Food web trophic control modulates tropical Atlantic reef ecosystems response to marine heat wave intensity and duration

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Abstract

1. Marine Heat Waves (MHWs) are episodes of anomalous warming in the ocean that can last from a few days to months. MHWs have different characteristics in terms of intensity, duration, and frequency and generate thermal stress on marine ecosystems. In reef ecosystems, they are one of the main causes of decreased presence and abundance of corals, invertebrates, and fish. The deleterious capacity of thermal stress often depends upon biotic factors such as resource availability (bottom-up control on predators) and predation (top-down control on prey). Despite the evidence of thermal stress and biotic factors affecting individual species, the combined effects of both stressors on the entire reef ecosystems are far less studied.

2. Here, using a food-web modeling approach, we estimated the rate of change in species' biomass due to different MHW scenarios based on their physical characteristics. Specifically, we modeled the mechanistic link between species' consumption rate and seawater temperature (thermal stressor), simulating species' biomass dynamics for different MHW scenarios under different trophic control assumptions (biotic factor).

3. We find that total reef ecosystem biomass declined by 10% ± 5% under MHWs with severe intensity and top-down control assumption. The bottom-up control assumption moderates the total ecosystem biomass reduction by 5% ± 5%. Irrespective of the MHW scenario and the trophic control assumption, the most substantial biomass changes occur among top, meso-predators, and corals (5% to 20% ± 10%).

4. Since habitat degradation may lead to reef ecosystems governed by top-down control on prey, our findings point to the critical importance of protecting reef ecosystems as a pivotal strategy to alleviate the impacts of thermal stress induced by MHWs. Overall, our results provide a unified understanding of the interplay between abiotic stressors and biotic factors in reef ecosystems under extreme thermal events, offering insights into present baselines and future ecological states for reef ecosystems.

1. Introduction

Marine Heat Waves (MHWs) are periods of unusually high ocean temperatures that last from a few days to several months. (Hobday et al., 2016). These extreme events have profound and widespread impacts on marine ecosystems services resulting in significant financial losses with associated socio-economic consequences (Smith et al., 2021 and 2023; Olivier et al., 2021). In this sense, understanding the response of marine ecosystems to climate change, particularly MHWs, has been acknowledged as a major societal challenge to allocate conservation efforts (Smith et al., 2021). Indeed, due to their abrupt nature, MHWs can rapidly push ecosystems beyond their resilience limits, hindering species adaptation and acclimatization processes (Gruber et al., 2021). Therefore, these extreme events pose a more severe threat to living species than long-term global warming. Several studies show that MHW occurrence has increased over the past century and suggest that these trends will continue in the future (Oliver et al., 2018, Frölicher et al., 2018). It is not only the projected increase in the occurrence of

MHWs that is a concern for society and ecosystems but also their changes in characteristics such as duration, intensity and frequency (Gupta et al., 2020). In this context, there is still a need to better understand how marine ecosystems respond to specific characteristics of MHWs.

The majority of studies report negative MHWs effects on reef ecosystems, especially on corals (IPCC, 2018). Coral death resulting from MHWs can lead to shifts in benthic community composition and alterations in ecosystem structure and functioning (Darling et al., 2019; Hughes et al., 2018; Ferrari et al., 2016). The severity and frequency of mass coral bleaching associated with MHWs have increased over the last decades, severely impacting shallow tropical reefs across the Pacific, Indian and Atlantic Oceans (Asner et al., 2022; Baum et al., 2023; Ferreira et al., 2021; Mohanty et al., 2021). Moreover, the magnitude of these impacts varies among regions. Coral mortality in the tropical South Atlantic Ocean is approximately 60% lower than in the Indo-Pacific and 50% lower than in the Caribbean sea (Mies et al., 2020). This observed spatial variability in the reef ecosystem responses indicates that biological factors modulate the thermal stress generated by MHWs.

Indeed, the abiotic stress induced by MHWs can be aggravated or moderated by biotic factors such as trophic interactions (Miller et al. 2014). This is because the amount of food a species eats (i.e.,the species' consumption rate) depends on sea water temperature, resource availability (bottom-up control on predators) and predation risk (top-down control on prey). For example, fish predator cues increase the effect of MHWs on copepod's reproduction and consumption rate (Truong et al. 2020). Reef damselfish *Stegastes nigricans* scares corallivorous fishes by defending its food resources and so it provides physiological resistance against MHWs to corals (Honeycutt et al. 2023). However, each of these examples does not quantify the minimum level of predation risk and resource availability that generates negative effects of MHWs on marine organisms. Thus there is an open area of research focusing on how biotic factors such as trophic interactions can modulate the MHWs negative impacts on marine organisms.

In this work, we used a food web modeling approach to address the following question: How do Atlantic tropical reef ecosystems respond to different marine heat wave characteristics, such as intensity and duration under different ecosystem trophic control assumptions? We hypothesized that if the intensity and duration of MHWs increase, then species' biomass would be negatively affected because an increase in sea water temperature negatively impacts species' consumption rate (Volkoff & Rønnestad, 2020). We expected that this reduction in species biomass would be more pronounced under a top-down trophic control assumption, because the effects of predation risk and elevated temperature are additive given that higher predation risk generates more physiological stress on prey (Miller et al. 2014, Global Change Biology). Moreover, we expected that MHW intensity would be the most detrimental MHW characteristic because intense MHWs induce extreme suboptimal temperature conditions impacting species' consumption rate (e.g. Smith et al., 2023 and Gruber et al., 2021).

2. Material and Methods

2.1 The Rocas Atoll reef ecosystem

In this study we used the Rocas Atoll as a study case. The Rocas Atoll is located in the tropical Southwest Atlantic. It is a pristine volcanic island that offers a natural laboratory for understanding the impact of thermal stress on tropical reef ecosystems (Figure 1a). Its isolation and protection status shield it from direct anthropogenic impacts such as pollution, urbanization, and fishing, making it an ideal location for studying the effects of MHWs (Longo et al., 2015, Brandão et al., 2017). However, since it is a shallow and non-turbid reef, it is more susceptible than coastal reefs to bleaching due to thermal stress (Glynn, 1996; Takahashi et al., 2004). This susceptibility was evidenced in 2019 when severe marine heatwaves caused the highest recorded bleaching events in the Southwestern Atlantic, affecting reefs in Rocas Atoll, Abrolhos coral reefs, and São Paulo rocky reefs (Banha et al., 2019; Duarte et al., 2020). Despite this, Rocas Atoll remains one of the most effective marine protected areas in the Southwestern Atlantic with minimal local anthropogenic impacts and it can serve as a natural model system for evaluating the MHWs impacts on species' biomass dynamics.

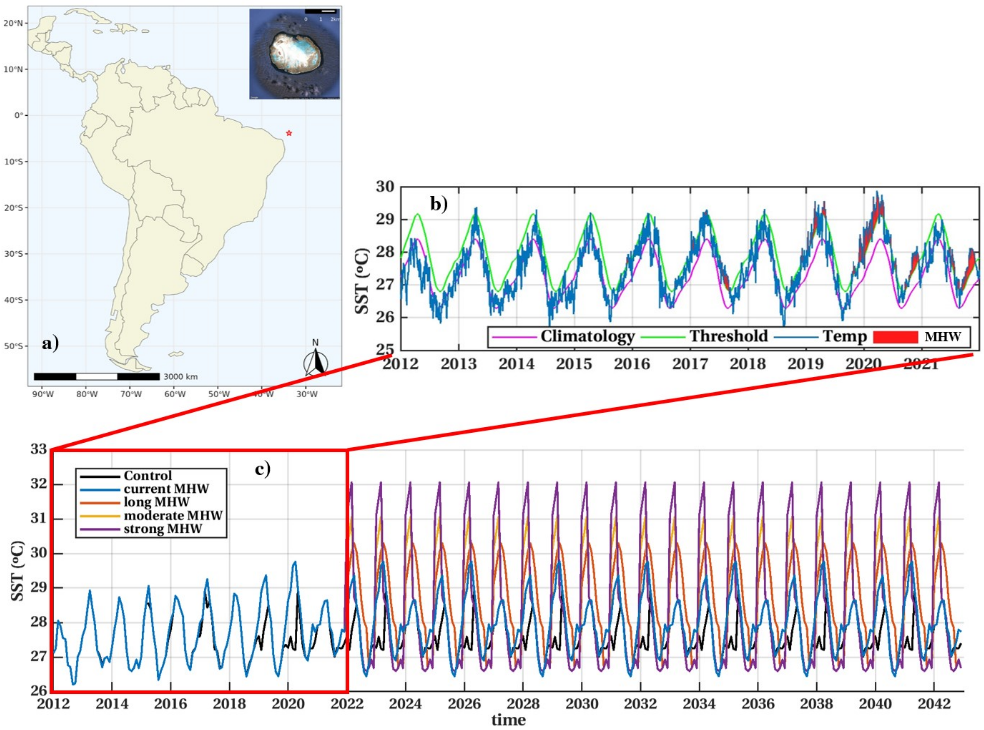

Figure 1 (a) Location of the Rocas Atoll (indicated with a red star) near Brazil, Southwest Atlantic Ocean. The satellite image of the Rocas Atoll was retrieved from Google Maps through *ggmap* package in R. (b) Sea Surface Temperature (SST) over the past decade, with detected Marine Heat Waves (MHWs) indicated in red. The threshold corresponding to the 90th percentile is indicated in green. The climatological mean computed over the period 1981-2021 is indicated in magenta. (c) Sea surface temperature time series used to force the ecosystem model under different scenarios of MHW events.

2.2 Marine heat waves detection using sea surface satellite data

MHWs were identified using the definition proposed by Hobday et al. (2016). According to their definition, MHWs are discrete and prolonged events characterized by anomalously warm water temperatures that exceed the seasonally-varying 90th percentile for a duration of more than five days (Figure 1b). This definition has been incorporated into a freely available software tool in Matlab developed by Zhao and Marin (2019).

The daily Sea Surface Temperature (SST) data utilized in this study were obtained from the National Oceanic and Atmospheric Administration Optimum Interpolation Sea Surface Temperature (NOAA OI SST V2.1; Reynolds et al., 2007). This data can be accessed freely on the NOAA website at https://www.ncei.noaa.gov/data/sea-surface-temperature-optimum-interpolation/v2.1/access/avhrr/. This data set is an interpolation of remotely sensed SSTs from the Advanced Very High-Resolution Radiometer (AVHRR) imager into a regular grid of 0.25° and daily temporal resolution from 1981 to the present. Our study focuses specifically on the period from 2012 to 2021, as in situ ecological information from Rocas Atoll is available from 2012 onwards. However, for the purpose of identifying MHWs, the reference period used spans from 1981 to 2021.

MHWs at Rocas Atoll have increased in intensity and duration since 2019 (Figure 1b). In particular, the year 2021 witnessed the longest mean MHW duration (90 days) and the most intense MHW event (1° above the climatological mean). We, therefore, focused on the period from 2019 to 2021 when analyzing the effects of past MHWs and defined scenarios considering the characteristics of the most extreme MHW of 2021 (see section 2.5).

2.3 Food web modeling approach

2.3.1 The Rocas Atoll Ecopath model

The food web model of the Rocas Atoll reef ecosystem was implemented within Ecopath-Ecosim software (EwE, v. 6.6.8 on Windows 11, https://ecopath.org/). The temporal dynamic module, Ecosim, simulates changes in the biomass, production, consumption, and diets of species/functional groups using a previous defined Ecopath model.

We updated the Rocas Atoll Ecopath model published by Capitani et al. (2021) by adding 13 species/functional groups. These are: particulate organic matter, dissolved organic matter, opportunistic pathogens microbes, mutualist microbes, sponges, fleshy macroalgae, crustose corraline algae, polychaeta, nudibranchia, nematoda, echinoderms/large gastropods, the black triggerfish *Melichthys niger* and the butterflyfish *Chaetodon* spp. We added these 13 components in order to provide a more realistic description of the trophic interactions present in the Rocas Atoll reef ecosystem. We aggregated several species into functional groups with other species of similar life history traits, diet composition and shared predators in the interest of keeping the model results easy to deal with. We refer the reader to the supplementary materials of this study and Capitani et al. (2021) for functional group composition and parameterization of the updated Rocas Atoll Ecopath model. Full details of the EwE modeling approach can be obtained from main references (Christensen and Walters 2004; Heymans et al., 2016).

2.3.2 Species biomass simulations over time and trophic control assumptions

The dynamic module Ecosim re-expresses the master equations of Ecopath as a system of differential equations to account for changes in species biomass, production and consumption over time due to changes in environmental parameters and mortality rates (Walters et al., 1997). In practice, the Rocas Atoll Ecopath model was used to set initial conditions for Ecosim simulations, and it was used to provide estimates of some of the consumption-related and production-related parameters of the Ecosim model. The system of differential equations is solved using an Adams-Bashford integration routine. The Ecosim prediction for type-i prey biomass to type-j predators biomass is of the functional form:

$$\frac{dB_i}{dt} = g_i \cdot \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (F_i + M_i + e_i) \cdot B_i \qquad (Eq. 1)$$

where B_i is the biomass of type-i prey; g_i is growth efficiency of type-i prey; Q_{ji} is consumption rate of prey i; Q_{ij} is consumption rate by all predators j; I is the immigration rate; F is fishing mortality and e is the emigration rate. Consumption rates Q are estimated following the 'foraging arena' concept (Ahrens et al. 2012; Walters et al., 1997) where species' biomass B is divided into two components, one vulnerable and other invulnerable to predation. For a given prey-predator couple (i, j), the consumption rate Q of prey i by predator j is estimated as follows (Eq.2):

$$Q_{ij} = \frac{\left(\frac{a_{ij} \cdot v_{ij} \cdot B_i \cdot B_j \cdot T_i \cdot T_j \cdot M_{ij}}{D_j}\right)}{v_{ij} + v_{ij} \cdot T_i \cdot M_{ij} + \left(\frac{a_{ij} \cdot M_{ij} \cdot B_j \cdot T_j}{D_j}\right)} \cdot S_{ij} f(e_e, t) \qquad (Eq. 2)$$

where, a_{ij} is the effective search rate for i by j, v_{ij} is the vulnerability rate expressing how fast the prey biomass i is available to predator j (e.g. biotic factor tested); B_i is the prey biomass; B_j is the predator biomass; T_i and T_j are the relative feeding time for prey and predator; M_{ij} is the mediation forcing effects; D_j is the effects of handling time as a limit to consumption rate and S_{ij} is a scalar multiplier (0 to 1) linked to a gaussian environmental response function

$f(e_e, t)$ to account for external abiotic stressors which change over time (e.g., sea water temperature).

It is important to note that the vulnerability rate v_{ij} is the main parameter related to the trophic control assumptions tested in this study. For values of v_{ij} greater than 2, a large increase in the prey biomass B_i results in a large increase in the predator consumption rate Q_{ij}. Thus, for values of v_{ij} greater than 2, the quantity of prey i biomass consumed by predator is mainly influenced by predator j biomass. The ecosystem is, then, under top-down trophic control. Conversely, when v_{ij} tends to 1, a large increase in prey biomass B_i has a lower impact on the predator consumption rate Q_{ij}; the ecosystem is, then, under bottom-up trophic control. Here we tested three trophic control assumptions: $v_{ij} = 1$ as bottom-up control assumption, $v_{ij} = 2$ as mixed trophic control assumption and $v_{ij} = 10$ as top-down control assumption.

2.3.3 Mechanistic link between sea water temperature and consumption rate in Ecosim

We applied species' thermal performance curves in Ecosim as gaussian environmental response functions. We used the thermal performance curves to modify the consumption rate Q_{ij} of each species/functional group, where the maximum consumption rate occurred at the optimum temperature, and consumption rates declined as temperature departed from the optimum (Eq. 2). For primary producers we used thermal performance curves to modify the primary producers' growth efficiency (g, Eq. 1). We defined the intercept between each species-specific thermal performance curve and the monthly average sea water temperature to calculate a scalar factor S_{ij} with a maximum multiplier of 1 for optimum temperature (Bentley et al., 2017). The scalar factor S_{ij} by definition declines as the average sea water temperature deviates from the optimum at a rate determined by the thermal performance curve standard deviations (Bentley et al., 2017; Serpetti et al., 2017; Corrales et al., 2018).

We used species distribution data and abundance to produce thermal performance curves following steps described by Waldock et al. (2019). For each species we: (1) produced a distribution model using the s-jSDM algorithm (Pichler and Hartig, 2021) to estimate the upper and lower thermal occurrence limits (as the 2.5% and 97.5% percentiles), then (2) we used a linear model to filter out the effect of predictors other than temperature (bathymetry, salinity, primary productivity and available phytoplankton carbon) on abundance, and lastly (3) we applied an additive model with temperature as sole predictor in the linear model residuals to project which temperature produces the highest abundance (Waldock et. al. 2019). To avoid collinearity issues, we combined environmental descriptors used in the s-jSDM and the linear models using a spatial principal component analysis. Since nearly all species we assessed are restricted to reefs, we trimmed all variables to include only cells with depths ranging between 0 and 30 m. We obtained reef fish biomass data (as abundance indicator) from Morais et al. (2017), percentage cover of sessiles organisms from Aued et al. (2018) and sea surface temperature rasters (alongside other environmental covariables used in the s-jSDM) from Bio-ORACLE (Assis et al. 2018). As not all species and/or functional groups had available data on abundance, we resorted to Aquamaps distribution repository to construct thermal performance curves based on temperature quantile distribution (Kaschner et al., 2019). Thermal performance curves for each species/functional group are presented in the supplementary materials, Figure 3.

2.3.4 MHWs scenarios

We conducted multiple temporal simulations to examine the impacts of MHWS on species' biomass. These simulations encompassed various scenarios of MHWs, including a scenario comprising MHWs with similar characteristics as the ones reported in the past (current MHW), one with longer lasting MHWs (long MHWs) and two with increased MHW intensity (ranging from moderate to strong) (Figure 2a). Each scenario involved running the ecosystem model (Figure 2b) over the period from 2012 to 2042, using temperature time series as the environmental driver (Eq. 2). The satellite-derived sea surface temperature time series for the period 2012-2021 was used in all the scenarios (Figure 1b), except for the control scenario. The sea surface temperature time series for this control scenario was built by removing the effects of MHWs: the sea surface temperature values during MHW events were replaced with climatological values (Figure 1c; black curve). Perturbations corresponding to each MHW scenario were introduced for the period 2022-2042. Details on the temperature time series for each scenario are provided in Table 1. For each scenario, the Ecosim model was run using the three trophic assumptions (Figure 2c).

Table 1 Marine Heat Waves (MHWs) scenarios used (see Fig. 3 for details about the methodological approach adopted).

Scenario	**Temperature forcing 2012-2021**	**Temperature forcing 2022-2042**	**Color in Figure 2c**
Control	Satellite Sea Surface Temperature (SST) with MHWs removed: MHW temperature values replaced by the climatological mean	Satellite SST from 2019-2021 with MHWS removed repeated 7 consecutive times over the period 2022-2042	black
Current	Satellite Sea Surface Temperature (SST)	Satellite SST from 2019-2021 repeated 7 consecutive times over the period 2022-2042	blue
Long	Satellite Sea Surface Temperature (SST)	Every year has a 10-month-long MHW with 1º above 90% percentile threshold	orange
Moderate	Satellite Sea Surface Temperature (SST)	Every year has a 3-month-long MHW with 2 º above the 90% percentile threshold	yellow
Strong	Satellite Sea Surface Temperature (SST)	Every year has a 3 month long MHW with 3 ° above the 90% percentiles threshold	purple

The model outputs were then used to compute the rate of change in biomass (R) for each species due to the occurrence of MHWs (Figure 2d and Eq. 3). This was accomplished by comparing the biomass of each scenario to the biomass of the control scenario. The calculation of R is defined as follows:

$$R = \frac{Biomass(S) - Biomass(control)}{Biomass(control)} * 100 \qquad (Eq. 3)$$

where S refers to a particular scenario (current, long, moderate or strong).

Species experiencing an increase in mean rate of change in biomass (positive R values) were considered as winners while those exhibiting a decrease (negative R values) were considered as losers.

We examined the effects of MHWs over different time scales. To assess the past impact of MHWs, we calculated the averaged R-value over the period from 2019 to 2022. For short-term effects, we computed the average R-value over the years 2023 to 2025. Additionally, we analyzed the long-term or accumulated effects by comparing the mean R-value in 2022 with that in 2042 (Figure 2d).

2.3.5 Ecosystem Indicators

We intended to describe the overall impacts of MHWs on the Rocas Atoll's reef ecosystem using four ecosystem indicators. We used Ecosim outputs to compute the relative changes of the four ecosystem indicators in the last year of the simulation (2042) with respect to 2022 (Figure 2e). These ecosystem indicators are: 1) biomass ratio of consumers to primary producers, defined as biomass units of consumers without the microbial community per unit of primary producers biomass (phytoplankton, macroalgae, turf algae and crustose coralline algae); 2) biomass ratio of corals to algae defined as biomass units of scleractinian corals per unit of benthic primary producers (macroalgae, turf algae and crustose coralline algae), 3) the biomass ratio of coral to sponges defined as biomass units of scleractinian corals per unit of sponges (i.e., phylum Porifera) and 4) total ecosystem biomass as the sum of primary producers and consumers biomass (excluding particulate organic matter and dissolved organic matter).

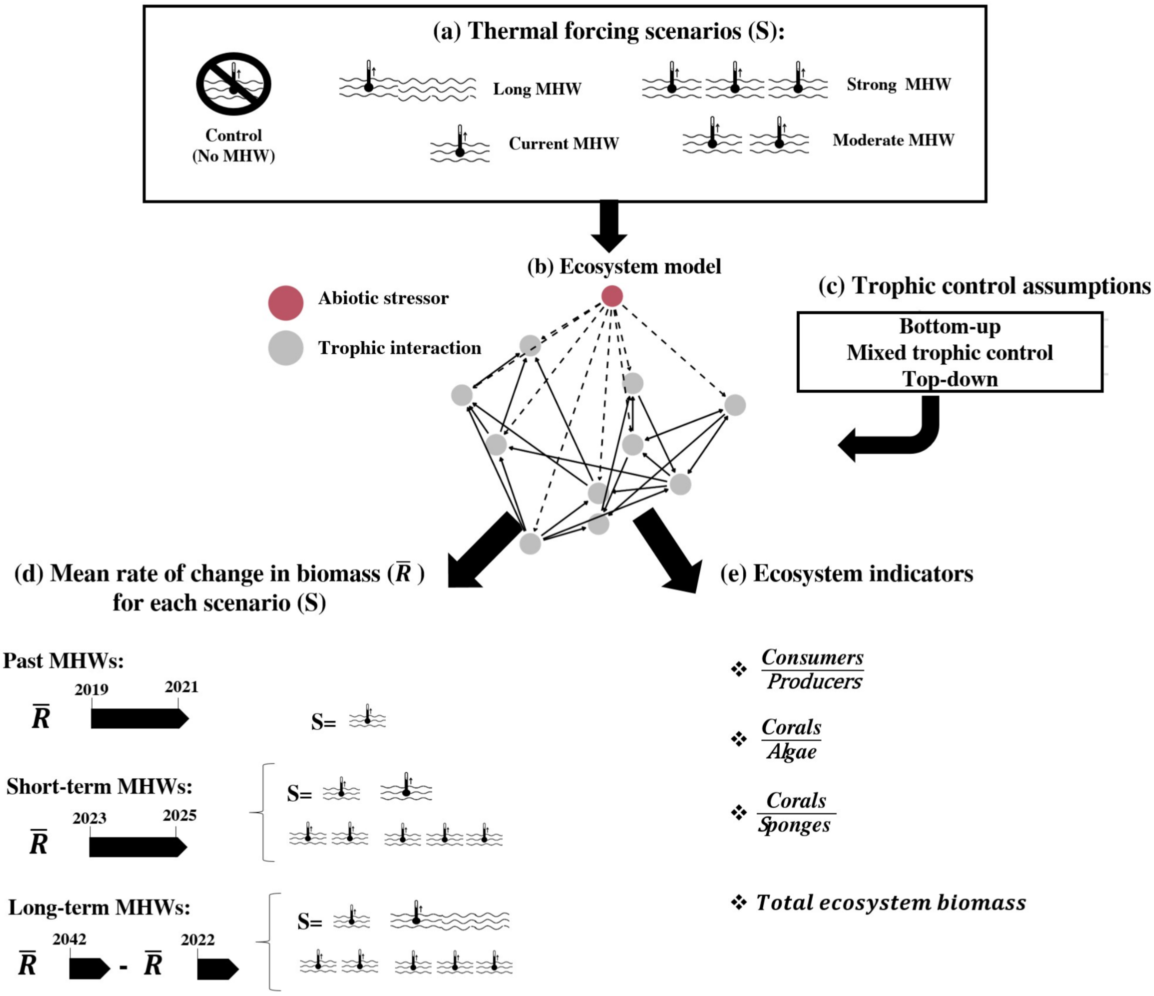

Figure 2 Summary of the methodological approach used in this study. (a) Thermal forcing scenarios of Marine Heat Waves (MHWs), (b) the ecosystem model for the Rocas Atoll, (c) three trophic assumptions used for the parameterization of the predator–prey interactions in the Ecosim model, (d) the rate of change in species' biomass due to MHWs averaged over different periods, and (e) the ecosystem indicators that were evaluated.

2.3.6 Uncertainty for species biomass simulations under MHWs scenarios

The Monte Carlo routine in Ecosim was used to perform sensitivity analyses for species biomass simulations under MHWs scenarios. This routine tests the sensitivity of Ecosim's output to Ecopath input parameters by drawing input parameters from a uniform distribution centered on the baseline Ecopath values with the coefficients of variation (CV) set to default 0.1 (Christensen and Walters 2004; Steenbeek et al., 2018). In our study, we set coefficients of variation as 0.1 for B (biomass per unit area), P/B (Production/Biomass), Q/B (Consumption/Biomass) parameters. We set coefficients of variation as 0.05 for the diet composition parameter of each species/functional group. We ran 500 Monte Carlo simulations for each scenario based on coefficients of variation to determine the error in the rate of change in biomass (R). We refer the reader to the "Error estimation of the rate of change in species' biomass" section in the supplementary material.

All statistical analyses were performed in R studio, an IDE for R v 4.3.1 (R Core Team, 2021) and Matlab (v R2017b). Within the R software, we used these packages for data aggregation and visualization *tidyverse* (v 2.0; Wickham et al., 2019). For spatial data analysis we used *rnaturaleart* (v 0.3.4; Massicotte et al. 2023), *ggmap* (v 3.0; Kahle & Wickham, 2019), *ggsn* (v 0.5; Baquero, 2022) and *ggspatial* (v 1.1.9; Dunnington et al .2023). *qgam* (v 1.3.4; Fasiolo et al. 2021), *sdmpredictors* (v 0.2.15; Bosh et al. 2023), *aquamapsdata* (v 0.1.4; Kaschner et al. 2019) for species' thermal performance curves.

3. Results

3.1 Marine heat waves impacts on species' biomass

3.1.1 Marine heat waves impact over the Past (2019-2021)

The largest changes in species' biomass for the period 2019-2021 (in some cases larger than 10%) occurred under the top-down control assumption (Figure 3). We found an increase in the mean rate of change of biomass of omnivore fish, herbivore fish, mutualistic microbes, and dissolved organic matter under mixed and top-down trophic control assumptions (Figure 3). The majority of the predicted changes were relatively small, not exceeding 5%, with error bars of similar magnitudes (Figure 3).

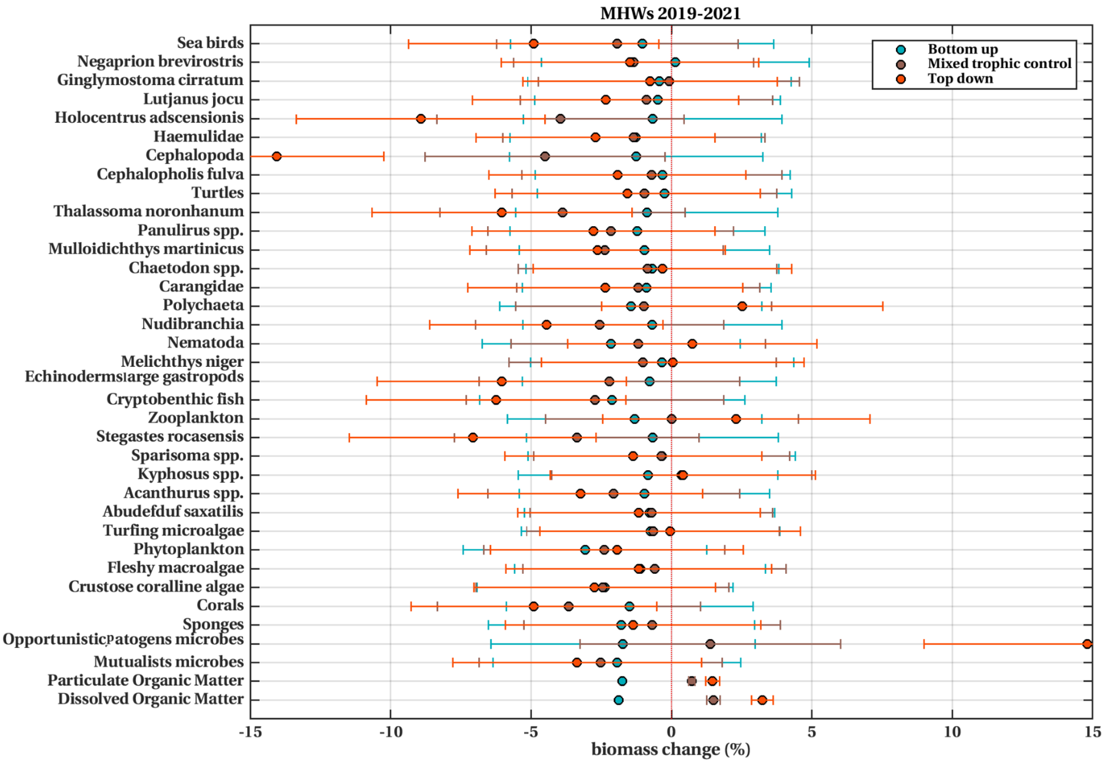

Figure 3 Species' biomass change under different ecosystem's trophic control assumptions (bottom-up, mixed and top-down) for the period 2019-2021. Dots represent the mean and the bars represent the respective error. Species/functional groups in the y axis are ordered by trophic level.

3.1.2 MHWs short-term impacts on species' biomass

Under the bottom-up assumption, the short-term (2023-2025) mean rate of change in species' biomass decreased by less than 17% (Figure 4a). Under the mixed trophic control assumption, dissolved organic matter, particulate organic matter, opportunistic microbes and sponges biomass increased across all MHW scenarios (Figure 5a and Figure 4 from Supplementary material). Under top-down assumption zooplankton and polychaeta increased in biomass (Figure 6a). Low-level predator fish *Holocentrus adscensionis*, nudibranchs, echinoderms and corals biomass decreased more than 40% under the long, moderate, and strong MHW scenarios, while opportunistic pathogens microbes biomass increased more than 50% (Figure 6a). Irrespective of the trophic control assumption, the strong MHW scenario induced the largest changes in biomass, while the long and moderate scenarios induced changes of a similar order of magnitude. Across all scenarios, keystone species such as sea birds, the nurse shark *Ginglymostoma cirratum* and the mid-level predator *Lujanus jocu* decreased in biomass.

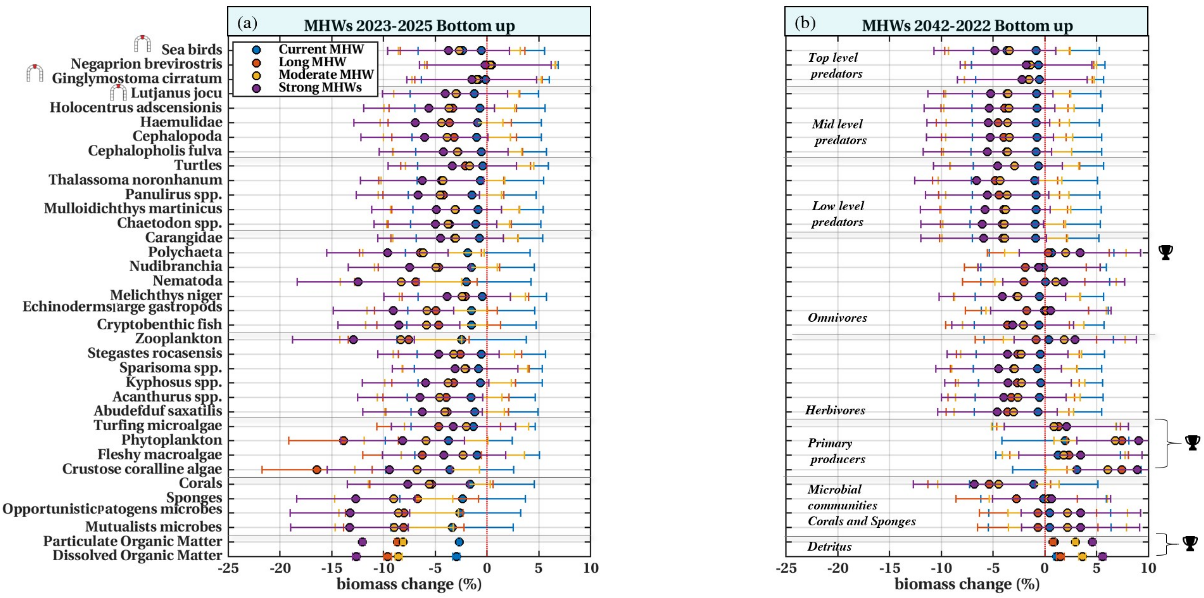

Figure 4 Short-term (a) and long-term (b) species' biomass change due to MHWs under the bottom-up trophic control assumption. Dots represent the mean and the bars the respective

error. Functional groups placed in the y axis are ordered by trophic level. Winners species are indicated with a black trophy.

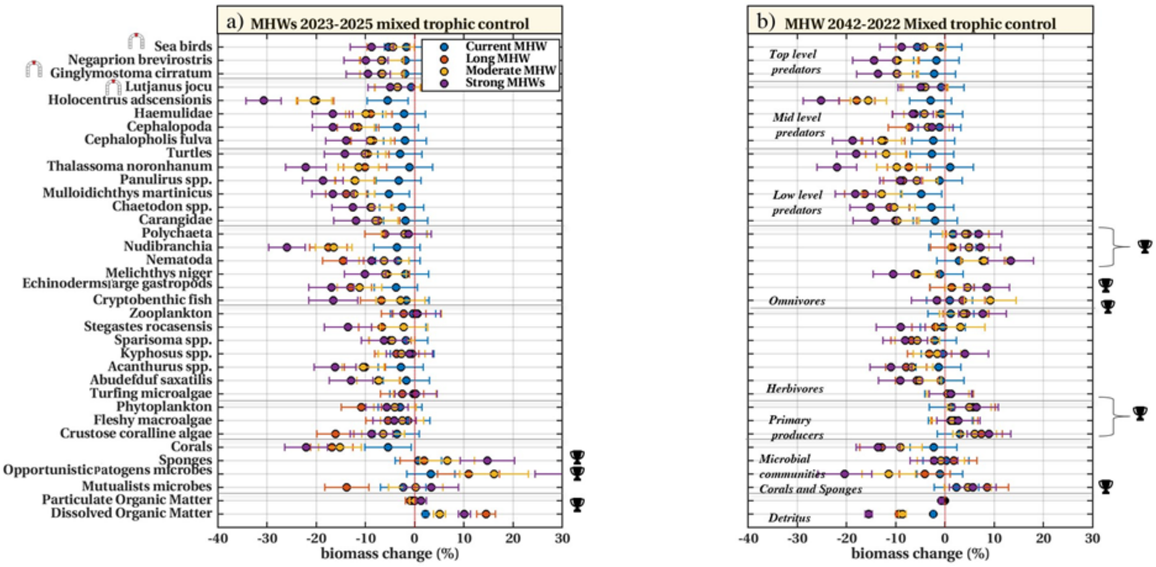

Figure 5 Short-term (a) and long-term (b) biomass' rate of change due to MHWs under the Mixed trophic control assumption. Dots represent the mean and the bars the respective error. Functional groups placed in the y axis are ordered by trophic level. Winners species are indicated with a black trophy.

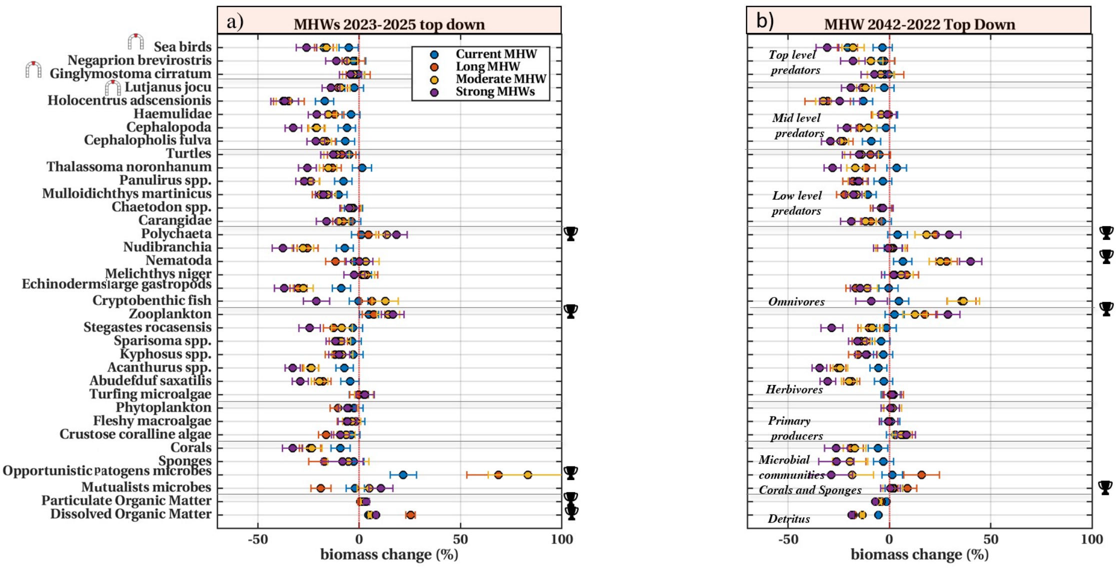

Figure 6 Short-term (a) and long-term (b) biomass's rate of change due to MHWs under the top-down trophic control assumption. Dots represent the mean and the bars the respective error. Functional groups placed in the y axis are ordered by trophic level. Winners species are indicated with a black trophy.

3.1.3 MHWs long-term impacts on species' biomass

The long-term impact of MHWs, considering the current scenario, is relatively small compared to the impacts induced by the strong, moderate, and long scenarios under all trophic control assumptions (Figures 4b, 5b and 6b).

We observed that the most negatively impacted species are low, top and mid-level predators (Figure 4b, Figure 5b 6b and Figure 4 from supplementary material) with the largest changes obtained with the top-down assumption. Sea birds, the butterfish *Cephalopholis fulva* and the Noronha wrasse *Thalassoma norohanum*, experienced ~40% biomass reduction under top-down control and the strong MHWs scenario (Fig. 7b).

We observed a general decline in species' biomass due to the cumulative effect of MHWs under the bottom-up assumption (Figure 4b). However, some species showed a biomass increase such as primary producers, detritus and polychaeta (Figure 4b). These positive changes in biomass were less than 5% and of the same order of magnitude as the error except for phytoplankton and crustose coralline algae.

Some species emerged as clear winners under specific MHWs scenarios under the mixed trophic control and top-down assumptions (Figure 5b and 6b). The majority of omnivores (except the black triggerfish *Melichthys niger*), primary producers and mutualistic microbes biomass increased by more than 7% (mixed trophic control) and 20 % (top-down control) (Figure 5b and 6b and Figure 4 supplementary material).

3.2 Relative changes in ecosystem indicators

We registered a general decrease for the ecosystem indicators under the top-down trophic control assumption (Figure 7). An exception is the coral/sponges ratio that showed an increase of 2% and 9% under the moderate and long MHWs scenarios (Figure 7).

MHWs with large intensity under the top-down control assumption lead to the most considerable changes in total ecosystem biomass (10%). Under bottom-up and mixed trophic control, total ecosystem biomass changes do not exceed 2%.

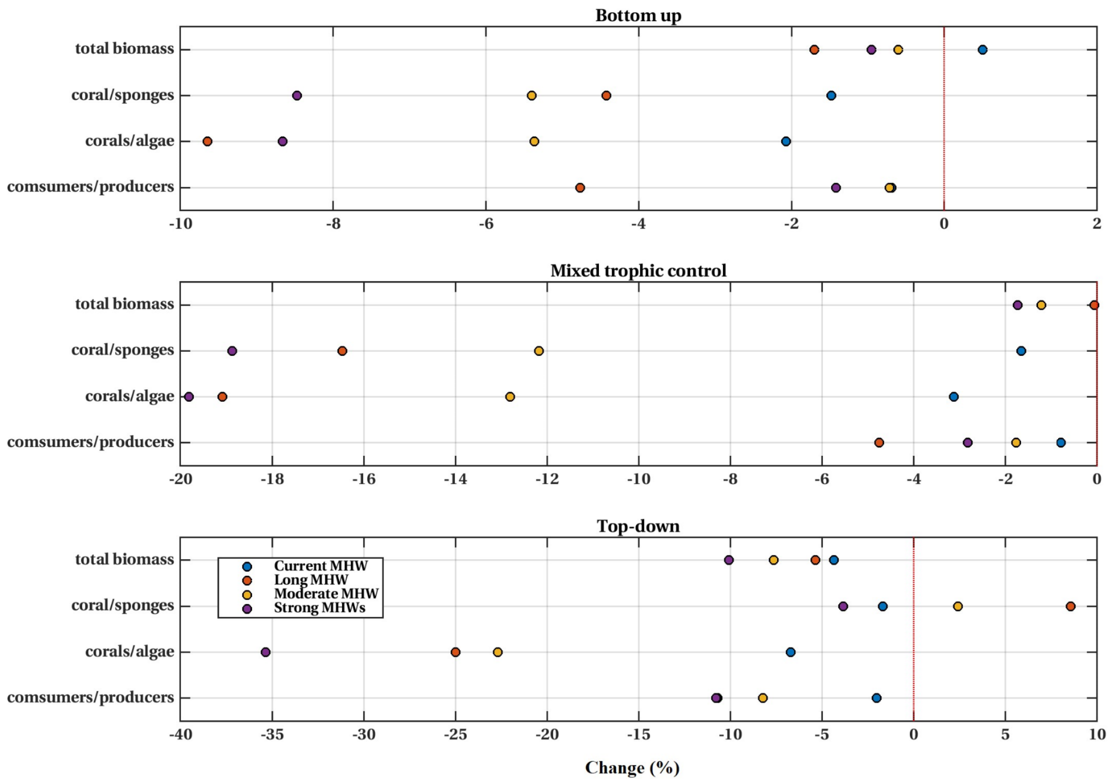

Figure 7 Ecosystem indicators percent change for each trophic control assumption and Marine Heat Waves (MHW) scenarios. The vertical red line indicates the 0% change.

4. Discussion

This study represents a comprehensive modeling exercise of the combined effects of abiotic stressor (MHWs) and biotic factor (food web trophic control) on tropical Atlantic reef ecosystems. Our results partially confirm our hypothesis that species' biomass changes are negatively impacted by the direct effects of thermal stress (i.e. intensity and duration of MHWs) and the indirect effects mediated by resource availability and predation risk (i.e. food web trophic control). On the other hand, as expected, we find a more pronounced reduction in species' biomass under the top-down trophic control assumption with, in particular, stronger MHWs. Overall, our results highlight that trophic interactions should be considered as an important biotic factor that conditions the resilience of reef ecosystems to the thermal stress in face of the expected increase in the number of MHWs.

4.1 Mechanisms leading to winners

Although the majority of species decline in biomass under the effect of MHWs regardless of their characteristics and the trophic control assumption, which agrees with our hypothesis, some species exhibit an increase in biomass and emerge as winners in particular circumstances. In fact, some studies have identified winners and losers in the Northeast Pacific after the 2013-2015 MHWs (Cavole et al., 2016) and after the 2014-2016 MHW affecting the West Coast of Canada and US (Free et al., 2023).

In most cases, we observed that these biomass increases are driven by trophic interactions. For instance, the short-term increase (over 2023-2025) in sponges biomass observed in all scenarios under the mixed trophic control assumption is probably due to the reduction of the main sponge predators, Nudibranchia and Polychaeta, as well as the increase in dissolved organic matter and zooplankton, which are the main components of the sponge's diet. However, in the long term, the rate of change in sponges' biomass is almost negligible. In the long term, primary producers emerge as winners in all scenarios under the bottom-up assumption, mainly because of the decrease in the biomass of herbivores and the increase of detritus, which is a source of nutrients. Additionally, the zooplankton increase observed in all scenarios under the top-down assumption is probably caused by the decrease in predators such as fish, corals, and sponges.

4.2 General Long-term Impact of MHWs in the Ecosystem

Under all MHWs scenarios and trophic control assumption, we observe a consistent decrease in the coral/algae indicator and consumer/producer indicator. The decrease in coral/algae indicator points at the ecosystem phase shift from coral to algae-dominated reef in all scenarios and under all trophic control assumptions. Since South Atlantic reef ecosystems are algae-dominated, the decrease in the ratio coral/ algae confirms a reef state with less habitat complexity and more pathogen microbial biomass as shown by Nelson et al. 2023. This is also consistent with previous studies that have documented shifts from coral-dominated reefs to reef systems characterized by turf and fleshy macroalgae (Barott and Rohwer, 2012, Pawlik et al., 2016). The model predicts that the transition towards algal dominance also results in a consistent increase in zooplankton.

The decrease in the consumers/producers indicator suggests that more primary producers' biomass is available to sustain consumers' biomass but also implies a decrease in consumers' biomass. The decrease in low, mid and top predators that occur under top-down and bottom-up assumptions results in the decrease in producers/consumers indicator. This indicator may also be related to the magnitude of intra and inter-specific competition for primary resources leading to shifts in ecosystem's trophic control (i.e., from bottom-up to top-down).

Finally, the decrease in the coral/ sponges indicator observed in the majority of scenarios suggests more sponges' biomass per reef unit area. The negative values associated with this indicator may be reflecting changes in the spatially competitive interactions between corals, sponges and algae. Moreover, this indicator may suggest an alteration in reef's biogeochemical cycling since sponges play a key role in transferring the energy and nutrients from dissolved organic matter to higher trophic levels (Rix et al. 2016).

Overall, the long-term changes in biomass towards lower trophic level species suggest a shortening of trophic chains and simplification of the food web.

4.3 Trophic control assumptions in the Rocas Atoll reef ecosystem

Since the Rocas Atoll reef ecosystem is highly preserved we hypothesized that the ecosystem is dominated by a bottom-up trophic control or by a mixed trophic control (Ahrens et al. 2012; Rehren et al., 2022). This means that in this ecosystem there is enough habitat heterogeneity to let prey hinder or escape from predators. In this sense, the relatively small changes that our food web model predicts under the bottom-up control are consistent with the changes reported in the literature for the Rocas Atoll under past MHW events (Gaspar et al., 2021). If a top-down control is assumed, we expect larger and non-linear changes in species' biomass. Indeed, under a top-down assumption, the amount of prey consumed by the predator is the product of $predator *$ prey biomass, (i.e., the predator biomass impacts on how much of the prey is consumed). Such a situation may occur when prey has no refuge and it is always taken upon being encountered by a predator. This top-down assumption is consistent with less protected ecosystems with higher habitat degradation, where both biotic factors and abiotic stressors are more prevalent. Consequently, our findings strongly suggest that protecting reef ecosystems can significantly alleviate the impacts of thermal stress-induced by MHWs.

4.4 Model limitations

It is important to consider several caveats associated with our analysis. First and foremost, the outcomes obtained in terms of biomass responses are intricately linked to the thermal performance characteristics of the species, encompassing their shape and magnitude. While we dedicated significant efforts to accurately compute these thermal performances, it is crucial to acknowledge that additional studies are necessary to enhance the level of certainty surrounding our findings.

Secondly, our model does not account for potential future acclimatization or adaptation mechanisms that species might undergo. This consideration holds substantial relevance, as species may have certain ability to adjust to changing environmental conditions over time (Garant 2020). It is a facet that merits attention for a more comprehensive understanding of the dynamics at play.

Lastly, a fundamental assumption underpinning our analysis is that the results hold validity predominantly for MHWs with extensive vertical and horizontal dimensions, thus potentially limiting species' capacity to seek out thermal refuges. However, it is worth noting that the applicability of our findings might differ in scenarios where MHWs exhibit distinct spatial characteristics. This, however, may be less relevant in our case study due to the shallower condition of our study area.

4.5 How realistic are the simulated MHWs?

Although climate models are known to have limitations in accurately reproducing extreme events near the coast and to have a too-coarse resolution, we investigate the projected temperature time series at Rocas Atoll using CMIP6 climate models (see Figure 5 in the Supplementary material) to assess the consistency of proposed scenarios with these model outputs.

As shown in Figure 1c, the "scenario long" implies MHWs reaching temperature with peaks of 30°C, moderate peaks of 31°C and strong peaks of 32°C. The analysis of projected time series from CMIP6 indicates that these temperature values are within a reasonable range. Specifically, peaks of 30°C and 31°C are recurrent in the majority of the climate models from the beginning of 2022, and some climate models show occasional peaks of 32°C during the period from 2022 to 2042. Interestingly, beyond 2042, the CMIP6 time series show peaks exceeding 35°C by the end of the century. This suggests that the reported changes in biomass described in this study could be far more extreme in the future. Despite the uncertainties associated with climate modeling, the CMIP6 time series raises important concerns about the potential impacts of such extreme temperatures on the marine ecosystem at Rocas Atoll.

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Conflict of interest

The contact author declares that neither of the authors has any competing interests.

Authors contribution

Camila Artana and Leonardo Capitani were involved in conceptualisation, methodology, investigation, formal analysis, visualization and writing original draft. Gabriel Santos Garcia was involved in methodology, review and editing. Ronaldo Angelini and Marta Coll were involved in conceptualisation, methodology, formal analysis, funding acquisition, supervision and review and editing. All authors contributed critically to the drafts and gave final approval for publication.

Statement on inclusion

Our study brings together authors from a number of different countries, including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. Whenever relevant, literature published by scientists from the region was cited; efforts were made to consider relevant work published in the local language.

Data availability statement

The raw data, the Rocas Atoll's food web model and the R code for data analysis that support the findings of this study are freely available in the GitHub repository: https://github.com/leomarameo7/MHW_trophic_interactions.The sea surface temperature from satellite data can be accessed freely on the NOAA website at https://www.ncei.noaa.gov/data/sea-surface-temperature-optimum-interpolation/v2.1/access/avhrr/.

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