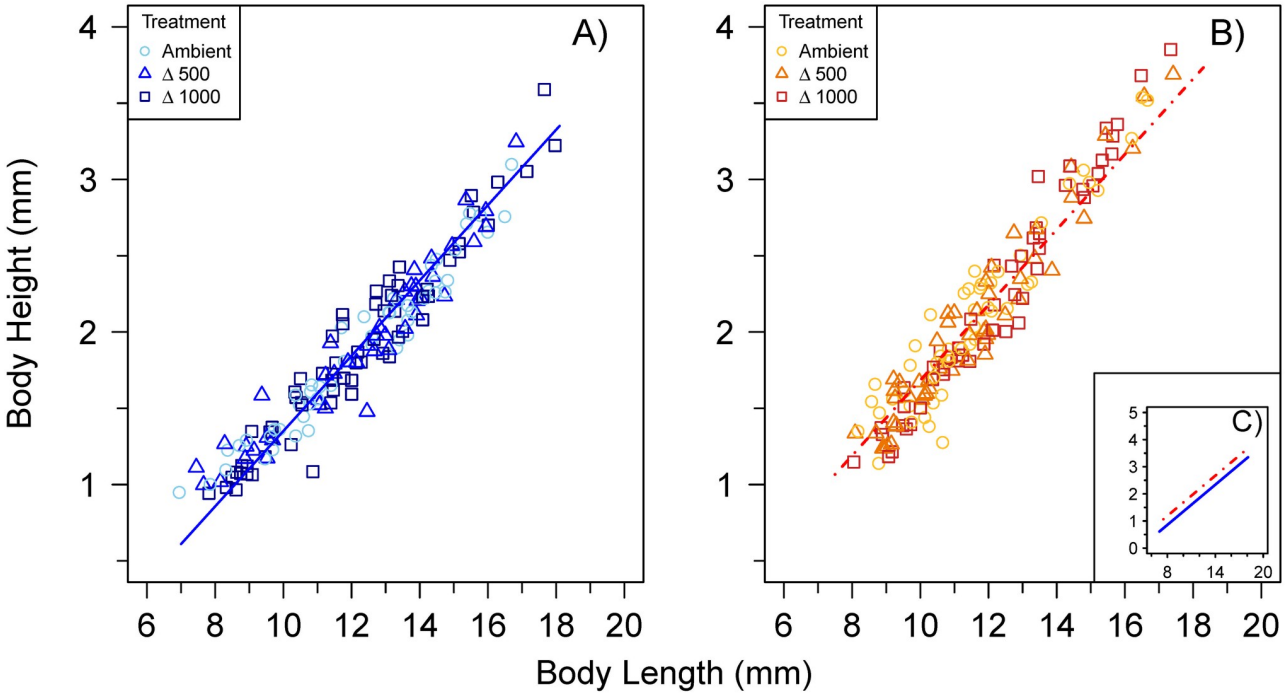


**Fig 2. Body height (BH) versus body length (BL) of European sea bass larvae reared at A) cold condition (15˚C) and B) warm condition (20˚C).** Symbols and colors indicate the $PCO_2$ treatment (A, Ambient $PCO_2$; Δ500, ambient + 500 μatm CO2; Δ1000, ambient + 1000 μatm CO2). Regression equations with mean (± SE) parameter estimates are: 15˚C, (n = 160) BH = 0.22(0.00)*BL—0.83(0.06), $R^2 = 0.93$, $p < 0.001$; 20˚C (n = 190) BH = 0.28 (0.01)*BL -1.14(0.07), $R^2 = 0.93$, $p < 0.001$). For clarity, both regression lines are compared in subpanel **C)** (insert).

https://doi.org/10.1371/journal.pone.0221283.g002

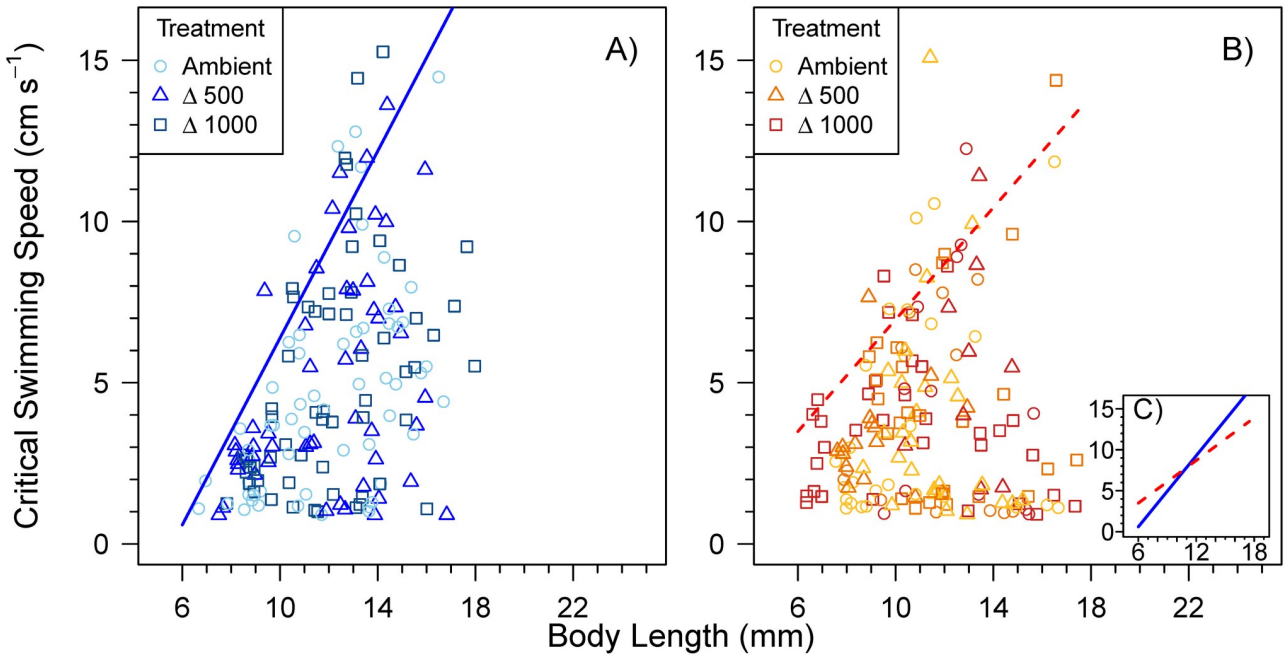


**Fig 3. Ontogeny of critical swimming speed ($U_{crit}$, cm $s^{-1}$) in larvae of European sea bass reared at A) cold condition (15˚C; n = 168) and B) warm condition (20˚C; n = 163).** Symbols and colors indicate $PCO_2$ levels treatment (A, Ambient $PCO_2$; Δ500, ambient + 500 μatm $CO_2$; Δ1000, ambient + 1000 μatm $CO_2$). The solid blue (cold) and dashed red (warm) lines shows the maximum $U_{crit}$ as defined by the 90$^{th}$ percentile (see text). For clarity, both lines are compared (see insert panel **C**).

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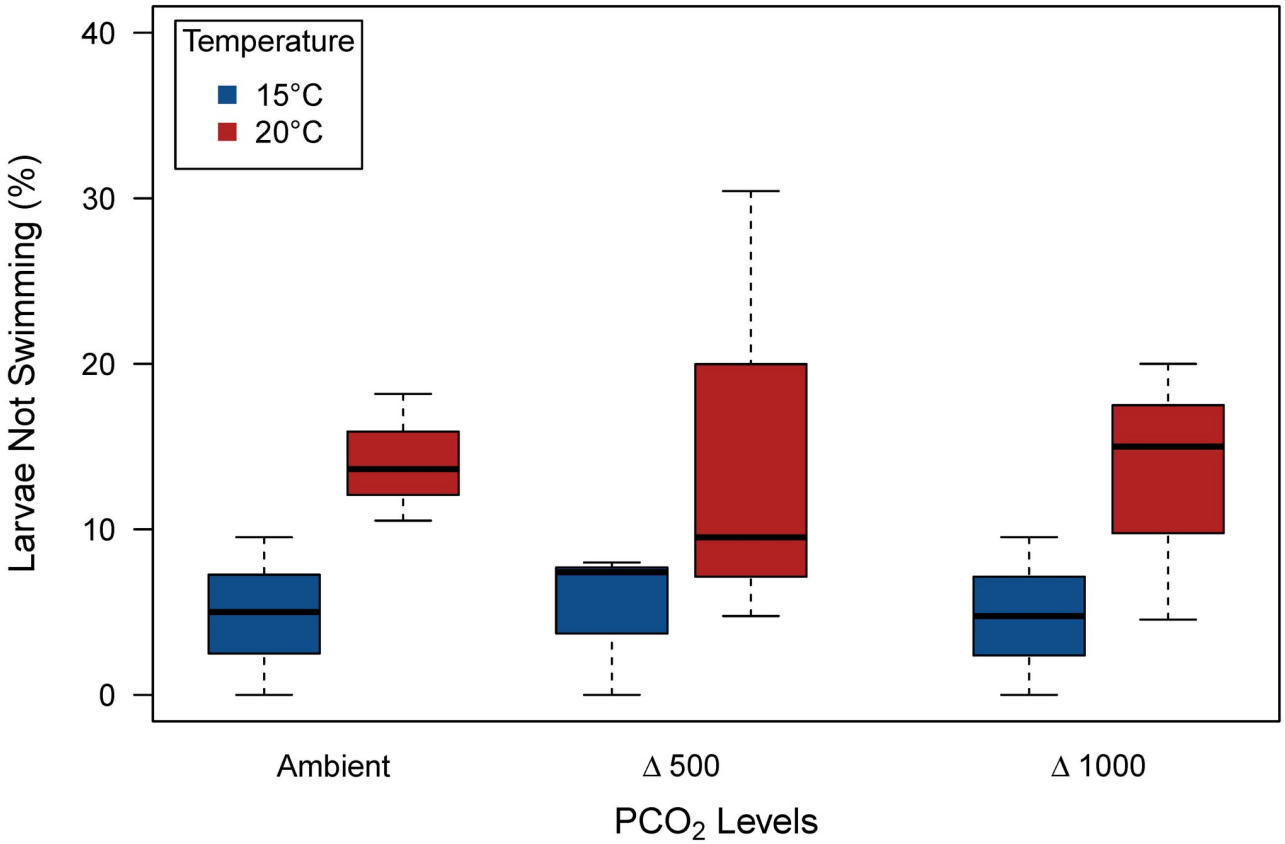


**Fig 4. Proportion (in %) of European sea bass larvae not swimming during the $U_{crit}$ trial in the cold (15˚C) and warm (20˚C) treatments at three $PCO_2$ levels (Ambient $PCO_2$; Δ500 = ambient + 500 μatm $CO_2$; Δ1000, ambient + 1000 μatm $CO_2$).**

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p = 0.94). There was no significant tank effect on the final model (ANOVA, p = 0.402). The $U_{crit}$ increased faster with BL in cold (15˚C) versus warm (20˚C) larvae and, at the end of the larval stage (16 mm BL) was 15.1 and 12.2 cm $s^{-1}$ at 15 and 20˚C, respectively.

In the 15˚C treatment, the coefficient of variation (CV) of $U_{crit}$ increased from 35.6 to 57.2% between notochord flexion (BL = 9.0 ± 0.2 mm) and post-flexion (BL = 12.9 ± 0.3 mm) stages. At 20˚C, the same life stages (BL = 9.1 ± 0.1 and 12.6 ± 0.2, respectively) had CVs of 46.9 to 73.1%. Some larvae were not able (or chose not) to swim beyond the minimum water velocity used during the acclimation period (0.8 cm $s^{-1}$ for 5 min). The percentage of larvae not swimming was significantly higher at 20˚C compared to 15˚C (ANOVA, p = 0.007, Fig 4).

## Swimming capacity of juveniles

The mean (± SE) $U_{crit}$ of juveniles reared in cold and warm conditions was 66.7 (0.7) and 79.2 (1.5) cm $s^{-1}$, respectively. There was no significant effect of $PCO_2$ treatment on $U_{crit}$ measured in cold (GLMM, p = 0.562) and warm conditions, respectively (ANOVA, p = 0.518). Although a group of 5 fish was tested in each trial, individuals became exhausted at different water velocities and our protocol allowed us to collect individual-level data. Large inter-individual differences were observed in $U_{crit}$, particularly among juveniles reared at warmer temperatures. Body sizes of fish tested in the cold and warm conditions differed, precluding direct comparison between temperatures (Fig 5, S2 Fig).

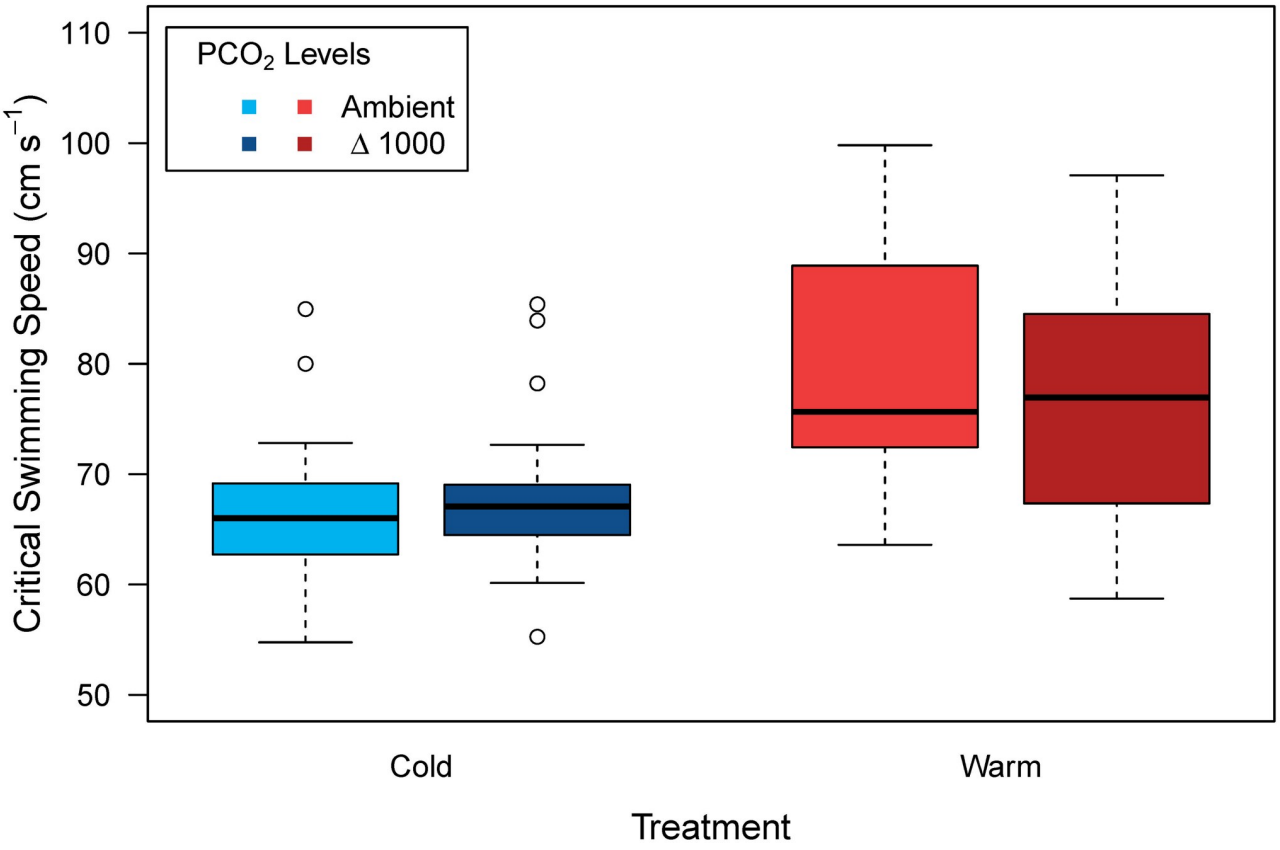


**Fig 5. Critical swimming speed ($U_{crit}$, cm $s^{-1}$) in 233 to 242 day post-hatch juvenile European sea bass in the cold (15˚C) and warm (20˚C) treatments at two $PCO_2$ levels: Ambient $PCO_2$ (n = 40 and n = 30, for cold and warm treatment, respectively) and Δ1000, ambient + 1000 μatm $CO_2$) (n = 33 and n = 30, for cold and warm treatment, respectively).** The raw data are shown in S2 Fig.

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## Discussion

Recent studies have examined the impact of OA and OAW on early life stage of teleost growth and survival [16, 17]. Large gaps in knowledge, however, persist, particularly on how long-term exposure to OAW may influence the performance of fish larvae and young juveniles. We investigated the effect of OAW on growth, development and swimming ability of European sea bass throughout larval and early juvenile ontogeny. Our results suggest that temperature, but not elevated $CO_2$, influenced growth, development and swimming performance. Our results also revealed a trade-off between swimming capacity and fast growth at warm temperatures, casting new light on the determinants of larval survival, dispersal, settlement pattern and recruitment [57, 58, 59].

### Effect of ocean acidification

Juvenile and adult European sea bass inhabit shallow estuaries where physicochemical parameters such as temperature and $PCO_2$ levels strongly fluctuate over short (diel) and longer (seasonal) time scales [60]. Thus, these life stages experience substantially more variation in water $PCO_2$ (e.g. daily variation up to 1 pH unit [61]) compared to early life stages. Measurements made between 1992 and 2004 within inner estuaries of the Loire and Gironde Rivers were 452 to 2780 μatm and 612 to 2829 μatm, respectively [62]. On the other hand, sea bass larvae develop in offshore waters where $PCO_2$ levels are generally stable (annual variation of <0.1 pH

units [63]). Taking this into account, it was expected that increased levels of $PCO_2$ might negatively affect the growth and/or swimming ability of larvae due to poorly developed acid-base regulation and the need to partition energy between homeostasis-related mechanisms and ecologically important activities.

Contrary to our expectations, the results of the present study indicated that life-long exposure to OA had no significant effect on the somatic growth rate and swimming capacity ($U_{crit}$) of sea bass larvae. A previous study on sea bass larvae, using similar exposure, rearing protocols and OA levels (Ambient, Δ500 and Δ1000 ($PCO_2$ = 650, 1150 and 1700 μatm)), also found no effect of OA on somatic growth at 19˚C [49]. These findings are in accordance with those reported in a recent meta-analysis conducted by Cattano et al., 2018 [64], highlighting no overall effects of high $CO_2$ on growth. A few studies, however, have reported impacts of OA on growth. For example, OA was associated with a higher growth rate in the clown anemonefish (*Amphiprion percula*) larvae [65] but slower growth rates were reported for gilthead seabream (*Sparus aurata*) [66] and decreased length-at-hatch for inland silversides (*Menidia beryllina*) [16].

Similar to our findings for growth rate, we also found no significant effect of OA on swimming capacity in sea bass larvae and juveniles. These results are in line with those in a number of other studies testing routine swimming characteristics [67, 68] or $U_{crit}$ [65, 69, 70] in marine fish larvae exposed to OA (Table 3). For example, Munday et al., 2009b [65] highlighted that swimming speed ($U_{crit}$) of the clown anemonefish (*Amphiprion percula*) larvae was unaffected by future OA scenarios. Similarly, Bignami et al., 2014 [71] did not observe a significant effect of high acidification on the swimming performance ($U_{crit}$ and mean routine swimming speed) of larval cobia (*Rachycentron canadum*) and mahi-mahi (*Coryphaena hippurus*). Although most studies on marine fish early life stages suggest that the physiological attributes related to swimming performance are not substantially impacted by levels of $PCO_2$ projected for the end of this century, some studies have reported impaired swimming duration and orientation [72] and reduced $U_{crit}$ as well as the average speed in response to a stimuli [73] (Table 3). Indeed, $U_{crit}$ was significantly lower, in juvenile yellowtail kingfish (*Seriola lalandi*) exposed to high (Δ500) $PCO_2$. This reduction in $U_{crit}$ values may be linked to 1) reduced motivation to swim and/or 2) reduced physiological performance, two traits that may differ according to individual variation [73]. It is worth noting that high inter-individual variability in $U_{crit}$ was observed across all treatments (CVs of 57 and 73% at 15 and 20˚C, respectively, for 9 to 13 mm BL). This large inter-individual variability, however, is generally observed in swimming studies in sea bass [74, 75, 76]. One hypothesis is that these large differences in swimming ability (e.g. maximum 10-fold in 15 mm larvae) also reflect variation in other behavioral traits such as boldness or willingness to swim. Using $U_{crit}$ as a performance test allowed us to compare swimming performance among treatments but also highlighted that results may not only reflect physiological limitation but also potentially inter-individual differences in behavior. Our results, together with these studies, highlight the species-specific nature of the responses to OA and the need for continued mechanistic (physiological-based) studies of potential impacts and the importance of publishing of studies that report no significant effects.

The fish used in the present study were the progeny of wild-caught adults acclimatized and maintained for about 5 years in the Aquastream aquaculture facility. These fish spawned at a pH of 7.6 which corresponds to our highest CO2 treatment. A number of studies have reported that parental exposure to an elevated level of CO2 may decreased the sensitivity of their progeny to OA [77, 78, 79]. In our study, therefore, the absence of differences in growth and swimming capacity observed among the three $PCO_2$ treatments could be the result of transgenerational plasticity. According to Griffith and Gobler, 2017 [80], however, the exposure of parents to a stressor (such as low pH) can also increase the sensitivity of their offspring to that stressor and that transgenerational plasticity is highly species-specific.

**Table 3. Summary of published studies investigating the impact of ocean warming (OW), ocean acidification (OA) and their combined effect (OAW) on swimming performance of early life stages (larvae, and juveniles) of marine fishes.**

| Species | | Stressor | Measurement | Life stage | T (˚C) | | $PCO_2$ (μatm) | | Results | Ref |
|---|---|---|---|---|---|---|---|---|---|---|
| Common name | Scientific name | | | | Cont | Treat | Cont | Treat | | |
| Anemonefish | *Amphiprion melanopus* | OW | $U_{crit}$ | L | 28 | 25 | ambient | - | Colder T induced slower development of swimming capacity | [81] |
| | | OAW | RSB | J | 28.5 | 30, 31.5 | 420 | 530, 960 | Elevated T alone reduced food consumption and foraging activity, combined with high $PCO_2$ these behaviors were increased | [82] |
| | *Amphiprion percula* | OA | $U_{crit}$ | L | 30 | - | 400 | 550, 750, 1030 | No effect | [65] |
| Cobia | *Rachycentron canadum* | OA | RSB/ $U_{crit}$ | L | ambient | - | 400 | 3500, 5400 | No effect | [83] |
| Dolphinfish | *Coryphaena hippurus* | OA | RSB/ $U_{crit}$ | L | ambient | - | 400 | 770 to 2100 | No effect | [83] |
| | | OA | RSB | L | 26 | - | 457 | 1671 | Swimming duration and vertical orientation frequency decreased with elevated $PCO_2$ | [84] |
| Yellowtail kingfish | *Seriola lalandi* | OAW | RSB/ $U_{crit}$ | J | 19.5 | 21, 25 | 589.4 | 462, 538.3, 959.8, 1010.6 | Ucrit and escape performances are enhanced by elevated T. High $PCO_2$ reduced $U_{crit}$ and distance moved after stimuli | [73] |
| Meagre | *Argyrosomus regius* | OAW | RSB | L | 20 | 24 | 350 | 1400 | T increased the time spent swimming. Elevated $PCO_2$ decreased the time spent swimming and lower capture success | [66] |
| Gilthead seabream | *Sparus aurata* | OAW | RSB | L | 18 | 22 | 350 | 1400 | Elevated PCO2 decreased the time spent swimming and lower capture success | [66] |
| Black seabream | *Spondyliosoma cantharus* | OA | RSB | L | 23.7 | - | 356.8 | 777, 2051.5 | Elevated $PCO_2$ decreased velocity and increased erratic swimming behaviors | [85] |
| Sand smelt | *Atherina presbyter* | OA | RSB | L | 15.9 | - | 537.1 | 2080.6 | No effect on routine swimming speed. Elevated $PCO_2$ increased the time to acquire shoaling behaviors and decreased laterization | [86] |
| | | OA | $U_{crit}$ | L | 16.4 | - | 600 | 1000, 1800 | No effect | [70] |
| Atlantic herring | *Clupea harengus* | OA | RSB | L | 5 to 10 | - | 370 | 1800, 4200 | No effect | [68] |
| Atlantic cod | *Gadus morhua* | OW | $U_{crit}$ | L | 6 | 10 | ambient | - | $U_{crit}$ decreased with elevated T before metamorphosis | [87] |
| | | OA | RSB | L | 7.2 | - | 370 | 1800, 4200 | No effect | [67] |
| | | OA | $U_{crit}$ | J | 5 | - | 528 | 3080, 5792 | No effect | [69] |
| European sea bass | *Dicentrarchus labrax* | OW | $U_{crit}$ | L | 18 | 21 | ambient | - | Swimming performance declined with temperature. | [30] |
| | | OAW | $U_{crit}$ | L, J | 15 | 20 | 650 | 1150, 1700 | $U_{crit}$ decreased with elevated T in larvae. No effect of $PCO_2$. | This Study |
| Shorthorn sculpin | *Myoxocephalus scorpius* | OW | $U_{crit}$ | L | 3 | 6 | ambient | - | $U_{crit}$ increased with elevated T before metamorphosis | [87] |

Abbreviations: T, temperature; $U_{crit}$, critical swimming speed; RSB, routine swimming behavior; L, larvae; J, juveniles; Cont, control; Treat, treatment.

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## Effect of temperature

Rearing at a warmer temperature (20 vs 15˚C) resulted in shorter larval stage duration and accelerated growth rate. These results agree with previous studies suggesting that sea bass larvae fed ad libitum display increased growth as temperatures increase to 22˚C [88, 89].

Temperatures supporting the maximum growth rate in sea bass larvae have not been estimated, but they are close to 22 to 24˚C in adults ~35 cm [74].

The impacts of temperature on performance traits of developing larvae can be complex due to the potential for different thermal optima for different physiological activities (e.g. multiple performances—multiple optima (MPMO) hypothesis [23]) and/or changes in thermal tolerance/optima during ontogeny. Increases in $U_{crit}$ with increasing temperature has been observed in the larvae of a variety of marine fish, including both tropical and temperate species, e.g. red and black anemonefish (*Amphiprion melanopus*) [81], shorthorn sculpin (*Myoxocephalus Scorpius*) [8], yellowtail kingfish (*Seriola lalandi*) [73] and Atlantic herring (*Clupea harengus*) [90]. This increased swimming performance was linked to changes in morphology and developmental rates, as well as to a decrease in water viscosity at warmer temperatures, which is especially relevant for cold-temperate species [91]. An increase in $U_{crit}$ with OW, however, is not expected to be universal but to be context- and species-specific [86]. This is the case with sea bass at the two temperatures tested in the present study. Just prior to metamorphosis and for the same body size, larvae reared at 15˚C displayed better swimming ability than larvae reared at 20˚C.

Thermal optima for performance measures such as $U_{crit}$ may change during ontogeny. In larger juvenile and adult sea bass maximum scope for activity ($MO_2max$) is between 22 and 24˚C, and coincides with optimal temperature for $U_{cirt}$ [74, 92]. Unfortunately no information is available on thermal performance curves for maximum scope for activity ($MO_2max$) nor $U_{crit}$ in sea bass larvae, but this and previous studies suggest that it is below 20˚C [30]. Temperature-dependent shifts in swimming ability may reflect temperature-dependent changes in developmental physiology affecting body shape and skeletal structure and/or muscle characteristics [93, 94, 95]. In our study, for the same BL, larvae were more streamlined at 15 compared to 20˚C. A streamlined body shape generally enhanced steady swimming while greater BH induced more irregular and more complex locomotor patterns (e.g. drastic changes in velocity or direction, fast-starts or rapid turns) [94], the velocity of the 20˚C-reared fish might then be affect by their rounder body shape. In addition, mitochondrial efficiency can decreased already at sublethal warm temperatures due to membrane associated problems (e.g. proton leak), with consequences for energy demanding processes like swimming. It might be that at 20˚C, sea bass larvae are already exposed to a sublethal warm temperature likely to affect mitochondrial structure and thus performance. Although, in a companion study [96], mitochondrial capacities for aerobic ATP production of permeabilized heart fibers were increased in juvenile sea bass reared at the warm versus the cold life condition. Juveniles have generally higher thermal optima than larvae, and this would indicate a rearrangement of biochemical pathways during ontogeny towards evolutionary thermal optima (colder for larvae than for juveniles).

## Trade-off between growth and swimming performance

Faster-growing individuals have better chances of survival by spending less time in life stages particularly vulnerable to mortality due to predators or starvation [97, 98, 99, 100]. Most fish, however, occur within habitats that are somewhat cooler than temperatures supporting maximum rates of growth [101]. This could be due to the need for a thermal-safety margin to survive sudden warming such as heat waves [102] or due to physiological trade-offs related to fast growth at relatively warm temperatures. For young larvae, rapid growth can lead to decrements in other fitness-related traits such as resistance to pathogens [103][91] longevity [104], energy storage [105], or locomotion [90]. In our study, sea bass larvae grew faster at 20˚C but displayed poorer swimming ability than larvae reared at 15˚C. The existence of a trade-off between growth and swimming ability has been reported in an increasing number of studies.

Studies on fathead minnow (*Pimephales promelas*) and Atlantic silversides (*Menidia menidia*) reported a negative correlation between growth rate and locomotory performance [106, 107]. A negative correlation between growth (compensatory after food deprivation) and sprint speed was reported for juvenile sea bass [108, 109].

The mechanisms behind the trade-off between fast growth and swimming ability have been poorly investigated, although several hypotheses have been proposed. First, the trade-off is based on the principle of energy allocation [110]. Rapid growth mobilizes more aerobic capacity leaving less energy dissipating capacity for locomotion [111, 107]. Early developmental stages have a relatively low aerobic capacity with factorial metabolic scopes around 1.5 and, thus, may be especially vulnerable to energy allocation conflicts [111, 112]. Second, rapid growth in fish can influence muscle characteristics including changes in the cellular structure and composition of muscle fibers [113] leading to poor locomotor performance. This may contribute to their higher swimming performance. Third, the relationship (and potential trade-off) between growth and swimming performance may have a genetic basis and can, therefore, be population-specific [114]. It would be interesting to study additional populations that inhabit different thermal regimes to test if trade-offs differ due to local adaptation.

## Conclusion

Our results indicate that, when fed *ad libitum*, European sea bass larvae are not impacted by projected future increases in levels of $PCO_2$ thanks to the use of physiological mechanisms allowing them to maintain growth and swimming performance. Life-time rearing at +5˚C above ambient influenced larval growth, development and swimming performance. Individuals reared at warmer condition grew faster but showed reduced swimming ability at metamorphosis. While growing faster reduced the duration of the larval phase, this reduction happened at the expense of swimming performance. Although the potential for local adaptation (adaptive capacity) is not known, our findings suggest that sea bass larvae of this Atlantic population may be negatively impacted by projected climate-driven warming (but not OA) under a business-as-usual (RCP8.5) scenario. These impacts appear to be due to physiological trade-offs between growth rate and $U_{crit}$. The physiological mechanism (i.e. limits in aerobic capacity and/or changes in energy partitioning) is unclear. The results of this and several other studies demonstrate that physiologically optimal thermal windows are stage-specific and appear more narrow (with a colder optimum) in larvae compared to juveniles. Finally, our study adds to the growing number of studies reporting no effects of OA or OAW on the swimming performance of marine fish larvae. Our review of this literature, however, also indicates that the impact of OA and/or OAW is species-specific.

## Supporting information

**S1 Fig. Experimental design and tanks transfer from larvae to juvenile stage.** Abbreviation: dph, days post-hatch.
(TIFF)

**S2 Fig. Critical swimming speed ($U_{crit}$, cm $s^{-1}$) in juvenile European sea bass reared at A) cold condition (15˚C; n = 73; 242 days post-hatch (dph)) and B) warm condition (20˚C; n = 60; 233 dph).** Symbols and colors indicate by $PCO_2$ levels treatment (A, Ambient $PCO_2$; Δ1000, ambient + 1000 μatm $CO_2$).
(TIFF)

**S1 Table. Light intensity during larval phase.** Abbreviation: dph, days post-hatch.
(PDF)

**S2 Table. Larval mortality (%) in the different larval rearing tanks.** Abbreviations: A, Ambient $PCO_2$; Δ500, ambient + 500 μatm $CO_2$; Δ1000, ambient + 1000 μatm $CO_2$; T, temperature, Rep, replicate tank.
(PDF)

**S3 Table. Juvenile mortality in % in the different tanks.** Abbreviations: A, Ambient $PCO_2$; Δ500, ambient + 500 μatm $CO_2$; Δ1000, ambient + 1000 μatm $CO_2$; T, temperature.
(PDF)

**S4 Table. Significance of terms for the 90% quantile regression model on the impact of water temperature and body length (BL) on the critical swimming speed ($U_{crit}$) in European sea bass larvae.** Abbreviation: DF, degrees of freedom.
(PDF)

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**Writing – review & editing:** Marta Moyano, Guy Claireaux, Sarah Howald, Felix C. Mark, José-Luis Zambonino-Infante, Myron A. Peck.

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