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Patterns of inter-populational and inter-individual variation in tolerance of sublethal progressive hypoxia and warming in the European seabass *Dicentrarchus labrax*

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We compared tolerance of acute progressive hypoxia and warming in the three recognized populations of European seabass, Atlantic (AT), West Mediterranean (WM) and East Mediterranean (EM), that have evolved within a North-West to South-East thermal gradient, from AT to EM. We reared progeny of captive broodstock in common garden at two temperatures, 18 and 24°C, representing summer temperatures in Atlantic and East Mediterranean, respectively. At about 1 year of age, hypoxia tolerance was evaluated with static respirometry, as critical saturation for regulation of standard metabolic rate (S_{crit}) and regulation index (RI); while warming tolerance was evaluated by swimming respirometry, as critical thermal maximum for aerobic swimming (CTS_{max}). We expected AT fish systematically to be least tolerant and EM most, with WM intermediate. At 18°C, the tolerance traits were similar among populations, but they responded differently when reared at 24°C. In AT and WM, S_{crit} increased—tolerance declined—from 18 to 24°C, whereas in EM it did not change. In AT and WM, RI did not change from 18 to 24°C whereas in EM it increased—tolerance increased, and EM had higher RI than WM at 24°C. In AT and EM, CTS_{max} was similar at 18 and 24°C whereas in WM it increased—tolerance increased, and WM had higher CTS_{max} than AT and EM at 24°C. Therefore, the EM population is able to avoid negative effects of warmer water on hypoxia tolerance, compared to AT and WM, but this was not related to improved thermal tolerance at the warmer temperature, where WM performed better than AT and EM. Consequently, the seabass exhibits inter-populational variation in tolerance of the stressors but patterns are complex and not consistent between hypoxia and warming. We explored some potential patterns of inter-individual variation in tolerance. We found no evidence that individuals relatively tolerant of hypoxia (low S_{crit} , high RI) were also relatively tolerant of warming (high CTS_{max}). There was evidence

of complex relationships with body mass, whereby tolerance of warming declined with increasing mass at 18°C but tolerance of hypoxia increased with mass at 24°C. Finally, the traits of tolerance were not dependent on individual standard metabolic rate at either temperature.

KEYWORDS

CTS_{max}, hypoxia, regulation index, standard metabolic rate, S_{crit}, warming, European seabass

1 Introduction

Fishes are an important component of human food security, provided by fisheries but also, increasingly, by aquaculture (1). Human-induced rapid environmental change (HIREC) is having profound effects on aquatic ecosystems globally, with poorly known consequences for wild and farmed fish populations. In aquatic habitats, there are two prominent elements of HIREC that can pose major physiological challenges to fish populations. It has been argued that the major threat is hypoxic episodes triggered by ongoing climate warming, nutrient pollution and changes in the water cycle (2–4). A further threat is the extreme summer heatwaves associated with the warming (5–7). Although hypoxic events and heatwaves can occur naturally in aquatic habitats, they are now increasing in frequency, intensity and duration across the globe (3, 6). It is important, therefore, to increase our understanding of the capacity of fish species and populations to tolerate these environmental stressors.

The European seabass *Dicentrarchus labrax* is a temperate coastal fish whose range extends from Norway to Senegal in the eastern Atlantic, and the entire Mediterranean (8). It is highly prized by commercial and sports fishermen, with the Atlantic the main area for fisheries, but it is also a key species in Mediterranean coastal and lagoon cage mariculture (72). Coastal and transitional ecosystems are particularly threatened by hypoxia and heatwaves (2, 9), and the Mediterranean is a climate change hotspot (10, 11), so it is valuable to investigate how well *D. labrax* tolerates hypoxia and warming. In fact, the effects of dissolved oxygen and temperature on the seabass, and the species' physiological responses to these environmental factors, have been studied relatively extensively [e.g., (12–18)]. Tolerance thresholds for progressive hypoxia and acute warming have been evaluated using loss of equilibrium (LOE) as an endpoint, in an incipient lethal oxygen saturation (ILOS) protocol or a critical thermal maximum (CT_{max}) protocol [e.g., (19, 20)].

However, none of these studies reported which European seabass population was under investigation. Three genetically distinguishable populations of European seabass exist across its geographical range: Atlantic (AT), West Mediterranean (WM) and East Mediterranean (EM) (8, 21). They started to diverge ~300,000 years ago (22, 23) in environments whose temperatures differed along a North-West to South-East gradient, from AT to EM (24). It is conceivable that the populations might now differ in their tolerance of temperature, due to processes of local adaptation (25, 26). At the same time, they may also exhibit differences in tolerance of hypoxia, if hypoxic episodes naturally occur less frequently in

coastal areas of the cooler oceanic Atlantic compared to the warmer Eastern Mediterranean basin.

Acute hypoxia and warming may share a common physiological mode of action in fishes, because both stressors challenge the capacity of the cardiorespiratory system to provide sufficient O₂ to respiring tissues. In hypoxia because availability falls, in warming because demand increases (27–29). This has stimulated research into whether tolerance of the two stressors is systematically interrelated, whereby tolerance of hypoxia is positively correlated to tolerance of warming. This has been investigated at the level of species (30), populations (31), and individuals within species (19, 20, 32–36). These studies mostly measured tolerance using ILOS and CT_{max} protocols and, although there was evidence of correlations at the level of species (30) and populations (31), there is very little evidence that inter-individual variation in tolerance of the two stressors was correlated (19, 20, 32, 34–36). This may, however, be because LOE occurs for different reasons at ILOS and CT_{max} (27, 34, 36, 37).

Sub-lethal protocols have been used to investigate correlations of individual tolerance of hypoxia and warming in fishes. In a tropical freshwater teleost, the Paraná pacu *Piaractus mesopotamicus*, there was a significant correlation between two measures of hypoxia tolerance, the critical oxygen saturation (S_{crit}) and the regulation index (RI), and the critical thermal maximum for aerobic swimming (CTS_{max}) (32). The S_{crit} and RI use static respirometry to evaluate the capacity of the cardiorespiratory system to regulate O₂ uptake unchanged from normoxic rates, as water O₂ availability diminishes in progressive hypoxia (38–41). The CTS_{max} uses fatigue from sustained exercise as endpoint when the fish is heated incrementally in a swim tunnel respirometer. Fatigue is attributed to an inability of the cardiorespiratory system to raise oxygen uptake and meet the combined oxygen demands of swimming plus the inexorable warming (42–45). A correlation among the sublethal traits may indicate that tolerance shares common physiological mechanisms but further work is needed on more fish species.

There has also been interest in evaluating whether body mass is significant for individual tolerance of hypoxia and warming in fishes, to gain insight into whether climate change impacts might be mass-dependent. Various studies have found that S_{crit} and RI are influenced by body mass although there is no clear consensus about the direction of effects, whereas there is evidence that CTS_{max} declines with increasing mass (32, 43, 46–51). It is also interesting to investigate whether individual S_{crit}, RI, and CTS_{max} depend on the magnitude of an individual's standard metabolic rate (SMR, an ectotherm's basal metabolic rate at their acclimation temperature).

Basal oxygen demand could affect an individual's capacity to assure supply in progressive hypoxia and there is evidence that European seabass with low SMR have higher CT_{max} (49, 52, 53).

Given that European seabass farming is in coastal areas and transitional ecosystems such as lagoons, which are particularly susceptible to hypoxic events and heatwaves, it is valuable to understand whether the populations may differ in their tolerance of sublethal hypoxic and thermal stress, as this may have implications for selecting broodstock for fish to be farmed in different areas of Europe. Understanding patterns of individual variation in tolerance of sublethal hypoxia and warming in the seabass can not only extend the knowledge base for fishes in general, but can also be a useful first step toward selection programs for improved tolerance in the species' farmed populations.

In this study we investigated Hypothesis 1 that the three seabass populations would differ in their tolerance of progressive hypoxia and acute warming, evaluated as S_{crit} , RI and CTS_{max} , with the AT population being less tolerant than EM, and WM intermediate. Fish were reared in common garden at two constant temperatures, 18 and 24°C, which represent summer temperatures in AT and EM, respectively (54, 55). Differences in tolerance among populations at a common temperature can therefore be attributed to local adaptation, whereas differences in tolerance across temperatures provide insight into populational plasticity in tolerance (56). We then evaluated the patterns of individual tolerance within populations at each acclimation temperature, with the Hypothesis 2 that individuals relatively tolerant of hypoxia were also relatively tolerant of warming. The final objective was to explore whether individual tolerance was related to body mass and SMR in the seabass, considering data at an overall species level.

2 Materials and methods

2.1 Animals

Experiments were performed on 120 seabass from the three populations, that were produced by artificial fertilization of captive broodstock and reared at the Ifremer marine research platform in Palavas-les-Flots (Occitania, France) as described in detail by Rodde et al. (54, 55). All fish were PIT-tagged for individual identification (Biolog-id, www.biolog-id.com) and, after experimentation for their individual feed efficiency at 18 and 24°C in a separate study (55), they were grouped into two tanks (vol. 1,000 L) supplied with biofiltered water at either 18°C (18 AT, 19 WM, and 25 EM) or 24°C (14 AT, 17 WM, and 27 EM) and a constant photoperiod of 12:12, for a minimum of 12 weeks prior to any further experimentation, during which time they were fed a commercial feed *ad libitum* by self-feeder (54).

2.2 Measures of oxygen uptake and determination of S_{crit} and RI by static respirometry

Static respirometry was performed as described in Rodde et al. (54). Briefly, 1 week before respirometry fish at each temperature were distributed into three holding tanks supplied with biofiltered water at the correct temperature (vol. 1,000 L,

18–22 fish randomly assigned per tank) and fed *ad-libitum* by hand, daily. Segregating into three tanks ensured that fish were not disturbed by netting/handling more than once when placing them in respirometer chambers. A single tank was then fasted for 24 h and, in the subsequent afternoon, the fish were rapidly netted from it, identified by a PIT tag and weighed. The fish were distributed into individual semi-transparent respirometry chambers (volume either 1.8 or 3.0 L according to their size, in a system of 32 chambers) and left for 12 h (overnight) to recover from handling. Chambers were submerged in two polyvinyl chloride trays (100 × 200 × 28 cm) supplied with aerated biofiltered seawater at either 18 or 24°C, trays were shielded behind opaque black plastic with fish in dim light at 12:12 photoperiod (54). The fish could see their conspecifics (57) and all of the fish themselves could be observed through small holes in the plastic curtain.

Oxygen uptake rate ($\dot{M}O_2$) was measured by intermittent stopped-flow respirometry (57, 58) as described in Rodde et al. (54) and McKenzie et al. (59), over a period of 24 h after the initial 12 h recovery. Water oxygen levels were measured and recorded each 10 s in the chambers by optodes (Firesting OXROB10 oxygen sensors, www.pyroscience.com) and associated oxygen meter (Firesting FSO2-O4) and software (Pyro Oxygen Logger) (54). At the end of this period, the flushing pumps of the respirometry system were switched off (at an external switch panel) and fish were left to consume the oxygen in the closed respirometry chambers, down to 10% O_2 saturation, with careful observation by experimenters. When oxygen saturation dropped to 10% in a chamber, the pump was turned back on to supply aerated, normoxic seawater. When all fish had returned to normoxia for at least 30 min, they were removed from their chambers and returned to their rearing tank. Background oxygen consumption due to bacterial respiration was then measured over 20 min in all chambers; background respiration was also measured in empty chambers throughout each respirometry series (57, 60). For the calculation of $\dot{M}O_2$, only slopes of $R^2 \geq 0.94$ from the intermittent closed cycle were used and rates were calculated as $mg\ O_2\ kg^{-0.8}\ h^{-1}$, considering the mass scaling coefficient of $b = 0.8$ for routine metabolic rate in European seabass (54, 61). Background respiration represented about 2% of $\dot{M}O_2$ by the fish, so no correction was applied. SMR was then calculated as described in Rodde et al. (54), as the 0.25 quantile of $\dot{M}O_2$ values over the 24 h period (62).

To then estimate S_{crit} and RI, measures of $\dot{M}O_2$ were resolved over 5-min intervals (35 sequential oxygen measurements) from 90 to 10% oxygen saturation, along the progressive decline in O_2 saturation in the closed respirometer chamber. This resulted in between 16 and 24 measurements per individual, depending upon how rapidly they consumed the oxygen in their chamber, which typically took from 70 to 120 min. Only slopes of $R^2 \geq 0.94$ were used and, as for SMR, rates were calculated as $mg\ O_2\ kg^{-0.8}\ h^{-1}$. The individual S_{crit} was calculated empirically, as the intersection between a horizontal line, drawn at SMR, and a least squares regression through $\dot{M}O_2$ values in the oxyconforming range of hypoxic oxygen saturations below SMR (32, 41, 49). The lower the S_{crit} , the greater the tolerance of hypoxia (40). The RI was also calculated empirically, based upon the concept of Mueller and Seymour (39). Briefly, we considered that if an individual maintained their routine $\dot{M}O_2$ unchanged between 90 and 10% saturation, this would be perfect regulation with an RI of 100% (RI

100). If, by contrast, routine $\dot{M}O_2$ declined in a straight line from the rate measured at 90% saturation down to the lowest $\dot{M}O_2$ at 10%, this would be complete conformity and an RI of 0% (RI 0). This line of conformity was calculated for each fish, from routine normoxic $\dot{M}O_2$ at 90% to the lowest hypoxic $\dot{M}O_2$, measured at 10%. At each measurement interval, the percentage regulation (%R) was calculated based on the prevailing $\dot{M}O_2$ as

$$\% R = \frac{\dot{M}O_2 - RI 0}{RI 100 - RI 0} * 100$$

and then the average of these measurements during progressive hypoxia taken as the overall RI for that individual. The higher the RI, the greater the tolerance of hypoxia (32, 39).

2.3 Determination of CTS_{max} in swim tunnels

This was performed with two Steffensen-type swim tunnels constructed in PVC and plexiglass (swim chamber volume 49 or 30L), on 10 fish per population per temperature. Two fish were captured at random from the three holding tanks described above and their PIT tag read, care was taken to avoid disturbing any one tank more frequently than once every 72 h, and the focal tank was fasted for 24 h before trials. Fish were caught in the afternoon and measured for mass, length, depth and width, to apply relative swimming speeds in body length per second (BL s^{-1}) and correct for the solid blocking effect (63), then placed into one of two tunnels provided with biofiltered seawater at the appropriate temperature. Fish were left to recover from handling stress overnight at a low swimming speed of 1BL s^{-1} . The next day, at 09:00 a.m., the current speed was increased by increments of 0.1 BL s^{-1} every 2 min until 2.5 BL s^{-1} . At 2.5 BL s^{-1} , all fish swam with a sustained aerobic body-caudal swimming gait. After 30 min at that speed, temperature was increased by 1°C every 30 min. If a seabass rested against the rear screen for at least 10 s, they were rapidly removed from the tunnel and placed in a recovery tank at their acclimation temperature for 30 min, then returned to their holding tank. Fatigue is not due to lack of endurance because the seabass can swim steadily at 2.5 BL s^{-1} for at least 8 h at their acclimation temperature, exceeding the duration of the CTS_{max} (44). The CTS_{max} was calculated as the last temperature step completed plus the proportion of the last temperature step that the fish tolerated prior to fatigue (42). $\dot{M}O_2$ measurements were made by sealing the swim tunnel for the last 15 min at each temperature step, and the highest $\dot{M}O_2$ was identified and denoted $\dot{M}O_{2max}$, as described in detail previously (42, 44). The $\dot{M}O_{2max}$ was taken as a measure of cardiorespiratory performance, which might provide insight into variation in CTS_{max} among populations and individuals.

2.4 Data and statistical analysis

All statistical analyses were performed in R 4.0.2 (73). In particular, analysis of variance (ANOVA) with interaction terms

with acclimation temperatures and populations or named ANOVAs followed by Tukey *post-hoc* tests. The normality of residuals was checked using the quantile-quantile method (comparing residual quantiles with theoretical normal quantiles). The homoscedasticity and independence of the residuals were checked by comparing the residuals with the fitted values from the models. The significance level was set at $p < 0.05$.

The following linear model was used to evaluate the effect of population and acclimation temperature on the phenotypic traits:

$$Y_{ijk} = \mu + P_i + T_j + PT_{ij} + \varepsilon_{ijk}$$

where Y_{ijk} is the phenotypic trait for population i (AT, WM or EM), acclimation temperature j (18 or 24°C), and individual k . Then, μ is a general mean, P a fixed effect of population, T a fixed effect of acclimation temperature, PT the interaction of these two effects, and ε_{ijk} the residuals ($\varepsilon_{ijk} \sim N(0; \sigma_e^2)$). Pairwise differences among populations and temperatures were further explored by Tukey *post-hoc* test.

Based upon the above analyses (see Section 3 below) correlations among traits were estimated with the Pearson coefficient, considering all populations together at each temperature and then all population and temperature data together. Dependence of tolerance traits on body mass and SMR was explored by least squares regression, considering all populations together at each temperature and then all population and temperature data together.

3 Results

The samples sizes and size of the fish from each population and temperature are shown in Table 1. For the hypoxia trials, body mass depended significantly on temperature, with fish at 24 being heavier than 18°C, but no effect of population or interaction. The populations did, however, differ significantly in mass at both 18 or 24°C, with WM significantly smaller than EM, and AT intermediate (Table 1). For the CTS_{max} trial, mass also depended significantly on temperature, increasing from 18 to 24°C within each population, but there were no effects of population or interaction—the populations did not differ in mass at either temperature. For forklength in CTS_{max} , there was a significant overall effect of temperature with fish being larger at 24 compared to 18°C. This effect was only significant within WM and EM, and populations did not differ in forklength at a common temperature (Table 1). Results of the linear model are carried in Table 2 and Supplementary Table S1.

3.1 Hypothesis 1, populations will differ in their tolerance of progressive hypoxia and acute warming

The seabass were carefully observed during progressive hypoxia and, although they hyperventilated vigorously, none of them showed any evidence of LOE. The averaged metabolic responses of the seabass populations showed a typical piscine oxygenator

TABLE 1 Mean values for body size, and traits of tolerance of hypoxia and warming, in three seabass populations, Atlantic (AT), West Mediterranean (WM) and East Mediterranean (EM), reared at two temperatures, 18 and 24°C.

Population	AT		WM		EM	
	18	24	18	24	18	24
Hypoxia						
<i>n</i>	20	24	18	25	23	29
Mass (g)	104 ± 34 ^{a,b}	140 ± 19 ^{c,d}	79 ± 22 ^a	129 ± 36 ^c	108 ± 26 ^b	155 ± 39 ^d
<i>S</i> _{crit} (% sat)	27.0 ± 1.1 ^a	34.2 ± 1.2 ^b	26.2 ± 1.4 ^a	33.3 ± 15 ^{b,c}	28.4 ± 25 ^a	32.6 ± 2.5 ^{a,b,c}
RI (% reg)	61.0 ± 4.7 ^{a,b}	61.2 ± 3.3 ^{a,b}	71.5 ± 2.9 ^{a,b}	54.7 ± 3.4 ^a	66.3 ± 2.7 ^a	69.9 ± 25 ^b
Warming						
<i>n</i>	10	9	10	11	10	8
Mass (g)	96 ± 25 ^a	269 ± 15 ^b	72 ± 24 ^a	189 ± 32 ^b	95 ± 34 ^a	210 ± 13 ^b
Forklength (mm)	193 ± 16 ^a	244 ± 53 ^b	182 ± 18 ^a	252 ± 11 ^b	196 ± 23 ^a	256 ± 12 ^b
CTS _{max} (°C)	30.9 ± 0.2 ^a	30.5 ± 0.9 ^a	30.9 ± 0.4 ^{a,b}	33.2 ± 0.7 ^b	31.4 ± 0.2 ^{a,b}	30.4 ± 1.1 ^a
$\dot{M}O_{2max}$ (mg kg ^{-0.8} h ⁻¹)	628 ± 55 ^a	444 ± 41 ^b	658 ± 54 ^a	558 ± 22 ^{a,b}	579 ± 33 ^{a,b}	533 ± 77 ^{a,b}

Mass and length are mean ± SD. Critical saturation for regulation of standard metabolic rate (*S*_{crit}), regulation index (RI), critical thermal maximum for aerobic swimming (CTS_{max}) and maximum oxygen uptake achieved during the CTS_{max} ($\dot{M}O_{2max}$) are mean ± SE. Within variables, a common superscript indicates no significant difference. Outputs of the linear model are in Table 2, see text for further details.

response, maintaining routine $\dot{M}O_2$ at normoxic rates until a critical oxygen level beyond which $\dot{M}O_2$ declined below SMR and toward zero (Supplementary Figure S1). In actual fact, all of the seabass populations showed increases in mean $\dot{M}O_2$ at intermediate levels of hypoxia, at both temperatures, although these were not accompanied by visible agitation (Supplementary Figure S1).

For *S*_{crit}, there was a significant effect of temperature but not of population, and an interaction of temperature and population that was not quite a significant result (Table 2). The *S*_{crit} of the three populations was statistically similar at 18°C; the overall *S*_{crit} increased from 18 to 24°C (Figure 1a, Table 1, Supplementary Table S1), indicating a decline in hypoxia tolerance. The effects of temperature were not, however, the same in all populations because *S*_{crit} increased significantly from 18 to 24°C in the AT and WM populations but not in the EM (Figure 1a, Table 1, Supplementary Table S1).

For RI, there was no significant effect of temperature or population, but a significant interaction (Tables 1, 2). The RI did not differ significantly among populations at 18°C and, although overall RI did not change with acclimation temperature, responses to temperature differed among populations (Figure 1b, Table 1, Supplementary Table S1). The RI did not change from 18 to 24°C for the AT and WM populations but it increased significantly in the EM and was significantly higher than the RI of the WM population at 24°C (Figure 1b, Table 1, Supplementary Table S1).

During the CTS_{max}, all individuals showed an increase in $\dot{M}O_2$ as temperature was increased in steps, with an overall exponential Arrhenius-type metabolic response (Supplementary Figure S2). They all eventually transitioned in swimming gait, from an entirely steady aerobic gait with rhythmic beating of the tail, to increasing engagement of unsteady anaerobic “burst-and-coast” episodes. This led to fatigue within <1 temperature increment (30 min). No individual showed any evidence of LOE in the swimming trials.

For CTS_{max}, there was no significant effect of temperature but a significant effect of population and a significant

temperature:population interaction (Table 2). There were no significant differences in CTS_{max} at 18°C (Figure 2a, Table 1, Supplementary Table S1). CTS_{max} did not change with an increase from 18 to 24°C in the AT and EM populations, but it rose significantly in the WM population. At 24°C, CTS_{max} of the WM population was significantly higher than the AT and EM populations (Figure 2a, Table 1, Supplementary Table S1). There is also evidence that CTS_{max} was more variable at 24°C, with outliers in all populations that we had no reason to disregard (Figure 2a).

With respect to cardiorespiratory performance in the CTS_{max}– $\dot{M}O_{2max}$ –there was a significant effect of temperature but not of population, and no interaction (Table 2). That is, $\dot{M}O_{2max}$ declined significantly with an increase from 18 to 24°C, and this was significant within the AT population, where the $\dot{M}O_{2max}$ at 24°C was significantly lower than its own population and WM at 18°C (Figure 2b, Table 1).

3.2 Hypothesis 2, individuals relatively tolerant of hypoxia are also relatively tolerant of warming

We focus on simple correlations between *S*_{crit}, RI and CTS_{max} at a species level, because the sample sizes per population at each temperature were limited. Furthermore, if the populations differed, which they did somewhat at 24°C, the distribution of individuals at species level can still inform us about whether relative tolerance is correlated within all individuals across the total sample. The individual *S*_{crit} and RI were negatively correlated at 24°C and when considering all data together, with quite high correlation coefficients (Figure 3a, Table 3). This is the expected pattern, a relatively hypoxia-tolerant individual would have a low *S*_{crit} and a high RI. There was, however, no correlation between *S*_{crit} or RI and

TABLE 2 Results of a linear model to investigate the effects of water temperature (18 vs. 24°C) and seabass population (Atlantic, Western or Eastern Mediterranean) on body mass, tolerance and performance variables.

	<i>F</i> -value	<i>P</i> -value
Body mass for hypoxia tolerance		
Temperature	66.703	<1 × 10⁻¹²
Population	10.048	<0.0001
Temp:Pop	0.502	0.606
S_{crit}		
Temperature	25.963	<0.001
Population	0.57	0.57
Temp:Pop	2.862	0.072
RI		
Temperature	0.440	0.508
Population	1.025	0.361
Temp:Pop	6.460	0.002
Body mass for thermal tolerance		
Temperature	161.690	<1 × 10⁻¹⁵
Population	3.364	0.042
Temp:Pop	1.212	0.306
CTS_{max}		
Temperature	1.176	0.283
Population	3.178	0.049
Temp:Pop	14.857	0.016
MO_{2max}		
Temperature	9.935	0.003
Population	1.665	0.199
Temp:Pop	1.327	0.274

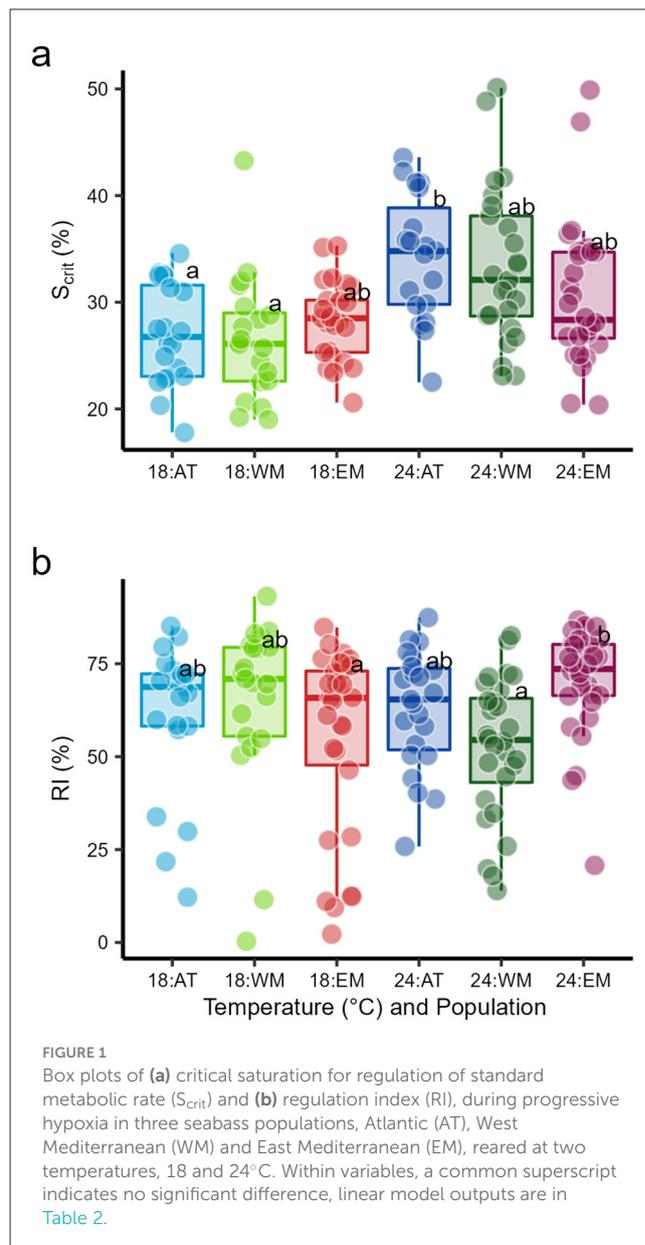
See text for further details.

Variables are critical saturation for regulation of standard metabolic rate (*S_{crit}*), regulation index (RI), critical thermal maximum for aerobic swimming (CTS_{max}) and maximum oxygen uptake achieved during the CTS_{max} (MO_{2max}). Temp:Pop, temperature by population interaction. Significant effects are in bold.

CTS_{max}, at either temperature or even when considering all data at both temperatures (Figures 3b, c, Table 3).

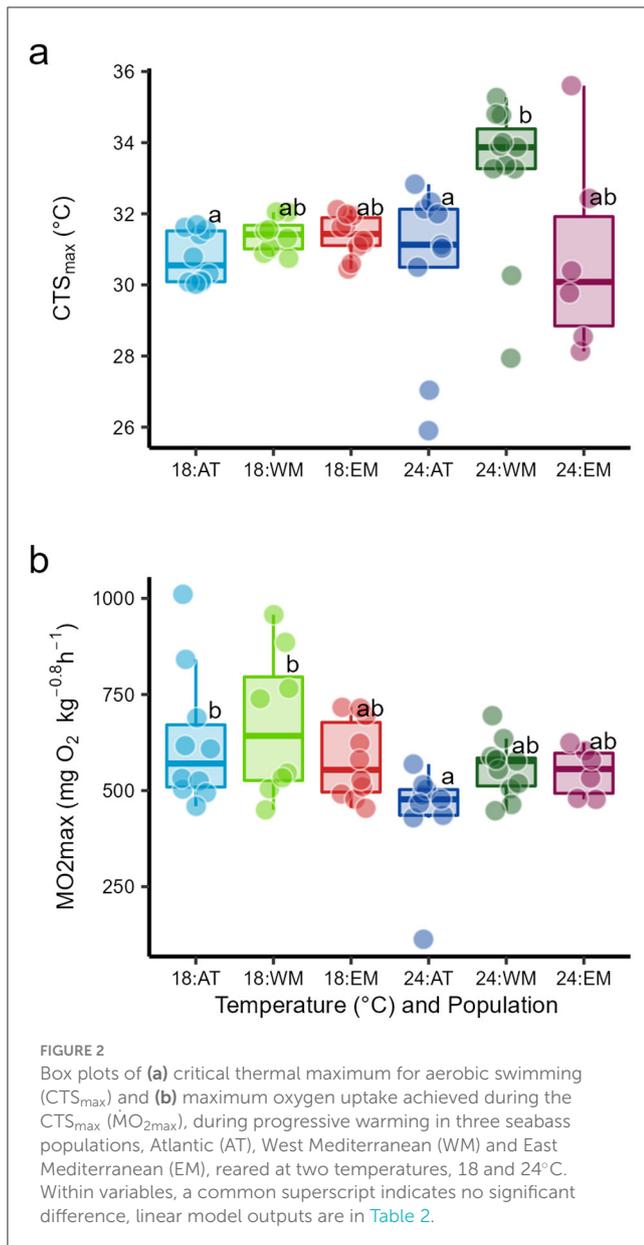
3.3 Exploration of the effects of individual body mass and standard metabolic rate on tolerance traits

There was no reliance of *S_{crit}* or RI on individual body mass at 18°C but a significant dependence on body mass at 24°C, whereby *S_{crit}* declined and RI increased, indicating improved tolerance with increasing mass, albeit with relatively low coefficients of determination. There were no significant effects of mass when data from both temperatures were combined (Figures 4a, b, Table 3). By contrast, CTS_{max} declined significantly with body mass at 18°C,



indicating poorer tolerance as mass increased, and mass explained almost 30% of the variation in CTS_{max} at this temperature. There was, however, no dependence on body mass at 24°C, or when all data were considered together (Figure 4c, Table 3).

The data for SMR of the three populations were reported in (54) as means for each population at each temperature. That study found no significant differences among SMRs at either temperature but that SMR was significantly higher at 24°C compared to 18°C in all populations. If the individual data are taken for each temperature, all populations considered, individual *S_{crit}* depended significantly upon individual SMR (Figure 5a, Table 3), and for all data together, SMR explained almost 30% of the variation in *S_{crit}*. By contrast, but individual RI did not depend on SMR (Figure 5b, Table 3). Individual CTS_{max} showed no evidence of a dependence on SMR (Figure 6a, Table 3), although it did depend on MO_{2max} at



24°C although the effect size was small in terms of coefficient of determination (Figure 6b, Table 3).

4 Discussion

The results support our Hypothesis 1 to the extent that the populations differed in their tolerance of sublethal hypoxia and warming. There was some evidence that the EM population was better able to cope with hypoxia at a warmer temperature but it was not systematically more tolerant than AT, with WM intermediate. In fact, somewhat paradoxically, the WM population was the least tolerant of hypoxia at the warmer temperature but the most tolerant of warming. We obtained no evidence for Hypothesis 2, that seabass individuals tolerant of hypoxia were also tolerant of warming, nor

of Hypothesis 3, that relative tolerance of the two stressors would depend upon individual SMR.

4.1 Hypothesis 1, populations will differ in their tolerance of progressive hypoxia and acute warming

These are the first data on comparative tolerance of HIREC-related stressors in the three European seabass populations. The finding that overall S_{crit} increased—hypoxia tolerance diminished—with an increase in temperature from 18 to 24°C is consistent with previous studies on other teleosts (40) and is attributed to an increase in SMR with temperature, such that the fish are defending a higher oxygen demand. Surprisingly, despite the quite extensive study of the physiology of hypoxia in seabass, dating back several decades (12, 14, 16–18), there is no published report of their S_{crit} . They have often been assumed to be quite tolerant of hypoxia because the juveniles inhabit enclosed coastal ecosystems such as estuaries and lagoons that are prone to hypoxia (64). Our S_{crit} measurements, of around 25% at 18°C and 30% at 24°C, indicate that the species has moderate hypoxia tolerance compared to other marine species at similar temperatures (40). Among the populations, the EM appeared better able to cope with hypoxia in warm water, based upon the absence of any change in S_{crit} within that population with warming.

The RI has been studied much less than S_{crit} in fishes but it is believed to provide a more accurate reflection of how well an animal regulates its oxygen uptake in progressive hypoxia because it integrates data throughout the exposure rather than simply revealing a threshold oxygen level (39, 41). It might be considered surprising that, in the seabass, overall RI did not decrease with the increase in temperature, given that overall S_{crit} decreased. This may be because RI was measured relative to an individual's actual normoxic MO_2 at each temperature, not in relation to their SMR, so that small changes in that routine MO_2 obscured effects of temperature. The RI in the seabass populations, ranging from 55 to 70%, is within the range of reports for other species such as the Paraná pacu with 79% at 26°C (32), the tropical freshwater mormyrid *Petrocephalus degeni* with 69–79% at 23°C (65), or the temperate marine tidepool sculpin *Oligocottus maculosus* with 60% at 12°C (66).

The finding that RI increased with warming in the EM population, and was significantly higher than the WM population at 24°C, is further evidence that the EM is better able to cope with hypoxia in warm waters. This may reflect local adaptation to hypoxia exposure at warm summer temperatures in the Eastern Mediterranean. The significant interaction between population and temperature for the effects of RI would also indicate differing levels of phenotypic plasticity in the hypoxia physiology of the three populations. The patterns of hypoxia tolerance require further study, not least because the low tolerance of the WM population at 24°C, based on their low RI, was linked unexpectedly to a relatively higher thermal tolerance at that temperature, based on their CTS_{max} .

This comparison of CTS_{max} among the seabass populations does not support the hypothesis that warming tolerance would

TABLE 3 Correlations among tolerance variables (Pearson correlation) and dependences of these variables on metabolic variables (least squares regression) in individuals from three seabass populations, Atlantic (AT), West Mediterranean (WM) and East Mediterranean (EM), reared at two temperatures, 18 and 24°C.

	18°C			24°C			All		
Pearson	<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>	<i>n</i>	<i>R</i>	<i>P</i>
S _{crit} vs. RI	61	−0.06	0.84	77	−0.577	0.002	138	−0.384	0.014
S _{crit} vs. CTS _{max}	30	−0.29	0.28	28	0.17	0.41	58	0.19	0.24
RI vs. CTS _{max}	30	−0.19	0.35	28	−0.13	0.54	58	−0.03	0.82
Regression		<i>R</i> ²	<i>P</i>		<i>R</i> ²	<i>P</i>		<i>R</i> ²	<i>P</i>
S _{crit} on mass	61	0.04	0.12	77	−0.172	<0.001	138	<0.01	0.66
RI on mass	61	0.04	0.07	28	0.063	0.023	58	<0.01	0.45
CTS _{max} on mass	30	−0.297	0.002	28	<0.01	0.85	58	<0.01	0.73
S _{crit} on SMR	61	0.19	0.15	77	0.208	0.045	138	0.290	<0.0001
RI on SMR	61	0.14	0.25	77	−0.03	0.75	138	0.04	0.66
CTS _{max} on SMR	30	<0.01	0.98	28	−0.09	0.39	58	−0.01	0.85
CTS _{max} on $\dot{M}O_{2max}$	30	0.119	0.062	28	0.193	0.019	58	0.061	0.059

Data are pooled by temperature and also considered overall (All).

S_{crit}, critical saturation for regulation of standard metabolic rate; RI, regulation index; CTS_{max}, critical thermal maximum for aerobic swimming; SMR, standard metabolic rate; $\dot{M}O_{2max}$, maximum oxygen uptake achieved during the CTS_{max}. Significant effects are in bold.

increase from a population that evolved in a relatively cool Atlantic compared to a warmer Eastern Mediterranean. A previous study, on the WM population (44), found a very similar mean value at 18°C ($30.3 \pm 0.4^\circ\text{C}$, $n = 8$) and that CTS_{max} was significantly lower than CT_{max} ($34.0 \pm 0.4^\circ\text{C}$) in the same individuals. A similar relationship of CTS_{max} to CT_{max} has been observed in other teleost species (42). The CTS_{max} has been argued to be valid measure of thermal tolerance in active fish species because swimming is important for their ecological performance and because fatigue may occur due to a similar mechanism in all species—an inability to meet the combined oxygen demands of aerobic swimming and progressive warming (37, 43, 45, 67).

The data also indicate that the CTS_{max} threshold is relatively insensitive to acclimation temperature over the range of 18–24°C for the seabass. It is interesting that there were no differences in CTS_{max} at 18°C but that, at 24°C, the WM population had higher thermal tolerance than the AT and EM populations. This difference in thermal tolerance should presumably be attributed to local adaptation to acute heat stress in the WM population. This population is known to colonize lagoons as summer feeding grounds and these enclosed habitats are prone to heatwaves, although they are also prone to concurrent hypoxia. Once again, the interaction of population and temperature on CTS_{max} may indicate populational differences in plasticity of tolerance, which deserve further investigation.

The significant decline in $\dot{M}O_{2max}$ from 18 to 24°C was unexpected because the species has been reported to have higher aerobic scope and growth at 24 compared to 18°C (13, 55). It is not clear why $\dot{M}O_{2max}$ was lower at 24°C, this may reflect consequences of rearing at a constant temperature, which is not ecophysiological realistic for temperate fish species. The fact that the decline in cardiorespiratory performance was only significant in the AT is a slight indication of a lower capacity to cope with warmer

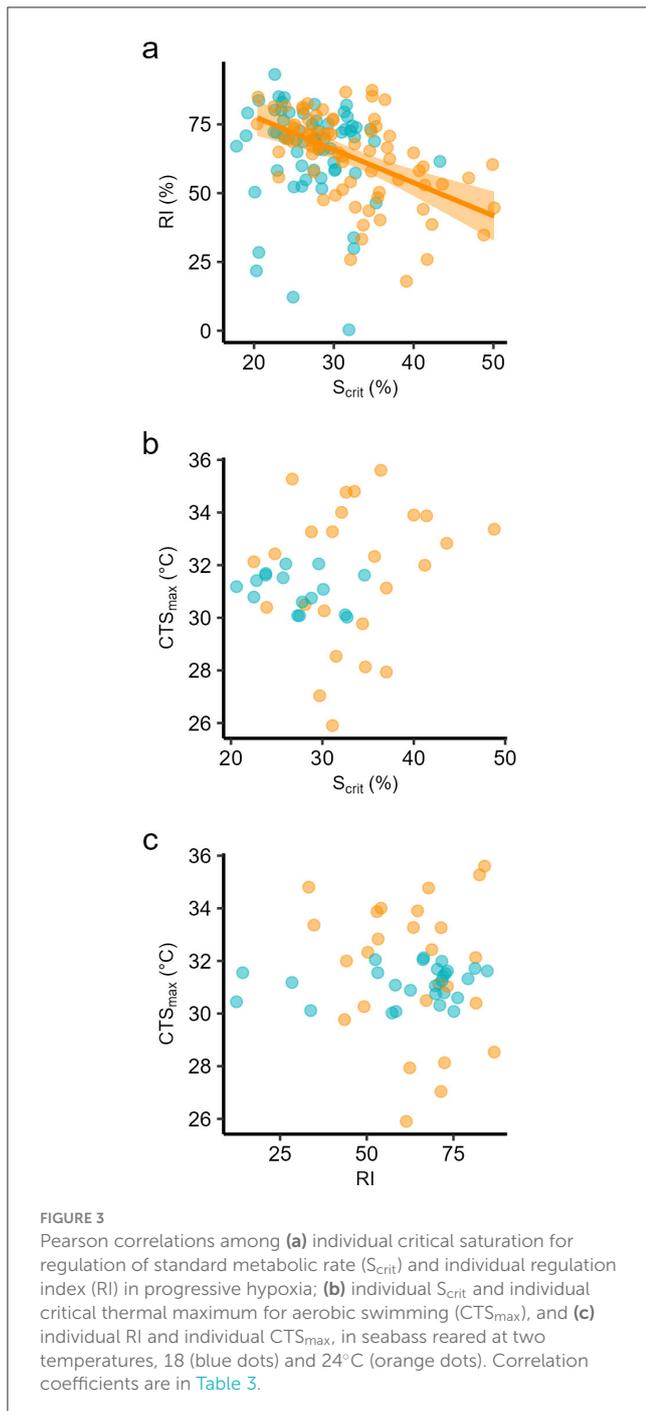
waters in this population, although it was not linked to a parallel decline in CTS_{max} from 18 to 24°C.

When considered together the data suggest that, in warmer waters, EM is somewhat more tolerant of hypoxia and WM of warming, with AT never being the best performer. The paradox of poor hypoxia but good warming tolerance in the WM clearly argues against our Hypothesis 2, for which we obtained no evidence whatsoever.

4.2 Hypothesis 2, individuals relatively tolerant of hypoxia are also relatively tolerant of warming

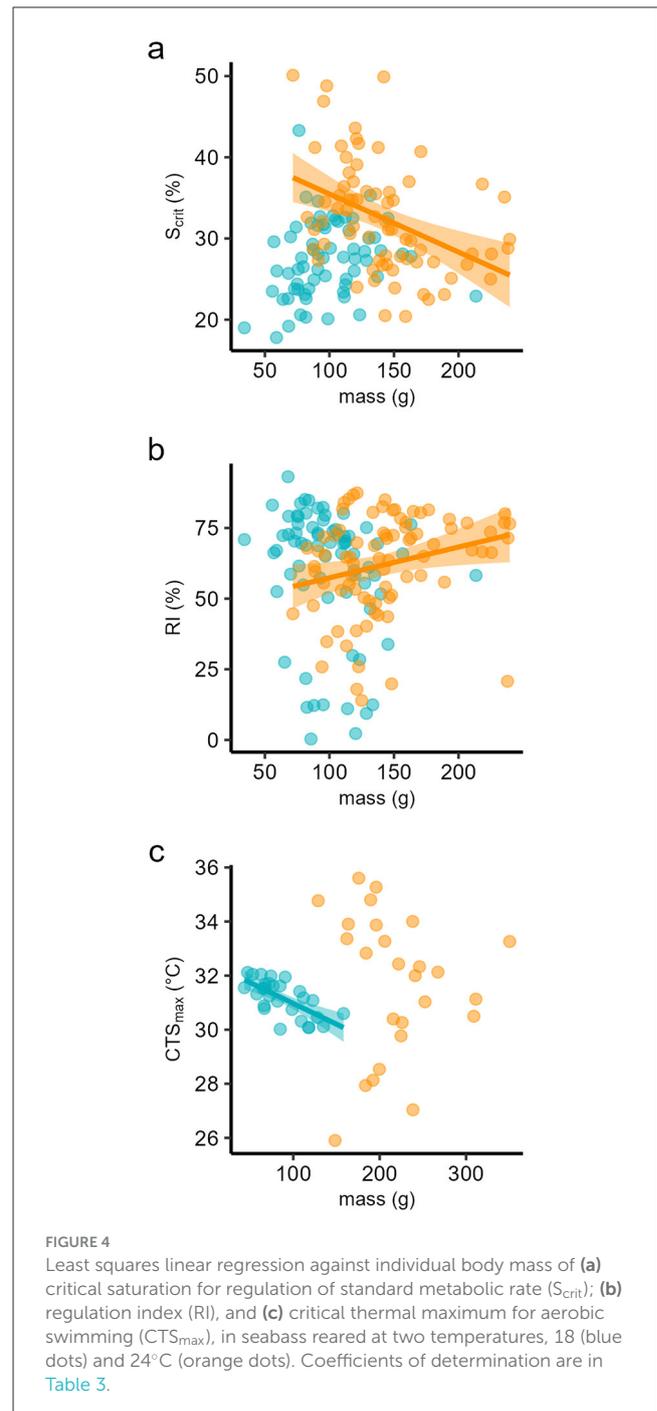
Despite previous indications that S_{crit}, RI and CTS_{max} might be correlated in individuals of the Paranà pacu, with those relatively tolerant of hypoxia being relatively tolerant of warming (32), we found no such evidence in the European seabass. The negative correlation of S_{crit} to RI is consistent with their relative relationship to hypoxia tolerance and indicates that they share a causal mechanism. That is, they both reflect aspects of cardiorespiratory capacity for regulation of aerobic metabolic rate as oxygen availability falls in progressive hypoxia (32, 39, 41, 49).

The endpoint in the CTS_{max}, fatigue from aerobic swimming, has been attributed to an inability of the cardiorespiratory system to meet the combined oxygen demands of exercise plus warming. This supposition is supported by the fact that fatigue is preceded by gait transition from aerobic to anaerobic swimming style, a response that has been observed in six teleost species so far [(42, 44, 45), D.J. McKenzie unpublished observations]. It is also supported by the positive correlation of CTS_{max} to $\dot{M}O_{2max}$ when all seabass were considered, irrespective of population or temperature. This positive

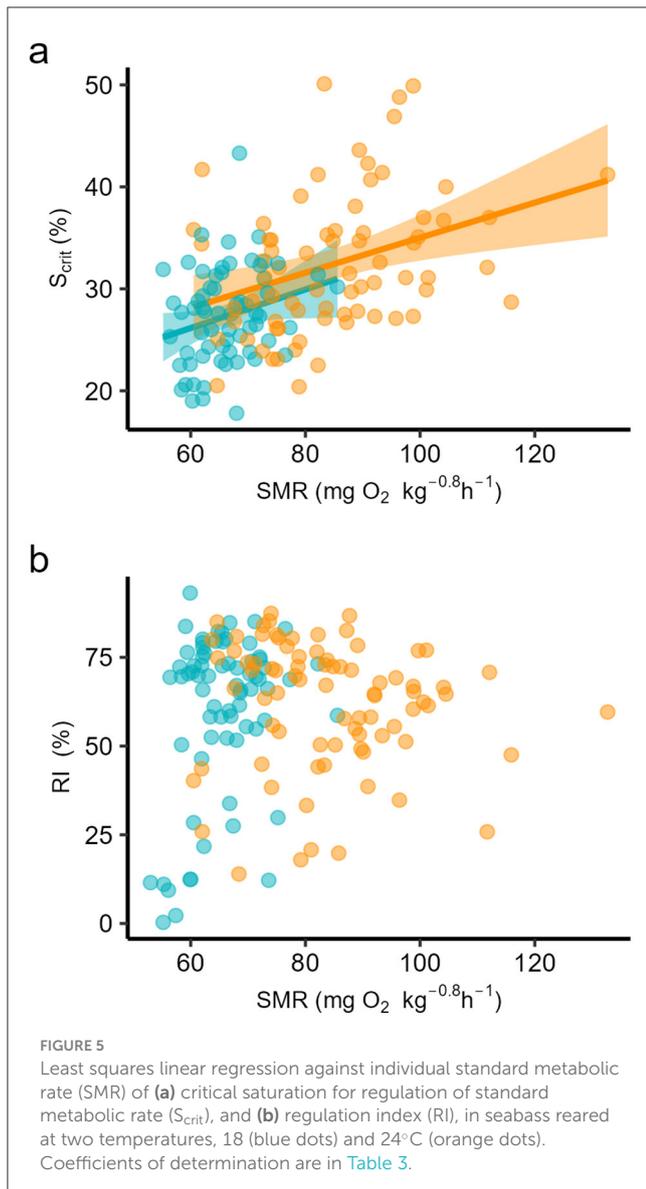


correlation has also been observed in a tropical freshwater teleost, the Nile tilapia *Oreochromis mossambicus* (43) and would also seem to indicate that individuals with a greater capacity to increase their oxygen supply, in response to increased demand due to warming, were relatively more tolerant.

The absence of any evidence of a correlation of S_{crit} or RI to CTS_{max} in the seabass would, therefore, argue against the notion that the endpoints share common underlying causal mechanisms. Given our good understanding of how oxygen uptake is regulated in hypoxia (38, 40, 41, 68), these results indicate that our understanding of the role of oxygen uptake in CTS_{max} is imperfect.



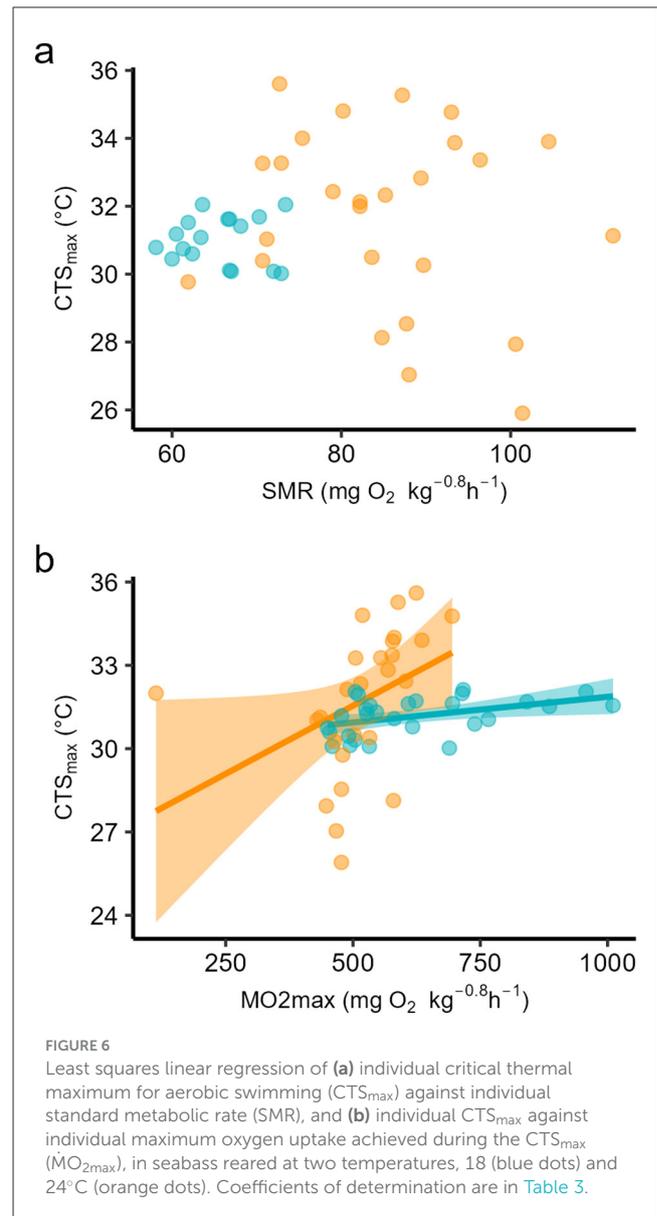
It is possible that cessation of swimming in a CTS_{max} does not occur due to an incapacity to provide oxygen to tissues, as recently argued for a tropical coastal marine species, the schoolmaster snapper *Lutjanus apodus*, because it showed no transition to anaerobic swimming prior to fatigue (69). For the seabass, however, there was a clear gait transition to anaerobic swimming prior to fatigue in all individuals in the CTS_{max} , a gait transition that is commonly assumed to indicate limitations in capacity for aerobic work in fishes (45, 69–71). It may indicate that individual CTS_{max} does not depend only upon intrinsic capacity for oxygen uptake, as hypoxia tolerance does, but also upon how the acute incremental



temperature increase affects the physiology and cardiorespiratory capacity of each individual. The mechanisms underlying cessation of swimming in a CTS_{max} protocol may therefore differ among species and this requires further research. Nonetheless, these sublethal endpoints are not proving more useful than LOE, at ILOS vs. CT_{max} , when investigating whether individual tolerance of hypoxia and warming are correlated in fishes (19, 20, 32, 34–36).

4.3 Exploration of the effects of individual body mass and standard metabolic rate on tolerance traits

Although there were significant effects of body mass on tolerance of hypoxia and warming, these were complex and to some extent contrasting, with overall small effect sizes. It is not



clear why hypoxia tolerance did not depend on mass at the cooler temperature but that both S_{crit} and RI showed a clear positive dependence at the warmer temperature. There is conflicting evidence about the effects of body mass on S_{crit} in fish species, with reports that it either decreases with mass (46, 49, 50), does not change (32, 47, 51), or increases (48). Little is known about effects of mass on RI in fishes, the current data on European seabass at 24°C are coherent with a previous report of an increase in RI with mass in Paraná pacu (32). At 24°C, the WM population had a lower S_{crit} and RI than the EM population, and also a lower body mass. Therefore, the difference in mass may have been a contributing factor to the difference in tolerance between these two populations.

It is also not clear why CTS_{max} depended on mass at 18°C but not at 24°C. The significant decline in CTS_{max} with mass at 18°C is coherent with a report for Nile tilapia, where tolerance declined significantly with mass (43). The contrasting effects of mass on

hypoxia and warming tolerance deserve further investigation, they certainly do not suggest that tolerance of the two stressors should be positively correlated among individuals. Future studies of the effects of mass on environmental tolerance within species should explore a mass range that is >1 order of magnitude, to improve explanatory power (42).

There was clear evidence of the positive correlation of SMR to S_{crit} observed in Gulf killifish *Fundulus grandis* (49), which would seem axiomatic since individuals with lower basal oxygen demand might be expected to be less challenged to regulate their metabolism in hypoxia. This finding in seabass is consistent with a previous study that found a correlations between individual SMR and the behavioral responses to hypoxia of aquatic surface respiration in the seabass (15). There was, however, no evidence of a dependence of S_{crit} on SMR in the Paranà pacu, which presumably reflects diversity of hypoxia physiology among fish species (32). The absence of any dependence of RI on SMR presumably is because the tolerance indicator is measured against routine $\dot{M}O_2$ in normoxia and does not contemplate basal oxygen demands, although SMR and routine metabolic rate, the average $\dot{M}O_2$ over 24h in the respirometers, were extremely closely correlated in the seabass in this study (54). In terms of thermal tolerance, a previous report found evidence that individual CT_{max} was related to SMR in European seabass (53) but we found no evidence that this was the case for CTS_{max} . There was some evidence of a dependence of CTS_{max} on overall cardiorespiratory performance, but the effect size was limited. More studies are therefore required, in more species, to evaluate the extent to which tolerance of environmental stressors might depend upon intrinsic metabolic phenotype in fishes but, to date, the evidence is inconclusive.

4.4 Conclusions and perspectives

This study provides the first comparative measures of tolerance of hypoxia and warming in the three genetic populations of the European seabass. Our hypothesis 1 was only partially supported, in that EM and WM fish were better able to cope with hypoxia and warming, respectively, than AT fish, which were never the best performers. Therefore, although the seabass shows inter-population variation in tolerance of hypoxia and warming, that presumably reflects processes of local adaptation, the pattern of variation does not simply reflect the broad scale thermal gradient over the species' geographic range. We also explored some potential patterns of inter-individual variation in tolerance. We found no evidence for Hypothesis 2 that, within the experimental subjects in general, individuals that were relatively tolerant of hypoxia (low S_{crit} , high RI) were also relatively tolerant of warming (high CTS_{max}). We found evidence that individual body mass explained some of the variation in tolerance at a species level although relationships were complex and effect sizes were small; and evidence that individual SMR affected hypoxia tolerance when measured as S_{crit} but had no effect on tolerance of warming when measured as CTS_{max} .

Clearly, there is a need to extend the knowledge base about patterns of intraspecific variation in tolerance of environmental stressors in fishes (26, 31, 32, 40, 56). The current results

do not really reveal one seabass population that is most tolerant of major stressors of HIREC, for application in cage mariculture, except the general conclusion that the AT population is not suited to farming in warm waters if these are subject to hypoxic or warming episodes. They also do not contribute greatly to our understanding of general principles that underly patterns of inter-individual tolerance of hypoxia and warming within all fish species, although this remains a worthwhile objective.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

The animal study was approved by C2EA–36 (Comité d'éthique en expérimentation animale Languedoc-Roussillon) under authorization APAFiS n° 2018100910598940. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JN: Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. CR: Data curation, Formal analysis, Investigation, Methodology, Validation, Writing – review & editing. FB: Investigation, Writing – review & editing. GS: Investigation, Writing – review & editing. AV: Investigation, Methodology, Resources, Writing – review & editing. HV: Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. MV: Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. FA: Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. DM: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Gen AI was used in the creation of this manuscript.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/frish.2025.1542342/full#supplementary-material>

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