RESEARCH ARTICLE

Damselfish face climate change: Impact of temperature and habitat structure on agonistic behavior

Thalles da Silva-Pinto¹, Mayara Moura Silveira¹, Jéssica Ferreira de Souza¹, Ana Luisa Pires Moreira¹, Edson Aparecido Vieira², Guilherme Ortigara Longo², Ana Carolina Luchiari¹*

¹ Laboratório de Peixes, Departamento de Fisiologia e Comportamento, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, Brazil, ² Laboratório de Ecologia Marinha, Departamento de Oceanografia e Limnologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Natal, Brazil

* analuchiari@yahoo.com.br

Abstract

Oceans absorb a huge part of the atmospheric heat, leading to the rise in water temperature. Reefs are among the most affected ecosystems, where the complex behavioral repertoire of fishes is usually an indicator of environmental impacts. Here, we examined whether temperature (28 and 34˚C) and habitat complexity (high and low) interact to affect the agonistic behavior (mirror test) of the dusky damselfish (Stegastes fuscus), a key species in Brazilian reefs because of its gardening capacity and territorial behavior. Higher temperatures altered basal behavior in both high and low-complexity conditions. Fish kept at 28˚C under the high-complexity condition were more aggressive than those at a higher temperature (34˚C) and in a low-complexity condition, which also exhibited lower dispersion. Our data show that changes in behavior of coral reef fish is associated to fluctuations in environmental conditions. Thus, it is important to implement management or conservation strategies that could mitigate global change effects.

1. Introduction

Global warming has been singled out as one of the most devastating effects of human activities [1], especially for oceans, which absorb around 90% of the atmospheric heat. For water-breathing ectothermic, physiological functioning depends on the thermal condition [2,3]. The rise in water temperature directly affects fishes’ metabolism, increasing respiration rate, nutritional requirements, and other physiological and behavioral responses such as reproduction and immunological defense [4–8]. Moreover, for the reef fishes the impact is exacerbated because algae and coral that make up reef’s structural foundation are even more sensitive to temperature rise. The three-dimensional structure and food source offered by the coral communities favor the establishment of hundreds of species, and the immediate impact of warming will be loss of diversity and changes in fish community composition [9,10].
Reef fishes exhibit a complex behavioral repertoire, and subtle changes in behavior are usually associated to fluctuations in environmental conditions [7]. Thus, reef fishes are important organisms in determining how environmental changes can modulate behavior and help us understand their potential influence on reef ecosystems. Environmental changes were shown to affect fish cognition [11], personality [12], reproduction patterns [13], social interactions, migration and even species diversity of reef dwellers [14].

Some reef-fish populations are sensitive to slight increases in water temperature [15], while others tolerate higher temperature variations [16,17]. The dusky damselfish (*Stegastes fuscus*) occurs along almost the entire Brazilian coast (from 5°S to 27°S), featuring a wide range of thermal gradients. Studies on a related species from the Pacific (*Chromis atripectoralis*) indicated that the thermal optimum is around 1°C above its regional maximum summer temperature (30°C; [17]). Damselfishes play an important ecological role by affecting the structure of benthic and coralline communities [18–20] and controlling algal diversity [21]. These species are largely territorial, exhibit aggressive behavior toward other herbivorous species and contribute to energy and nutrient transfer in reef environments, as a result of their gardening ability [22].

If global warming projections for the end of this century materialize, ocean water temperatures may increase 2–4°C on average, and important conditions for preserving marine life will be affected [23,24], including the structural complexity of reefs [25]. In this study we evaluated whether water temperature and structural complexity of the habitat affect mobility patterns, tank occupation, and behavioral profile of the damselfish *Stegastes fuscus*. For this, we subjected the animals to classic mirror test and observed if animals kept at high temperature and barren conditions (mimicking the worst forecast scenario for the future) present significant changes in behavior when compared to fish kept at natural temperature and enriched or barren habitat. As increase in temperature raises the metabolic rate of fish and promotes direct influences in behavior, we suggest that natural aggressive behavior of *S. fuscus* would be affected.

### 2. Materials and methods

#### 2.1 Animal sampling and holding conditions

Animals were collected from Pirambúzios beach (6°03’25”S and 35°05’53”W), Nisia Floresta, Rio Grande do Norte state, Northeastern Brazil, as authorized by the Brazilian Institute of Environment and Natural Resources (IBAMA License Number 62318-1/2018). The tide pools that form at this beach serve as a refuge for various marine communities [26]. The average maximum coastal water summer temperature is 30°C [27], but reaches 36°C in the tide pools (critical temperature occurring only at low tide and for short periods of time), salinity remains between 36 and 40ppt, and pH is around 8.0 [28].

Dusky damselfish (*S. fuscus*) were collected from the tide pools in two sampling moments (average size and weight of 8.99 ± 1.04 cm, 18.83 ± 4.29 g and 8.27 ± 0.80 cm, 13.41 ± 2.99 g at the first and second capture, respectively) using a cast net (3m diameter, 10mm mesh size). Fish were immediately stored in 30-L containers with seawater and air stones to maintain oxygen level. Next, they were taken to the laboratory and placed in glass tanks (33 x 30 x 30 cm; 25L) at the Fish Vivarium, Department of Physiology and Behavior, Federal University of Rio Grande do Norte. Saltwater was previously prepared (Red Sea Salt, Red Sea, Houston, USA) and the tanks filled. Salinity was maintained at 36ppt, and a 12:12H light:dark cycle was established.

Every 12 tanks formed a closed recirculating system, in which water was kept aerated and filtered (mechanical, chemical and biological filters) and maintained at a controlled...
temperature by a thermostat. Fish were individually held in isolated tanks to avoid physical confrontation and damages. One system (12 tanks) was kept at 28°C, the average water temperature on the Brazilian coastal reefs where animals were sampled [27], and the other (12 tanks) at 34°C, the expected warming of tropical oceans projected to occur by the end of this century [24]. Since 34°C is considered the long-term thermal limit for several species of reef fish [17], it represents the worst global warming scenario. To reach 34°C, tanks at 28°C were subjected to a 0.5°C temperature increase every 2 hours for 24h. Tanks were also enriched or kept clean to provide a complex or barren habitat, respectively. The high-complexity habitat consisted of covering the walls and bottom of the tank with wallpaper simulating marine gravel substrate, and including a shelter (6 x 6 x 15 cm hollowed brick) and plastic plants in the tanks. The barren (low-complexity) habitat contained none of the aforementioned items and the tank was kept completely clean. Thus, four groups were formed: “complex habitat at 28°C” (28C group–n = 12); “complex habitat at 34°C” (34C group–n = 06); “barren habitat at 28°C” (28B group–n = 9); and “barren habitat at 34°C” (34B –n = 9). Fish were kept in these conditions for 1 month before the behavioral tests. They were fed twice a day ad libitum with frozen *Artemia salina*, shrimp paste and dried food pellets (algae-based tetra marine salt granules).

When any type of disease/injury was observed during the 30-day period or when fish stopped feeding for more than 5 days, fish were excluded from the behavioral test, resulting in groups with different sample sizes. A total of twelve fish were excluded from the tests. Following the research data collection, all animals used were euthanized using clove oil anesthetic. All animal procedures were authorized by the Animal Ethics Committee of the Federal University of Rio Grande do Norte (CEUA 100.12/2018).

2.2 Behavioral tests

The experimental tanks (40 x 20 x 25cm, 15L) were filled with water under the same conditions and temperature as the stocking systems where each group was maintained, and an air stone provided constant aeration. The tanks were covered with white paper to prevent the fish from having any contact with the outside environment, but the right and the front walls remained uncovered for experimental purposes. A white partition was placed in front of the right wall, but could be removed when needed, allowing the fish to see a mirror positioned at 45° [28–31]. In this position, one corner of the tank (Q1) was closer to the mirror than the other (Q2). On the opposite sides of the mirror (Q3 and Q4) were areas of less interactivity with the mirror image, where less responsive animals were expected to remain longer (Fig 1). The uncovered front wall allowed a camera (SONY® DCR-SX45) to record fish behavior (camera positioned 50 cm from the tank), while another camera (SONY® DCR-SX45) was placed 1m above the tank in order to record fish movements. Fish were not fed during behavioral tests.

Fish from the 4 stocking conditions (28C, 34C, 28B, 34B) were individually placed in the center of experimental tank, and after a 2-min acclimation period, behavior was recorded from the overhead and frontal cameras. During the first 5 min of recording, the white partition prevented the fish from seeing the mirror. The partition was then removed and fish behavior was recorded for another 5 min. The animals were then returned to the stock tanks.

Behavior recorded by the frontal camera was visually tracked to identify aggressive displays directed toward the mirror. The number and type of displays were quantified. *Attacks* where considered when the fish approached the mirror from the front or the side quickly and/or successively, opening its mouth and trying to bite the side of the tank in contact with the mirror, and *Threats* when it erected its dorsal, pelvic and anal fins close to the mirror. *Immobility* was considered when the fish remained still for 2s or more, *Vigilance* when it moved through the tank fins down, and *Substrate nibbling* when it bit any possible particle at the bottom of the
tank (no food was offered, thus it was recorded as a typical foraging behavior observed in nature). Locomotion was recorded from the overhead camera and analyzed using tracking software developed in MatLab [32]. The overhead view made it possible to divide the bottom of the tank into 4 quadrants: Q1 was the closest to the mirror, Q2 the side area where the mirror offered a more distant view of the image, and Q3 and Q4 were the back areas (Fig 1; see video at https://www.youtube.com/watch?v=wz_aOkjumOA&feature=youtu.be). The time spent in each quadrant and average swimming speed were measured. For speed, calculations are performed on a series of frames to produce quantified measurements of the animal behavior. It is known the position of the animals for each frame of the video, and the number of frames per second. Thus, the series of frames is analyzed, and the number of frames changed in a certain time is used to estimate the animal’s movement.

2.3 Statistical analysis

All comparisons were performed through independent analyses before and after mirror exposure. We decided not to use ‘time’ as a factor due to the dependence between two periods and because analysis of time spent in each quadrant (see details below) would result in two dependent factors in the same analysis (‘time’ and ‘quadrant’).

The effects on mobility were evaluated using swimming velocity and immobility time. Each variable was compared separately between ‘temperature regime’ (fixed, ‘28˚C’ and ‘34˚C’) and ‘habitat complexity condition’ (fixed, ‘complex’ and ‘barren’), and the respective interaction, applying two-way ANOVA. Data were checked for normality (Komogorov-Smirnov test) and homoscedasticity (Levene test), and when a divergence was observed (swimming velocity and immobility time after mirror exposure) square-root transformation was applied. For significant sources of variation, posthoc pairwise comparisons were evaluated using the Student-Newman-Keuls test.

The effects on aggressive behavior were assessed considering the time spent in each quadrant, related to mirror position, as a proxy of aggressiveness level (see methods). Since the time spent in one quadrant is dependent on the others, repeated measures ANOVA was performed for each of them, with ‘temperature regime’ (‘28˚C’ and ‘34˚C’) and ‘habitat complexity’
('complex' and 'barren') as fixed factors, and 'quadrant' (Q1, Q2, Q3 and Q4) as the repeated measure. Data were square-root transformed and Greenhouse-Geisser correction was applied when epsilon was lower than 0.75 [33]. For significant sources of variation, the differences were highlighted by applying descriptive analysis [34].

Behavioral effects were evaluated using a multivariate approach. After the data on percentage of behaviors were square-root transformed, they were used to build a resemblance matrix with Bray-Curtis distance. To test homogeneous dispersion, data were assessed using the PERMDISP procedure (permuted dispersion, which tests for homogeneity of dispersions). Following these procedures, PERMANOVA with 999 permutations [35] was carried out using the same model applied in univariate comparisons for swimming velocity and immobility time. For significant sources of variations, pairwise comparisons were performed and SIMPER analyses conducted to highlight the behaviors that most contributed to these differences.

The univariate analyses (two-way and repeated measures ANOVA tests) were performed in the software Systat 12 and the multivariate procedures (PERMANOVA and SIMPER tests) in the software Primer 6 with PERMANOVA add-on.

3. Results

Swimming velocity varied between habitat complexity depending on the temperature regime, both before and after mirror exposure (Table 1 and S1 Data). The differences between habitat complexity occurred only at 34 degrees. Fish from the complex habitat decreased velocity before mirror exposure and those from the barren habitat increased it after the same exposure (Table 1 and Fig 2). For immobility time, we observed an effect only after mirror exposure, where fish from barren tanks showed a decrease at 34˚C (Table 1 and Fig 2).

The time spent in different quadrants under the two temperature regimes depended on habitat complexity, both before and after mirror exposure (Table 2). Before exposure at 28˚C, the fishes spent more time in quadrant 4 (lower aggressiveness), with a greater difference observed when the habitat was barren (28C versus 28B). At 34˚C, although the fishes also spent more time in quadrant 4, the opposite was observed, with a larger difference when the

| Table 1. Two-way ANOVA to compare ‘Swimming velocity’ and ‘Immobility time’ between temperature (28 and 34˚C) and habitat structure (complex and barren) in the dusky damselfish before and after mirror exposure. |
|---|
| Swimming velocity |
| Before mirror | After mirror |
| (KS–p = 0.128; L–p = 0.718) | (KS–p = 0.061; L–p = 0.493) |
| Source | DF | MS | F | P | MS | F | P |
| Temp. | 1 | 0.55 | 0.14 | 0.714 | 1.14 | 6.32 | 0.017 |
| Compl. | 1 | 2.14 | 0.53 | 0.471 | 2.39 | 13.20 | 0.001 |
| T x C | 1 | 33.60 | 8.34 | 0.007 | 2.81 | 15.55 | < 0.001 |
| Error | 32 | 4.03 | | | | | |
| Before mirror | After mirror |
| (KS–p = 0.457; L–p = 0.141) | (KS–p = 0.125; L–p = 0.373) |
| Source | DF | MS | F | P | MS | F | P |
| Temp. | 1 | 18.67 | 0.01 | 0.941 | 19.73 | 4.26 | 0.047 |
| Compl. | 1 | 4.08 | 0.00 | 0.973 | 24.43 | 5.27 | 0.028 |
| T x C | 1 | 12892.76 | 3.80 | 0.060 | 33.49 | 7.23 | 0.011 |
| Error | 32 | 108674.99 | | | | | |

Square root-transformed data were used for swimming velocity after mirror exposure in order to achieve ANOVA assumptions. Bold p-values correspond to significant effects. KS–Kolmogorov-Smirnov test for normality; L–Levene test for homoscedasticity; Temp./T–temperature; Compl./C–complexity of the habitat. DF = degrees of freedom, MS = mean squared

https://doi.org/10.1371/journal.pone.0235389.t001
habitat was structurally more complex (Fig 3). After mirror exposure, fishes remained longer in quadrant 1 (i.e. more aggressive) under both temperature regimes. However, fish at 28˚C showed a greater behavioral change (from quadrant 4 to quadrant 1), while fish at 34˚C occupied the other quadrants (less aggressive when compared to quadrant 1). Also, fish from complex habitat remained longer in quadrant 1 than fish from barren habitat (Fig 3).

Aggressive and locomotor behavior differed due to the temperature before mirror exposure and the interactive effect of temperature and habitat complexity after mirror exposure (Two-Way PERMANOVA, Table 3). Before mirror exposure, more threat behavior occurred at 34˚C and more vigilance, immobility and feeding at 28˚C (Fig 4 and Table 4). However, there was a trend to a habitat complexity effect at 34˚C, resulting in more threat behavior in the barren condition and more vigilance in its complex counterpart (Fig 4 and Table 4). After mirror exposure, attack behavior became more frequent (almost absent before mirror exposure) and an integrative effect between temperature regime and habitat complexity was observed (Fig 4).

Table 2. Repeated Measures ANOVA for comparisons of time spent in each quadrant considering the different temperatures (28 and 34˚C) and environments (complex and barren) in the dusky damselfish before and after mirror exposure.

| Source     | Between subjects | Within subjects |
|------------|------------------|-----------------|
|            | DF   | MS    | F   | P    | MS    | F   | P    |
| Temp.      | 1    | 1.17  | 0.32 | 0.575 | 1.86  | 0.76 | 0.390 |
| Compl.     | 1    | 3.19  | 0.88 | 0.357 | 8.80  | 3.61 | 0.067 |
| T x C      | 1    | 10.50 | 2.88 | 0.100 | 0.60  | 0.25 | 0.624 |
| Error      | 32   | 3.65  |      |       |       |      |      |
| Quadr.     | 3    | 181.44| 13.90| < 0.001| 166.46| 16.27| < 0.001|
| Q x T      | 3    | 0.92  | 0.07 | 0.942 | 27.26 | 2.67 | 0.075 |
| Q x C      | 3    | 2.90  | 0.22 | 0.817 | 1.97  | 0.19 | 0.832 |
| Q x T x C  | 3    | 47.50 | 3.64 | 0.029 | 33.06 | 3.23 | 0.044 |
| Error      | 96   | 13.05 |      |       |       |      |      |

Data were square-root transformed and p-values were subjected to Greenhouse-Geisser correction. Bold p-values correspond to significant effects. Temp./T - temperature; Compl./C - complexity of the habitat; Quadr/Q - quadrant. DF = degrees of freedom. MS = mean squared.

https://doi.org/10.1371/journal.pone.0235389.t002
Overall, there were more attacks at 28°C when compared to 34°C, but habitat complexity played a larger role at 34°C, with more attacks and threats when the habitat was barren and more immobility and vigilance when it was complex (Fig 4 and Table 4).

### 4. Discussion

We observed that changes in temperature and complexity affect mobility and aggressiveness in the dusky damselfish (*S. fuscus*). An increase in water temperature from 28 to 34°C (mimicking global warming predictions) and a decrease in habitat complexity (mimicking the loss of complexity due to coral mortality predicted in global warming scenarios) increased motor activity and decreased the emission of typical agonistic displays. This result suggests that environmental temperature and structure affect the natural behavioral repertoire of *S. fuscus* and thus, the strength of interspecific competition may be disturbed and affect habitat use and the interactions in the reef community. Although the species shows high behavioral plasticity [36], it may require longer to properly cope with drastic environmental changes.

It is forecasted that the rate of warming will accelerate in the near future [37–39]. Thermal stress, one of the leading direct climate-related threats to reef ecosystems [40], may result in increased frequency and intensity of coral bleaching [41], algae population decline [42] and dispersion of reef species [43,44]. Warming may lead to increased metabolic activity in fishes, potentially causing cardiac and ventilatory overload [15] and consequent reduction in the

---

### Table 3. Two-way PERMANOVA comparing the set of behaviors under different temperatures (28 and 34°C) and habitat structures (complex and barren) in the dusky damselfish before and after the mirror exposure.

| Source  | DF | MS      | Pseudo-F | P-perm | MS      | Pseudo-F | P-perm |
|---------|----|---------|----------|--------|---------|----------|--------|
| **Before mirror** (PERMDISP-\(p = 0.930\)) |     |         |          |        |         |          |        |
| Temp.   |    | 2997.4  | 4.77     | 0.007  | 1166.8  | 2.91     | 0.060  |
| Compl.  |    | 2065.3  | 3.29     | 0.051  | 636.8   | 1.59     | 0.205  |
| T x C   |    | 1884.9  | 3.00     | 0.069  | 2258.5  | 5.64     | 0.009  |
| Error   |    | 628.42  |          |        | 400.5   |          |        |

**After mirror** (PERMDISP-\(p = 0.057\))

Data were square-root transformed in order to better achieve homogeneous dispersion. Bold \(p\)-values correspond to significant effects. Temp./T—temperature; Compl./C—complexity of the habitat. DF = degrees of freedom, MS = mean squared, PERMDISP = permuted dispersion.

https://doi.org/10.1371/journal.pone.0235389.t003
animal's aerobic scope [45]. Thermal stress was already shown to cause behavioral changes that are usually followed by reduced ability to exploit resources [46], decreased immunity response [47,48], reproductive losses [6,49], and failure to recognize environmental cues [50,51]. A recent study on butterflyfishes showed reduced aggression due to reef's complexity loss [4].

The dusky damselfish appears to tolerate some temperature variation: it can withstand acute temperature increase caused by seawater entrapped in small tide pools that can reach 36°C (personal observation). However, their tolerance time-range seems to be narrow (i.e., only 4–6 hours of the low tide). In this scenario, fish seem to reduce locomotion and the percentage of time invested in agonistic behaviors until the flow returns to higher levels, and the animals have access to the open sea. In contrast, the present study imposed a more extended period of high temperature (30 days), and \textit{S. fuscus} tolerance zone may have been exceeded to enter the resistance zone. Warming caused a decrease in costly displays (threats, attacks) that were replaced by more economical ones, such as vigilance. Although fish spent more time close to the mirror (after mirror exposure), showing that warming did not affect the ability to

**Table 4. SIMPER results for the behaviors that most contributed to the differences observed after pairwise comparison for significant effects obtained in PERMANOVA.**

| Behavior | Before mirror | After mirror |
|----------|---------------|--------------|
| 28 vs. 34 | 28C vs. 34C | 28C vs. 34B | 28B vs. 34B | 34C vs. 34B |
| Immobility | 3\textsuperscript{rd} (28) | 3\textsuperscript{rd} (34C) | 4\textsuperscript{th} (28C) | 2\textsuperscript{nd} (28B) | 4\textsuperscript{th} (34C) |
| Vigilance | 2\textsuperscript{nd} (28) | 4\textsuperscript{th} (34C) | 2\textsuperscript{nd} (28C) | 3\textsuperscript{rd} (28B) | 3\textsuperscript{rd} (34C) |
| Feeding | 4\textsuperscript{th} (28) | | | | |
| Threat | 1\textsuperscript{st} (34) | 2\textsuperscript{nd} (28C) | 1\textsuperscript{st} (34B) | 1\textsuperscript{st} (34B) | 1\textsuperscript{st} (34B) |
| Attack | 1\textsuperscript{st} (28C) | 3\textsuperscript{rd} (28C) | 4\textsuperscript{th} (28B) | 2\textsuperscript{nd} (34B) | |

For each comparison between two conditions, behaviors were ranked in terms of contribution. The code in parentheses indicates the condition in which the behavior was more frequent: 28°C, 34°C, Complex—C or Barren—B.

https://doi.org/10.1371/journal.pone.0235389.t004
notice a conspecific invader, it changed the way fish interact with the intruder. Thus, increased water temperatures seem to affect the behavioral trade-off between signaling and fighting against the intruder, a result that is consistent with our prediction.

The locomotor patterns observed in *S. fuscus* did not indicate loss of swimming velocity (Fig 2), as found in other species of damselfish [52–55]. The decreased aggression observed in increased water temperature may be related to nutritional deficit following temperature rise and complexity loss, as an economic strategy to cope with increased metabolism [4, 56,57]. Therefore, the ecological relations of the damselfish with the coral reef community would be compromised.

We observed that fish kept in the barren environment exhibited more aggressive displays than those in a complex environment, similar to what occurs with salmonids [58]. Overall levels of aggression tend to be higher in less complex environments [12], given that more aggressive animals have preferential access to resources [59] or more mating opportunities [60]. Thus, it seems that barren environments, where there are fewer habitat sharing options, lead to a single solution: increased aggressiveness to guarantee territory, even if it involves more stress and higher energy costs.

Although the combination of high temperature and barren condition was the worst for *S. fuscus*, the enrichment of the 34˚C ambient seemed to compensate thermic stress, as suggested by Goldenberg et al. [61]. Other authors have shown that enrichment increases neurogenesis and decreases anxiety-like behavior in fish [62,63]. Several other studies have discussed the importance of environmental complexity, which seems to favor behavioral plasticity [64,65] and decline stress levels [66,67], in addition to affecting reef predation and competition rates [68,69]. The structural complexity of the habitat is related to ecologically diverse environments with high fish abundance [70], because a more complex environment provides elevated niche and resource variability [71], producing areas that can harbor more biological diversity and fish biomass when compared to less structurally complex environments [72,73]. Thus, habitat structure may ultimately change the behavioral pattern of species [74]. As such, the reef ecosystem complexity, which is considered of utmost importance for species diversity and richness [25,75–78], is being threatened by the global warming, and many species that occur exclusively on reefs are endangered.

The predicted global warming will affect species distribution and lead to profound changes in the three-dimensional structure of reefs [79]. In our study, we heated the tank water to the temperature predicted for the end of this century (34˚C) and maintained it for one month, observing several behavioral effects on the dusky damselfish (*S. fuscus*) that may have cascading effects on reef community. Rather than overall effects on the reef, our results suggest ocean warming reduces the damselfish ability to maintain their territories and consequently control other species’ growth by their gardening role. Losing territory size due to decreased aggressiveness is likely to scale up and affect interaction networks in the reefs (e.g., gardening, competition, predation, foraging, reproduction, navigability, and niche partitioning). Changes in behavior are only the tip of the iceberg of many and much more harmful changes, and strategies to mitigate global warming effects are urgently needed to prevent such a future adverse scenario.

**Supporting information**

**S1 Data.**

(XLSX)

**Author Contributions**

**Conceptualization:** Guilherme Ortigara Longo, Ana Carolina Luchiari.
Formal analysis: Thalles da Silva-Pinto, Edson Aparecido Vieira.

Methodology: Thalles da Silva-Pinto, Mayara Moura Silveira, Jéssica Ferreira de Souza, Ana Luisa Pires Moreira.

Resources: Ana Carolina Luchiari.

Supervision: Ana Carolina Luchiari.

Writing – original draft: Ana Carolina Luchiari.

Writing – review & editing: Thalles da Silva-Pinto, Mayara Moura Silveira, Jéssica Ferreira de Souza, Ana Luisa Pires Moreira, Guilherme Ortigara Longo, Ana Carolina Luchiari.

References

1. Zanna L, Khatiwala S, Gregory JM, Ison J, Heimbach P. Global reconstruction of historical ocean heat storage and transport. 2019;116. https://doi.org/10.1073/pnas.1808838115

2. Clarke A, Fraser KPP. Why does metabolism scale with temperature? Funct Ecol. 2004; 18: 243–251. https://doi.org/10.1016/j.tree.2004.08.041 x

3. Handeland SO, Imsland AK, Stefansson SO. The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. Aquaculture. 2008; https://doi.org/10.1016/j.aquaculture.2008.06.042

4. Keith SA, Baird AH, Hobbs JPA, Woolsey ES, Hoey AS, Fadli N, et al. Synchronous behavioural shifts in reef fishes linked to mass coral bleaching. Nat Clim Change. 2018; 8: 986–991.

5. Clarke A, Johnston NM. Scaling of metabolic rate with body mass and temperature in teleost fish. 1999; 68: 893–905.

6. Miranda LA, Chalde T, Elisisio M, Strüssmann CA. Effects of global warming on fish reproductive endocrine axis, with special emphasis in pejerrey Odontesthes bonariensis. Gen Comp Endocrinol. 2013; 192: 45–54. https://doi.org/10.1016/j.ygcen.2013.02.034 PMID: 23500677

7. Wong BBM, Candolin U. Behavioral responses to changing environments. Behav Ecol. 2015; 26: 665–673. https://doi.org/10.1093/beheco/aru183

8. Klein C, Jonas W, Iggena D, Empl L, Rivalan M, Wiedmer P, et al. Exercise prevents high-fat diet-induced impairment of flexible memory expression in the water maze and modulates adult hippocampal neurogenesis in mice. Neurobiol Learn Mem. 2016; 131: 26–35. https://doi.org/10.1016/j.nlm.2016.03.002 PMID: 26968656

9. Lindahl ULF, Marcus CO. The 1997 / 1998 Mass Mortality of Corals: Effects on Fish Communities on a Tanzanian Coral Reef. 2001; 42: 127–131. https://doi.org/10.1016/S0025-326X(00)00167-3

10. Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J. Dynamic fragility of oceanic coral reef ecosystems. PNAS. 2006;103. https://doi.org/10.1073/pnas.0600693103 PMID: 16709673

11. Salvanes AGV, Moberg O, Ebbesson LOE, Nilsen TO, Jensen KH, Braithwaite VA. Environmental enrichment promotes neural plasticity and cognitive ability in fish. Proc R Soc B Biol Sci. 2013; 280: 13. https://doi.org/10.1098/rspb.2013.1331 PMID: 23902903

12. Church KDW, Grant JWA. Does increasing habitat complexity favour particular personality types of juvenile Atlantic salmon, Salmo salar? Anim Behav. 2018; 135: 139–146. https://doi.org/10.1016/j.anbehav.2017.11.006

13. Pankhurst N, Munday PL. Effects of climate change on fish reproduction and early life history stages. Mar Freshw Res. 2011; 62: 1015–1026. https://doi.org/10.1017/MF10269

14. Lees K, Pitois S, Scott C, Frid C, MacKinson S. Characterizing regime shifts in the marine environment. Fish Fish. 2006; 7: 104–127. https://doi.org/10.1111/j.1467-2979.2006.00215.x

15. Nilsson GE, Crawley N, Lunde IG, Munday PL. Elevated temperature reduces the respiratory scope of coral reef fishes. Glob Chang Biol. 2009; 15: 1405–1412. https://doi.org/10.1111/j.1365-2486.2008.01767.x

16. Munday PL., Jones GP., Pratchett MS., Williams AJ. Climate change and the future for coral reef fishes. Fish Fish. 2008; 261–285. https://doi.org/10.1111/j.1467-2979.2008.00281.x

17. Rummer JL, Couturier CS, Stecky JAW, Gardiner NM, Kinch JP, Nilsson GE, et al. Life on the edge: Thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. Glob Chang Biol. 2014; 20: 1055–1066. https://doi.org/10.1111/gcb.12455 PMID: 24281840
18. Ceccarelli DM, Jones GP, McCook LJ. Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. Oceanogr Mar Biol Annu Rev. 2001; 39: 355–389. https://doi.org/10.1016/j.chemphys.2005.03.003

19. Hata H, Kato M. A novel obligate cultivation mutualism between damselfish and Polysiphonia algae. Biol Lett. 2006; 2: 593–596. https://doi.org/10.1098/rsbl.2006.0528 PMID: 17148297

20. Ceccarelli DM. Modification of benthic communities by territorial damselfish: a multispecies comparison. Coral Reefs. 2007; 26: 13. https://doi.org/10.1007/s00338-007-0275-1

21. Hixon MA, Brostoff WN. Damsel fish as keystone species in reverse: Intermediate disturbance and diversity of reef algae. Science (80-). 1983; 511–513. https://doi.org/10.1126/science.220.4596.511 PMID: 17816223

22. Jones GP. Interactions between herbivorous fishes and macro-algae on a temperate rocky reef. J Exp Mar Bio Ecol. 1992; 159: 217–235. https://doi.org/10.1016/0022-0981(92)90038-C

23. Lough J. Climate and climate change on the great barrier reef. In: Johnson JE, Marshall PA (eds) Climate change and the great barrier reef: a vulnerability assessment. Great Barrier Reef Marine Park Authority. 2013; Townsville. pp.15–50.

24. IPCC (The Intergovernmental Panel on Climate Change). The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. 2013; United Kingdom. Cambridge University Press.

25. Munday PL, McCormick MI, Nilsson GE. Impact of global warming and rising CO2 levels on coral reef fishes: what hope for the future? J Exp Biol. 2012; 215: 3865–3873. https://doi.org/10.1242/jeb.074765 PMID: 23100485

26. Metaxas A, Scheibling RE. Community structure and organization of tidepools. Mar Ecol Prog Ser. 1993; 98: 187–198. https://doi.org/10.3354/meps098187

27. CoralReefWatch May.26. NOAA Satellite and Information Service. Thermal History 2019; [accessed 2019 May26]. https://coralreefwatch.noaa.gov/product/thermal_history/

28. Leão ZMAN, Dominguez JML. Tropical coast of Brazil. Mar Pollut Bull. 2000; 41: 112–122. https://doi.org/10.1016/S0025-326X(00)00105-3

29. Barlow GW, Rogers W, Fraley N. Do Midas cichlids win through prowess or daring? It depends. Behav Ecol Sociobiol. 1986; 19: 1–8. https://doi.org/10.1007/BF00309396

30. Earley RL, Hsu Y, Wolf LL. The use of standard aggression testing methods to predict combat behaviour and contest outcome in Rivulus marmoratus dyads (Teleostei: Cyprinodontidae). Ethology. 2000; 106: 743–761. https://doi.org/10.1046/j.1439-0310.2000.00586.x

31. Arnott G, Beattie E, Elwood RW. To breathe or fight? Siamese fighting fish differ when facing a real opponent or mirror image. Behav Processes. 2016; 129: 11–17. https://doi.org/10.1016/j.beproc.2016.05.005 PMID: 27234172

32. Pinheiro-da-Silva J, Silva PF, Nogueira MB, Luchiari AC. Sleep deprivation effects on object discrimination task in zebrafish (Danio rerio). Anim Cogn. 2017; 20: 159–169. https://doi.org/10.1007/s10071-016-1034-x PMID: 27646310

33. Girden E. 1992. ANOVA Repeated Measure. Newbury Park, CA. Sage.

34. Quinn GP, Keough MJ. Experimental design and data Analysis for Biologists. Cambridge: Cambridge University Press; 2002. https://doi.org/10.1192/bjp.112.483.211-a

35. Anderson MJ. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 2001; 26: 32–42.

36. Medeiros PR, Moreira ALP, Medeiros AMA. Local variations in microhabitat use by Stegastes fuscus (Cuvier, 1830) (Teleostei: Pomacentridae) in a tropical reef of Brazil. Braz. J. Biol. Sci. 2016; 6: 375–384. https://doi.org/10.21472/bjbs.030613

37. Meissner KJ, Lippmann T, Gupta AS. Large-scale stress factors affecting coral reefs: Open ocean sea surface temperature and surface seawater aragonite saturation over the next 400 years. Coral Reefs. 2012; 31: 309–319. https://doi.org/10.1007/s00338-011-0866-8

38. Collins WJ, Fry MM, Yu H, Fuglestvedt JS, Shindell DT, West JJ. Global and regional temperature-change potentials for near-term climate forcers. Atmos Chem Phys. 2013; 13: 2471–2485. https://doi.org/10.5194/acp-13-2471-2013

39. Mizuta R, Arakawa O, Ose T, Kusunoki S, Endo H, Kitoh A. Classification of CMIP5 Future Climate Responses by the Tropical Sea Surface Temperature Changes. Sola. 2014; 10: 167–171. https://doi.org/10.2151/sola.2014-035

40. Brierley AS, Kingsford MJ. Impacts of climate change on marine organisms and ecosystems. Curr Biol. 2009; 19: R602–R614. https://doi.org/10.1016/j.cub.2009.05.046 PMID: 19640499
41. Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, et al. Global warming and recurrent mass bleaching of corals. Nature. 2017; 543: 373–377. https://doi.org/10.1038/nature21707 PMID: 28300113

42. Sominson EJ, Scheibling RE, Metaxas A. Kelp in hot water: I. Warming seawater temperature induces weakening and loss of kelp tissue. Mar. Ecol. Prog. Ser. 2015; 573: 89–104. https://doi.org/10.3354/meps11438

43. Holbrook SJ, Schmitt RJ, Stephens JS. Changes in an Assemblage of Temperate Reef Fishes. 1997; 7: 1299–1310. https://doi.org/10.1890/1051-0761(1997)007[1299:CIAATJ]2.0.CO;2

44. Vergés A, Doropoulos C, Malcolm HA, Skye M, García-Pizá M, Marzinelli EM, et al. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. Proc Natl Acad Sci. 2016; 113: 13791–13796. https://doi.org/10.1073/pnas.1610725113 PMID: 27849585

45. Johansen JL, Jones GP. Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. Glob Chang Biol. 2011; 17: 2971–2979. https://doi.org/10.1111/j.1365-2486.2011.02436.x

46. Navarro JM, Paschke K, Ortiz A, Vargas-Chacoff L, Pardo LM, Valdivia N. The Antarctic fish Harpagifer antarcticus under current temperatures and salinities and future scenarios of climate change. Prog Oceanogr. 2018; https://doi.org/10.1016/j.pocean.2018.09.001

47. Klein RD, Borges VD, Rosa CE, Colares EP, Robaldo RB, Martinez PE, et al. Effects of increasing temperature on antioxidant defense system and oxidative stress parameters in the Antarctic fish Notothenia coriiceps and Notothenia rossii. J Therm Biol. 2017; 68: 110–118. https://doi.org/10.1016/j.jtherbio.2017.02.016 PMID: 28689712

48. Martinez D, Vargas-Lagos C, Oyarzun R, Loncoman CA, Pontigo JP, Yáñez AJ, et al. Temperature modulates the immunological response of the sub-antarctic nototheniid fish Eleginops maclovinus injected with Piscirickettsia salmonis. Fish Shellfish Immunol. 2018; 82: 492–503. https://doi.org/10.1016/j.fsi.2018.08.042 PMID: 30165153

49. Miller GM, Kroon FJ, Metcalfe S, Munday PL. Temperature is the evil twin: effects of increased temperature and ocean acidification on reproduction in a reef fish. Ecol Appl. 2015; 25: 603–620. https://doi.org/10.1890/14-0559.1 PMID: 26214908

50. Allan BJM, Domenici P, Munday PL, McCormick MI. Feeling the heat: The effect of acute temperature changes on predator-prey interactions in coral reef fish. Conserv Physiol. 2015; 3: 1–8. https://doi.org/10.1093/conphys/cov039 PMID: 26214908

51. Warren DT, Donelson JM, McCormick MI. Extended exposure to elevated temperature affects escape response behaviour in coral reef fishes. PeerJ. 2017; 5: e3652. https://doi.org/10.7717/peerj.3652 PMID: 28828253

52. Gardiner NM, Munday PL, Nilsson GE. Counter-gradient variation in respiratory performance of coral reef fishes at elevated temperatures. PLoS One. 2010; 5. https://doi.org/10.1371/journal.pone.0013299 PMID: 20949020

53. Johansen JL, Steffensen JF, Jones GP. Winter temperatures decrease swimming performance and limit distributions of tropical damselfishes. Conserv Physiol. 2015; 3: 1–12. https://doi.org/10.1093/conphys/cov039 PMID: 27293724

54. Nilsson GE, Östlund-Nilsson S, Munday PL. Effects of elevated temperature on coral reef fishes: Loss of hypoxia tolerance and inability to acclimate. Comp Biochem Physiol—A Mol Integr Physiol. 2010; 156: 389–393. https://doi.org/10.1016/j.cbpa.2010.03.009 PMID: 20233610

55. Killen SS, Mitchell MD, Rummer JL, Chivers DP, Ferrari MCO, Meekan MG, et al. Aerobic scope predicts dominance during early life in a tropical damselfish. Funct Ecol. 2014; 28: 1367–1376. https://doi.org/10.1111/1365-2435.12296

56. Hiscock K, Southward A, Tittley IAN, Hawkins S. Effects of changing temperature on benthic marine life in Britain and Ireland. 2004; 362: 333–382. https://doi.org/10.1002/acq.628

57. Punzón A, Serrano A, Sánchez F, Velasco F, Preciado I, González-Irusta JM, et al. Response of a temperate demersal fish community to global warming. J Mar Syst. 2016; 161: 1–10. https://doi.org/10.1016/j.jmarsys.2016.05.001

58. Højesjø J, Johnsson J, Bohlin T. Habitat complexity reduces the growth of aggressive and dominant brown trout (Salmo trutta) relative to subordinates. Behav Ecol Sociobiol. 2004; 56: 286–289. https://doi.org/10.1007/s00265-004-0784-7

59. Ward AJW, Thomas P, Hard PB, Krause J. Correlates of boldness in three-spined sticklebacks (Gasterosteus aculeatus). Behav Ecol Sociobiol. 2004; 55: 561–568. https://doi.org/10.1007/s00265-003-0751-8

60. Myhre LC, Forsgren E, Amundsen T. Effects of habitat complexity on mating behavior and mating success in a marine fish. Behav Ecol. 2013; 24: 553–563. https://doi.org/10.1093/beheco/ars197
61. Goldenberg SU, Nagelkerken I, Marangon E, Bonnet A, Ferreira CM, Connell SD. Ecological complexity buffers the impacts of future climate on marine consumers. Nat. Clim. Change. 2018; 8: 229–233. https://doi.org/10.1038/s41558-018-0199-2 PMID: 29608759

62. von Krogh K, Sørensen C, Nilsson GE, Øverli Ø. Forebrain cell proliferation, behavior, and physiology of zebrafish, Danio rerio, kept in enriched or barren environments. Physiol. Behav. 2010; 101: 32–39. https://doi.org/10.1016/j.physbeh.2010.04.003 PMID: 20385156

63. Näslund J, Johnsson JI. Environmental enrichment for fish in captive environments: effects of physical structures and substrates. Fish Fish. 2016; 17: 1–30.

64. Rossi C, Angelucci A, Costantin L, Braschi C, Mazzantini M, Babbini F, et al. Brain-derived neurotrophic factor (BDNF) is required for the enhancement of hippocampal neurogenesis following environmental enrichment. Eur J Neurosci. 2006; 24: 1850–1856. https://doi.org/10.1111/j.1460-9568.2006.05059.x PMID: 17040481

65. Strand DA, Utne-Palm AC, Jakobsen PJ, Braithwaite VA, Jensen KH, Salvanes AGV. Enrichment promotes learning in fish. Mar Ecol Prog Ser. 2010; 412: 273–282. https://doi.org/10.3354/meps08682

66. Poubder KC, Mitchell JL, Thomson JS, Pottinger TG, Buckley J, Sneddon LU. Does environmental enrichment promote recovery from stress in rainbow trout? Appl Anim Behav Sci. 2016; 176: 136–142. https://doi.org/10.1016/j.applanim.2016.01.009

67. White LJ, Thomson JS, Poubder KC, Coleman RC, Sneddon LU. The impact of social context on behaviour and the recovery from welfare challenges in zebrafish, Danio rerio. Anim Behav. 2017; 132: 189–199. https://doi.org/10.1016/j.anbehav.2017.08.017

68. Almany GR. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia. 2004; 141: 105–113. https://doi.org/10.1007/s00442-004-1617-0 PMID: 15197644

69. Almany GR. Does Increased Habitat Complexity Reduce Predation and Competition in Coral Reef Fish and competition reduce habitat predation complexity Does increased in coral reef fish assemblages? Oikos. 2014; 106: 275–284. https://doi.org/10.1111/j.0030-1299.2004.13193.x

70. Gratwicke B, Speight MR. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J Fish Biol. 2005; 66: 650–667. https://doi.org/10.1111/j.1095-8649.2005.00629.x

71. Friedlander AM, Parrish JD. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J Exp Mar Bio Ecol. 1998; 224: 1–30. https://doi.org/10.1016/S0022-0981(97)00164-0

72. Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK. Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs. 2017; 36: 561–575. https://doi.org/10.1007/s00338-017-1539-z

73. Kovalenko KE, Thomaz SM, Warfe DM. Habitat complexity: Approaches and future directions. Hydrobiology. 2012; 685: 1–17. https://doi.org/10.1007/s10750-011-0974-z

74. Braithwaite VA, Salvanes AGV. Environmental variability in the early rearing environment generates behaviourally flexible cod: Implications for rehabilitating wild populations. Proc R Soc B Biol Sci. 2005; 272: 1107–1113. https://doi.org/10.1098/rspb.2005.3062 PMID: 16024371

75. Risk M. Fish diversity on a coral reef in the Virgin Islands. Atoll Res Bull. 1972; 153: 1–7. https://doi.org/10.5479/si.00775630.153.1

76. Luckhurst BE, Luckhurst K. Analysis of the influence of substrate variables on coral reef fish communities. Mar Biol. 1978; 49: 317–323. https://doi.org/10.1007/BF00455026

77. Roberts C, Ormond R. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar Ecol Prog Ser. 1987; 41: 1–8. https://doi.org/10.3354/meps041001

78. Grigg RW. Effects of sewage discharge, fishing pressure and habitat complexity on coral ecosystems and reef fishes in Hawaii. Mar Ecol Prog Ser. 1994; 103: 25–34. https://doi.org/10.3354/meps103025

79. Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 2003; https://doi.org/10.1038/nature01286 PMID: 12511946