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Effects of exposure to elevated temperature and different food levels on the escape response and metabolism of early life stages of white seabream, *Diplodus sargus*

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"We are the first generation to feel the effect of climate change and the last generation who can do something about it".

-Barack Obama, Former USA President

"Twenty-five years ago people could be excused for not knowing much, or doing much, about climate change. Today we have no excuse".

-Desmond Tutu, Former Archbishop of Cape Town

"What you do makes a difference, and you have to decide what kind of difference you want to make".

-Dr Jane Goodall, Scientist & Activist

"By polluting the oceans, not mitigating CO_2 emissions and destroying our biodiversity, we are killing our planet. Let us face it, there is no planet B".

-Emmanuel Macron, President of France

Resumo

O final da fase larvar é um período crítico na vida dos peixes, sujeito a elevadas taxas de mortalidade, principalmente devido à predação. O sucesso nesta fase é, então, modelado pela capacidade de escapar a predadores. A literatura sugere que o aumento da temperatura pode afetar a resposta de fuga e metabolismo, contudo poucos estudos têm focado na resposta aguda e potencial de aclimatação, através da plasticidade de desenvolvimento. Aqui, pretendemos avaliar os efeitos da exposição aguda e de longo prazo a temperaturas elevadas na resposta de fuga e taxas metabólicas padrão (SMR), nas fases iniciais de *Diplodus sargus*. Adicionalmente, como a disponibilidade alimentar pode modelar a resposta ao aquecimento, testámos os efeitos da exposição a temperatura elevada e indisponibilidade de alimento, como fatores individuais e em interação, na resposta de fuga e SMR. Os tratamentos de temperatura foram ajustados à temperatura ambiente (19°C) e elevada (22°C). Os tratamentos de alimentação foram estabelecidos como *ad libitum* e alimentação reduzida (50% do *ad libitum*). A resposta de fuga e SMR foram medidos após a temperatura elevada ser atingida (exposição aguda) e após 4 semanas (exposição a longo prazo). O aquecimento agudo teve um efeito significativo na resposta de fuga e aumentou ligeiramente a SMR. Contudo, a longo prazo, parece existir uma aclimatação da resposta de fuga e SMR. A indisponibilidade de alimento, ao interagir com a temperatura elevada, levou a um aumento da latência e redução da SMR, sugerindo que os peixes regulam as taxas metabólicas em função da disponibilidade alimentar.

Palavras-Chave: Aclimatação de desenvolvimento, Alterações climáticas, Comportamento, *Diplodus sargus*, Fisiologia.

Abstract

The end of the pelagic larval stage is a critical period in the life of fish, subject to high mortality rates, mostly due to predation. Success at this stage is then modulated by the ability to escape from predators. The literature suggests that an increase in temperature can affect escape response and fish metabolism, however few studies have focused on the acute sensitivity responses and the potential for acclimation through developmental plasticity. Here, we aimed at evaluating the acute and long-term effects of exposure to warming conditions on the escape response and Standard Metabolic Rates (SMR) of early life stages of the white seabream, *Diplodus sargus*. Additionally, as food availability may modulate the response to warming, we further tested the effects of long-term exposure to high temperature and food shortage, as individual and interacting drivers, on escape response and SMR. Temperature treatments were adjusted to ambient temperature (19°C), and a high temperature (22°C). Feeding treatments were established as *ad libitum* and short fed (50% of *ad libitum*). Escape response and SMR were measured after the high temperature was reached (acute exposure), and after 4-weeks (long-term exposure). Acute warming had a significant effect on escape response, and slightly increased SMR. In the long-term, however, there seems to be an acclimation of the escape response and SMR. Food shortage, interacting with high temperature, led to an increase in latency response and a significant reduction in SMR, which suggests that fish might regulate metabolic rates as a function of food availability.

Key-words: Behaviour, Climate change, Developmental Acclimation, *Diplodus sargus*, Physiology.

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Introduction

In recent decades, the intensification of the release of carbon dioxide (CO_2) and other polluting gases of anthropogenic origin into the atmosphere has led to profound changes in the physical and chemical properties of ocean water (Sabine *et al*., 2004; Kwan *et al*., 2017), with consequences to marine life in general (Brierley & Kingsford, 2009; Pankhurst & Munday, 2011; Domenici *et al*., 2019). It is estimated that the ocean absorbs 25% of CO_2 and 93% of the heat that is not dissipated from the earth (Bates *et al*., 2012; Balmaseda *et al*., 2013). This warming will initially take place in the shallower layers, but will slowly move to deeper waters (Levin & Le Bris, 2015; Cheng *et al*., 2019). Projections developed by the Intergovernmental Panel on Climate Change (IPCC) point out that, by 2100, partial CO_2 levels in the open ocean can reach values close to 1000 ppm and temperature can increase up to 4 °C (IPCC, 2014).

Ocean warming poses several challenges to marine organisms, potentially affecting reproduction (Donelson *et al*., 2010; Miller *et al*., 2015), behaviour (Nagelkerken & Munday 2015, 2016), physiology (Alfonso *et al*. 2021), locomotion (Herbing, 2002; Green & Fisher, 2004), and growth (Neuheimer *et al*., 2011; Rountrey *et al*., 2014). However, the effects of higher temperature on marine species may be more complex than the simple relationship between individual performance and temperature (Harley *et al*., 2006). Adding to the impacts on performance and physiology, the increase in temperature will have further effects on species interactions, such as predator-prey (Anderson *et al*., 2001; Allan *et al*., 2015, 2017; Bastille-Rousseau *et al*., 2018). Avoiding predators is crucial to improve individual fitness and survival, and it has been shown that, in fish, increasing temperature can substantially impact behaviour and locomotor performance components of an escape response (Warren *et al*., 2017; Domenici *et al*. 2019). Increasing temperature will also increase physiological rates, which will have further effects on reproduction, growth and feeding rates (Rangel *et al*., 2018; Pilakouta *et al*., 2020). The Standard Metabolic Rate (SMR), which represents the minimum rate of energy production to keep the animal at rest (White & Kearney, 2013), is one of the most used physiological characteristics to assess individual fitness. As an early response to warming, individual SMR is expected to change to compensate the increase in temperature. Yet, a prolonged exposure to these new environmental conditions might provide the organisms time to acclimate, if the benefit-cost ratio is favorable (Rummer *et al*., 2014). However, to fully comprehend how metabolism will be affected by increasing temperature, a better understanding of organisms' thermal sensitivity is necessary (Rangel *et al*., 2018). Q_{10} is one of the most used thermal sensitivity measures and represents the rate of change in metabolic rates with an increase or decrease of 10 °C (Rangel *et al*., 2018). For most fish species, the mean Q_{10} value lies between 2 and 3 (Clarke & Fraser, 2004), despite being dependent on factors such as thermal regime (Donelson & Munday, 2012), and phylogeny (Clarke & Johnston, 1999).

Frequently, experimental studies addressing the effects of environmental stressors on behavioural and physiological responses of fish are held under optimal feeding conditions, which might mask the real response of individuals to the stressor (Chick & Van Den Avyle, 2000). In the natural habitat, where food resources are finite and not always available, the available energy may not be sufficient to support all biological functions, with some maximized in detriment of others (McMahon *et al*., 2019). Climate change is also expected to limit food availability, due to increased ocean stratification, which will isolate the surface layers of nutrient-rich deep waters (O'Connor *et al*., 2009), potentially affecting primary production, with cascading effects to the entire trophic web (O'Connor *et al*., 2009; Lewandowska *et al*., 2014). Thus, addressing the interacting effects of food availability and increasing temperature on species response assumes particular relevance (Cominassi *et al*., 2020), but, to date, has been poorly investigated.

Here, we aimed at evaluating the effects of higher temperature and food availability, as individual and interacting stressors, on the escape response and SMR of late-stage larvae of white seabream, *Diplodus sargus*. Early life stages are a critical stage in the life cycle of fish (Searcy & Sponaugle, 2001), marked by high mortality rates, mostly due to predation (Almany & Webster, 2006), which can lead to a bottleneck effect and affect the population dynamics, including recruitment (Searcy & Sponaugle, 2001). The white seabream, a highly important commercial species (Sá *et al*., 2008), has a wide geographical distribution, being mainly abundant on the Atlantic coast and Mediterranean Sea (Froese & Pauly, 2019). After a dispersive larval phase, in the plankton, late-stage larvae move to coastal regions, in particular the tidal zones, to settle, grow and reproduce (Vigliola *et al*., 1998; Macpherson & Raventós, 2006).

To assess the effects of elevated temperature and food availability, larval fish were reared in a fully crossed experimental design with two temperatures and two food levels. The temperature treatments were set to an ambient temperature (19 ºC), typically found in their habitat, and the high temperature scenario to +3 ºC, which reflects acute heating events and is in line with projected future climate change conditions, according to the IPCC RCP scenario 8.5 (IPCC 2014; Hobday *et al*., 2018). Escape responses and SMR were measured immediately after high temperature was attained, and after a 4-weeks exposure period to temperature and food treatments. This approach allowed us to address: 1) the acute response to temperature increase;

2) the potential to acclimate to increasing temperature; and 3) the single and interacting effects of temperature and food levels. In view of all known effects of temperature on neural and sensory capacity, temperature is expected to have a detrimental effect on latency and directionality, but a beneficial one on responsiveness and locomotor parameters of the escape response (Warren *et al*., 2017; Domenici *et al*. 2019). Moreover, the SMR is expected to increase as temperature rises, by increasing biochemical reactions in the short term (Norin *et al*., 2019; McMahon *et al*., 2020), but in the long-term exposure it is expected that a thermal acclimation will occur (Donelson *et al*., 2011). The presence of food shortage conditions will likely amplify the negative effects of high temperature (Bignami *et al*., 2017). Thus, we expect that most notorious effects in behaviour and metabolism will be observed when fish are exposed to the interacting effects of temperature and food shortage.

Methods

Fish rearing and experimental setup treatments

White seabream, *Diplodus sargus*, larvae, at the age of 48 days post hatch, were provided by EPPO, an Aquaculture Research Station (IPMA – Olhão, Portugal). Fish were transported to ISPA fish facilities and placed in an 80 L tank, enriched with artificial algae and sediment, with temperature (19 ºC), salinity (35) and photoperiod (14L:10D) matching the conditions found at the EPPO station. Fish were left in this tank for 10 days, and then transferred to individual 30 L tanks, also enriched with algae and sediment, at a density of 25 individuals per tank, and left to acclimate to the new tanks for 3 days. Subsequently, fish were randomly assigned to four treatments: A) ambient temperature (19 ºC) and fed *ad libitum*, B) ambient temperature (19 ºC) with reduced feeding (50% of *ad libitum*), C) increased temperature (22 ºC) and fed *ad libitum*, and D) increased temperature (22 ºC) with reduced feeding (50% of *ad libitum*). Fish were randomly allocated to two replicate treatment tanks. Having only two replicates may limit our ability to estimate variation, but dividing the fish randomly will remove any potential tank effect during rearing. Temperature in treatments C and D were stepwise increased about 1 °C per day, using heaters, to avoid any stress and heat shock associated with rapid temperature changes (Gardiner & Munday, 2010), until +3 ºC above the ambient temperature treatment was reached. Once the experimental temperature was reached, the food treatments started. Fish at the *ad libitum* treatments were daily fed with 0.8 g of commercial fish feed (SPAROS, Olhão, Portugal), 5 times per day, while fish in short fed treatments were daily fed with 0.4 g (50% of *ad libitum*), 5 times per day. Fish were exposed for 4-weeks to these conditions. Temperature and salinity were daily measured, and other water quality parameters, such as ammonia, nitrates and nitrites, were monitored twice a week, and kept below critical levels. Tanks were daily cleaned, to remove excess of food, and were equipped with filtrations systems, ensuring water quality throughout the experimental period.

Escape response and SMR were measured at two timepoints: 1) immediately after high temperature was attained, and 2) after a 4-weeks exposure period to temperature and food treatments. Each individual was tested only once.

Standard Metabolic Rate and thermal sensitivity

Prior to trials, fishes were fasted for 24 h to ensure a post-absorptive state. Individuals were then transferred to a 100 ml o-ring sealed cylinder chamber connected via a tube to a 100 L aquarium with controlled temperature clean water (to minimize bacterial respiration). After being transferred, individuals were left in the chamber for one hour with constant water circulation, to acclimate before SMR measurement. Afterwards, the water flow inside the chamber was stopped and the individual kept in the closed chamber for 10 minutes, in which the oxygen consumed values were recorded.

After the measurement, the water flow inside the chamber was opened again so that oxygen levels inside the respirometry chamber could reach 100% saturation. The fish was then removed, and the oxygen consumption analyzed with the chamber empty to determine the background respiration. The SMR value was determined using the following formula:

$$MO_2 = \frac{\text{Chamber volume} * \text{Slope of oxygen consumption}}{\text{Weight (Kg)} * \text{Time (hours)}} - \text{Background}$$

During tests, the oxygen saturation levels were constantly monitored, to ensure that it remained above 80%. Temperature inside the chamber was maintained by submerging the respirometry chambers in water baths with heaters. Once the experiment was completed, the fish were weighed, and total and standard lengths registered. Ten to twelve individuals were analyzed per treatment, at the two timepoints.

From the oxygen consumption data, the thermal sensitivity was also analyzed, through the Q_{10}, using the following formula:

$$Q_{10} = \left(\frac{\text{Rate } 22\ ^{\circ}\text{C}}{\text{Rate } 19\ ^{\circ}\text{C}} \right)^{10\ ^{\circ}\text{C} / (22\ ^{\circ}\text{C} - 19\ ^{\circ}\text{C})}$$

Escape response

Experimental trials were conducted over a period of 2-4 days in a temperature-controlled room. The experimental setup used to assess the escape response was based on protocols established by Warren *et al* (2017), which involves presenting a stimulus to effectively elicit a startle response to the fish. Fish were individually transferred to a test arena, which consisted of a circular transparent acrylic enclosure (19 cm in diameter) placed in a tank, with a water depth of 8 cm, to limit vertical movements during the escape response. Water temperature in the arena matched the temperature of the treatment of origin, and was replaced every three trials. After a habituation period of 5 to 10 minutes, the startle response was elicited by dropping a weight, attached to a wire so that it just touched the surface of the water and did not collide with the individual. To provide a sudden stimulus, the weight was dropped through a PVC tube, to not elicit a visual stimulation before mechanical stimulation. The escape response was recorded using a high-speed video camera (Sony Cyber-Shot DSC-RX100M4), and a mirror was positioned at a 45 ° angle from the arena, so that the fish movement could be recorded to minimize visual disturbances (Figure 1). The test arena was surrounded by a covered structure (black curtains). Once the escape response experiment was complete, the fish was weighed, and total and standard lengths registered.

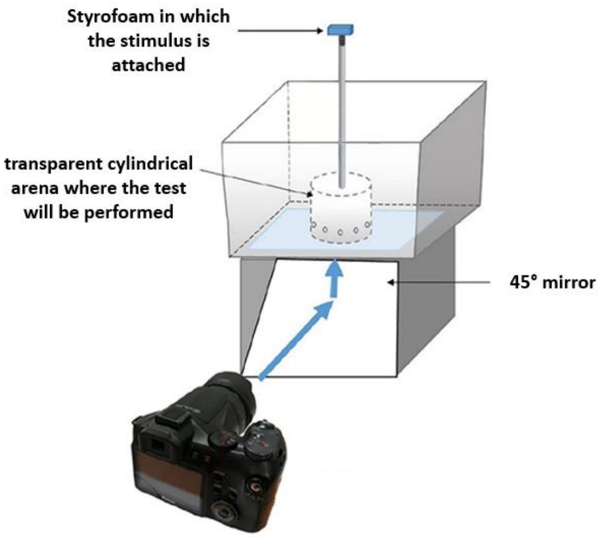

Figure 1 - Experimental setup of the escape response test. Adapted from McCormick *et al* (2017).

Escape response analysis included: responsiveness (proportions of fish that responded to the stimulus with C-Start or S-Start), directionality (defined by the movement of the head away or toward the side stimulus), latency (interval between the initiation of the stimulus and the response developed by the individual), escape distance (distance travelled during the response), and maximum speed (maximum acceleration reached during escape response), and were chosen as they are considered reliable indicators of fish escape performance (Walker *et al*., 2005). Videos were converted into frames (300 frames per second for latency analysis and 10 frames per second for maximum speed and escape distance analysis), and analyzed using the imageJ software with the manual tracking plugin.

Data analysis

Homogeneity of variances and normality were analyzed using the residual model. Responsiveness and directionality were analyzed using the Chi-square test. Latency (ms), maximum speed (converted to body length s^{-1} to control for any size effect), escape distance (cm), SMR (mg O_2 Kg^{-1} h^{-1}), weight (g) and total length (cm) were analyzed using a generalized linear model (GLM) with Gamma distribution and Tukey's HSD post hoc tests to examine differences between treatments. Independence and leverage were used to perform model validation. Temperature (2 levels: ambient and high) and food availability (2 levels: *ad libitum* and short fed) were used as explanatory variables according to each above-mentioned dependent variables. These variables were analyzed at each timepoint (acute and prolonged exposure) and between timepoints. Values are reported as means ± standard error (S.E.), and p-values below 0.05 were considered significant.

Data analysis was conducted in R statistical software (v4.1), using “lme4” and “nlme” package for running GLM models (R Core Team, 2018).

Results

Temperature effects on body condition, escape response and Standard Metabolic Rate

Fish weight differed between ambient and high temperature at the acute exposure timepoint, with a mean value of 0.142 ± 0.013 g at 19 °C and 0.208 ± 0.028 g at 22 °C (t= 2.172, N=35, *p*=0.037, Figure 2). Weight increased significantly after 4-weeks of exposure, both at ambient (t=13.48,N=37, *p*< 0.001) and high temperature (t=7.906, N=37, *p*<0.001), but no significant differences between treatments were detected (Supplementary Material Table S1).

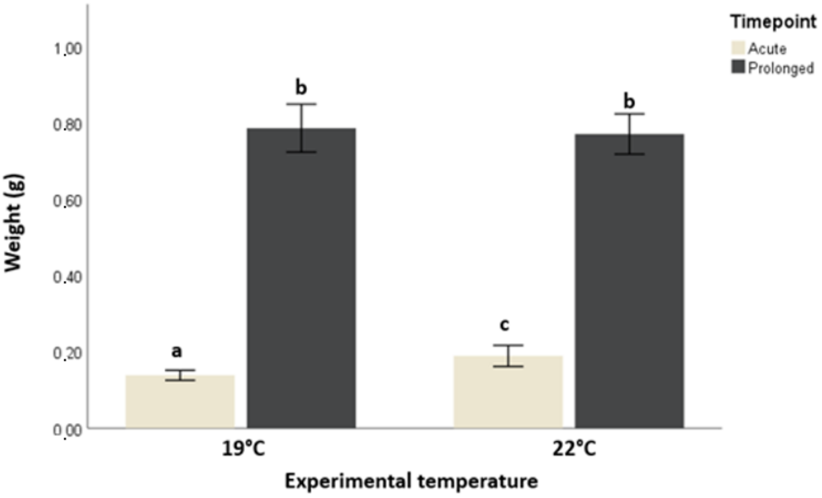

Figure 2 - Weight (grams) of *Diplodus sargus* larvae reared under ambient and high temperature treatments, following an acute and prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

Opposite to weight, total length did not differ between treatments at the onset of the experiment (Supplementary Material Table S1), averaging 2.180 ± 0.087 cm at 19 °C, and 2.205 ± 0.088 cm at 22 °C. Fish grew during the 4-week exposure period in both treatments, averaging 3.635 ± 0.113 cm at 19 °C (t=9.386, N=37, *p*<0.001), and 3.682 ± 0.079 at 22 °C (t=10.23, N =37, *p*<0.001). Similar to weight, total length did not differ between treatments at this timepoint (Supplementary Material Table S1, Figure 3).

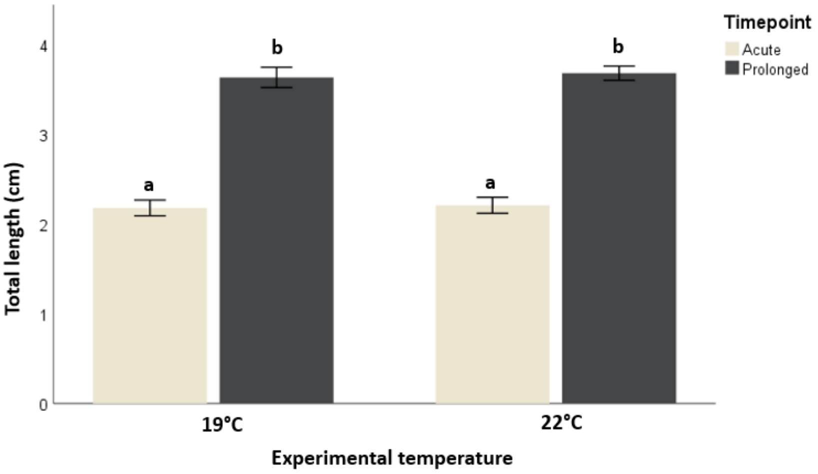

Figure 3 - Total length (centimeters) of *Diplodus sargus* larvae reared under ambient and high temperature treatments, following an acute and prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

At the acute exposure timepoint, 95% of individuals from ambient temperature responded to stimuli with a C-Start or S-Start, while at 22 °C the percentage of responsive individuals decreased to 80%. However, this difference was not significant between treatments (Supplementary Material Table S2). After 4-weeks of exposure, the responsiveness is reduced by 5% in both treatments, however this reduction is not significant either at ambient temperature (Supplementary Material Table S2), or at high temperature (Supplementary Material Table 2). Similarly, no significant differences between treatments were detected at this timepoint (Supplementary Material Table S2).

Like responsiveness, directionality did not differ between treatments in the acute exposure timepoint (Supplementary Material Table S2). At 19 °C only one individual moved in the direction of the stimulus, while at 22 °C all fish moved in the opposite direction of the stimulus. After 4-weeks of exposure, no significant differences in directionality in ambient temperature (Supplementary Material Table S2) and high temperature (Supplementary Material Table S2) were observed. No differences were found between treatments at this timepoint (Supplementary Material Table 2).

The acute exposure to high temperature did not affect latency response (Supplementary Material Table S3), neither did a prolonged exposure (Supplementary Material Table S3, Figure 4). At ambient temperature, latency to respond to the stimulus did not change with exposure time (Supplementary Material Table S3), but at higher temperature, latency increased from 16.5 ± 4.11 ms to 32.21 ± 11.311 ms after 4-weeks of exposure. However, there was high variability associated to this response, and this increase was not significant (Supplementary Material Table S3).

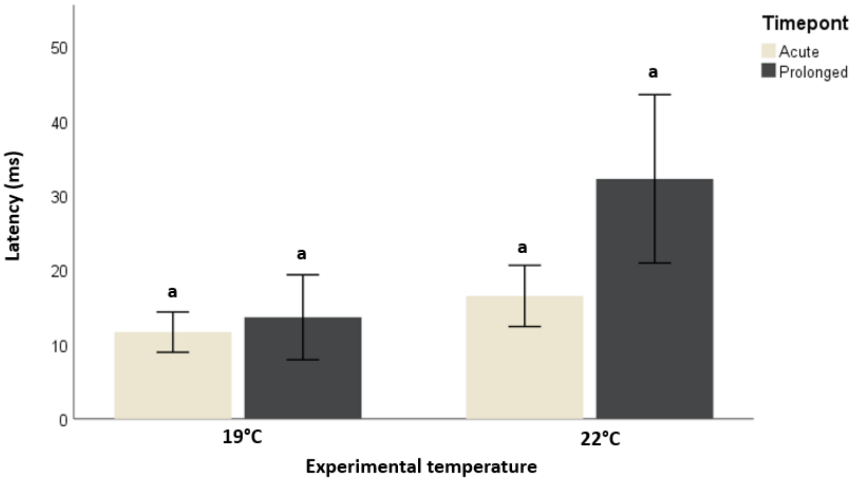

Figure 4 - Latency (millisecond) of *Diplodus sargus* larvae reared under ambient and high temperature treatments, following an acute and prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

Temperature did play a significant effect on the maximum speed attained after an acute exposure (t=2.399, N=35, *p*=0.022, Figure 5). At 19 °C a maximum acceleration of 16.609 ± 1.748 BL s^{-1} was recorded, which increased to 23.152 ± 2.042 BL s^{-1} at 22 °C, corresponding to a 40% increase. At ambient temperature, maximum speed did not change with exposure time (Supplementary Material Table S3), but interestingly, after a prolonged exposure to 22 ºC, maximum speed reduced significantly, from 23.152 ± 2.042 BL s^{-1} to 14.299 ± 1.223 BL s^{-1} (t=0.473, N=37, *p*<0.001), which is similar to maximum speed values attained by larvae kept at ambient temperature.

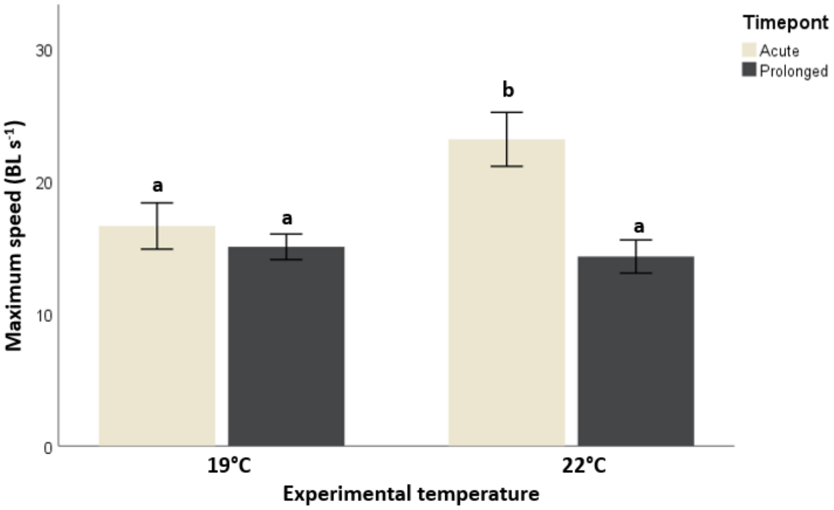

Figure 5 - Maximum speed (body length per second) of *Diplodus sargus* larvae reared under ambient and high temperature treatments, following an acute and prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

After an acute exposure to 22 ºC, larvae covered twice the distance as a response to the stimulus compared to larvae under ambient temperature (6.894 ± 0.717 cm vs 14.096 ± 3.433 cm) (t=2,865, N=35, *p*=0.007, Figure 6). Escape distances did not differ between timepoints, within each temperature treatment. At 19 °C the escape distance increased 32.3% between timepoints (Supplementary Material Table S3), while at 22 °C there was an opposite trend, decreasing by about 19.5% after 4-weeks of exposure (Supplementary Material Table S3). The prolonged exposure to 22 ºC, though, led to escape distances similar to the ones covered by larvae kept at ambient temperature (Supplementary Material Table S3), as it was seen for maximum speed.

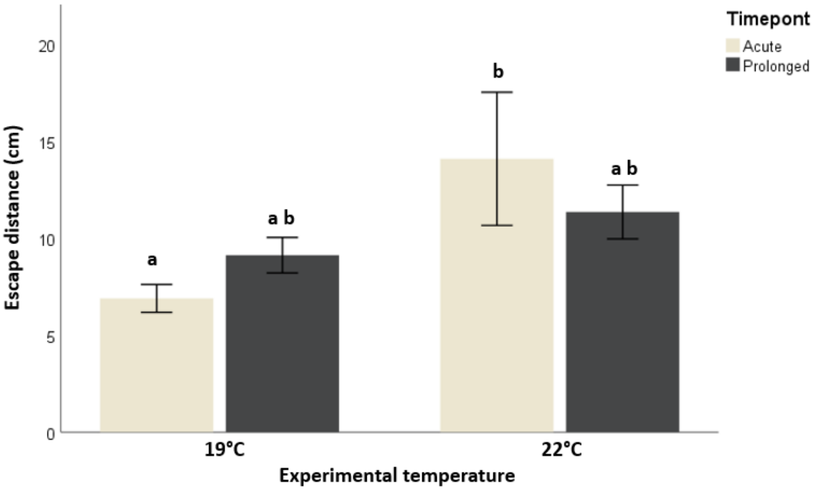

Figure 6 - Escape distance (centimeters) of *Diplodus sargus* larvae reared under ambient and high temperature treatments, following an acute and prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

Regarding metabolism (Figure 7), an acute exposure to 22 ºC led to an increase of SMR of about 13%, although not significant (Supplementary Material Table S4), and a prolonged exposure to this temperature was not reflected in changes in oxygen consumption in rest either, in comparison to the ambient temperature (Supplementary Material Table S4). The SMR slightly decreased between timepoints at ambient temperature, although not significantly (Supplementary Material Table S4), while at 22 ºC there was a significant reduction of more than 37% in oxygen consumption after a 4-week exposure (t=-3.368, N=37, *p*=0.003).

With acute exposure to elevated temperature, a Q_{10} of 2.25 was recorded. After 4-weeks of exposure, the Q_{10} decreased to 1.05.

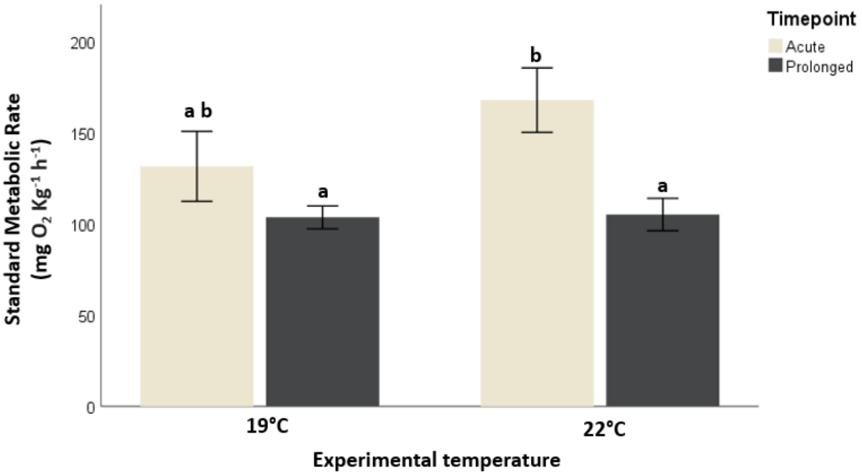

Figure 7 - Standard Metabolic Rate (milligram of oxygen per kilogram per hour) of *Diplodus sargus* larvae reared under ambient and high temperature treatments, following an acute and prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

Combined effects of temperature and food availability on body condition, escape response and Standard Metabolic Rate

At 19 °C, a mortality rate of 5.88% was recorded in the *ad libitum* treatment after a 4-week exposure, which increased to 10% with the reduction of food availability, although not statistically significant (Supplementary Material Table S5). However, at 22 ºC, a significant increase in mortality rates was observed ($X^2(1)=7.111$, N=100, *p*=0.008), from 2% in the *ad libitum* treatment to 18% in the short fed treatment.

Body weight did not show significant differences between treatments (Supplementary Material Table S6), with values ranging between 0.7 ± 0.056 g and 0.786 ± 0.063 g (Figure 8).

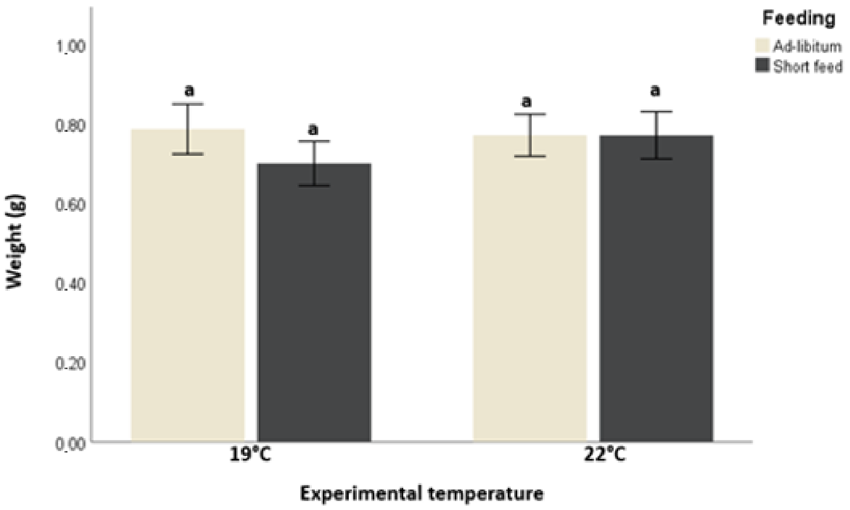

Figure 8 - Weight (grams) of *Diplodus sargus* larvae reared under *ad libitum* and short fed treatments, at ambient and high temperature, following prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

Likewise, total length did not differ between treatments (Supplementary Material Table S6), with values ranging from 3.474 ± 0.11 cm to 3.721 ± 0.101 cm (Figure 9).

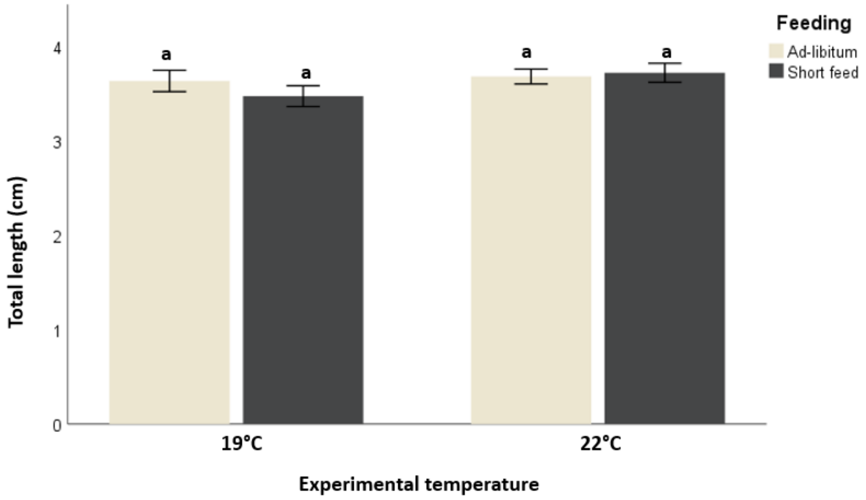

Figure 9 - Total length (centimeters) of *Diplodus sargus* larvae reared under *ad libitum* and short fed treatments, at ambient and high temperature, following prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

At both ambient and high temperatures, responsiveness did not change with feeding regime (Supplementary Material Table S7), ranging from 90 to 94.74% at 19 ºC, and 75 to 78.57% at 22 ºC. Likewise, temperature did not affect responsiveness between feeding regimes (Supplementary Material Table S7). Similarly, directionality did not differ between feeding treatments in both temperatures (Supplementary Material Table S7), with more than 90% of all individuals across all treatments responding in the opposite direction to the stimulus (Supplementary Material Table S7).

At ambient temperature, food availability did not significantly affect latency response (Supplementary Material Table S8), although there was a tendency to increase with food shortage, from 13.633 ± 5.7 ms to 28.817 ± 9.557 ms (Figure 10). At 22 ºC, a similar pattern is observed. Latency increased with short food availability, from 32.214 ± 11.306 ms to 81.6 ± 33.868 ms, but the high variability of responses prevents from finding significant differences (Supplementary Material Table S9). When well fed (*ad libitum*), latency did not differ between ambient and high temperatures (Supplementary Material Table S8 e S9). However, the combination of high temperature and short food availability significantly increased latency response (t = 2.883, N=33, *p*=0.005).

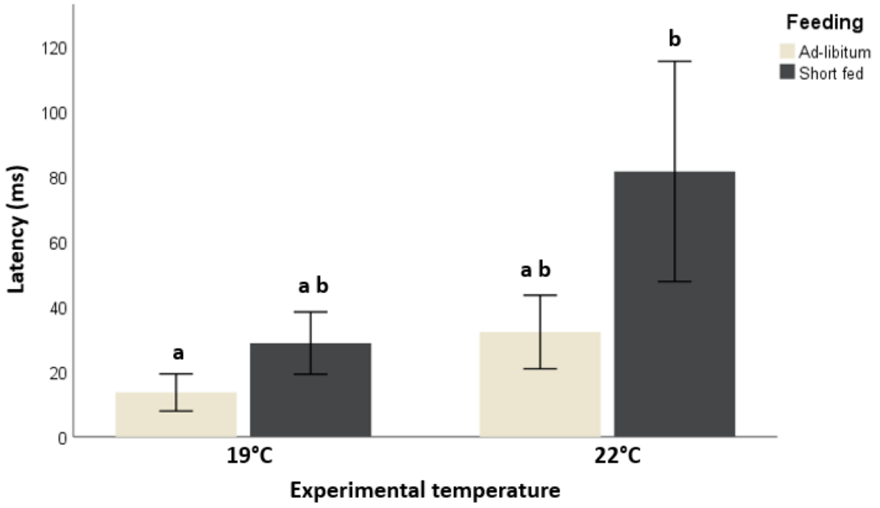

Figure 10 - Latency (millisecond) of *Diplodus sargus* larvae reared under *ad libitum* and short fed treatments, at ambient and high temperature, following prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

Maximum speed attained in the escape response was not affected by food shortage, in neither temperature treatments (Figure 11, Supplementary Material Table S8), ranging from 14.645 ± 1.345 to 15.032 ± 0.967 BL s^{-1} at 19 °C, and from 11.886 ±1.307 to 14.299 ± 1.125 BL s^{-1} at

22 ºC. The combination of high temperature and short food led to a small decrease of the maximum speed, although not significant (Supplementary Material Table S8).

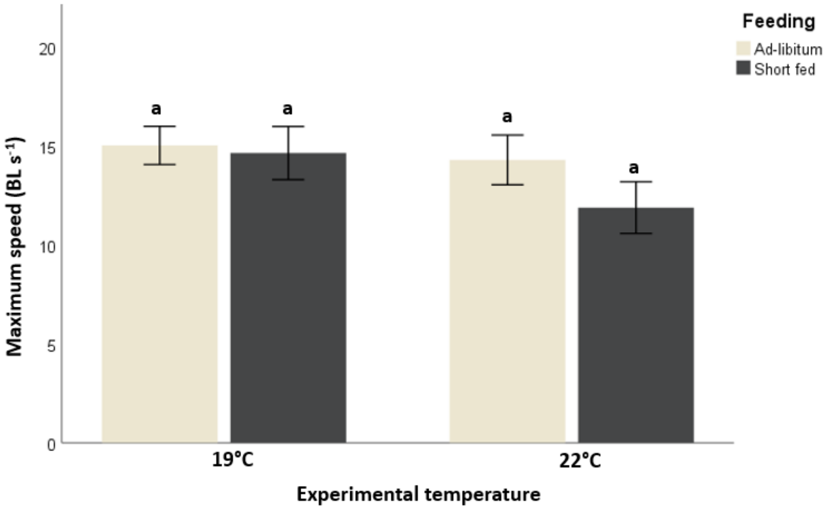

Figure 11 - Maximum speed (body length per second) of *Diplodus sargus* larvae reared under *ad libitum* and short fed treatments, at ambient and high temperature, following prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

Likewise, different feeding regimes did not affect the escape distance covered by larvae reared at ambient and high temperatures (Supplementary Material Table S8). Nevertheless, and as seen for maximum speed, the interaction of high temperature and short food availability lead to a decrease in the covered distance (15.15%), but not significant (Supplementary Material Table S8).

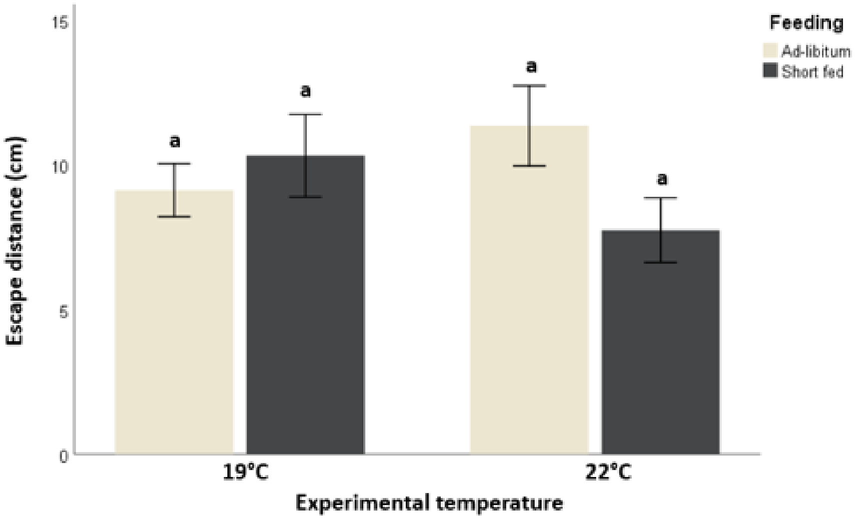

Figure 12 - Escape distance (centimeters) of *Diplodus sargus* larvae reared under *ad libitum* and short fed treatments, at ambient and high temperature, following prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

As for metabolism, food availability together with temperature had a significant effect on SMR (Figure 13). SMR decreased between feeding conditions at 19 °C, from 103.645 ± 6.289 mg O_2 Kg^{-1} h^{-1} to 80.775 ± 9.984 mg O_2 Kg^{-1} h^{-1}, although this decrease is marginally non-significant (Supplementary Material, Table S11). With exposure to 22 °C, significant differences were observed between feeding regimes (t=-3.377, N=20, *p*=0.004), with SMR decreasing from 105.210 ± 8.888 mg O_2 Kg^{-1} h^{-1} in the *ad libitum* condition to 68.474 ± 8.020 mg O_2 Kg^{-1} h^{-1} under short fed conditions. SMR did not differ significantly between temperature treatments in the *ad libitum* (Supplementary Material Table S10) and short fed condition (Supplementary Material Table S11).

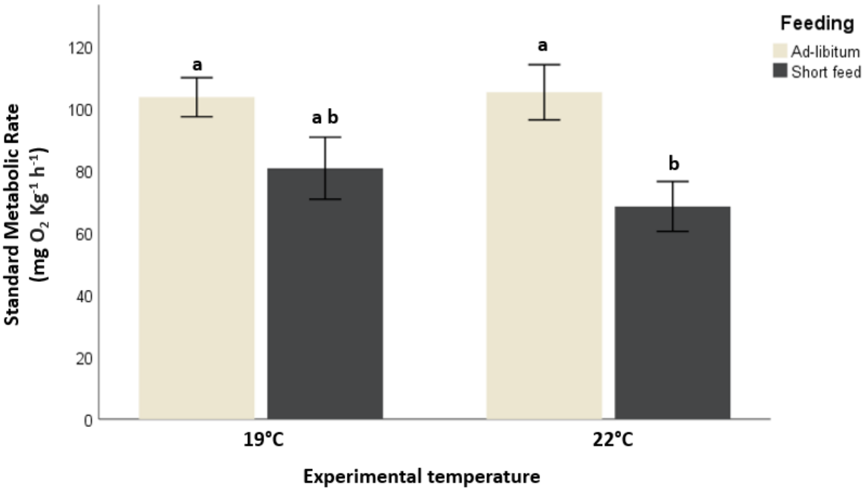

Figure 13 - Standard Metabolic Rate (milligram of oxygen per kilogram per hour) of *Diplodus sargus* larvae reared under *ad libitum* and short fed treatments, at ambient and high temperature, following prolonged exposure. Letters represent significant differences between treatments. Values are reported as mean ± S.E.

Discussion

Evaluating how temperature affects the escape response of marine species is essential to understand how predator-prey interactions will be affected by climate change (Gilman *et al*., 2010). Here, we observed that a rapid increase in temperature caused changes in the locomotor parameters of the escape response - distance and escape velocity - of white seabream, but not in the non-locomotor elements - responsiveness, directionality and latency. Changes in locomotor parameters with temperature must be associated with an increase in the muscle shortening speed, which contributes to an increase in muscle power and, consequently, a greater locomotor performance (Wakeling *et al*., 2000), which corroborates the higher maximum speed and escape distance observed in the current study after a rapid increase in temperature. These results contradict those obtained by Allan *et al* (2017) in the tropical ward's damselfish (*Pomacentrus wardi*), in which the authors found a tendency to reduce the maximum speed (from values close to 0.45 m s^{-1} to 0.3 m s^{-1}) and the escape distance (from 30 cm to 20 cm) with increasing warming. The authors argue that the decrease in maximum speed and escape distance is related to the rapid increase in SMR and maintenance, or slow increase in MMR, which in turn will reduce the Aerobic Scope and, consequently, decrease the energy available for all processes that are not related to homeostasis, which include the locomotor parameters of the escape response (Domenici *et al*., 2019). In fact, several studies in tropical fish species have reported an increase in the SMR, between 67% and 100%, with a rapid increase of 3°C - lemon damsel (*Pomacentrus moluccensis*) (Grenchik *et al*., 2013), yellowstriped cardinalfish (*Ostorhinchus cyanosoma*), and doederlein's cardinalfish (*Ostorhinchus doederleini*) (Nilsson *et al*., 2009). Even higher increases in SMR have been reported - Munday *et al* (2009) found, in yellowstriped cardinalfish and doederlein's cardinalfish, a 122% increase in SMR (from 225 mg O_2 Kg^{-1} h^{-1} to 500 mg O_2 Kg^{-1} h^{-1}), with the same 3 °C increase. This was not the case in our current study, where we only observed a slight increase in SMR after an acute exposure to +3 °C. Similarly, Kemp (2009) reported, in white seabream adults subjected to an acute increase of 6 °C, a trend (not significant) of increasing SMR, from 0.362 mg O_2 $g^{-0.86}$ h^{-1} to 0.440 mg O_2 $g^{-0.86}$ h^{-1}. The literature suggests that the most significant effects of temperature increase will be on tropical species, because the thermal regime they live in are closer to their thermal limits (Sunday *et al*., 2011; Rummer *et al*., 2014). The limited temperature effect on SMR, observed in our study, is supported by the Q_{10} value (2.25) obtained after the acute temperature increase, which suggests that the white seabream is thermally sensitive to temperature. This value is in line with the Q_{10} values obtained in this species (2.07) (Kemp, 2009), but also in other species which also use the intertidal regions, such as the goby *Caffrogobius caffer* (1.82) (Kemp, 2009), the giant goby (*Gobius cobitis*) (2.10) (Berschick *et al*., 1987) and the rockpool blenny (*Hypsoblennius gilberti*) (2.30) (Graham, 1970). Nevertheless, the effects of acute temperature increase on metabolism were less significant compared to tropical species, which Q_{10} values range between 4.2 and 5.7 (Nilsson *et al*., 2009).

Contrary to what has been described in the literature, the responsiveness, directionality and latency did not differ with temperature. Szabo *et al* (2008) and Warren *et al* (2017) described that the increase in temperature will generate a greater responsiveness due to changes in the balance between excitatory and inhibitory synaptic transmission. However, the observed tendency for a reduction in responsiveness may suggest a decrease in overall activity, as proposed by Yocom & Edsall (1974) and Webb & Zhang (1994).

Interestingly, the results of the present study suggest that white seabream will be able to fully compensate the acute thermal effects on locomotor parameters and SMR after prolonged exposure to 22 °C. After 4-weeks of exposure, the maximum acceleration, escape distance and SMR approached the values obtained at ambient temperature, suggesting the existence of a thermal acclimation. The literature clearly points out that prolonged exposure to high temperatures will contribute to the acclimation of SMRs, by increasing mitochondrial efficacy (Perry & Gilmour, 2010), as has already been verified in Atlantic halibut (*Hippoglossus hippoglossus*) (Gräns *et al*., 2014), shorthorn sculpin (*Myoxocephalus scorpius*) (Sandblom *et al*., 2014), egyptian mouth-brooder (*Pseudocrenilabrus multicolor*) (McDonnell & Chapman, 2016) and three-spined stickleback (*Gasterosteus aculeatus*) (Pilakouta *et al*., 2020). There are also evidences of thermal acclimation of the locomotor parameters of the escape response. Johnson & Bennett (1995) demonstrated that goldfish (*Carassius auratus*) can compensate the effects of high temperature exposure on escape velocity, after 4-weeks of exposure. Similar results were observed in golden gray mullet (*Chelon auratus*) and trinidad guppies (*Poecilia reticulata*), in which it was found that the escape velocity did not differ between fish acclimated to different temperatures, which indicates the existence of full compensation after 30 to 70 days of exposure (Muñoz *et al*., 2012; Killen *et al*., 2015). Nevertheless, there are also signs of lack of acclimation. For example, in the common carp (*Cyprinus carpio*), after 2-weeks of exposure to high temperatures, changes in muscle fiber levels were induced, and thermal acclimation was not achieved (Wakeling *et al*., 2000). Thermal acclimation, despite all the costs involved, namely the lower investment in other activities, will allow the conservation of fitness that will be essential for adapting to a changing environment (Angilletta *et al*., 2003; Donelson *et al*., 2011). However, this regulation will only be possible if the temperature change occurs within the thermal range of the species (Evans, 1990).

The Q_{10} value also supports the thermal acclimation hypothesis of white seabream at elevated temperatures. After 4-weeks of exposure, a Q_{10} value of 1.05 was obtained, which, being close to 1, suggests an independence between metabolic rates and temperature (Farrell, 2011; Seebacher *et al*., 2015). This value also suggests that temperature may not have a significant effect on physical condition through changes in metabolism, as this would be associated with values greater than 2 (Sandblom *et al*., 2014). In fact, we did observe a significant increase in weight after the acute temperature increase, at which point Q_{10} value reached 2.25. Most species have a thermal range, in which a slight increase in temperature may be beneficial to the body condition through greater energy supply, greater number of substrate-enzyme complexes and higher rates of diffusion (Takasuka & Aoki, 2006). However, if the increase in temperature exceeds higher pejus temperatures, the condition may be negatively affected by the existence of a cardiac output unable to support high metabolic rates (Neuheimer *et al*., 2011).

After 4-weeks of exposure, no differences in weight and total length were observed between temperature conditions. Since the literature suggests that the increase in temperature will contribute to an increase in growth rates (Brander, 1995: Green & Fisher, 2004), we were expecting to have larger fish at 22 ºC. The lack of differences in total length may then suggest that the costs associated with establishing acclimation may be involving a lower energy investment in body growth (Angilletta, 2009; Donelson *et al*., 2011).

Reducing food availability did not affect fish escape response within each temperature treatment, however it significantly decreased SMR at 22 ºC. This shows that the escape response is maintained even if metabolic changes related to food limitation are taking place (Domenici & Blake, 1997; Yan *et al*., 2015). This maintenance, namely of locomotor parameters, may indicate the absence of differences, between feeding conditions, in the concentration of ATP, PCr and glycogen, which are the main energy sources used during the escape response (Kieffer *et al*., 1997; Kieffer, 2000). Thus, the results obtained suggest that white seabream larvae, subject to reduced food availability, do not exercise energy conservation and have the ability to preserve the anaerobic capacity, as a way to ensure the escape of predators in famine circumstances (Skajaa & Browman, 2007; Gingerich *et al*., 2010). However, it must be hypothesized that a 50% reduction in food availability may have not been enough to change the condition and behaviour of this species. Although food shortage did not induce changes in the escape response, by itself, the interaction of high temperature and reduced food availability significantly increased latency compared to the control treatment (19°C + *ad libitum*). We discuss this result in the light of the energy-saving hypothesis, which suggests that under stressful conditions, individuals can model their response, namely by increasing latency, if they do not consider the stimulus as a high-threat risk factor, in order to conserve energy (Ramasamy *et al*., 2015). In the current study, the stimulus intensity may not have been considered a high threat factor.

The exposure to different food levels was limited to 4-weeks, and it is likely that a longer exposure duration would lead to different results, as the effect of food availability may only be felt after 30 days of exposure (Skajaa & Browman, 2007). Sullivan & Somero (1983) demonstrated in sablefish (*Anoplopoma fimbria*), that after 24-weeks of food restrictions, the activity of Lactate Dehydrogenase and Pyruvate Kinase (enzymes associated with white muscles, fundamental in anaerobic swimming) was reduced by 75%. Likewise, Yang & Somero (1993) demonstrated in California scorpionfish (*Scorpaena guttata*) and shortspine thornyhead (*Sebastolobus alascanus*), that the concentration of anaerobic enzymes was significantly reduced after 90 to 115 days of exposure. Thus, we can hypothesize that an increase in duration of food restrictions will contribute to the change in the activity of anaerobic enzymes associated with white muscles, structural degradation of muscle proteins and atrophy of muscle fibers, which will prevent muscle contraction, ultimately affecting escape response performance (Gingerich *et al*., 2010; Killen *et al*., 2014).

The reduction in food availability led to a decreasing trend (22%) of the SMR at 19 °C. These results are less meaningful than those obtained in species of the Cyprinidae family, which show a 40% reduction in SMR in individuals kept under food restrictions conditions (Wieser *et al*., 1992); in the rainbow trout (*Oncorhynchus mykiss*), in which 68% reductions in resting oxygen consumption were described (Alsop & Wood, 1997); and in California scorpionfish and shortspine thornyhead, in which 60% and 66% reductions in resting oxygen consumption were reported, after 90 to 115 days of exposure, respectively (Yang & Somero, 1993). The interaction of food limitation and high temperature had a significant effect on SMR, with almost 35% reduction compared to fish fed *ad libitum* at 19 °C. These results are in line with those obtained in juveniles of european perch (*Perca fluviatilis*), in which there was a 57% reduction in resting oxygen consumption after 14 days of exposure to high temperatures and food restrictions (Mehner & Wieser, 1994). This suggests that fish regulate their metabolic rates depending on the food availability and/or temperature, to minimize the effects on body condition (O'connor *et al*., 2000). The difference in SMR effects between species can be explained by more or less significant effects of food availability on the biochemical composition of tissues, on the reduction of the relative size of certain organs and on the synthesis and turnover of proteins and cellular components (O'connor *et al*., 2000). This decrease in the volume of certain organs and protein synthesis may also contribute to the loss of physical condition.

Contrary to our expectations, the total length and weight did not differ between the two feeding conditions. It is likely that these two variables may have been significantly reduced soon after the introduction of food restrictions, as described by Ziegelbecker & Sefc (2021). But later growth rates and weight have increased to values close to *ad libitum* treatments, suggesting that white seabream larvae invested in body condition, perhaps through a reduction of activity levels, which is consistent with the need to reduce risks of predation (Ziegelbecker & Sefc, 2021). Unfortunately, we did not assess fish activity levels under the different treatments, therefore we can only speculate that individuals under food restrictions and high temperature were less active as a saving-energy strategy. Prolonged exposure to food restrictions may also have allowed individuals to adapt to these conditions, through greater digestive efficiency (Kotrschal *et al*., 2014) or adjustments in metabolic rates (O'connor *et al*., 2000). However, we can also hypothesize that a 50% reduction in food availability may not be sufficient for stress levels to be significantly higher than those of *ad libitum* treatment. The increase in stress levels may indicate an increase in cortisol levels, which, by presenting a high affinity for hepatic receptors, may contribute to an increase in the catabolism of carbohydrates and amino acids in the liver and muscles, leading to a loss of physical condition (Boon *et al*., 1991; Gingerich *et al*., 2010). The absence of differences in cortisol concentration between feeding conditions, has already been demonstrated in chinook salmon (*Oncorhynchus tshawytscha*) (Barton *et al*., 1988) and white sucker (*Catostomus commersonii*) (Bandeen & Leatherland, 1997).

Mortality was higher in short fed treatments, ranging between 10% and 18%. This indicates that food availability plays a more important role in survival than temperature, but the combined effect of these two drivers significantly increased mortality rate. Exposure to low food availability, in addition to affecting the synthesis of cellular components and internal organ volume, will contribute to the atrophy of adipose tissues and reduced immune capacity, which will have an impact on growth and survival in the early stages of development (Park *et al*., 2012). This reduction in immune capacity will be particularly relevant given the increased development of pathogens at high temperatures (Martins *et al*., 2011). The interaction of reduced food availability with increasing temperature on SMR might further contribute to increased oxidative stress and mortality, through lactic acidosis and heart failure (Farrell, 2009; Bignami *et al*., 2017).

Conclusion

The main objectives of this study were to: 1) evaluate the acute response to temperature increase; 2) analyze the potential for acclimation to increased temperature; and 3) evaluate the effect of temperature and food availability, as individuals and interacting factors, on escape response and Standard Metabolic Rate.

The results obtained show that the acute increase in temperature increases the locomotor parameters of the escape response, but does not significantly affect the non-locomotor parameters and SMR. After prolonged exposure to 22 °C, the locomotor parameters and SMR approach the values obtained at ambient temperature, suggesting the existence of an acclimation process. The escape response is maintained under conditions of reduced food availability, at both temperatures. However, the interaction of this stressor with increasing temperature significantly increased latency and reduced SMR. This indicates the existence of a metabolic regulation for the maintenance of the body condition.

Altogether, this study suggests that white seabream may be able to preserve its predator-prey relationships, but will undergo metabolic changes with variations in temperature and food availability. However, the results here obtained are quite conservative, as the temperature level selected as high (22 ºC) is still within the thermal regime that the species may experience in the natural habitat. Temperature was a driver for biological changes in our case, but future extreme temperature conditions might actually act as a true stressor, inducing much severe and negative consequences for fish (Boyd & Hutchins, 2012). Therefore, it would be important for future experiments to include a greater thermal amplitude, in which 3 temperature treatments would be used: 19 °C (current average temperature), species threshold temperature (which would represent future average temperature), and +3 °C than current maximum temperature (which would represent a stress response to ocean warming). Also, from the perspective of future work, it would be relevant to assess at what rates the acclimation process occurs. Species with faster acclimation rates will be able to adapt better to the rapid rise in temperature and present a competitive advantage, in relation to species with slower acclimation rates (Angilletta, 2009). It would also be important to evaluate the escape response in white seabream as a group, considering that it is a species that lives in schools (Froese & Pauly, 2019). In addition, it would be relevant to determine how predators will respond to climate change in terms of predator-prey interactions (capture rates, attack rates and maximum speed reached during attack) and metabolism, and to develop a broader multi-stress analysis (Domenici *et al.*, 2019). Moreover, climate change will not only involve changes in temperature and food availability, but also changes in $p\text{CO}_2$ and dissolved oxygen. Thus, the results obtained represent only the tip of the iceberg when it comes to the effects of environmental changes on the escape response and SMR. The action of climate change will have profound effects on behaviour and physiology in the early stages of development, which will affect the structure and dynamics of populations and, ultimately, lead to the disappearance of species unable to adapt.

Ethics statement

This study was performed under approval of DGAV (permit 0421/000/000/2020) and according to the University's animal ethics guidelines.

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Attachments

I-State of art

1. Ocean warming and impacts on physical, chemical and biological ocean processes

Human action has strongly influenced the climate through the emission of polluting gases, such as carbon dioxide and methane, which originate from the burning of fossil fuels, agriculture, and deforestation (Koerner & Klopatek, 2002; Caro *et al*., 2014; Pearson *et al*., 2017). These gases contribute to the greenhouse effect by preventing the dissipation of heat that is reflected on the surface of the planet (Figure 14) (Houghton, 2009). Carbon dioxide, in particular, accounts for 77% of the anthropogenic greenhouse effect (Laffoley & Baxter, 2016). The Intergovernmental Panel on Climate Change (IPCC) reports a global temperature rise of 0.85 °C since the end of the 19th century and an acceleration of this warming rate over the last three decades, of around 0.2 °C per decade (IPCC, 2014). This extra heat is mostly absorbed by the ocean, initially by the surface layers, but slowly this heat will move to deeper waters (IPCC, 2014). IPCC projects that ocean temperature can increase 1 to 4 °C until the end of this century, depending on the RCP (representative concentration pathway) scenario (IPCC, 2014).

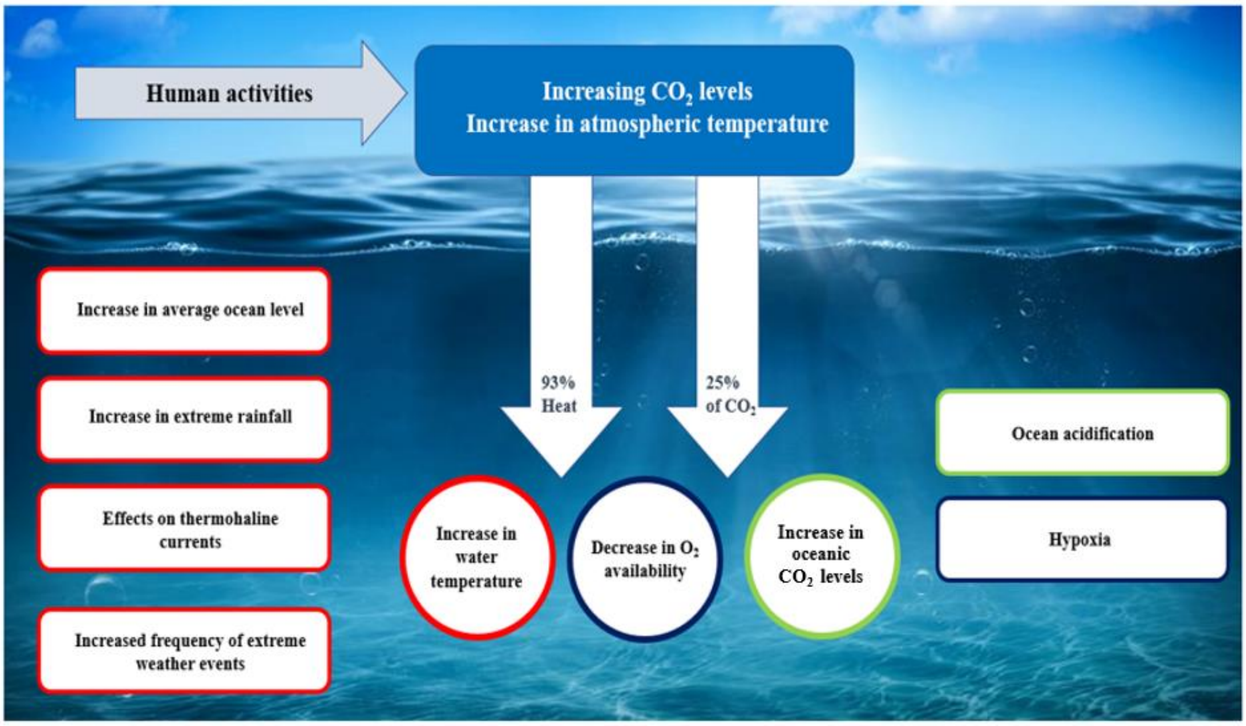

Figure 14 - Abiotic changes caused by climate change.

The distribution of this extra heat will not be uniform across the planet, and it is expected that the northern hemisphere and tropical regions will suffer from a higher warming (Laffoley & Baxter, 2016). Data collected between the beginning of the 19th century and 2001, showed a greater heating tendency in the oriental tropical Atlantic (1.2 - 1.6 °C), while the tropical regions of the Indian and Pacific suffered an increase between 0.8 and 1 °C (NOAA, 2020). Changes in ocean temperature will have vast consequences on the physical and biogeochemical processes, including the increase in frequency of extreme phenomena and the rise of sea level (Webster *et al*., 2005; Poloczanska *et al*., 2009; Min *et al*., 2011), resultant from the melting of the polar ice caps and thermal expansion of the water (Kuhlbrodt & Gregory, 2012; Chen *et al*., 2013). During the 20th century, the sea level rise was about 1.7 mm / year, however in this century it is expected that the increase will be faster, reaching up to 0.5 to 0.8 meters by 2100 (Rahmstorf, 2007; Herr, 2009). Rising sea levels are the main threat to coastal ecosystems and will cause a reduction in water quality, eradicate nursery areas for many fish and crustacean species, reduce biodiversity and release a large amount of stored CO_2, as a result of melting ice caps, thus intensifying global warming (Ewel *et al*., 1998; Nagelkerken *et al*., 2008).

The combined action of temperature with melting sea ice and increased precipitation may affect thermohaline currents, by slowing or blocking them (Marotzke, 2000; Clark *et al*., 2002; Latif *et al*., 2006). This may prevent oxygenated surface waters from moving to depth, which will have strong implications for life in deep environments (Matear & Hirst, 2003; Vaquer-Sunyer & Duarte, 2008; Henson *et al*., 2017; Breitburg *et al*., 2018). There will also be a reduction in the concentration of dissolved O_2, due to the inverse correlation that warmer waters have on O_2 solubility (Matear & Hirst, 2003; Vaquer-Sunyer & Duarte, 2008; Henson *et al*., 2017; Breitburg *et al*., 2018). The reduction in O_2 concentration may have direct consequences on the biogeochemical cycle of nitrogen, iron and carbon (Sarmiento *et al*., 1998; Archer & Johnson, 2000; Zehr & Kudela, 2011; Steinberg & Landry, 2017). When O_2 reaches values below 5 µmol Kg^{-1}, nitrate replaces O_2 as the final electron receptor (Keeling *et al*., 2009), which leads to a loss of nitrogen in the ocean through denitrification and an increase in the supply of nitrate, which is an element that inhibits primary production (Keeling *et al*., 2009). Productivity may also be affected by the increase in ocean stratification, which will restrict the supply of nutrients to photosynthetic organisms (Dave & Lozier, 2010; Lozier *et al*., 2011; Roxy *et al*., 2016; Henson et al., 2017). This will result in a reduction in the flow of energy to higher trophic levels (Moran *et al*., 2010). Projections indicate that primary productivity will suffer a reduction of 2 to 20% by 2100, in low and medium latitude regions, and an increase in the Arctic and Antarctic Ocean, due to the reduction of sea ice (Doney *et al*., 2012).

These changes in ocean patterns will have major ecological consequences, such as latitudinal shifts, behaviour changes, side effects in reproduction and the destruction of certain habitats, such as coral reefs (Laffoley & Baxter, 2016; Alfonso *et al*. 2021).

2. Consequences of ocean warming on marine organisms

The increase in water temperature will have direct and indirect effects on a wide variety of marine organisms, spanning from corals, seabirds and marine mammals (Hoegh-Guldberg, 1999; Hughes *et al*., 2003; Berteaux *et al*., 2006; Learmonth *et al*., 2006; Pankhurst & Munday, 2011; Sydeman *et al*., 2012). Corals develop under conditions close to their maximum temperature limits, which maximize reproduction and growth (Rodolfo-Metalpa *et al*., 2008). However, if the temperature exceeds these limits, corals will be subjected to the bleaching process, which have the potential to affect reproduction, growth, increase susceptibility to disease and ultimately lead to death (Hoegh-Guldberg *et al*., 2007). These events will reduce coverage and change the three-dimensional structure of coral reefs, thus eliminating the habitat of numerous resident species and increasing coastal risks in face of climatic phenomena (Baker *et al*., 2008). Unlike corals, the impacts of climate change on marine mammals will be more difficult to predict, given the dependence on multiple factors, such as the temporal and geographic scales at which these changes occur, longevity and generation time (Evans & Raga, 2012). However, it is expected that with increasing temperature there will be an increase in the development of pathogens, a greater susceptibility of hosts to infectious agents and the loss of breeding, resting and feeding habitats, due to the rise in sea level (Harvell *et al*., 2002; Derocher *et al*., 2004; Ferguson *et al*., 2005). But the main threat will be changes predicted to occur at the level of biological productivity, as a result of changes in the upwelling process in coastal areas, in mix of nutrients and currents (Evans & Bjørge, 2013). The reduction in nutrient availability will hamper the growth of phytoplankton, which will have a cascading effect across the food web, particularly affecting species with very restricted diets (Simmonds & Isaac, 2007). In view of this, many marine mammals may change their geographic distribution (Evans & Raga, 2012). However, species with limited geographic distributions may not be able to follow food availability (Moore & Huntington, 2008). This change in prey distribution is the main effect of climate change on seabirds as well (Laffoley & Baxter, 2016).

2.1 Consequences of ocean warming on fish

Fish are also likely to change their geographical distribution in response to water temperature, which will change the composition of communities (Poloczanska *et al*., 2013). Globally, the communities' structure is expected to be tropicalized, or redefined, as warm water species are expected to become more abundant in temperate regions, and temperate species decrease their density or move to higher latitudes (Vergés *et al*., 2019). Projections for more than 800 invertebrates and fish species indicate that the latitudinal distribution of organisms could be altered between 10 and 100 km per decade, in a more extreme climate change scenario (Jones & Cheung, 2015). The arrival of new species in temperate and subpolar regions will have a strong impact on marine ecosystems and trophic webs, as they can exert strong predation, herbivory or competition with local species (Vergés *et al*., 2014). Also, some predator species may lose their food sources as their prey migrates to higher latitude regions (Vergés *et al*., 2014). Changes in water temperature will exert their effects at several organism-levels. In fish, higher temperature may have effects on reproductive processes through the hypothalamus-pituitary -gonadal axis (HPG axis) (Pankhurst & Munday, 2011). This complex is responsible for the release of gonodotrophic hormones into the gonotrophic cells of the hypophysis, which stimulate the synthesis and consequent release of the Luteinizing hormone (LH) and the Follicle-Stimulating hormone (FSH) (Zohar *et al*., 2010), responsible for controlling maturation events and stimulating early stages of gametes development, respectively (Pankhurst & Munday, 2011). With increased temperature, the action of the endocrine system may be compromised due to conformational changes in LH, FSH, its receptors and a set of enzymes important to steroid hormone synthesis, causing its inhibition (Pankhurst & Munday, 2011).

Alternatively, temperature can act on reproduction by activating a hormone-mediated stress response (Miller *et al*., 2015). Stress promotes the activation of a catecholamine-measured response and longer activation of the hypothalamus-pituitary-interrenal axis (HPI axis) (Pankhurst *et al*., 2011). This will lead to an increase in blood levels of 1alfa-hydroxycorticosterone in elasmobranchs and steroid cortisol in teleosts (Pankhurst *et al*., 2011). In the short term, exposure to high concentrations of steroid cortisol results in increased energy availability, but in the long term may have suppressor effects on immunological functions, growth and reproduction (Espelid *et al*., 1996; Schreck *et al*., 2001). However, there is no scientific consensus on the effects on the HPI complex and consequently on reproduction (Pankhurst & Munday, 2011). Studies in *Salmo salar* (Pankhurst & Munday, 2011), *Cyprinus carpio* (Pankhurst *et al*., 1995), *Carassius auratus* (Lister *et al*., 2008) and *Pagrus auratus*

(Pankhurst *et al.*, 1995) shows that cortisol does not affect steroid hormone levels and consequently reproduction, which contradicts data obtained for *Oreochromis mossambicus* (Foo & Lam, 1993) and *Salmo truta* (Schreck, 2010).

Temperature plays a crucial role in fish early life stages, and eggs are perhaps the most heat sensitive stage (Rombough, 1997). Thus, as the oceans heat up, egg mortality will increase significantly, especially in tropical species whose thermal limits are closer to being reached (Figueira *et al*., 2009). This will happen unless fish adapt their spawning time so that embryonic development occurs at an optimal temperature (Pankhurst & Munday, 2011). Such changes seem quite likely to occur, as gametogenesis is temperature-dependent in a wide variety of species and reproduction can be inhibited long before the thermal limits for egg survival are reached (Pankhurst & Munday, 2011). The effects of ocean warming are not limited to direct egg mortality, but can also increase embryonic development rates (Kucharczyk *et al.*, 1997). This acceleration in development will imply a reduction of the incubation period, which is also dependent on the size of the eggs (larger eggs have larger incubation periods) (Pankhurst & Munday, 2011). Thus, climate change may shorten the incubation period by minutes or hours in small eggs, and hours or days in larger eggs (Rombough, 1997). This effect will be more significant in high latitude species with longer incubation periods (Rombough, 1997). Reduction of embryonic development will have effects on larval survival, as hatching may occur in a non-optimal period, such as periods of greater predation or lower food availability (Pankhurst & Munday, 2011).

Temperature can affect several aspects of larval stages, namely larval phase duration, metabolism and growth (Benoît *et al.*, 2000). Growth rates will increase with warming, and studies have shown that temperature can explain 90% of the variation in growth rates in some cohorts of certain species (Sponaugle & Cowen, 1996; Green & Fisher, 2004). Acceleration of growth will reduce the period until yolk sac absorption, metamorphosis and pelagic larval phase duration (PLD) (Pankhurst & Munday, 2011). The relationship between PLD and increased growth rates will have a strong influence on the size of individuals at the time of settlement and confer a survival advantage, as predation rates at this stage are the highest in the entire fish life cycle (O'Connor *et al.*, 2007). The effects of temperature on PLD will be more pronounced in cold water species, however tropical species may see their pelagic larval phase reduced between 4 and 8% at each 1°C increase (Munday *et al.*, 2009).

Moreover, as already mentioned, metabolism is likely to be altered, as climate change intensifies (Doney *et al.*, 2012). Metabolic rates (i.e. oxygen consumption per mass unit) will increase with ocean warming, and organisms may need to increase food intake to overcome such metabolic needs (Pankhurst & Munday, 2011). In face of sharp rises in temperature, increased metabolism and dietary needs can affect marine species at the level of recruitment, making it variable or inhibiting it (Sponaugle & Cowen, 1996). If there is no increase in food consumption, there may be a decrease in activity levels, which in turn may affect routine swimming, food search (Nowicki *et al*., 2012) and social behaviour (Bartolini *et al*., 2015).

2.1.1 Effects of warming on fish aerobic metabolism

Most marine species are ectotherms, whose biochemical reactions, cellular processes and, consequently, metabolism are dependent on environmental conditions (Angilletta *et al*., 2002; Schulte, 2015). Aerobic Scope is defined as the difference between the Maximum Metabolic Rate (MMR) and the Standard Metabolic Rate (SMR), and represents the energy available to support all processes beyond basic requirements, such as reproduction, digestion, locomotion and growth (Auer *et al*., 2015A; Auer *et al*., 2015B; Norin *et al*., 2019). The SMR refers to the minimum metabolic rates that guarantee life without affecting the cellular level (Weibel *et al*., 2004; Norin & Malte, 2011). MMR, on the other hand, is defined as the maximum energy that can be metabolized aerobically by an individual and marks the transition to anaerobic metabolism, as a result of intense efforts with reduced flow of O_2 (Weibel *et al*., 2004; Norin & Malte, 2011). Changes in oxygen consumption may arise due to variations in the size of individuals or environmental conditions, such as hypoxia and temperature (Clarke & Johnston, 1999; Pörtner & Peck, 2010).

The increase in temperature is expected to increase the SMR, through the development of a series of physiological responses used to counter environmental changes (Chabot *et al*., 2016). MMR will also increase with warming, however at a slower rate than SMR (Chen *et al*., 2015). This will reduce the Aerobic Scope strip and reduce the energy available for many functions (Pörtner & Knust, 2007).

The oxygen and capacity limited thermal tolerance (OCLTT) hypothesis, developed by Pörtner & Knust, (2007), assumes that the performance of the Aerobic Scope has an asymmetric temperature-dependent curve and that the oxygen supply becomes limited in extreme thermal conditions (Figure 15) (Schröer *et al*., 2009). The acquisition of O_2 is maximized between lower and upper pejus temperatures (T_p) (temperature that marks a significant reduction in the Aerobic Scope), ensuring the normal functioning of vital processes, such as reproduction and feeding (Pörtner, 2010). Next to the upper pejus temperature is the optimum temperature (T_{opt}) of the Aerobic Scope, in which the individual reaches the maximum fitness (Norin *et al*., 2014; Norin *et al*., 2019). However, organisms spend a short period of time at T_{opt} during their life cycle because it is not necessary for the most carried out activities (Farrell, 2016).

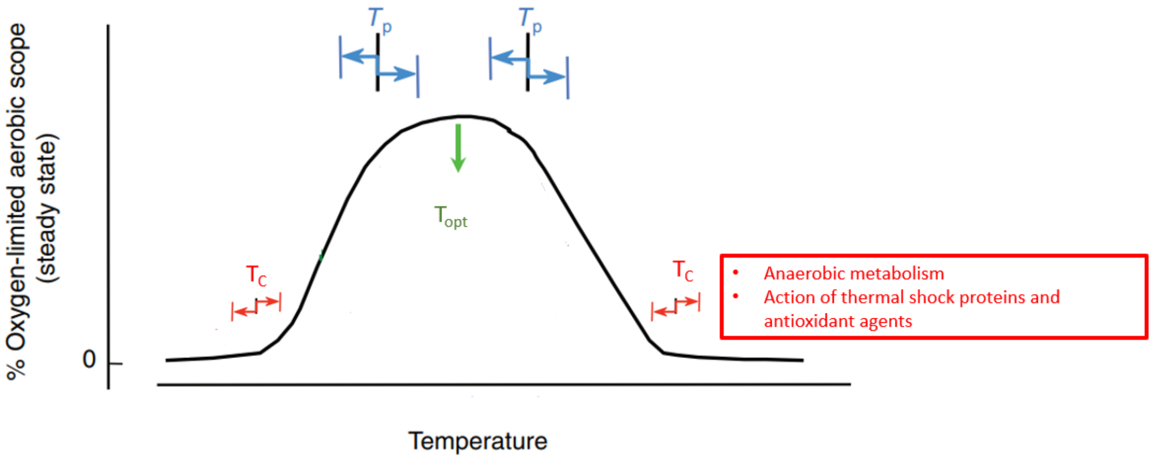

Figure 15 - Model proposed by the OCLTT hypothesis and the performance range of the species *Zoarces viviparus*. T_p- pejus temperature; T_{opt}- optimal temperature and T_c-critical temperature (figure adapt from Pörtner & Knust, 2007).

When T_p are exceeded, circulatory and respiratory systems are no longer able to respond to oxygen needs (Lannig *et al*., 2004). Thus, there is a progressive loss of fitness as the Aerobic Scope is reduced (Nilsson *et al*., 2009; Rummer *et al*., 2014). When the critical temperature (T_c) is reached, the Aerobic Scope reaches a value equal to zero and there is a transition to anaerobic metabolism and cell and membrane impairment (Pörtner, 2010). To counteract this reduction in structural integrity, antioxidant defenses and heat shock proteins are produced, but whose action is short-lived (Pörtner, 2010). The temperature at which the different processes occur will vary between species through the ability to deal with extreme conditions, geographic distribution and migratory efforts (Auer *et al*., 2015B; Norin *et al*., 2019). The temperature can be readjusted throughout the life cycle, as a result of the type of habitat (shallow water or deep water) and also the abundance and quality of food (Farrell, 2016). During periods of hunger there is a decrease in oxygen consumption and activity, to conserve energy reserves (Cook *et al*., 2000). The lack of food may also act on the Aerobic Scope by slowing the growth rates, thus allowing to maintain the ability to obtain O_2 from the environment (Audzijonyte *et al*., 2019; Meyer & Schill, 2020).

Currently the scientific community is divided on the acceptance of the OCLTT hypothesis. This controversy arises due to the uncertainties that the mechanisms associated with this hypothesis prevail in ectothermic species with increasing temperature, especially in the long-term (Jutfelt *et al*., 2018). It has already been shown, in species subject to acute thermal effects, that the limitation of oxygen in tissues can be determinant in the deterioration of the performance of organisms (Claireaux & Lefrançois, 2007; Pörtner & Knust, 2007). However, several of the studies not cited by Pörtner do not support oxygen limitation as a key factor in species performance, stressing that the OCLTT hypothesis is not universal (Clark *et al*., 2013; Jutfelt *et al*., 2014; Schulte, 2015).

This hypothesis has several limitations associated with its development, namely the lack of scientific evidence to support certain assumptions, the existence of ill-defined concepts (e.g pejus temperature) that make biased analyzes favorable and the assertion that oxygen limitation is the main cause of the effect on reproduction, growth, among other factors, has not been empirically proven (Jutfelt *et al*., 2018). In addition, Pörtner *et al* (2017) points to the OCLTT hypothesis as mechanistic, despite the fact that much of the evidence supporting the hypothesis results from correlations between processes, which prevents the determination of the cause-effect relationship. Recent studies have supported the existing doubts regarding the OCLTT hypothesis (Jutfelt *et al*., 2018). Through meta-analyses, Lefevre (2016) failed to define optimal temperatures for the Aerobic Scope in various species after acute and long-term exposures, which negates one of the fundamental principles developed by Pörtner. Brijs *et al* (2015) and Ern *et al* (2016) demonstrated that manipulation of O_2 levels had no effect on thermal tolerance until low critical oxygen levels were achieved.

In conclusion, there is no consensus regarding the OCLTT hypothesis. Although there is some scientific evidence that supports the hypothesis, many studies contradict the assumptions developed by Pörtner. It is, therefore, essential that the OCLTT hypothesis is revised, and its assumptions clarified so that they can be experimentally tested.

2.1.2 Effects of warming on fish behaviour

The first response by animals to a changing environment is predominantly through modification of their behaviour, which in turn has the potential to affect species interactions and ecological processes (Candolin & Wong 2012). Avoiding predators is crucial to individual fitness and survival, and it has been shown that increasing temperature can substantially impact the behaviour and locomotor performance components of escape response in fish (Allan *et al*., 2017; Domenici *et al*. 2019). Escape response is an essential element in the anti-predatory mechanisms of a wide variety of species (Domenici, 2010). As a result, it has been studied in several scientific areas, including biomechanics, neurophysiology, behavioural ecology and kinetics (Eaton *et al*., 2001). Initially it was assumed that the escape response was a stereotypical behaviour, with little variation between species and the performance to be maximized by natural selection (Marras *et al*., 2011). However, the intensification of studies demonstrated that it is a highly varied process among its components, with coefficients of variation between 20 and 40% (if stereotyped it would be close to 10%) (Domenici & Kapoor, 2010).

This anti-predatory mechanism is described as having three phases: phase 1 - the body folds with a minimum translation of the center of the body; phase 2 - second curvature of the body and adjustment in the escape trajectory; and phase 3 - the individual develops a continuous swim, however in some cases phase 2 may be absent (Domenici, 2010; Domenici & Hale, 2019). The first two phases are controlled by Mauthner Cells/M Cells (reticulospinal neuron pair) and their associated systems, which receive sensory inputs from different sources and develop an adequate response to stimulus (Zottoli & Faber, 2000; Preuss & Faber, 2003; Kohashi & Oda, 2008). During the first phase, two movement patterns can be generated, C-Start and S-Start, which have distinct motor systems (Figure 16) (Hale, 2002).

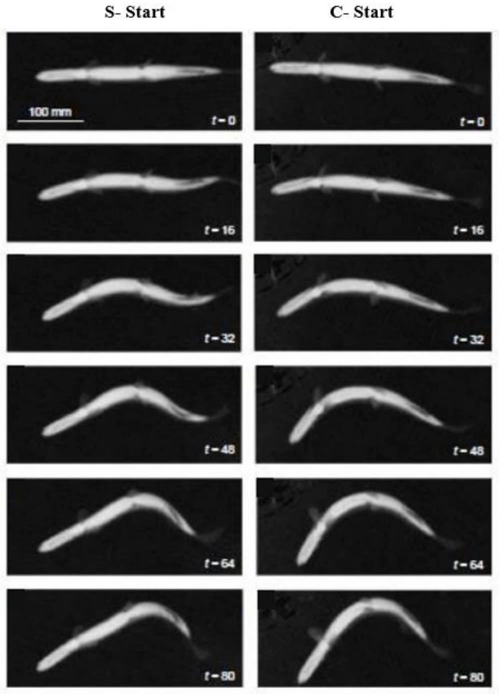

Figure 16 - Motion patterns associated with escape response. Start of the S-Start (top, left) and C-Start (top, right) movement (Domenici & Hale, 2019).

C-Start is described as a C-shaped body flexion resulting from a unilateral contraction (Bohórquez-Herrera *et al*., 2013). In the occurrence of a stimulus only the nearest Mauthner cell is activated, with the production of a single action potential (Domenici & Hale, 2019). The activity of the Mauthner Cell is propagated along the axon, passes through the spinal cord and stimulates motor neurons and interneuron (Preuss & Faber, 2003; Liao & Fetcho, 2008). The spinal cord's commissural neurons will inhibit the activation of contralateral neurons from the same site (Satou *et al*., 2009). All this complex mechanism will lead to a C-shaped curvature of the body and allows the individual to move away from the threat (Domenici & Hale, 2019). This movement pattern, despite being a characteristic element of the escape response, can also be observed in routine swimming and sustained swimming (swimming that occurs for more than 200 meters) (Webb & Fairchild, 2001).

S-Start is a movement not as frequent as C-Start and consists in the development of an S-shaped body curvature, in which the head and the tail fin are positioned in opposite directions (Fashingbauer *et al*., 2019). Unlike C-Start, S-Start Mauthner cells are activated simultaneously and bilaterally by a stimulus in the caudal region (Liu & Hale, 2017). In the spinal cord of this same region, the stimulus will trigger a rapid response in the local circuits, which inhibits the action of motor neurons and prevents the action potentials of Mauthner cells from generating a caudal flexion (Domenici & Hale, 2019). Thus, the action potential developed by one of the M cells is responsible for the bending that occurs in the caudal region and the action potential of the other Mauthner cell triggers the curvature in the rostral region (Domenici & Blake, 1997; Preuss & Faber, 2003). However, Liu & Hale (2017) came to demonstrate that stimulation in the caudal region could allow the development of C-Start, with unilateral or bilateral activation of M cells.

After development of S-Start or C-Start, phase 2 of the escape response may occur (Domenici & Hale, 2019). This phase is dependent on the occurrence of double-bend (i.e. a new contraction); if only the bending of phase 1 (single-bend) is developed, phase 2 will not occur (Domenici & Hale, 2019). Double-bend responses allow individuals to achieve speeds above single-bend due to additional contraction and bending (Fleuren *et al*., 2018). Thus, although the energy costs of each have never been assessed, double-bends will require greater energy needs (Fleuren *et al*., 2018).

Over the last two decades, the study of escape response has made significant progress towards a more integrated approach to the whole process, including swimming performance and non-locomotive variables (Domenici, 2010; Domenici & Kapoor 2010). Within the non-locomotors components, there is latency (interval between the initiation of the stimulus and the response developed by the individual), the reaction distance (distance between the stimulus and the individual at the start of the escape response), directionality (defined by the movement of the head away or toward the side stimulus) and responsiveness (proportions of fish that responded to the stimulus with C-Start or S-Start) (Fuiman *et al.*, 2006; Domenici, 2010; Domenici & Hale, 2019). These variables will be dependent on multiple ecological and behavioural factors (Domenici, 2010). Among these factors is the approximation speed and frontal profile of the predator (Domenici & Hale, 2019). Slowly approaching predators with a narrow frontal profile are able to catch prey even before they have the ability to react (Domenici & Hale, 2019). The type of stimulus can also influence non-locomotor parameters (Domenici, 2010). For example, Batty (1989) demonstrated that latency to a mechanoacoustic stimulus was significantly lower compared to visual stimuli.

In addition to the factors mentioned above, the non-locomotor variables of the escape response are also dependent on environmental factors, such as oxygen availability and temperature (Preuss & Faber, 2003; Lefrançois *et al*., 2005). It has already been described that the increase in temperature results in greater responsiveness due to individuals becoming hyperexcitable, as a result of the change in the balance between inhibitory and excitatory synaptic transmission (Szabo *et al*., 2008; Domenici *et al*., 2019). However, this hyperexcitability is also observed with the decrease in temperature (Domenici *et al*., 2019).

In view of this hyperexcitability at reduced temperatures, there are changes in the properties of Mauthner cells, namely in the sensory process time that will increase 100% (Domenici, 2010). This, in turn, will increase the latency period, which is also observed with the increase in temperature (Preuss & Faber, 2003; Szabo *et al*., 2008).

Since the latency is highly related to the reaction distance, the increase in temperature will reduce the reaction distance by changing the properties of Mauthner cells, as mentioned above (Allan *et al*., 2017). Temperature increase may also reduce directionality due to a higher neural driving speed that reduces the time between inputs in Mauthner Cells (Domenici, 2010), as demonstrated by Allan *et al* (2017), who reported that 50% of the juveniles of ward's damselfish head in the direction of stimulus when exposed to a 3 °C increase.

3. Plasticity as a response to environmental changes

Given the impact of climate change on behaviour and physiology (as described in the above sections), the persistence of species is dependent on their ability to respond to such changes through latitudinal changes, adaptive evolution or phenotypic plasticity (Hoffmann & Sgrò, 2011; Guillaume *et al*., 2016). Although these are three important mechanisms, latitudinal changes will only be viable if the species has a good dispersal capacity and there are suitable habitats available (Guillaume *et al*., 2016). Adaptive evolution will also have limitations, if populations have high mortality rates during adaptation, population will disappear before a tolerance to the stressor is developed (Bell & Gonzalez, 2009). Thus, phenotypic plasticity may play a key role in the adaptability of organisms (Guillaume *et al*., 2016).

There has been an increased interest in phenotypic plasticity as a way for organisms to maintain and even increase their fitness, in response to increased temperature and acidification (Donelson *et al*., 2011; Bonduriansky *et al*., 2012; Munday *et al*., 2013; Salinas *et al*., 2013). The concept of phenotypic plasticity is based on the recognition of a differential expression of phenotypes through environmental conditions, involving changes in behaviour, morphology and physiology (Angilletta, 2009; Donelson *et al*., 2011). However, these responses to the new environment will depend on the rates at which environmental changes occur (Donelson *et al*., 2016). Gradual changes will allow a better adjustment to existing conditions, while faster changes involved higher energy expenditure associated with a delayed response (Terblanche *et al*., 2007; Chown *et al*., 2009; Peck *et al*., 2009; Donelson *et al*., 2016). Phenotypic plasticity can function as a response to daily or seasonal variations (reversible acclimation) or as a permanent response to environmental conditions (developmental acclimation) (Angilletta, 2009). Developmental plasticity can arise as an intragenerational response, in which the individual responds to the stress factor during one stage of development to improve fitness in the next stage (Angilletta, 2009) or an intergenerational response, which involves a response from parents throughout their life cycle, with the aim of improving the fitness of their offspring (Beaman *et al*., 2016). This fitness improvement is a result of a better nutrition, transmitting hormones, proteins, somatic factors or epigenetic markers, provided by the parents, which improve gene regulation in the new environment (Bonduriansky & Day, 2009; Marshall & Morgan, 2011; Grenchik *et al*., 2013). However, the transmission of these factors can come from both parents or just one of them (Vehmaa *et al*., 2012; Shama *et al*., 2014). Studies already carried out show that parents exposed to conditions of acidification and high temperatures will provide their offspring a greater capacity to tolerate these conditions (Donelson *et al*., 2012; Miller *et al*., 2012; Thor & Dupont, 2015). This suggests that transgenerational plasticity will allow populations to respond to climate change and minimize the bottleneck effect, which is felt in the early stages of development (Munday *et al*., 2013). However, although the phenotypic plasticity provides a better adaptation to the environment, it will involve costs associated with changes in cells and tissues (Angilletta, 2009). Cellular responses include changes in membranes (Hazel, 1995; Crockett, 1998) or the expression of new proteins, namely heat shock, whose functioning involves additional expenditure of energy that could be used for other activities (Angilletta, 2009).

Future research should focus on transgenerational plasticity, with the aim of understanding which phenotypic characteristics will respond transgenerationally, whether the benefits of transgenerational acclimation will be maintained over the long-term, and how transgenerational acclimation will interact with genetic adaptation (Hoffmann & Sgrò, 2011; Munday *et al.*, 2013; Munday, 2014). This will allow us to understand the phenotypic response over several generations and, consequently, understand how species will be affected by climate change (Donelson *et al.*, 2018). However, the results obtained through transgenerational plasticity must be carefully analyzed, so that there is no direct extrapolation that this will be the response of organisms in their natural environment (Donelson *et al.*, 2016). The immediate increase in stress factors to projected values for the future, may not represent the plasticity capacity that will be verified over multiple generations over a period of 50 to 100 years, as the interaction between transgenerational and developmental pathways are not considered (Donelson *et al.*, 2016).

4. Implications of food restriction under ocean warming scenarios

Experimental studies, conducted in lab-controlled environments, represent an extremely valuable tool for a better understanding of the effects of ocean warming on organisms. However, most of the studies are carried out under optimal feeding conditions, which in highly unlikely to occur in the aquatic environment (Batty *et al.*, 1993; Chick & Van Den Avyle, 2000; Lyon *et al.*, 2008; Miller *et al.*, 2015). The phytoplankton concentration will vary regionally and seasonally depending on the availability of nutrients and light radiation, the stratification of the water column, the existence of upwelling processes and the presence or absence of sea ice, which reduces the light reaching the ocean (Fiedler *et al.*, 1991; Wang *et al.*, 2014; Schofield *et al.*, 2018). With the intensification of climate change, there may be an increase in the stratification of the ocean, which will isolate the cold and nutrient-rich waters from the surface layers (Behrenfeld *et al.*, 2006; O'Connor *et al.*, 2009). This will restrict the growth of phytoplankton and limit the biomass of zooplankton, as well as all other organisms inserted in the trophic web (O'Connor *et al.*, 2009).

Herein, food restriction is a phenomenon that many species are subject to throughout their life cycle and is described as having three physiologically distinct phases, which are defined by the type of compounds that are catabolized (Belkhou *et al.*, 1991; Caruso *et al.*, 2010). During phase 1 there is an increase in the catabolism of proteins, fats and glycogen; in phase 2, lipids become the main source of energy; and in phase 3, lipids reach their critical value and protein tissues begin to be catabolized more quickly (Volkoff, 2012). However, the ability to tolerate hunger varies between species, with some tolerating only a few days or weeks, while others, such as *Anguilla anguilla*, are able to survive several years without feeding (McCue, 2010). Currently, there are a large number of studies that analyze the effects of food deficiency on different biological aspects, such as reproduction, growth and development, immune system, behaviour and, above all, metabolism (Sumpter *et al*., 1991; Pulgar *et al*., 1999; Skajaa & Browman, 2007; Caruso *et al*., 2010; Chatzifotis *et al*., 2011; Penghan *et al*., 2016). The most common metabolic response is the mobilization of energy and nutrients that are stored in the muscles and liver, with a reduction in body mass (Volkoff, 2012). The poor body condition may compromise the immune system due to effects on hemolytic activity and reduction of mucus secretion by epithelial cells, which protect individuals from chemical and bacterial injuries (Caruso *et al*., 2010, Caruso *et al*., 2012). The reduction in body mass may also reduce the size of the deposited eggs, which in turn will affect hatch rates and size of larvae at hatch (Pankhurst & Munday, 2011). After hatching, larvae exposed to food restriction most likely become less efficient predators, which will increase energy expenditure and decrease growth rates (Jonas & Wahl, 1998). Furthermore, slower growth will increase the duration of life phases most vulnerable to predation, which may indicate a significant reduction in survival rates (Chick & Van Den Avyle, 2000). The increase in predation rates may also arise from an increase in the duration and extent of demand for food and a decrease in alarm signals, due to the lack of reserves that prevent individuals from investing more energy in anti-predatory signals (Lienart *et al*., 2014; Lienart *et al*., 2016). But it can also result from lapses in the decision-making process, reduced ability to detect predators and escape response performance, namely in responsiveness, escape speed and reaction distance, especially when exposed to long-term food restrictions. (Fuiman, 1993; Jonas & Wahl, 1998; Chick & Van Den Avyle, 2000). Contrary to what happens in escape swimming, sustained swimming will be affected in the short-term through effects on muscle contraction, resistance and alteration of aerobic enzyme activity (Gingerich *et al*., 2010). This will lead to settlement failures, which may reach 80% in some species (Booth & Hixon, 1999).

Future works should address variations in food availability. *Ad libitum* feeding conditions will prevent determining the real impacts of the stressor, as there is no energy expenditure associated with predation, escape from predators, among other factors, and all energy will be used to counteract the stress factor, as mentioned above. At the same time, it will be critical to determine the boundary condition levels at which effects on behaviour and physiology become evident (Skajaa & Browman, 2007).

5. Early life stages as the lifeline

The embryonic and larval phases are marked by rapid development that involves morphological, behavioural and ecological changes, and a high mortality rate that can reach 99% in some species (Gosselin & Qian, 1997; Searcy & Sponaugle, 2001; McCormick & Hoey, 2004). Hence, in this period there is a bottleneck effect that will determine recruitment rates (Almany & Webster, 2006; Jenkins & King, 2006).

Several hypotheses have been established to explain the variability in recruitment, Hjort (1914) proposed that the transition between the depletion of the yolk sac and the beginning of exogenous feeding, is a critical period that would determine the success of recruitment. Later, Cushing (1975) presented the synchrony hypothesis, which explained that the synchronism between the maximum production of larvae and the plankton blooms will allow greater survival and growth of the larvae, and thus guarantee the success of recruitment (Cushing, 1990). Subsequently, predation and growth were integrated as key factors that could influence recruitment (Searcy & Sponaugle, 2001). Houde & Hoyt (1987) proposed the hypothesis of the duration of the larval phase as a key element for recruitment, whose reduction will make the larvae less vulnerable to predation. Miller *et al* (1988) came to demonstrate that mortality is dependent on size. However, none of these hypotheses directly points to abiotic factors as the cause of the variation in larval characteristics and, consequently, recruitment (Nunn *et al*.,2007; Zhang *et al*., 2016).

The first stages of development are particularly sensitive to environmental changes, due to the high surface/volume ratio and inefficient ionic regulation mechanisms, which do not guarantee the maintenance of the internal ionic environment (Falk, 2005; Jonz & Nurse, 2006; Bromhead *et al*., 2015). Many of the physical processes associated with environmental changes have been described as having effects on the survival of eggs and larvae (Peck *et al*., 2012). The increase in temperature during the incubation period will have a strong influence on the growth and swimming ability of the larvae (Vagner *et al*., 2019). Batty *et al* (1993) demonstrated in Atlantic herring (*Clupea harengus*), that an increase of 2 °C above the optimal temperature during the incubation period significantly reduced the swimming capacity. This reduction in locomotor parameters may be associated with the development of skeletal deformations (Dionísio *et al*., 2012) or a reduction in the interval between the time when maximum speed is reached and when fatigue is achieved (Vagner *et al*., 2019). The increase in temperature will also increase development rates, which will reduce the period of greatest vulnerability to predation and, consequently, mortality rates (Sponaugle & Pinkard, 2004). The literature suggests that the increase in development rates will favor recruitment, and it has been verified in several reef species that warm years are associated with good recruitment events (Meekan *et al*., 2001; Meekan *et al*., 2003). However, increasing temperature may also make recruitment variable in some species (Sponaugle & Cowen, 1996). Although development rates increase with temperature, their effectiveness does not, which will imply increase food intake to support increased metabolic rates (Pankhurst & Munday, 2011). This will be particularly difficult as climate change and their effects on productivity advance (Doney et al., 2012). Larvae might be more vulnerable to starvation, which will increase mortality rates and lead to variable recruitment or even recruitment failure (Pankhurst & Munday, 2011). The increase in development rates will decrease the size of larvae at the time of settlement, which will increase mortality in later stages and dilute the reduction in mortality during the larval stage (Sponaugle & Pinkard, 2004). This will imply a reduction in the number of breeding individuals within the population, with consequent impacts on population dynamics (Sponaugle & Pinkard, 2004).

6. White seabream, *Diplodus sargus*

The white seabream, *Diplodus sargus* (Linnaeus, 1758), is a teleost fish from the Sparidae family. It is a bento-pelagic species with a demersal behaviour (Pajuelo & Lorenzo, 2002). This species has an oval body, raised ventrally and a bipartite tail (FAO, 2011). Adults typically range between 15 and 30 cm, however may reach a maximum length of 45 cm (Pavlidis & Mylonas, 2011).

It is a subtropical and temperate species, which has spread along the Mediterranean, Black Sea, Indian and Atlantic coasts, from the Bay of Biscay to Cape Verde and Angola to South Africa, including the Canary Islands and Madeira (Froese & Pauly, 2019). The preferred habitat of *Diplodus sargus* is coastal regions with sandy or rocky backgrounds (Pereira *et al*., 2010). It is commonly found at 50 meters deep in the Mediterranean, however it can reach up to 150 meters (Vaz, 2011). It is an euryhaline species that moves to brackish waters in the spring and returns to the sea in late autumn (Malheiro, 2007).

Juveniles of this species are omnivorous, feeding mostly on amphipods, larvae and algae (Vaz, 2011). Adults are carnivores, feeding preferably on molluscs, algae, polychetes, echinoderms and crustaceans (FAO, 2011). It has already been observed that adults form clusters close to ports, where they feed on fish that are discarded by fishermen (Vaz, 2011). This indicates that adults besides carnivores are also necrophagous (Vaz, 2011).

This species has a gregarious behaviour and adults form quite numerous groups (Froese & Pauly, 2019). Juveniles form smaller groups, between 10 and 30 individuals (Caballero, 2002). Within these groups there is a well-defined hierarchical structure, at least under laboratory conditions, which is affected by socio-environmental factors that can increase the occurrence of aggressive behaviours between elements (Caballero, 2002).

Diplodus sargus is a protandric hermaphrodite species, in which males convert to females when the number of these in the population decreases (Vaz, 2011). This strategy allows to maintain the appropriate proportion of both sexes, thus ensuring reproductive success (Morato, 2003). This reversal of sex begins during the third year and completes in the fifth, being characterized by the degeneration of the male gonads, followed by oogenic development leading to the formation of the oocytes (Lenfant, 2003).

Sexual maturity is reached at 2 years and reproduction occurs between the months of January and June, depending on the location (Vaz, 2011). At lower latitudes it is found that the spawning period starts earlier and extends longer, as the latitude increases the spawning period becomes later and with shorter duration (Morato, 2003). Thus, it is possible to verify that temperature plays a fundamental role in the beginning and duration of reproduction in this species (Morato, 2003). The larvae after one month adrift in their pelagic form, are settle in shallow benthic areas, where they remain for several months (Harmelin-Vivien *et al*., 1995). By reaching 4 to 5 cm in length, juveniles leave the nursery areas and join the adult populations (Lenfant, 2003).

7. Knowledge gaps

The ocean warming is a reality that will bring numerous challenges to marine species, with the increasing frequency of heat wave events and seasonal temperature increase (Alfonso *et al*., 2021). Much progress has been made in understanding how climate change will affect the behaviour and physiology of species, but there is a lack of knowledge about how this will alter species interactions, population dynamics and, ultimately, the structure of communities (Nagelkerken & Munday, 2016). At the species level, studies have mainly focused on the effect of isolated stressors on anti-predatory and foraging behaviour, in small tropical species (Nagelkerken & Munday, 2016). Thus, there is a poor comprehension of the effects of multiple stressors on species from temperate and subpolar regions, and it is not possible to generalize the results already obtained to species from these geographic regions, because the response of organisms is dependent on multiple factors, such as their genetic base, vital history and metabolic abilities (Somero, 2010; Comte & Olden, 2017). In addition, many of the ecological processes associated with climate change (hypoxia and food availability) have not yet been analyzed in detail. In view of all this, it is essential and urgent to develop studies that focus on species from temperate and subpolar regions and in which different stress factors are carefully selected. This will make it possible to unravel the complex web of behavioural and physiological interactions, enabling the development of a predictive model of how communities will change as climate change advances (Nagelkerken & Munday, 2016). In addition to those already mentioned, there are many other biologically important questions that have not yet been answered, which limit our ability to make the link between effects at the individual level and at the level of populations and communities. Among these are 1) the changes in energy allocation in behavioural processes and in the condition of individuals, 2) the synergistic and antagonistic effects of multiple stressors on behaviour and metabolism, and 3) the effect of temperature on connectivity, through changing the size of individuals in settlement (O'Connor *et al.*, 2007; Wilson *et al.*, 2010).

Given all the known effects of climate change on marine species, there has been an increased interest in phenotypic plasticity, as a way for organisms to respond in the short and long-term to environmental changes (Donelson *et al.*, 2011). Much progress has been made in this area in an attempt to understand the potential for transgenerational acclimation and the effect-cause relationships between environmental conditions and genes and physiological phenotypes, the information of which is extremely important in reinforcing the genomic data that will determine whether or not the introduction of conservation measures (Veilleux *et al.*, 2015). However, despite all the reinforcement in this area and its importance for the introduction of conservation measures, it remains unclear whether the acclimation potential will cover anti-predatory behaviors, namely the escape response, whose results obtained so far do not be clear (Domenici *et al.*, 2019).

The multifactorial nature of climate change has made it difficult to understand how species and communities will be affected (Gunderson et al., 2016). Temperature increase, acidification and reduction of oxygen solubility have been widely studied (Guinotte & Fabry, 2008; Doney *et al.*, 2009; Capotondi *et al.*, 2012; Keeling *et al.*, 2014; Cheng *et al.*, 2019), but climate change will also involve changes in nutrient availability, by increasing stratification that will isolate surface layers from nutrient-rich deep water (O'Connor *et al.*, 2009). Thus, the understanding of how this variable will interact with the other stress factors associated with climate change is very relevant, but so far it has been little investigated.

8. References

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II-Supplementary Material

Table S1 - GLM analysis. Effects of temperature on weight and total length of *Diplodus sargus*. Comparisons between treatments in acute exposure and between timepoints, at ambient and high temperatures. Est-Estimates, Std error-Standard error. Significant differences (p<0.05) are indicated in bold.

Model: GLM (Gamma)
Variable: Weight and Total length

	Est	**Std error**	**t value**	***p***
Weight:				
Acute exposure	0.378	0.174	2.172	**0.037**
Ambient temperature between timepoints	1.706	0.127	13.480	**<0.001**
High temperature between timepoints	1.310	0.166	7.906	**<0.001**
Total length:				
Acute exposure	0.053	0.056	0.937	0.355
Ambient temperature between timepoints	0.496	0.053	9.386	**<0.001**
High temperature between timepoints	0.458	0.045	10.23	**<0.001**

Table S2 - Chi-square analysis. Effects of temperature on responsiveness and directionality of *Diplodus sargus*. Comparisons between treatments in acute exposure and between timepoints, at ambient and high temperatures. Est-Estimates, Std error-Standard error.

Chi-square test
Variable: Responsiveness and Directionality

	Value	***p***
Responsiveness:		
Acute exposure	2.057	0.151
Ambient temperature between timepoints	0.36	0.548
High temperature between timepont	0.165	0.684
Directionality:		
Acute exposure	2.918	0.233
Ambient temperature between timepoints	1.333	0.513
High temperature between timepont	1.792	0.408

Table S3 - GLM analysis. Effects of temperature on latency, maximum speed and escape distance of *Diplodus sargus*. Comparisons between treatments in acute exposure and between timepoints, at ambient and high temperatures. Est-Estimates, Std error-Standard error. Significant differences (p<0.05) are indicated in bold.

Model: GLM (Gamma)
Variable: Latency, Maximum speed and Escape distance

	Est	**Std error**	**t value**	***p***
Latency:				
Acute exposure	0.403	0.357	1.128	0.268
Ambient temperature between timepoints	0.196	0.472	0.416	0.680
High temperature between timepoints	0.365	0.365	0.998	0.325
Maximum speed:				
Acute exposure	0.315	0.131	2.399	**0.022**
Ambient temperature between timepoints	-0.097	0.125	-0.777	0.442
High temperature between timepoints	-0.473	0.106	-4.449	**<0.001**
Escape distance:				
Acute exposure	0.672	0.234	2.865	**0.007**
Ambient temperature between timepoints	0.281	0.147	1.915	0.064
High temperature between timepoints	-0.173	0.228	-0.756	0.455

Table S4 - GLM analysis. Effects of temperature on Standard Metabolic Rates of *Diplodus sargus*. Comparisons between treatments in acute exposure and between timepoints, at ambient and high temperatures. Est-Estimates, Std error-Standard error. Significant differences (p<0.05) are indicated in bold.

Model: GLM (Gamma)
Variable: Standard Metabolic Rates

	Est	Std error	t value	*p*
Acute exposure	0.244	0.180	1.355	0.189
Ambient temperature between timepoints	-0.239	0.169	-1.411	0.174
High temperature between timepoints	-0.468	0.139	-3.368	**0.003**

Table S5 - Chi-square analysis. Mortality rate in *Diplodus sargus* after prolonged exposure to ambient (19 ºC) and high (22 ºC) temperature, crossed with *ad libitum* and short fed treatments.

Chi-square test
Variable: Mortality rate

	Value	*p*
Between 19 °C	0.501	0.479
Between 22 °C	7.111	0.008
Between *ad libitum* treatments	1.042	0.307
Between short fed treatments	1.420	0.233

Table S6 - GLM analysis. Effects of temperature and feeding treatment on weight and total length of *Diplodus sargus*. - A: *ad libitum* x ambient temperature; B: *ad libitum* x high temperature; C: short fed x ambient temperature; and D: short fed x high temperature. Est-Estimates, Std error-Standard error.

Model: GLM (Gamma)
Variable: Weight and Total length

	Est	**Std error**	**t value**	***p***
Weight:				
A*B	-0.048	0.037	-1.318	0.192
A*C	0.002	0.038	0.063	0.950
A*D	-0.063	0.044	-1.449	0.152
Total length:				
A*B	0.015	0.042	0.364	0.717
A*C	-0.044	0.044	-1.012	0.315
A*D	0.022	0.050	0.438	0.663

Table S7 - Chi-square analysis. responsiveness and directionality in *Diplodus sargus* after prolonged exposure to ambient (19 ºC) and high (22 ºC) temperature, crossed with *ad libitum* and short fed treatments.

Chi-square test
Variable: Responsiveness and Directionality

	Value	***p***
Responsiveness:		
Between *ad libitum* treatments	1.723	0.189
Between short fed treatments	2.141	0.143
Between 19 °C treatments	0.308	0.579
between 22 °C treatments	0.066	0.789
Directionality:		
Between *ad libitum* treatments	3.571	0.168
Between short fed treatments	0.633	0.426
Between 19 °C treatments	1.337	0.512
Between 22 °C treatments	1.200	0.549

Table S8 - GLM analysis. Effects of temperature and feeding treatment on latency, maximum speed and escape distance of *Diplodus sargus*. - A: *ad libitum* x ambient temperature; B: *ad libitum* x high temperature; C: short fed x ambient temperature; and D: short fed x high temperature. Est-Estimates, Std error-Standard error. Significant differences ($p<0.05$) are indicated in bold.

Model: GLM (Gamma)
Variable: Latency, Maximum speed and Escape distance

	Est	**Std error**	**t value**	***p***
Latency:				
A*B	0.510	0.451	1.131	0.262
A*C	0.760	0.472	1.612	0.112
A*D	1.551	0.538	2.883	**0.005**
Maximum speed:				
A*B	-0.047	0.113	-0.414	0.680
A*C	-0.046	0.118	-0.391	0.697
A*D	-0.225	0.134	-1.675	0.099
Escape distance:				
A*B	0.202	0.167	1.211	0.230
A*C	0.145	0.174	0.833	0.408
A*D	-0.179	0.199	-0.900	0.372

Table S9 - Post Hoc Tukey analysis of latency in *Diplodus sargus* after extended exposure. Comparisons between treatments- A: *ad libitum* x ambient temperature; B: *ad libitum* x high temperature; C: short fed x ambient temperature; and D: short fed x high temperature. Est-Estimates, Std error-Standard error. Significant differences (p<0.05) are indicated in bold.

Variable: Latency
Timepoint: Prolonged exposure

	Est	**Std error**	**t value**	***p***
A*B	0.510	0.451	1.131	0.262
A*C	0.760	0.472	1.612	0.112
A*D	1.551	0.538	2.883	**0.005**
B*C	0.250	0.458	0.545	0.948
B*D	1.040	0.526	1.991	0.190
C*D	0.791	0.544	1.453	0.465

Table S10 - GLM analysis. Effects of temperature and feeding treatment on Standard Metabolic Rates of *Diplodus sargus*. - A: *ad libitum* x ambient temperature; B: *ad libitum* x high temperature; C: short fed x ambient temperature; and D: short fed x high temperature. Est-Estimates, Std error-Standard error. Significant differences (p<0.05) are indicated in bold.

Model: GLM (Gamma)
Variable: Standard Metabolic Rates

	Est	**Std error**	**t value**	***p***
A*B	0.043	0.139	0.310	0.758
A*C	-0.371	0.155	-2.391	0.078
A*D	-0.429	0.137	-3.126	**0.004**

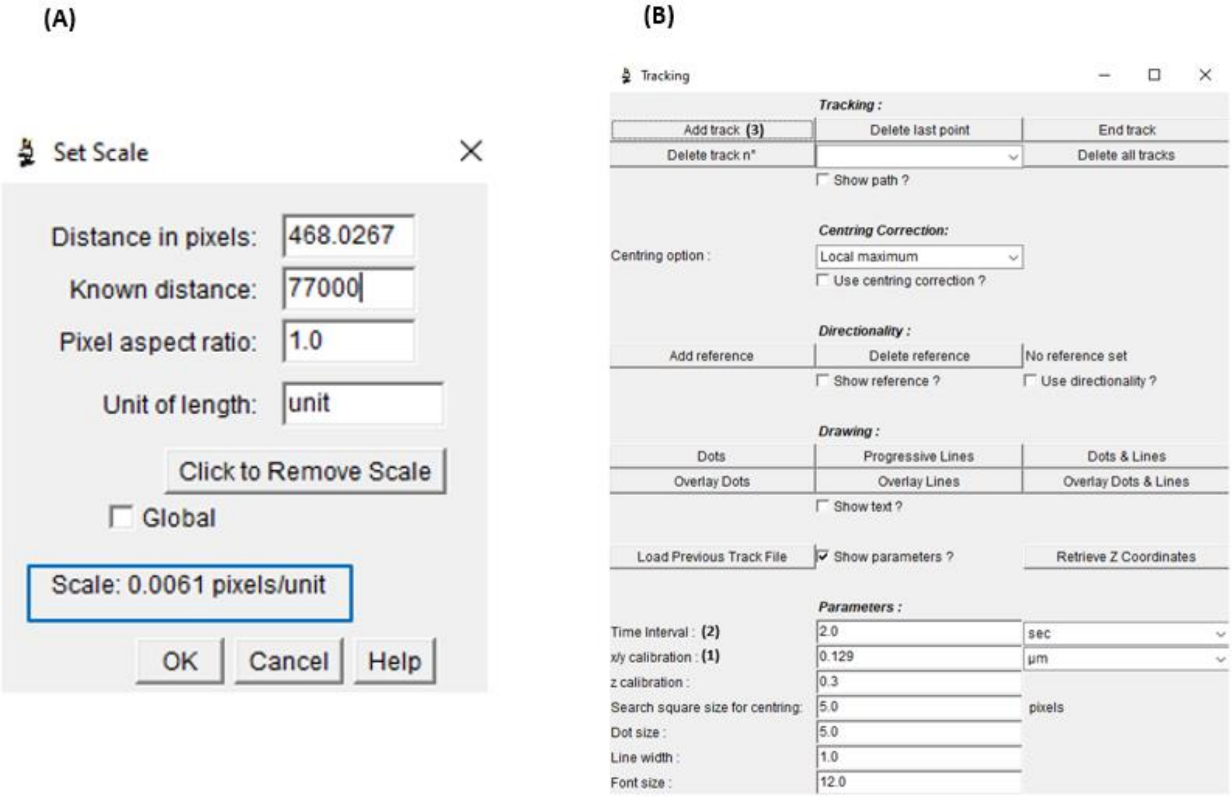
Table S11 - Post Hoc Tukey analysis of Standard Metabolic Rate in *Diplodus sargus* after extended exposure. Comparisons between treatments - A: *ad libitum* x ambient temperature; B: *ad libitum* x high temperature; C: short fed x ambient temperature; and D: short fed x high temperature. Est-Estimates, Std error-Standard error. Significant differences (p<0.05) are indicated in bold.

Variable: Standard Metabolic Rate
Timepoint: Prolonged exposure

	Est	**Std error**	**t value**	***p***
A*B	0.043	0.139	0.310	0.758
A*C	-0.371	0.155	-2.391	0.078
A*D	-0.429	0.137	-3.126	**0.009**
B*C	-0.414	0.166	-2.499	0.060
B*D	-0.472	0.140	-3.377	**0.004**
C*D	-0.058	0.152	-0.382	0.981

III-Protocol for using the imageJ manual tracking plugin

- Open image sequence in ImageJ by going to file, import and image sequence.
- Go to analysis and then set scale.
- Set calibration with known distance in µm. Remove pixel per unit value (Figure 17A).
- Open Manual Tracking.
- Set x/y calibration (1, Figure 17B), which is found in the unit/pixel unit of measure. Thus, it is necessary to divide 1 by the pixel/unit value obtained previously.
- Define time interval (2, Figure 17B), according to the period between frames.
- Start tracking (3, Figure 17B).



(A)

Distance in pixels: 468.0267
Known distance: 77000
Pixel aspect ratio: 1.0
Unit of length: unit
☐ Global
Scale: 0.0061 pixels/unit

(B)

☐ Show path ?
Centring option : Local maximum
☐ Use centring correction ?
No reference set
☐ Show reference ?
☐ Use directionality ?
☐ Show text ?
☑ Show parameters ?
Time Interval : (2) 2.0 sec
x/y calibration : (1) 0.129 µm
z calibration : 0.3
Search square size for centring: 5.0 pixels
Dot size : 5.0
Line width : 1.0
Font size : 12.0

Figure 17 - (A) Determination of scale, with emphasis on the value of pixels per unit. **(B)** User interface in manual tracking. (1) x/y position calibration, (2) time interval calibration and (3) start tracking.