

## Article

# Effects of Water Temperature and Structural Habitat Complexity on the Routine Swimming Speed and Escape Response of Post-Settlement Stage White Seabream

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**Abstract:** Coastal habitats are increasingly threatened by multiple anthropogenic-related activities, which include ocean warming and loss of structural habitat complexity. These two pressures have the potential to severely affect the structure and function of marine biodiversity. Early life stages of many fish species recruit to coastal habitats at the end of their pelagic phase, benefiting from access to food, shelter and protection. However, changes in temperature have been shown to influence ecologically relevant behaviours in post-settlement stage fish, and the loss of structural habitat complexity has been related to low recruitment and deleterious behaviours of fish in coastal habitats. Here, we evaluated the individual and interactive effects of prolonged exposure to increasing temperature and changed structural habitat complexity on routine swimming speed and escape response of post-settlement white seabream, *Diplodus sargus* (Linnaeus, 1758). Fish were reared under different temperatures (control 19 °C; high 22 °C) and structural habitat complexity (low and high) scenarios, in a cross-experimental design, and the routine swimming and escape responses were analyzed after 6 weeks of exposure. Change in temperature did not induce alterations at the behavioural level, but loss of structural habitat complexity increased speed and distance travelled during routine swimming, and responsiveness to a stimulus during the escape response behaviour. The interaction of the two factors did not influence performance. Determining how species are affected by changes in their environment, and the mechanisms that underlie these changes, will be critical to understanding the fish recruitment and populations' fitness and survival.

**Keywords:** early life stages; *Diplodus sargus*; global change; habitat degradation



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## 1. Introduction

Marine coastal ecosystems are increasingly threatened by climate change stressors. Since the Industrial Revolution, the release of greenhouse gases into the atmosphere has increased at unprecedented rates [1,2] leading to an increasingly warmer planet. The ocean retains more than 90% of the excess heat released into the atmosphere [3], and, according to the Intergovernmental Panel on Climate Change (IPCC) models, ocean water temperatures may increase by 2–4 °C on average until the end of the century [4]. However, climate changes do not occur in isolation from other threats. Marine coastal ecosystems are heavily impacted by other anthropogenic-related activities, such as the over-exploitation of resources, pollution, excess of nutrients, bottom trawling and dredging [5]. Together, these pressures have been driving the degradation and/or complete loss of the habitat complexity of coastal ecosystems around the world [6], affecting their ecological and economic value [7].

Structurally complex, shallow, coastal habitats typically support higher abundance and biodiversity than less complex habitats [8], by providing a greater diversity of resources,

such as food, refuges and microhabitats. Currently, these habitats are becoming rarer across temperate marine environments [9,10], and their loss has been associated with the low recruitment of littoral fishes that use coastal habitats as nursery areas (e.g., in the Mediterranean Sea [11]).

The increasing warming of the seawater surface will most certainly alter coastal landscapes, with far-reaching consequences for the structure and function of marine ecosystems and organisms [12,13]. Here, we investigated the effects of increased water temperature and decreased structural habitat complexity on the routine swimming speed and escape response of post-settlement stage white seabream, *Diplodus sargus* (Linnaeus 1758). Both routine swimming and escape performance are key behavioural traits for species fitness and survival, influencing the ability of fish to find food and escape from predators [14,15]. The white seabream is a highly important commercial species, abundant on the Atlantic coast and in the Mediterranean Sea [16]. After a dispersive larval phase in the plankton for approximately 1 month [17], larvae move to coastal regions to settle. Settlers of 1–1.5 cm total length colonize very shallow, sheltered coastal areas at <2 m depth between late spring and early summer (review by [18]). They preferably recruit microhabitats with coarse sand, gravel, pebbles or boulders [19]. Only later in the ontogeny (<6 cm total length) may they disperse to deeper waters to join larger shoals of conspecifics [18]. There is little information regarding the daily activity patterns of white seabream juveniles, but Macpherson [20], based on field observations, suggested little variation in aggregation or habitat use in settlers throughout the day.

To assess the effects of elevated temperature and structural habitat complexity on fish routine speed and escape response, individuals were reared in a fully-crossed experimental design, with two temperatures and two structural complexities, for a 6-week period. The temperature treatments were set to a control temperature (19 °C), which can be found in the seabream's natural habitat [21], and the high-temperature scenario of +3 °C (22 °C), which is in line with projected future climate change conditions [22]. On the Portuguese coast, white seabream settle during the spring–summer months, when the average temperature ranges from 15 °C to 18 °C, but can reach up to 20–23 °C in warmer years [21]. Although the high-temperature scenario (22 °C) selected for this study can occasionally be experienced by the species, the goal of the study was not to test a thermal stress response curve, by exposing fish to more extreme temperature treatments, but instead to test the response to a prolonged exposure to a temperature that is likely to become the “new normal” in white seabream habitats during the settlement phase. The high structural complexity habitat was constructed by adding substrate and plastic plants to the tanks, while a completely clean tank, without the aforementioned items, was used to simulate a low complexity habitat. The temperature has been shown to alter predator–prey kinematics, with warming promoting an increased speed and escape response due to the effect of temperature on muscle performance and power output, which tend to increase at higher temperatures (review by [23]). Habitat complexity also has the potential to influence risk assessment and predator–prey interactions by providing access to shelter and changing the visibility and detection of both prey and predators [24,25]. We, therefore, predicted that a high temperature would increase the routine swimming speed of white seabream and enhance their escape response, and a low structural habitat complexity would make the fish more vigilant and respond to a stimulus faster.

## 2. Materials and Methods

### 2.1. Experimental Design

Experiments took place from late April to early June 2021. White seabream, *D. sargus*, individuals, at the age of 48 days post-hatch with an average total length of 2 cm, were provided by IPMA's Aquaculture Research Station, currently known as EPP0 (Olhão, Portugal). The fish were transported to ISPA—Instituto Universitário fish facilities, and were placed in an 80-L acclimation tank, enriched with artificial algae and sediment, with a temperature (19 °C), salinity (35) and photoperiod (14 L:10 D) matching the conditions

found at the EPP0 station. The fish were fed five times per day with commercial fish feed (SPAROS, Olhão, Portugal), until satiation. After a 10-day period, the fish were randomly distributed among four treatment groups, and among two replicate 30-L tanks within each group, for a total of eight tanks ( $n = 13$  fish per tank). The four treatments were set as follows: control temperature and low complexity habitat; control temperature and high complexity habitat; high temperature and low complexity habitat; high temperature and high complexity habitat. The temperature was maintained at  $19.40 \pm 0.02$  °C for the control temperature treatments, and  $21.87 \pm 0.03$  °C in the high temperature treatments. The temperature was gradually increased throughout a 3-day period, to avoid the stress and heat shock associated with rapid temperature changes. To simulate a high complexity habitat, tanks were enriched with medium-sized gravel on the bottom and artificial marine plants; low-complexity tanks were kept clean, with no environmental enrichment.

Tanks were equipped with mechanical, biological, chemical and ultraviolet filtration, ensuring water quality throughout the experimental period. 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 cleaned daily, to remove excess food.

The fish were maintained under these conditions for a 6-week period, and subsequently tested for routine swimming and escape response. Individuals were randomly sourced from both replicate tanks per treatment ( $n = 22$ – $26$  for each treatment). Experimental trials were conducted over a period of 2–4 days in a temperature-controlled room, to minimize temperature fluctuations during the trials. Each individual was tested only once. After each test, the fish were euthanized with an excessive dose of MS222, and the standard length (SL) was measured.

## 2.2. Routine Swimming and Escape Response

The experimental setup used to assess the routine swimming and escape response followed [26], and was based on, the protocol of [27]. Briefly, each fish was placed in an experimental circular arena (19 cm diameter) filled with artificial seawater and at a height of 8 cm, to limit vertical movement. The temperature in the arena matched the temperature of the original treatment, and the water was changed every three trials to maintain the temperature conditions. We cannot exclude the influence of chemical cues left in the water from one fish to the next during the three-trial period, however, observations did not suggest altered behaviours during the acclimation phase. After 10 min of acclimation, fish routine swimming was recorded for 2 min 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 without further visual disturbances. Furthermore, a black curtain isolated the experimental arena. After recording routine swimming, an escape response was elicited by dropping a tapered weight attached to a wire above the water's surface. The weight was dropped through a PVC tube so that the visual stimulus could be minimized before the mechanical stimulus. Caution was taken so that the weight only touched the water's surface, without hitting the fish.

The routine swimming analysis included minimum, average and maximum swimming speed (body length per second, to control for any size effect), and total distance traveled (cm) [14]. The escape response analysis included responsiveness (% of fish that responded to the stimulus), directionality (opposite or towards the stimulus, %), latency (time that fish takes to respond to the stimulus, milliseconds), escape distance (distance travelled during the response, cm) and maximum escape speed (body length per second). These are reliable indicators of fish escape response behaviour [28].

Videos were converted into frames (300 frames per second for latency analysis and 10 frames per second for maximum escape speed, escape distance and routine swimming analysis), and were analyzed using the imageJ software 1.53v with the manual tracking plugin.

### 2.3. Statistical Analysis

Linear mixed-effects models were used to estimate the size of the fixed effects of temperature and habitat complexity, and their interaction with standard length (SL) and the behavioural responses of fish: average routine swimming speed, total distance covered during routine swimming, latency of escape response, escape response speed and distance. As fish size can influence behavioural responses, SL was included as a fixed effect for the analysis of routine speed and escape response as well. The tank was included as a random effect, to account for shared variations among measurements from the same tank. In all analyses, we first considered a full model that contained coefficients for the intercept (reference group was the control temperature, complex habitat treatment), temperature treatment, habitat complexity, their interaction and length. This version of the model thus allowed for any differences in the effects of temperature among complex habitat treatments (and vice versa). If the interaction term was non-significant (i.e.,  $p > 0.05$ ) the interaction term was dropped, and the analyses were rerun as an additive model. Additive models summarized the overall effects by averaging the temperature effects across complex habitat treatments and averaging the complex habitat effects across temperature treatments. A chi-square test of independence was performed to evaluate the effects of temperature and habitat complexity on the responsiveness and directionality of the escape response.

All analyses were performed in R Version 4.2.1, using the package lme4.

### 3. Results

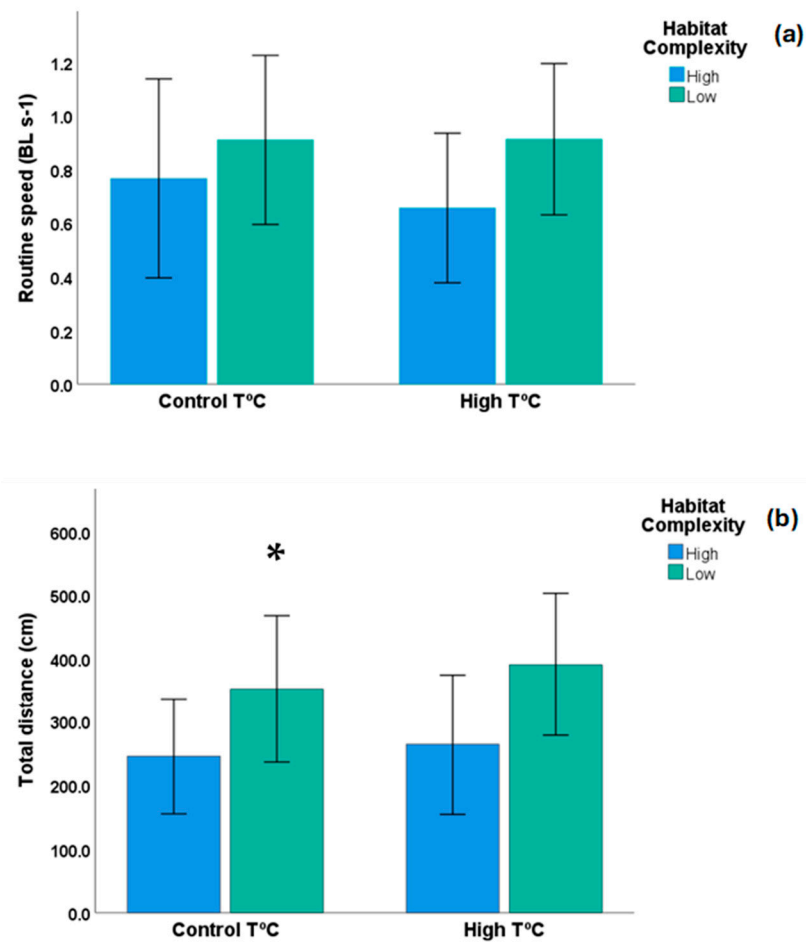
The seabream reared for 6 weeks under higher temperatures were significantly larger than the fish reared at the control temperature ( $p = 0.019$ , Tables 1 and S1). Contrary to temperature conditions, habitat complexity did not induce changes in body size ( $p = 0.303$ , Tables 1 and S1), and neither did the interaction of temperature and habitat complexity and, therefore, the interaction term was dropped from the models.

**Table 1.** Summary of mean  $\pm$  standard error (Mean  $\pm$  SE) of length, routine swimming and escape response of white seabream in the four treatments: control temperature and high complexity habitat; control temperature and low complexity habitat; high temperature and low complexity habitat; high temperature and high complexity habitat.

Variables	Control T °C $\times$ High Complex	Control T °C $\times$ Low Complex	High T °C $\times$ Low Complex	High T °C $\times$ High Complex
Standard length (cm)	3.22 $\pm$ 0.11	3.41 $\pm$ 0.09	3.62 $\pm$ 0.91	3.60 $\pm$ 0.12
Aver routine speed (BL/s)	0.85 $\pm$ 0.19	0.91 $\pm$ 0.16	0.91 $\pm$ 0.14	0.66 $\pm$ 0.15
Routine distance (cm)	271.96 $\pm$ 47.85	351.34 $\pm$ 75.84	389.93 $\pm$ 56.09	275.94 $\pm$ 62.13
Responsiveness (%)	89	100	100	86
Directionality (%)	88	96	95	94
Latency (ms)	41.84 $\pm$ 14.04	24.27 $\pm$ 4.05	21.45 $\pm$ 5.04	20.64 $\pm$ 4.84
Escape distance (cm)	2.89 $\pm$ 0.44	2.90 $\pm$ 0.42	3.01 $\pm$ 0.51	2.60 $\pm$ 0.37
Max escape speed (BL/s)	2.70 $\pm$ 0.24	2.94 $\pm$ 0.24	2.82 $\pm$ 0.27	2.69 $\pm$ 0.34

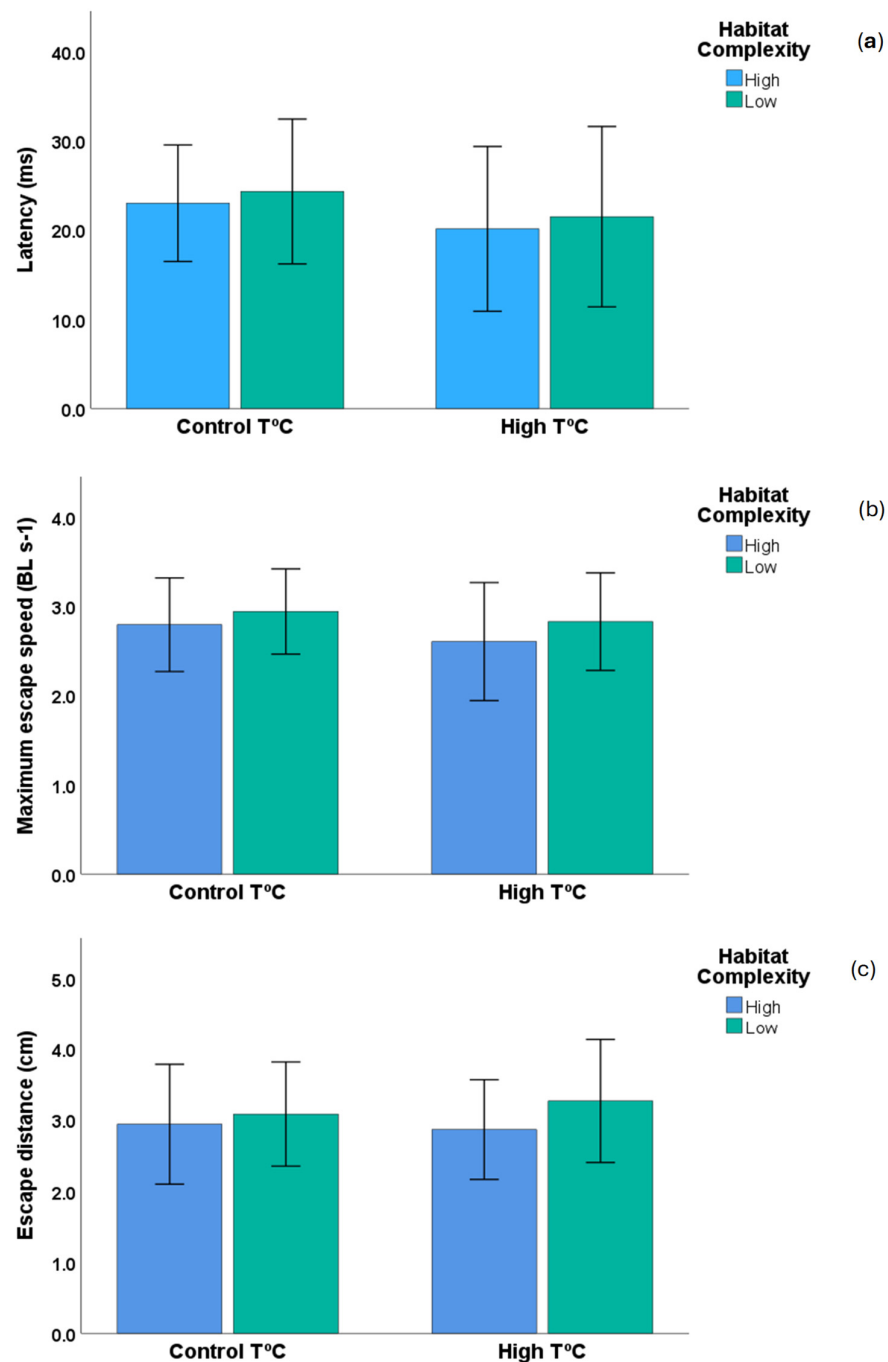
The temperature had no effect on the routine swimming speed ( $p = 0.519$ ) or the travelled distance ( $p = 0.301$ ) of the white seabream (Figure 1, Tables 1 and S1). The interactive effects of temperature and habitat complexity were not significant, so the interaction term was dropped from the models. Routine swimming speed moderately increased in fish under low structural complexity ( $p = 0.063$ , Figure 1, Tables 1 and S1), which also covered a significantly greater distance during the 2 min trial, when compared to fish reared in a more structurally complex environment ( $p = 0.015$ , Figure 1, Tables 1 and S1).

Length significantly influenced speed and distance, with larger fish presenting higher speeds ( $p < 0.001$ ) and longer travelled distances ( $p = 0.05$ ) (Figure 1, Table S1).



**Figure 1.** The effect of temperature and habitat complexity on average swimming speed (a) and total distance travelled (b) during routine behaviour of white seabream. Bold \* represent significant differences. The reference case for this experiment is the control temperature, high complexity habitat treatment.

Regarding the escape response, exposure to higher temperature did not influence non-locomotor variables: responsiveness ( $p = 0.526$ ), directionality ( $p = 0.527$ ) and latency ( $p = 0.689$ ) (Tables 1, S1 and S2), neither the escape distance ( $p = 0.750$ ) and maximum speed ( $p = 0.869$ ) attained during the response (Figure 2, Tables 1 and S1). The interactive effects of temperature and habitat complexity were not significant, so the interaction term was dropped from the models. Habitat structure did influence the responsiveness of fish ( $p = 0.023$ ), with 100% of fish from low-complexity environments responding to the stimulus (Tables 1 and S2). Other than responsiveness, habitat complexity did not affect the remaining components of the escape response: directionality ( $p = 0.336$ ), latency ( $p = 0.713$ ), escape speed ( $p = 0.312$ ) and distance ( $p = 0.461$ ) (Figure 2, Tables 1, S1 and S2). Similarly to the routine speed, the length significantly affected the maximum speed attained during escape response, with larger fish sustaining higher speeds ( $p = 0.006$ , Table S1).



**Figure 2.** The effect of temperature and habitat complexity on latency of response (a), maximum escape response (b) and escape distance (c) of white seabream.

#### 4. Discussion

Habitat complexity can influence the perception of predation risk [29], through changes in shelter availability, changes in visibility and predator detection [24]. A low-structured environment may appear risky, making fish more exposed to risk, and, therefore, more stressed and in a permanently vigilant state. Accordingly, in our study, fish exposed to a low-complexity habitat displayed increased activity (increased routine speed and distance travelled) and higher responsiveness to a predatory stimulus. Increased locomotor activity of fish reared in a low-complexity environment has been described in zebrafish [30], brown trout [31] and Atlantic salmon [32], which may reflect an increase in anxiety-like behaviors [33,34]. We also hypothesized that a low-complexity environment would also



increase a fast start response, but our data do not indicate altered kinematic performance. While responsiveness has been considered as being under some behavioural control, the kinematic components of the escape response (speed, distance) are physiologically determined and are more automatic [35]. It therefore seems that, in our experimental conditions, white seabream reared in a low-complexity environment were able to conserve their escape performance. A word of caution is needed when interpreting these results, though. The experimental arena for routine swimming and escape response was a novelty for fish of the high-complexity habitat, as it lacked environmental enrichment, so stress could be induced on fish from the complex habitat and promote a change in behavior that in fact is not caused by the differences in the rearing environment. Although this could be a possibility, after the acclimation phase we did not observe signs of behavioural stress responses, such as freezing, staying closer to the arena walls, or erratically swimming. We therefore consider that the obtained results are a reliable indicator of a response to the rearing environment.

Living in a more structured environment did not induce changes in the growth of white seabream in the present study, which contrasts with the findings of several other authors who reported higher growth rates in gilthead seabream [36], Atlantic salmon [37], black rockfish [38] and catfish [39] exposed to physical enrichments, compared to those reared in barren tanks. These authors also reported lower levels of aggression in the fish reared in an enriched environment, which could explain the better growth performance as energy spent on fighting is instead allocated to growth. In our study, we did not measure aggression levels, but daily observations indicated that fish in higher complexity environments had a more dispersed shoal structure, therefore decreasing the likelihood of aggressive interactions.

While structural complexity led to altered routine activity and responsiveness in white seabream, exposure to higher temperature did not induce changes at these behavioural levels, which contradicts the literature that frequently points to increased swimming and escape performance under warming conditions [40–42]. The white seabream has a wide thermal range and can withstand acute temperature increases in more confined habitats, such as tide pools, which could explain the lack of significant results at the behavioural performance level. However, tolerance to extreme temperatures must be time-limited (during low tide, or for a few days during heatwave events, for example), and prolonged exposure to such critical temperatures will certainly impose thermal stress with more far-reaching consequences [43]. Our experimental design was not intended to test acute thermal stress responses, but instead to address the responses to prolonged exposure to a scenario predicted for the end of the century, which may become the “new normal” for the species. In this sense, our data suggest that a future scenario of 22 °C will not affect the routine and escape performance of post-settlement stage white seabream, as already seen by Almeida et al. [26]. Nonetheless, we did find an increased body size of fish under higher temperature conditions, which is not unexpected, as warming usually promotes fish growth within a suitable temperature range [44,45].

There are a few recent studies in the literature that examined the effects of structural complexity on fish (e.g., [33,34,36,46–48]), but their scope is frequently related to welfare under captivity, and is, therefore, more focused on aquaculture/model species and stress-related endpoints (growth performance, anxiety-like behaviours, brain function). Other studies have made a great contribution to this field by looking at the effects of habitat degradation in the wild, but are focused on tropical reef fish species (e.g., [49–51]). To the best of our knowledge, the current study is the first to address the effects of both increasing temperature and low-complexity environment on an ecologically meaningful response in late-stage larvae of a temperate reef fish species. Overall, our results highlight the important role that habitat structure plays in fish anti-predator responses. However, to better understand how species are affected by changes in their natural landscape, we suggest future studies test different levels of habitat complexity and temperature scenarios and further investigate the mechanisms that underlie these changes. Clearly, this is an

aspect that warrants further study, and this knowledge will be critical for understanding the dynamics of change in a fish community.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/oceans5010003/s1>, Table S1: Summary of effects of temperature (control and high) and habitat complexity (high and low) on routine swimming speed and escape response of white seabream. The reference case for this experiment is the control temperature, high complexity habitat treatment. Tank is included as a random effect to account for shared variation among measurements from the same tank. Random effects associated with Tank represent the variation in tank means. Bold and \* *p*-values highlight significant effect ( $p < 0.05$ ). Table S2: Summary of Chi-square results for the effects of temperature (control and high) and habitat complexity (high and low) on responsiveness and directionality of the escape response of white seabream.

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**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** The data presented in this study are available on request from the corresponding author.

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