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Camila Artana, Leonardo Capitani, Gabriel Santos Garcia, Ronaldo Angelini, Marta Coll. Food web trophic control modulates tropical Atlantic reef ecosystems response to marine heat wave intensity and duration. *Journal of Animal Ecology*, In press, 10.1111/1365-2656.14107 . hal-04604849

HAL Id: hal-04604849

<https://hal.science/hal-04604849>

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RESEARCH ARTICLE

Intraspecific Variation in Ecology and Evolution

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

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Funding information

Triatlas project, Grant/Award Number: 817578; ProOceans project, Grant/Award Number: RETOS-PID2020-118097RB-I00

Handling Editor: Cristina Linares

Abstract

1. Marine heatwaves (MHWs) are episodes of anomalous warming in the ocean that can last from a few days to years. MHWs have different characteristics in terms of intensity, duration and frequency and generate thermal stress in marine ecosystems. In reef ecosystems, they are one of the main causes of the decreased presence and abundance of corals, invertebrates and fish. The deleterious capacity of thermal stress often depends on biotic factors, such as the trophic control of predators on prey. Despite the evidence of thermal stress and biotic factors affecting individual species, the combined effects of both stressors on entire reef ecosystems are much less studied.
2. Here, using a food web modelling approach, we estimated the rate of change in species' biomass due to different MHW characteristics. Specifically, we modelled the mechanistic link between species' consumption rate and seawater temperature (thermal stressor), simulating species' biomass dynamics for different MHW characteristics under different trophic control assumptions (top-down, mixed trophic control and bottom-up).
3. We find that total reef ecosystem biomass declined by $10\% \pm 5\%$ under MHWs with severe intensity and a top-down control assumption. The bottom-up control assumption moderates the total ecosystem biomass reduction by $5\% \pm 5\%$. Irrespective of the MHW characteristics and the trophic control assumption, the most substantial biomass changes occur among top, mesopredators and corals (5% to $20\% \pm 10\%$).

Camila Artana and Leonardo Capitani contributed equally to this work.

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4. We show that reef ecosystems where predators exert top-down control on prey are prone to suffer species abundance declines under strong MHW events. We identify food web trophic control as a crucial driver that modulates the impacts of 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.

KEYWORDS

bottom-up, climate change, Ecopath and Ecosim, marine heatwaves, reef fish, species' biomass, thermal performance, top-down

1 | INTRODUCTION

Marine heatwaves (MHWs) are periods of unusually high ocean temperatures that last from a few days to several years (Hobday et al., 2016). These extreme events have profound and widespread impacts on biodiversity and marine ecosystem services (such as provisioning, regulating habitat and cultural services), resulting in significant financial losses with associated socio-economic consequences (Smith et al., 2021, 2023). Several studies show that MHW occurrence has increased over the past century and suggest that these trends will continue in the future (Frölicher et al., 2018; Oliver et al., 2018). Not only is the projected increase in the occurrence of MHWs a concern for society and ecosystems, but also their changes in characteristics such as duration, intensity and frequency (Sen Gupta et al., 2020). 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). In this sense, we still need to better understand how marine ecosystems respond to the specific characteristics of MHWs.

Temperature is one of the most important abiotic factors that influence species physiology due to its impact on overall metabolism and energy regulation (Volkoff & Rønnestad, 2020). Species exhibit a range of temperatures within which their physiological processes are optimized (Clarke, 2017; Martin & Huey, 2008). MHWs have the potential to rapidly push species beyond these optimal temperature ranges and their resilience limits, affecting species biomass (Gruber et al., 2021; Szuwalski et al., 2023). Under suboptimal conditions, species consumption rates are reduced as consumers surpass the thermal thresholds of optimal physiological performance (Csik et al., 2023; Englund et al., 2011). Therefore, given their abrupt nature, MHWs can negatively influence the species population dynamics on relatively short timescales (Gomes et al., 2024; Smale et al., 2019).

Trophic interactions can modulate the MHW effects on marine species (Harvey et al., 2022; Tekwa et al., 2022). This is partially because species consumption rates depend also on prey vulnerability to predators (i.e. on trophic control) (Allen et al., 2022; Preisser et al., 2005). For example, the effects of MHWs on copepods physiology (reproduction and consumption rate) are amplified when fish

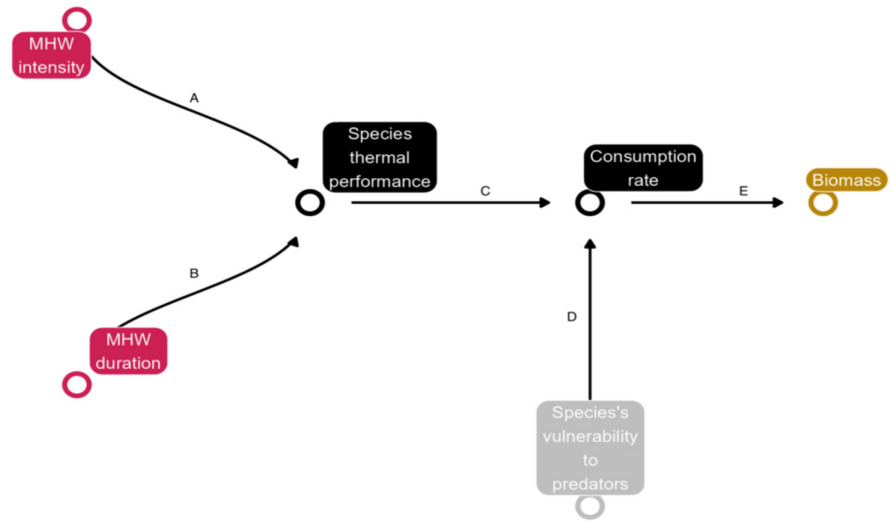
predator is present (Truong et al., 2020). Reef damselfish *Stegastes nigricans* scare corallivorous fishes by defending its food resources, and so it provides physiological resistance to corals against MHW stress (Honeycutt et al., 2023). However, each of these examples does not quantify the minimum level of prey vulnerability to predators that generate negative effects of MHWs on marine organisms. Therefore, there is still an open area of research focusing on how biotic factors, such as trophic interactions, can mediate the negative impacts of MHW on marine organisms.

The International Panel on Climate Change has reported the severe negative effects of MHWs on reef ecosystems worldwide (IPCC, 2019). The Southwestern tropical Atlantic reef ecosystem is a unique case where low cover of hard corals and macroalgae coexist in high turbidity and nutrient load conditions (Aued et al., 2018). Coral mortality is approximately 60% lower in the Southwestern tropical Atlantic than in the Indo-Pacific and 50% lower than in the Caribbean Sea (Mies et al., 2020). This has been attributed to their deeper bathymetric distribution, higher tolerance to nutrient enrichment, higher morphological resistance and more flexible symbiotic associations (Mies et al., 2020). Whether tropical Atlantic reef ecosystems would be resilient in future scenarios of longer-lasting and more intense MHWs remains an open question.

In this work, we used a food web modelling approach to address the following question: How do Atlantic tropical reef ecosystems respond to different MHW characteristics, such as intensity and duration, under different ecosystem trophic control assumptions? We hypothesized that:

- If the intensity and duration of MHWs increase then the species' biomass would decrease because the species' consumption rate decreases as it diverges from the species's thermal optimal performance (Clarke, 2017; Volkoff & Rønnestad, 2020) (Figure 1A–B–C–E).
- Given a defined MHW by its intensity and duration, the decrease in species biomass would be more pronounced under high prey vulnerability to predators because higher predator trophic control negatively impacts species' consumption rate (Allen et al., 2022; Bentley et al., 2017; Preisser et al., 2005) (Figure 1D–E).
- MHW intensity would be the most detrimental characteristic

FIGURE 1 Directed acyclic graph representing the research hypothesis. Variables are represented by nodes, with directed edges pointing from cause to effect. The species' vulnerability to predators is shown in grey, and it represents the trophic control influence on the species' consumption rate. The MHW exposure is represented by the magenta colour. The outcome, species' biomass, is represented in gold.



because it induces extreme suboptimal temperature conditions impacting species' consumption rate (e.g. Gruber et al., 2021; Smith et al., 2023) (Figure 1A–C).

2 | MATERIALS AND METHODS

2.1 | The Rocas Atoll reef ecosystem

In this work, we used the Rocas Atoll reef ecosystem as a study case (Figure 2a). The Rocas Atoll is located in the tropical Southwest Atlantic. 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. Rocas Atoll susceptibility to warming was evidenced in 2019 when severe MHWs caused the highest recorded bleaching events in the Southwestern Atlantic (Banha 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 laboratory for evaluating the MHW impacts on species' biomass dynamics.

2.2 | Marine heatwave detection using sea surface satellite data

We identified MHWs using the definition proposed by Hobday et al. (2016). We defined MHWs as discrete and prolonged events characterized by anomalously warm water temperatures that exceed the seasonally varying 90th percentile for more than 5 days (Figure 2b). This definition has been incorporated into a freely available MATLAB software tool developed by Zhao and Marin (2019).

We obtained the daily Sea Surface Temperature (SST) data used in this study 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 on reef fish biomass and benthic cover from Rocas Atoll is available from 2012 onwards. However, to identify MHWs, the reference period used spans from 1981 to 2021.

MHWs at Rocas Atoll have increased in intensity and duration since 2019 (Figure 2b). 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 analysing the effects of past MHWs and defined scenarios considering the characteristics of the most extreme MHW of 2021 (see Section 2.3.5).

2.3 | Food web modelling 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 previously defined Ecopath model.

We updated the Rocas Atoll Ecopath model published by Capitani et al. (2022) by adding 13 species/functional groups. These are particulate organic matter, dissolved organic matter, opportunistic pathogen microbes, mutualist microbes, sponges, fleshy macroalgae, crustose coralline algae, polychaeta, nudibranchia, nematoda,

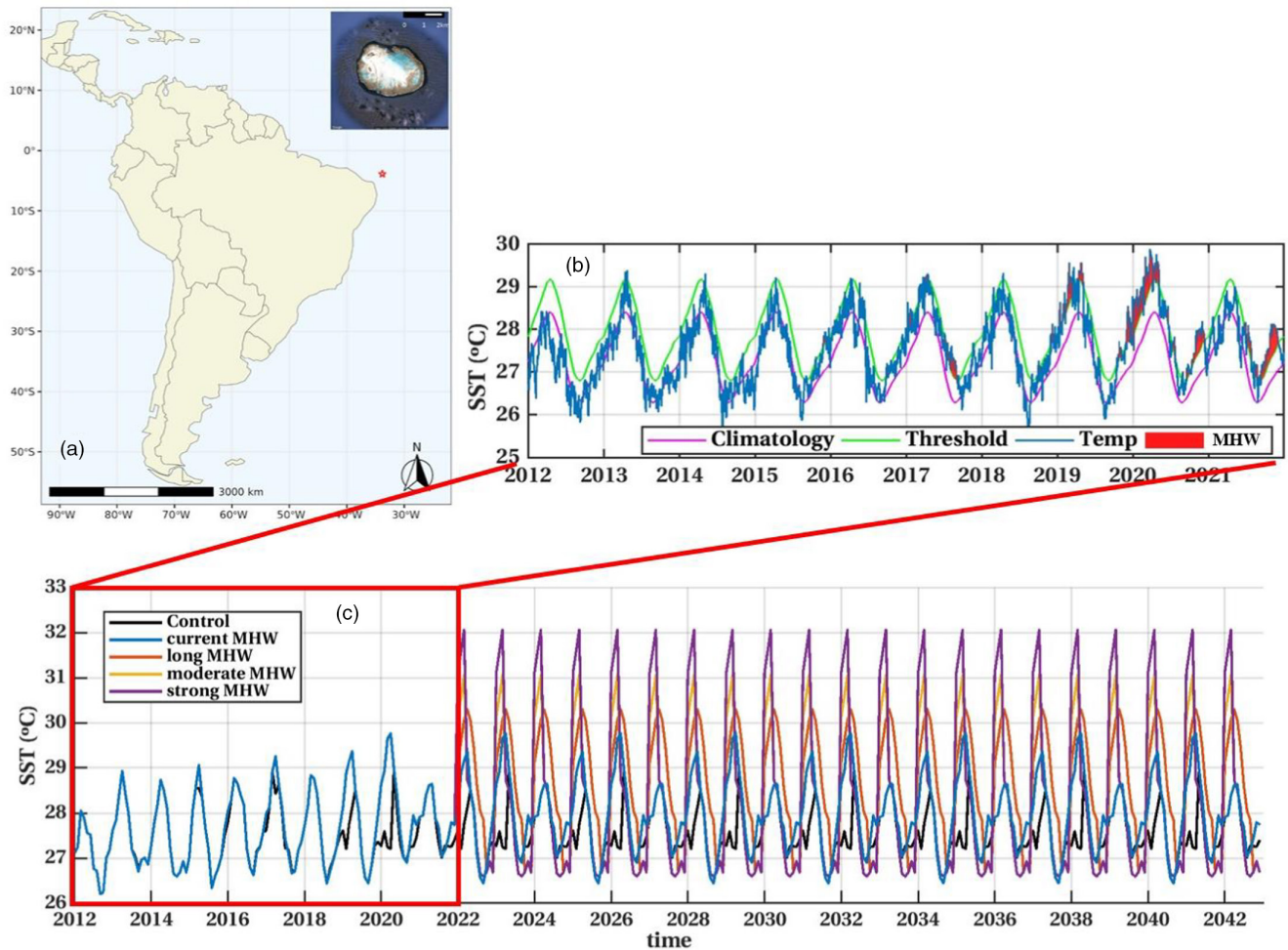


FIGURE 2 (a) Location of the Rocas Atoll (indicated with a red star) near Brazil, southwest Atlantic Ocean. The satellite image of Rocas Atoll was retrieved from Google Maps using the *ggmap* package in R. (b) Sea surface temperature (SST) over the past decade, with detected marine heatwaves (MHWs) indicated in red. The threshold corresponding to the 90th percentile is indicated in green. The climatological mean calculated over the period 1981–2021 is indicated in magenta. (c) Time series of sea surface temperature used to force the ecosystem model under different scenarios of MHW events.

echinoderms/large gastropods, the black triggerfish *Melichthys niger* and the butterflyfish *Chaetodon* spp. We added these 13 components 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. We refer the reader to the [Supporting Information S1](#) of this study and Capitani et al. (2022) for the composition and parameterization of the functional group of the updated Rocas Atoll Ecopath model (Figures S1 and S2; Table S1). Full details of the EwE modelling approach can be obtained from the main references (Christensen & Walters, 2004; Heymans et al., 2016).

2.3.2 | Species biomass simulations over time

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 Ecosim prediction for type- i prey biomass to type- j predators biomass is of the functional form:

$$\frac{dB_i}{dt} = g_i \times \sum_j Q_{ji} - \sum_j Q_{ij}, \quad (1)$$

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 . Consumption rates Q are estimated following the 'foraging arena' concept (Ahrens et al., 2012; Bentley et al., 2017; Walters et al., 1997), where species' biomass B is divided into two components, one vulnerable and the 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 (Equation 2):

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

where, a_{ij} is the effective search rate for i by j , v_{ij} is the vulnerability rate expressing how much the prey biomass i is available to predator j (e.g. trophic control assumption tested in this study, see next section); 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 (set to 2 in this study); D_j is the effects of handling time as a limit to consumption rate (set to 1 in this study) and S_{ij} is a scalar multiplier (0 to 1) linked to a skewed normal environmental response function $f(e_e, t)$ to account for external abiotic stressors which change over time (e.g. sea water temperature).

2.3.3 | Trophic control assumptions

The vulnerability of prey to predators is defined by the parameter v_{ij} (Equation 2). The v_{ij} parameter ranges from 1 to 100. It represents the predation mortality the prey experiences. The higher the v_{ij} parameter the higher is the predator trophic control on prey. Therefore, values close to 1 represent a bottom-up control on prey, while values larger than 2 represent a top-down control on prey. In this study, 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. The prey vulnerability is related to reef habitat complexity, as prey can be in states that are or are not vulnerable to predation (Ahrens et al., 2012; Bentley et al., 2017). For instance, they can hide when not feeding, being only subject to predation when leaving their shelter to feed.

2.3.4 | Mechanistic link between sea water temperature and consumption rate in Ecosim

We used species distribution data and abundance to produce thermal performance curves following the steps described by Waldock et al. (2019). For each species with available information about biomass or relative abundance, we: (1) produced community-wide species (one for reef fish biomass and the other for the relative abundance of benthic organisms) distribution models using the s-jSDM algorithm (Pichler & 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 a sole predictor in the linear model residuals to find the temperature which 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 shallow reefs, we trimmed environmental variables to include only areas with depths ranging between 0 and 30m. We obtained reef fish biomass data (as an abundance indicator) from Morais et al. (2017), percentage cover of sessile 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 abundance data, we resorted to the Aquamaps distribution repository to define thermal performance curves based on temperature quantile distribution (Ready et al., 2010). Thermal performance curves for each species/functional group are presented in Figure S3.

We applied species' thermal performance curves in Ecosim as negatively skewed normal 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 optimal temperature, and consumption rates declined as temperature departed from the optimal (Equation 2). For primary producers, we used thermal performance curves to modify the primary producers' growth efficiency (g , Equation 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} (Equation 2) with a maximum multiplier of 1 for optimum temperature (Bentley et al., 2017). The scalar factor S_{ij} declines as the average seawater temperature deviates from the optimum at a rate determined by the thermal performance curve standard deviations (Bentley et al., 2017; Corrales et al., 2018; Serpetti et al., 2017).

2.3.5 | MHW 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 similar to those reported in the recent past (current MHW), one with longer-lasting MHWs (long MHWs), and two with increased MHW intensity (ranging from moderate to strong) (Figure 3a). Each scenario involved running the Ecosim model (Figure 3b) from 2012 to 2042, using temperature time series as the environmental driver (Equation 2). We used the satellite-derived sea surface temperature time series for the period 2012–2021 in all scenarios (Figure 2b), except for the control scenario. We built the time series of sea surface temperature for this control scenario by removing the effects of MHWs: we replaced the sea surface temperature values during MHW events with climatological values (Figure 2c; black curve). We introduced perturbations corresponding to each MHW scenario for the period 2022–2042. We provide details of the temperature time series for each scenario in Table 1. We ran the Ecosim model for each scenario using the three trophic assumptions (Figure 3c).

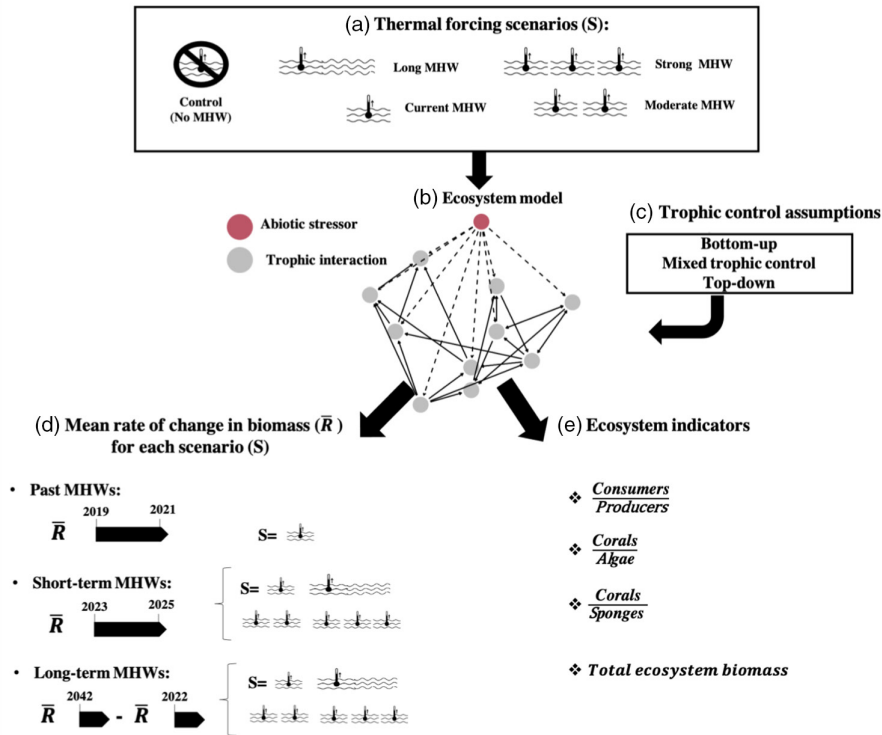


FIGURE 3 Summary of the methodological approach used in this study. (a) Thermal forcing scenarios of marine heatwaves (MHWs), (b) the ecosystem model for the Rocas Atoll, (c) three trophic assumptions used for the parameterization of the predator–prey interactions in the Ecosim model, (d) the rate of change in species' biomass due to MHWs averaged over different periods and (e) the ecosystem indicators that were evaluated.

Scenario	Temperature forcing 2012–2021	Temperature forcing 2022–2042	Colour in Figure 2c
Control	Satellite Sea Surface Temperature (SST) with MHWs removed: MHW temperature values replaced by the climatological mean	Satellite SST from 2019 to 2021 with MHWs removed repeated seven consecutive times over the period 2022–2042	Black
Current	Satellite Sea Surface Temperature (SST)	Satellite SST from 2019 to 2021 repeated seven consecutive times over the period 2022–2042	Blue
Long	Satellite Sea Surface Temperature (SST)	Every year has a 10-month-long MHW with 1° above 90% percentile threshold	Orange
Moderate	Satellite Sea Surface Temperature (SST)	Every year has a 3-month-long MHW with 2° 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

TABLE 1 Marine heatwave (MHW) scenarios used (see Figure 3 for details on the methodological approach adopted).

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

$$R = \frac{\text{Biomass (S)} - \text{Biomass (control)}}{\text{Biomass (control)}} \times 100, \quad (3)$$

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

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

We examined the effects of MHWs on different time scales. To assess the past impact of MHWs, we calculated the averaged R -value from 2019 to 2022. For short-term effects, we computed the average R -value from 2023 to 2025. Furthermore, we analysed the long-term or accumulated effects by comparing the mean R -value in 2022 with that in 2042 (Figure 3d).

2.3.6 | Ecosystem indicators

We described 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 3e). These ecosystem indicators are (1) the 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) the 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).

2.3.7 | Uncertainty for species biomass simulations under MHW scenarios

We used the Monte Carlo routine in Ecosim to perform sensitivity analyses for species biomass simulations under MHW scenarios. This routine tests the sensitivity of Ecosim's output to Ecopath input parameters by drawing input parameters from a uniform distribution centred on the baseline Ecopath values with the coefficients of variation (CV) set to default 0.1 (Christensen & 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 [Supporting Information S1](#).

We performed the statistical analyses in R studio, an IDE for R v 4.3.3 (R Core Team, 2024) and MATLAB v R2017b (The MathWorks Inc., 2017).

3 | RESULTS

3.1 | Marine heatwave impacts on species' biomass

3.1.1 | Marine heatwaves impact over the recent past (2019–2021)

We found that the mean biomass changes induced by past MHWs are generally negative (Figure 4). The largest negative changes in species' biomass for 2019–2021 (in some cases larger than 10%)

occurred under the top-down control assumption. Cephalopoda presented the largest negative change of the order of 14% under the top-down assumption. Despite the general negative tendency, some species did show a slight biomass increase under the top-down and mixed trophic control assumption. This is the case for certain omnivorous and herbivorous fishes, opportunistic microbes and dissolved and particulate organic matter under mixed and top-down trophic control assumptions (Figure 4). However, these increases are relatively small, not exceeding 3%, except for opportunistic microbes that show an increase of 15% under the top-down assumption. Overall, most of the predicted changes were relatively small, not exceeding 5%, with error bars of similar magnitudes (Figure 4).

3.1.2 | MHWs short-term impacts on species' biomass

Regardless of the MHW scenario, we observed a species biomass decrease of 35 species over 36 under the bottom-up control assumption and of 30 species under the mixed trophic control assumption and of 24 under the top-down control assumptions (Figures 5a, 6a and 7a). Under the bottom-up assumption, the short-term (2023–2025) mean rate of change in species' biomass decreased by up to 17% (Figure 5a). Mixed trophic control assumption with long MHW scenario induced a decrease of 30% for *Holocentrus adscensionis*, 25% in nudibranchs and 23% in corals. Under the top-down control assumption and the long, moderate and strong MHW scenarios, low-level predator fish *Holocentrus adscensionis*, nudibranchs, echinoderms and corals biomass decreased by more than 40% (Figure 7a).

Dissolved organic matter, opportunistic microbes and sponges biomass increased across all MHW scenarios under mixed trophic control (Figure 6a). Polycheta, zooplankton, opportunistic microbes, dissolved organic matter and particulate organic matter increased across all MHW scenarios under the top-down assumption (Figure 7a). In particular, opportunistic pathogens microbes biomass increased by more than 50% in the long, moderate and strong MHW scenarios.

Regardless 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 seabirds, the nurse shark *Ginglymostoma cirratum*, and the mid-level predator *Lujanus jocu* decreased in biomass.

3.1.3 | MHWs long-term impacts on species' biomass

In the long term, we observed, regardless of the MHW scenario, a species biomass decrease in 23 species over 36 under the bottom-up control assumption and 20 under the mixed and top-down

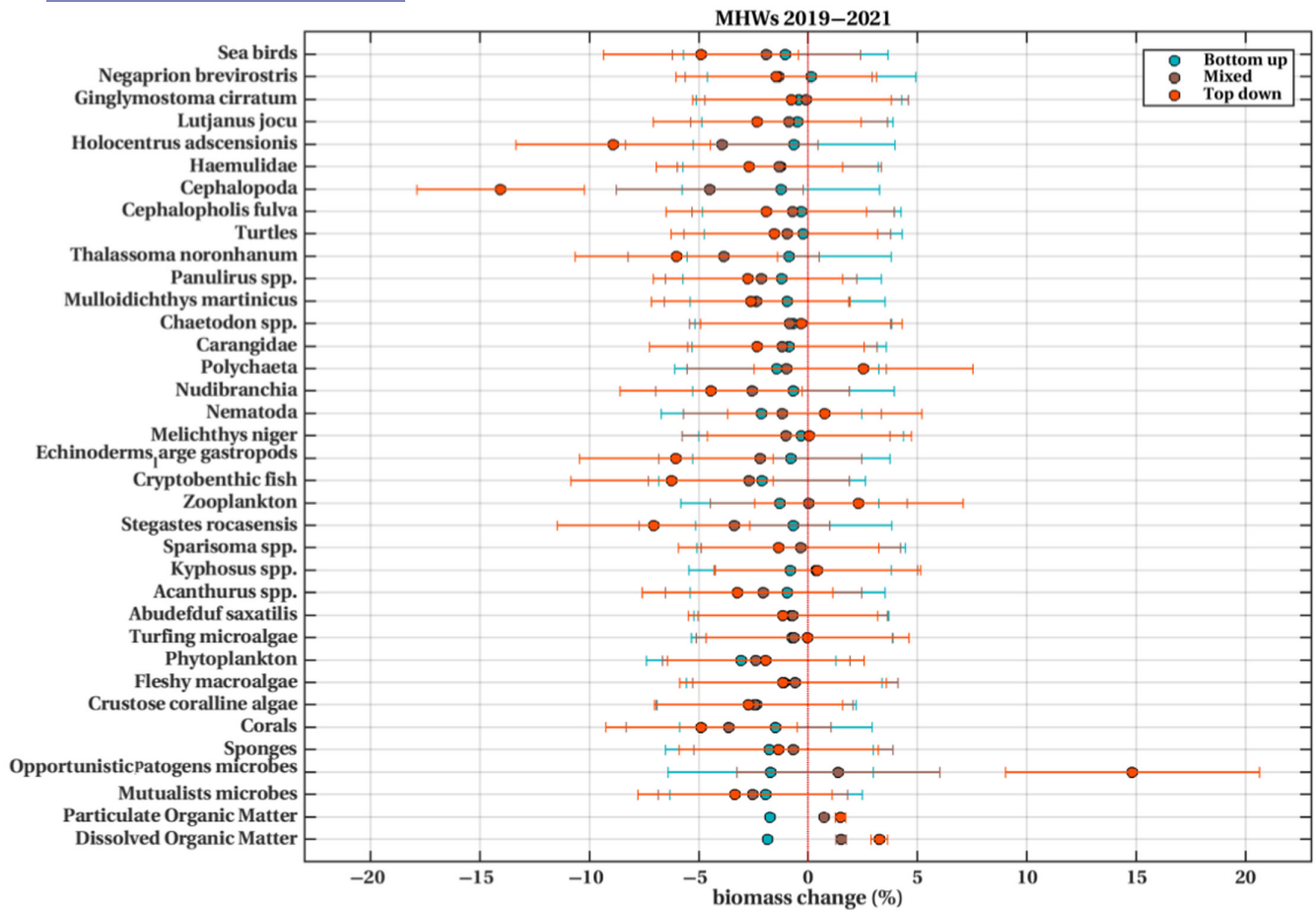


FIGURE 4 Species' biomass change under different ecosystems' trophic control assumptions (bottom-up, mixed and top-down) for 2019–2021. Dots represent the mean, and bars represent the respective error. Species/functional groups on the y-axis are ordered by trophic level.

control assumptions. The species most negatively impacted are low, top and mid-level predators (Figures 5b, 6b and 7b; Figure S4) with the largest changes obtained with the top-down assumption. For instance, seabirds, the butterflyfish *Cephalopholis fulva*, and the Noronha wrasse *Thalassoma noronhanum*, experienced ~40% biomass decrease under top-down control and the strong MHW scenario (Figure 7b).

Some species emerged as winners under specific MHW scenarios. Under the bottom-up assumption, primary producers, detritus and polychaeta showed a biomass increase (Figure 5b). 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. Positive changes are considerably greater under mixed trophic control and top-down assumptions (Figures 6b and 7b). The biomass of most omnivores (except the black triggerfish *Melichthys niger*), primary producers, and mutualistic microbes increased by more than 7% (mixed trophic control) and 20% (top-down control) (Figures 6b and 7b; Figure S4).

The long-term impact of MHWs, considering the current scenario, was relatively small compared to the impacts induced by the

strong, moderate and long scenarios under all trophic control assumptions (Figures 5b, 6b and 7b).

3.2 | Relative long-term changes in ecosystem indicators

Under all trophic control assumptions, we observed a general decrease for the ecosystem indicators (Figure 8). An exception is the coral/sponges ratio, which showed an increase of 2% and 9% under the moderate and long MHW scenarios under the top-down control assumption, and the total ecosystem biomass that showed an increase of less than 1% in the current MHW scenario under the bottom-up assumption (Figure 8).

MHWs with large intensity under the top-down control assumption led to the most considerable negative changes in the ecosystem indicators. In particular, we observed that the total ecosystem biomass decreased by almost 10%, and the coral/algae ratio decreased by 35% under long MHW scenario. For bottom-up control, long MHWs lead to the largest negative changes in the total ecosystem biomass, coral/algae

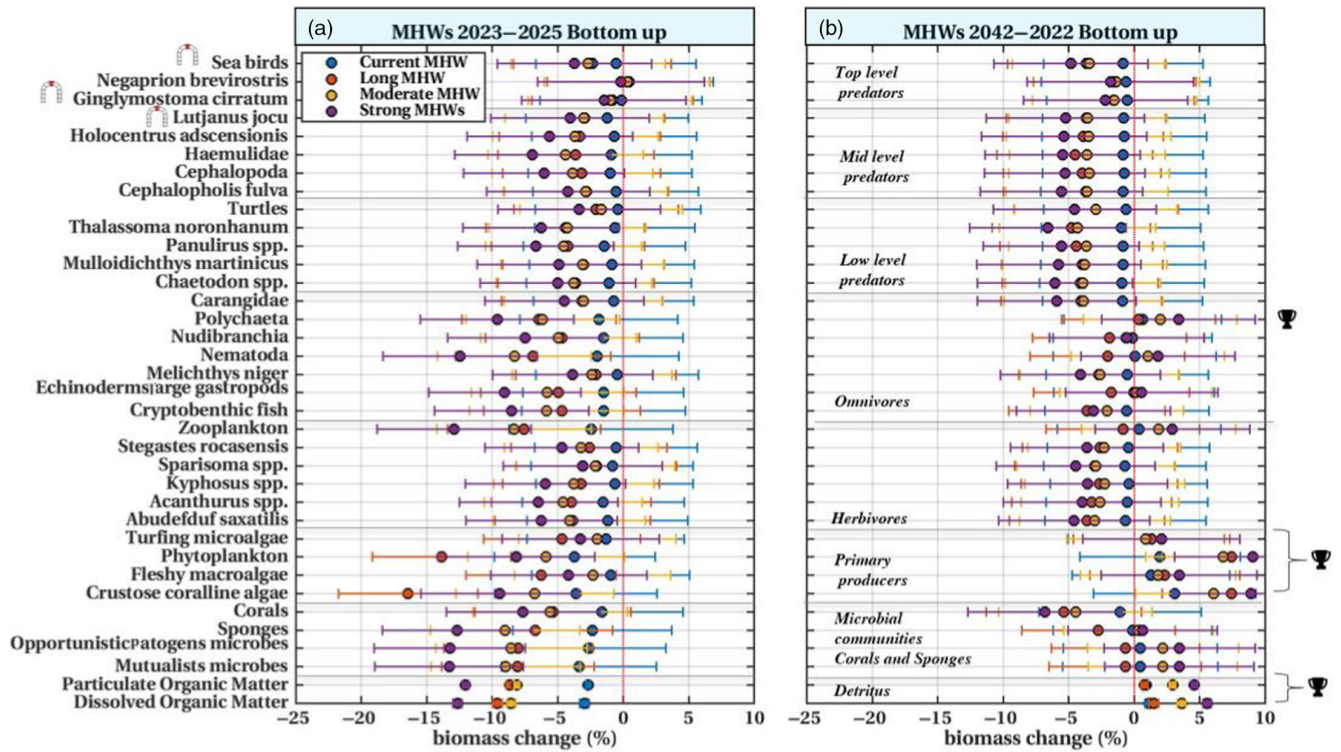


FIGURE 5 Short-term (a) and long-term (b) species' biomass change due to marine heatwaves (MHWs) under the bottom-up trophic control assumption. Dots represent the mean and the bars the respective error. Functional groups placed in the y-axis are ordered by trophic level. Winner species in all MHW scenarios are indicated with a black trophy. The arch symbol on the y-axis indicates the keystone species.

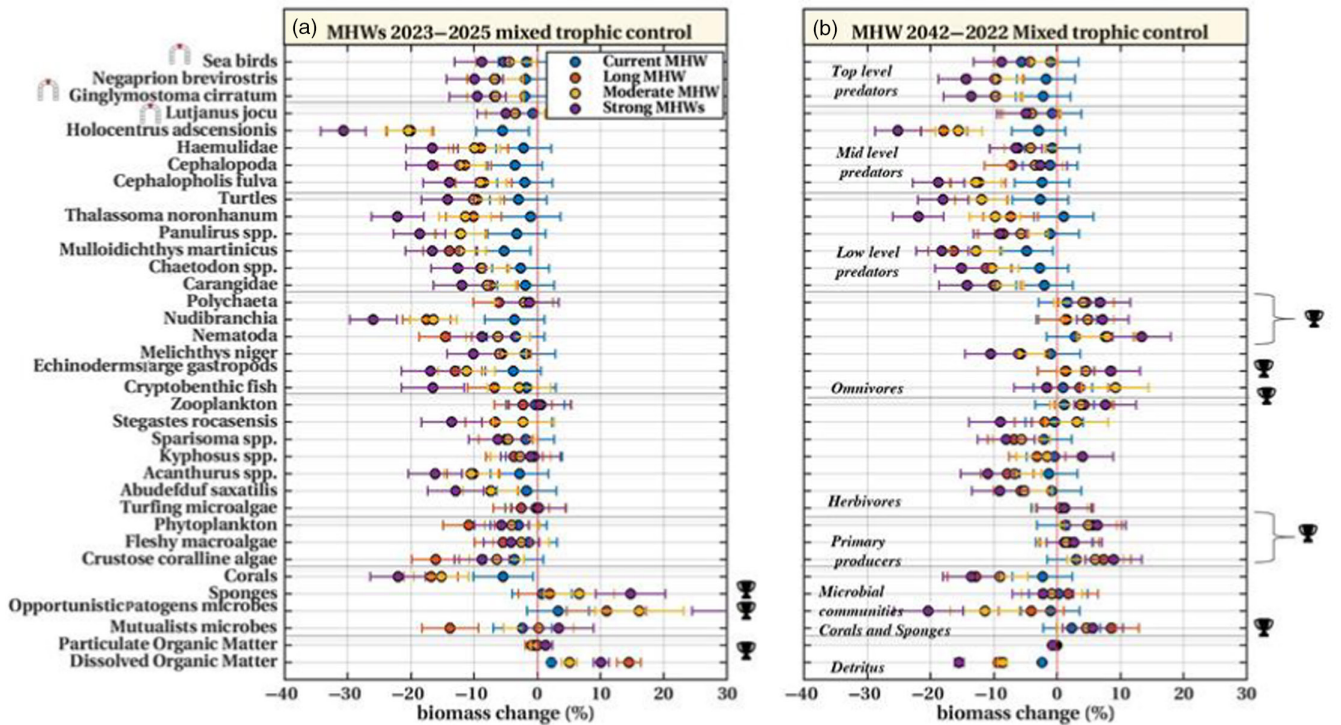


FIGURE 6 Short-term (a) and long-term (b) biomass rate of change due to marine heatwaves (MHWs) under the mixed trophic control assumption. Dots represent the mean, and the bars the respective error. Functional groups placed in the y-axis are ordered by trophic level. Winner species in all MHW scenarios are indicated with a black trophy. The arch symbol on the y-axis indicates the keystone species.

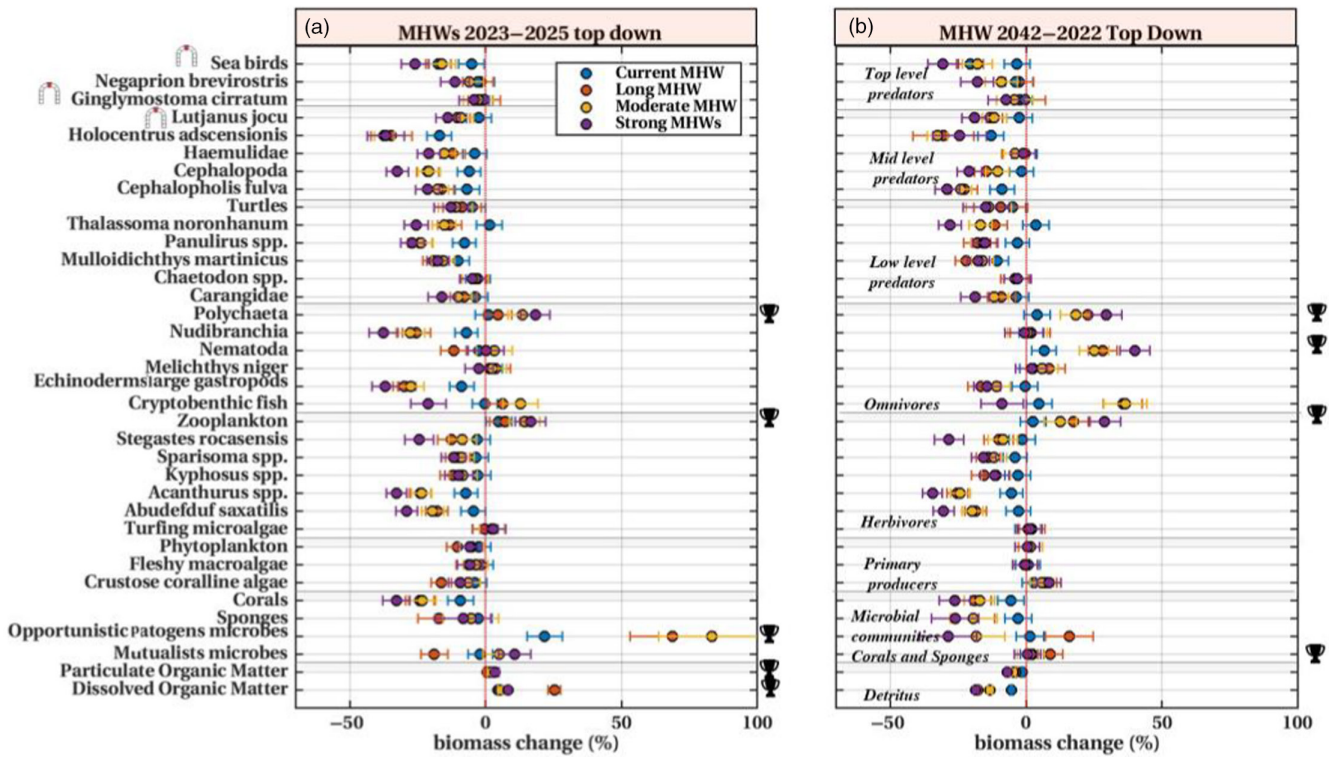


FIGURE 7 Short-term (a) and long-term (b) biomass's rate of change due to marine heatwaves (MHWs) under the top-down trophic control assumption. Dots represent the mean and the bars the respective error. Functional groups placed in the y-axis are ordered by trophic level. Winner species in all MHW scenarios are indicated with a black trophy. The arch symbol on the y-axis indicates the keystone species.

ratio and consumers/producers ratio. Under bottom-up and mixed trophic control, total ecosystem biomass changes did not exceed 2%.

4 | DISCUSSION

This study represents a comprehensive modelling exercise of the combined effects of thermal stress (MHWs) and biotic factors (food web trophic control) on an insular tropical Atlantic reef ecosystem. We partially confirmed our hypothesis that MHW thermal stress negatively impacts species' biomass. Moreover, we confirmed that the negative impact of MHW on species biomass dynamics is modulated by the vulnerability of prey to predators. As we expected, we found a more pronounced reduction in species' biomass under the top-down trophic control assumption with stronger MHWs. Overall, our results highlight that trophic interactions should be considered an essential biotic factor that conditions the resilience of reef ecosystems to the thermal stress in face of the expected increase in the number, magnitude and duration of MHWs.

4.1 | Mechanisms leading to winners

Although most species decline in biomass under the effect of MHWs regardless of their characteristics and the trophic control assumption, we found that some species exhibit an increase in biomass and

emerge as winners. Some studies have identified winners and losers in the Northeast Pacific after the 2013–2015 MHW (Cavole et al., 2016) and after the 2014–2016 MHW affecting the west coast of Canada and the United States (Free et al., 2023). In most cases, we observed that trophic interactions drive these increases in biomass. For instance, the short-term increase (over 2023–2025) in sponge biomass observed in all MHW 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 MHW scenarios under the bottom-up assumption, mainly because of the decrease in herbivore biomass and the increase in detritus, which is a source of nutrients. Additionally, the increase in zooplankton observed in all scenarios under the top-down assumption is probably caused by the decrease in its predators, such as fish, corals and sponges. Therefore, we identified predator release and increased resource availability as the main mechanisms that lead to winners under the different MHW scenarios.

4.2 | General long-term impact of MHWs

Under all MHW scenarios and trophic control assumptions, we observed a consistent decrease in the coral/algae ratio and

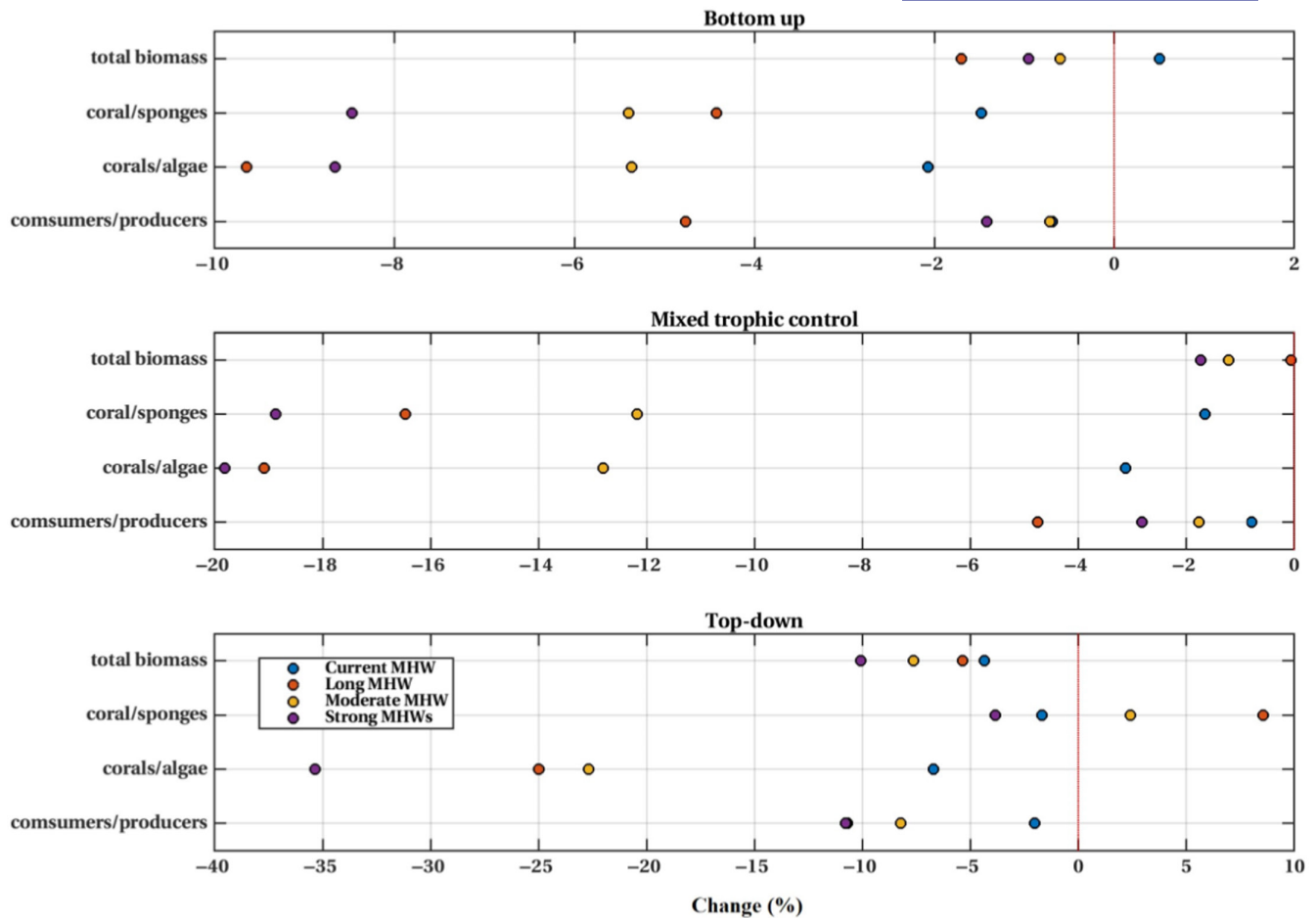


FIGURE 8 Percent change in ecosystem indicators for each trophic control assumption and marine heatwaves (MHW) scenarios. Total ecosystem biomass is the sum of primary producers' and consumers' biomass (excluding particulate organic matter and dissolved organic matter). The vertical red line indicates the 0% change.

consumer/producer ratio indicators. The decrease in coral/algae ratio points to an ecosystem phase shift from coral to algae-dominated reef. Since the majority of Southwestern Atlantic reef ecosystems are algae-dominated (Aued et al., 2018), the decrease in the coral/algae ratio suggests a reef state with less habitat complexity and more pathogen microbial biomass (Nelson et al., 2023). This is also consistent with previous studies that have documented shifts from coral-dominated reefs to reef ecosystems characterized by turf and fleshy macroalgae (Barott & Rohwer, 2012; Pawlik et al., 2016).

The decrease in the consumers/producers ratio suggests that more primary producers' biomass is available per capita and also implies a reduction in consumers' biomass. The decline in low, mid and top predators that occur under top-down and bottom-up assumptions results in a decrease in consumers/producers ratio. This ratio may also be related to the magnitude of intra and interspecific competition for primary producers, which may lead to changes in the ecosystem's trophic control (i.e. from bottom-up to top-down) (Jochum et al., 2012). Finally, the decrease in the coral/sponge ratio observed in most scenarios suggests more sponge biomass per unit of reef area. The decrease in the ratio may reflect changes in the

spatially competitive interactions between corals, sponges and algae. This is in agreement with studies that suggest that some coral reefs may become sponge reefs in the future because corals and sponges respond differently to changes in the environment (Bell et al., 2013). This could have important implications in the 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 observed changes in the ecosystem indicators, reflected by an increase in lower trophic level biomass and a decrease in higher trophic level biomass, imply a shortening of the food chain length and a simplification of the reef food web.

4.3 | Trophic control assumptions in the Rocas Atoll reef ecosystem

We have found that species' biomass dynamics underwent relatively small changes under low prey vulnerability to predators. Indeed, the total ecosystem biomass reduction is of the order of $5\% \pm 5\%$ under the bottom-up assumption. These results are

consistent with the changes reported in the literature for the Rocas Atoll ecosystem under past MHW events (Gaspar et al., 2021). Since the Rocas Atoll reef ecosystem is highly preserved, we hypothesize that the ecosystem is dominated by a bottom-up or by a mixed trophic control (Ahrens et al., 2012; Rehren et al., 2022). This means that there is enough habitat complexity in this ecosystem to allow prey to hide or escape predators. If instead top-down control is assumed, we expect larger and nonlinear changes in species' biomass (Rehren et al., 2022). In fact, under a top-down assumption, the amount of prey consumed by the predator is the product of $predator \times prey$ biomass (i.e. the predator biomass impacts how much of the prey is consumed). Such a situation may occur when the prey has no refuges to hinder and suffers a high mortality via predation. High vulnerability of prey to predators is linked with lower reef habitat complexity (Almany, 2004; Johnson, 2006). Consequently, our findings suggest that protecting reef ecosystems by preserving habitat complexity can significantly alleviate the impacts of thermal stress induced by MHWs (Geffroy et al., 2015; Wilson et al., 2008).

4.4 | Model limitations

The agreement between the model results and existing literature regarding past MHWs (2019–2021) underscores the reliability of the food web model as a valuable tool for assessing species biomass changes under different MHW scenarios. However, it is important to consider several caveats associated with our analysis. First and foremost, species biomass dynamics are intricately linked to the species' thermal performance characteristics, encompassing their shape and uncertainty. In this study, species' thermal performance curves were defined by the shape of a negatively skewed normal distribution. However, there is no scientific consensus about the species' thermal performance shape and whether they change in time and space (Khelifa et al., 2019; Rezende & Bozinovic, 2019; Sinclair et al., 2016). We acknowledge that additional studies are necessary to enhance the level of certainty surrounding our findings. We suggest that long-term monitoring studies of species population dynamics and mesocosm experiments are needed to further improve the characterization of species' thermal performances.

Second, our model does not account for future potential adaptation mechanisms that species might undergo. This consideration is of substantial relevance, as some species may have a certain ability to adjust to changing environmental conditions over time (Garant, 2020). For example, when warm temperatures compromise fitness, species can change their geographical location (Harvey et al., 2022). This is an issue 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 should be noted 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 S5) to assess the consistency of proposed scenarios with these model outputs.

As shown in Figure 2c, the 'scenario long' implies MHWs reaching temperature with peaks of 30°C, moderate peaks of 31°C and strong peaks of 32°C. The majority of the projected time series from CMIP6 show peaks of similar magnitude. Specifically, peaks of 30°C and 31°C are recurrent in 50% of the climate models from the beginning of 2022 to 2025, and some climate models show occasional peaks of 32°C 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 modelling, the CMIP6 time series raises important concerns about the potential impacts of such extreme temperatures on the Rocas Atoll reef ecosystem.

5 | CONCLUSIONS

By comprehensively examining the response of an insular tropical Atlantic reef ecosystem to the combined influence of MHW characteristics and trophic interactions, our work sheds new light on how and why MHWs will have important effects on species biomass dynamics. We have found that food web trophic control modulates the impacts of thermal stress induced by MHWs. Our work leads to a better understanding of how abiotic and biotic factors interact within reef ecosystems, providing insights into current benchmarks and potential future ecological conditions in face of intensified prolonged and more frequent MHW events. Our results point to the importance of protecting reef ecosystems as a key strategy to alleviate the thermal stress caused by MHWs, and serve as a call for proactive conservation measures that can effectively respond to the challenges posed by MHWs to marine ecosystems.

AUTHOR CONTRIBUTIONS

Camila Artana and Leonardo Capitani contributed equally. They 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.

ACKNOWLEDGEMENTS

This study is a contribution to the European Union's Horizon 2020 research and innovation programme under grant agreement no. 817578 (Triatlas project) and the Spanish funded ProOceans project (Ministerio de Ciencia e Innovación, Proyectos de I+D+I, RETOS-PID2020-118097RB-I00). MC and CA acknowledge institutional support of the 'Severo Ochoa Centre of Excellence' accreditation (CEX2019-000928-S) to the Institute of Marine Science (ICM-CSIC). We thank the Brazilian Long-Term Ecological Research Program (*Programa de Pesquisas Ecológicas de Longa Duração—PELD*) to support long-term research and monitoring in Rocas Atoll reef ecosystem funded by the Brazilian government and coordinated by the CNPq (*Conselho Nacional de Desenvolvimento Científico e Tecnológico*).

CONFLICT OF INTEREST STATEMENT

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

DATA AVAILABILITY STATEMENT

The raw data, the Rocas Atoll's food web model and the R and matlab codes 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/>.

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.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Snapshot representation of the Rocas Atoll's Ecopath model by 2012 year.

Figure S2: Diet proportions for prey i and predator j used in the Rocas Atoll Ecopath model.

Figure S3: Species' thermal performance curves obtained by modeling species habitat suitability and then statistically filtering out the effect of variables other than temperature.

Figure S4: Short-term (left) and long-term (right) MHWs impacts on species' biomass for bottom up, mixed trophic control and top-down trophic control assumptions.

Figure S5: Sea Surface Temperature Time series from CMIP6 model and SSP5-8.5 scenario at the Rocas Atoll location.

Table S1: Basic estimates of the Rocas Atoll Ecopath model for all species/functional groups.

How to cite this article: Artana, C., Capitani, L., Santos Garcia, G., Angelini, R., & Coll, M. (2024). Food web trophic control modulates tropical Atlantic reef ecosystems response to marine heat wave intensity and duration. *Journal of Animal Ecology*, 00, 1–15. <https://doi.org/10.1111/1365-2656.14107>