**Title**

**#1 Ocean warming degrades the food web in tropical reef ecosystems**

**#2 Degradation of tropical reef ecosystems by ocean warming**

**Abstract**

Climate change is affecting life on Earth in many levels, from affecting metabolic responses of individuals to causing shifts in species distributions and community composition, which may scale up to the ecosystem level by affecting its energy flux, nutrient cycling and stability. A less evident but not less important impact are climate-driven shifts in food webs, which are overlooked due to the paucity of data and difficulty to generate reliable models. We developed a food web model of a tropical near-pristine reef ecosystem and analyzed changes on living biomass and fish biomass partitioning across trophic levels as a response to climate change scenarios over the 21st century. By the end of the century, total living biomass is expected to decrease by 1%, 8 % and 44% under the low, medium and high emissions scenarios, respectively. As total fish biomass decrease under high emissions scenario, ecosystem structure will shift from a system with greater relative abundance of herbivorous/detritivorous fish and suspensivorous benthic invertebrates, to a system typified by relatively more invertivorous fishes, suspension feeding zooplankton, and algal turfs that thrives while corals collapse. This climate-driven community shift is likely to degrades the food web by altering the dominant flows of energy, potentially favouring heterotrophic microbial growth, coral disease and reducing ecosystem resilience and services. Besides providing a predictive framework, our results highlight how the risk of severe biodiversity losses from climate change in tropical pristine reef ecosystems can scale up and affect the entire food web and thus energy flow and ecosystem functioning.

**Introduction**

Human-induced climate change is affecting ecosystems in all continents and oceans (Sunday et al. 2012; McCauley et al. 2015; Lotze et al. 2019). Rising temperatures will transform ecosystems into new configurations, towards more homogeneous and less stable biological communities (Sydeman et al. 2015; Nolan et al. 2018). The predicted ocean warming under high greenhouse-gas emissions scenarios will severely affect species distribution, abundance and extinction rates (Bryndum‐Buchholz et al. 2019; Pörtner 2019). Beyond species, climate change will affect entire food webs that control the dynamics and stability of biological communities, as well as energy and matter flow within and across ecosystems (Zhang et al. 2017; Gibert 2019). Although overlooked due to lack of data and difficulties in generating reliable models, predicting changes in food webs can help us to understand the structure and dynamics of these novel and simplified ecosystems that are likely to emerge under climate change scenarios (Blanchard et al. 2012; O’Gorman et al. 2017).

Coral reefs are among the most diverse and sensible ecosystems on planet, being severely impacted by human-induced climate change (Burrows et al. 2011; Hughes et al. 2017; Sully et al. 2019). Major impacts on these ecosystems include coral bleaching and mortality leading to loss of structural complexity and diversity (Graham and Nash 2013; Magel et al. 2019), shifts in species distribution (Pecl et al. 2017) and changes in the ecosystem trophic structure with increasing algal cover prompting a higher importance of microbes in the energy flow (i.e., microbialization; Haas et al. 2016). Besides ecosystem functioning, the degradation of coral reefs threatens important services, including fisheries and tourism (REFs), on which millions of humans rely (Pratchett et al. 2014; Hughes et al. 2017).

To form a better view of the ocean warming impacts on reef ecosystems, we investigated the potential future effects of human-induced ocean warming on reef food webs using a near-pristine tropical reef ecosystem in the South Atlantic Ocean as a model, the Rocas Atoll. We fitted the model based on primary data obtained in the field along a seven-year time series complemented with data from the literature. Species were assigned to guilds based on their diet and feeding behaviour, including the way they capture, store, and transfer energy across trophic levels (Mouillot et al. 2014; Madin et al. 2016). The model incorporated species-specific thermal tolerances and functional responses in order to test the impact of warming under three projected scenarios (Representative Concentration Pathways; RCP 2.6, 4.2 and 8.5) predicted by the Intergovernmental Panel on Climate Change (van Vuuren et al. 2011). For each scenario, we ran temporal simulations for the biomass of several reef fish species, critical consumers in reef food webs, and of other organisms within several trophic guilds (e.g.,plankton, macroalgae, corals, macro and micro invertebrates, seabirds and sea turtles). We found that within 55 years, most taxa are likely to experience dramatic declines in biomass, affecting energy and matter flow through the entire food web, leading to a general degradation of the ecosystem.

**Results**

**General description of the Rocas Atoll reef food web**

The reef food web of the Rocas Atoll was dominated by algal primary producers, particularly algal turfs and the red macroalgae *Digenea simplex*, which accounted for 74% and 19% of the total living biomass (1089.9 g·m-2), respectively (Figure 1). The decomposition of this algae biomass generates detritus, accounting for 1% of the total biomass. Micro and macro invertebrates combined accounted for 4% of the total living biomass, while reef fish accounted for 2%. Algal turf, macroalgae and detritus were the main food items for micro invertebrates, macro invertebrates and herbivorous/detritivorous fish (40-70% of their diet). Reef sharks, sea birds and cephalopods occupied a similar position in the highest trophic levels, ranging between levels 3.2 and 3.5. They had a generalist diet, with each item representing less than 10% of diet composition. Total reef fish biomass was estimated in 24.2 g·m-2, from which herbivorous/detritivorous fish accounted for 49% followed by invertivorous fish (22.5%), generalist predators (19.7%) and reef sharks (8.8%; Figures 1, 2).

**Fig.1.** Food web of the Rocas Atoll ecosystem (year 2012). Each species is shown as a circle and its size is proportional to the biomass’ square root. The food web’s groups are represented by their trophic levels (TL, y-axis) and linked by predator-prey relationships showed as lines representing the relative prey’s contribution in the predator’s diet. Organisms’ shapes are not to scale.

**Simulated biomass changes under ocean warming scenarios**

We ran simulations on biomass dynamics based on fish time-series data and using temperature projections from 2018 to 2100. We present species-specific biomass dynamics and compare each warming scenario relative to a hypothetical future with no changes in sea temperature by 2100 (*status quo* scenario) using average relative biomass’ percent variation. Current average seawater temperature in Rocas Atoll’s is 27.3ºC, which by 2100, is expected to rise 0.5ºC, 1.3ºC and 3ºC under the low (RCP 2.6), intermediate (RCP 4.5) and high (RCP 8.5) emissions scenarios, respectively. Total living biomass (1089.9 g·m-2), is expected to decrease by 1% under RCP 2.6, by 8 % under RCP 4.5, and by 44 % under RCP 8.5.

Regarding the total fish biomass dynamics, the RCP 4.5 and RCP 8.5 scenarios began to diverge from RCP 2.6 and *status quo* scenarios in 2040. There was a continuous overlap of the confidence intervals of total biomass dynamics among all scenarios until 2075, when a steep decline started to occur under the RCP 8.5, which deviated from the other scenarios (Figure 2). Under the *status quo* scenario, total fish biomass reached an average of 27.2 g·m-2 by 2100, which was close to that predicted under the RCP 2.6 scenario (27.7 g·m-2; Figure 2). The RCP 4.5 scenario predicted a decreasing average of 17.3%, and the RCP 8.5 an 86% decrease in total fish biomass, estimated to reach 3.7 g·m-2 (Figure 2).

**Fig. 2** Model projections of total fish biomass dynamics under climate change scenarios and changes in fish biomass partitioning across trophic levels. 95% confidence intervals around the mean are shown for trend lines. Bar graphics represent trophic guild mean percent contribution based on the relative difference in biomass among trophic guilds for total fish biomass under climate change scenarios.

Model simulations also predict alterations on the trophic structure of the fish assemblage. Herbivores and detritivores (currently 49% of total fish biomass), would have the major declines between ~30% and ~20% under RCP 4.5 and RCP 8.5, respectively (Figure 2 and Figure 3). Invertivorous fish (currently 22.5% of total fish biomass) could represent ~ 40% and ~ 50% of total fish biomass under these projected scenarios, despite the decrease in biomass (Figure 2 and Figure 3). Generalist predators and reef sharks maintained similar biomass proportions under all scenarios (~ 20% and 10%, respectively) but also with a reduction in biomass (Figure 2 and Figure 3). Under the 1.3°C and 3°C warming scenarios (RCP 4.5 and RCP 8.5, respectively), biomass decreased by 28% and 88% for reef sharks, 15% and 8.5% for generalist predators, 7% and 74% for invertivorous fish, 23% and 94% for herbivorous/detritivorous fishes (see details in Supplementary Materials 2; Figure S4). Under the medium and high emissions scenarios, the trophic composition of the reef fish assemblages is likely to change from an herbivorous/detritivorous dominated assemblage to an invertivorous one by 2100 (Figure 2; see details for the relative biomass changes in Supplementary Materials 2).

**Fig. 3** Projections of fish biomass dynamics in the Rocas Atoll reef ecosystem under climate change scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

Biomass of almost all no-fish groups also decreased under RCP 4.5 and RCP 8.5 scenarios, but with variable magnitudes (Fig. 4; see details in Supplementary Materials 2). Most of these species-specific biomass dynamics overlapped due to the high uncertainty of parameters. The biomass reductions were more pronounced under the high emissions scenario, specifically after the year 2075. The biomass of major primary producers, such as the macroalgae *Digenea simplex*, algal turfs, and phytoplankton, declined by 58%, 42%, and 66%, respectively. Corals (mainly *Siderastrea stellata*), which also contribute to primary production, had gradual losses according to the warming scenario. Under low emissions scenario, corals declined by 8%, while under medium emissions scenario they decreased by 61%, with prevision to be locally extinct by 2075 under the 3°C warming scenario (RCP 8.5).

The biomass of lobsters (mainly *Panulirus* spp.) and sea turtles are predicted to decline by 99% and seabirds by 89% under RCP 8.5. Under the RCP 2.6 scenario, the biomass of lobsters declined by 45% and by 85% under the RCP 4.5. Sea turtle’s biomass will decrease 13% under RCP 2.6 and 47% under RCP 4.5, while the biomass of seabirds, macro, and micro invertebrates remained unchanged under both lower and medium scenarios (RCP 2.6 and 4.5, respectively). Biomass dynamics of macro and micro invertebrates decreased by 69% under the RCP 8.5 scenario. Conversely, zooplankton biomass remained unchanged under the RCP 2.6 but experienced a 37% increase (RCP 4.5) and a 111% increase (RCP 8.5), respectively.

**Fig. 4** Projections of no-fish species biomass dynamics in the Rocas Atoll reef ecosystem under climate change scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

**Discussion**

Marine food webs are at risk of collapse due to ocean warming (Bryndum‐Buchholz et al. 2019; Lotze et al. 2019; Blowes et al. 2019), particularly in reef ecosystems where synergistic human related impacts have caused drastic changes (Hughes et al. 2017; Hughes et al. 2018; Beyer et al. 2018). We predicted that an increase in temperature higher than 1.3ºC will cause a loss between 1% and 44% of total living biomass in Rocas Atoll reef ecosystem by 2100. These values were even worst considering fish biomass, which can undergo a reduction of 86% in the high emissions scenario. This decrease in biomass across trophic levels will cause the ecosystem to shift from dominance of herbivorous/detritivorous fish and benthic suspension/deposit-feeding invertebrates to a system typified by relatively more invertivorous fishes, suspension-feeding zooplankton, and algae turfs. Such composition shift may result in diminishing trophic interactions, like predation and herbivory, jeopardizing the stability and ability of this system to maintain the current configuration, being prone to reach different species-poor alternative stable states (Fung et al. 2011; Houk et al. 2018). The predicted increase in the relative abundance of algal turfs and macroalgae can increase the amount of algal-derived dissolved organic carbon, thereby fuelling heterotrophic microbial growth and coral disease (Haas et al. 2016; McDole Somera et al. 2016). Under the worst warming scenario, corals could be locally extinct within 55 years. Therefore, this tropical reef ecosystem is likely to be simplified as a consequence of having its food web severely degraded under more extreme warming scenarios.

Our results support the expected outcome that tropical reef ecosystems may be particularly vulnerable to suffer local extinctions of several species caused by climate warming (Rummer et al. 2014; Barlow et al. 2018). Experimental evidence indicates that in the long term (i.e, more than 90 days) activity and survival of tropical marine organisms could be compromised just 2-3°C above present seawater temperatures (Nguyen et al. 2011). A recent modelling study reports that in between 4% (RCP 2.6) and 49% (RCP 8.5) of marine species will be exposed to temperatures beyond their realized thermal niche in tropical South Atlantic Ocean before 2060 (Trisos et al. 2020). Deleterious impacts of climate warming on ectotherms will be amplified if food intake is also reduced, either because warming reduces standing food resources or because it restricts foraging time (Huey and Kingsolver 2019). Most of the species of the Rocas Atoll ecosystems are living close to their thermal maximum (28-30ºC), having narrow realized thermal limits. Consequently, a large number of species occurring close to their upper realized thermal limits and concomitant shortage of food resources may explain the overall severe decline biomass projected in our study.

Despite the empirical evidence that small increases in temperature can significantly affect individual performance, many reef fishes have large latitudinal ranges, spanning thermal gradients similar to the temperature increases predicted due to global warming (Feary et al. 2010; Longo et al. 2019). Rocas Atoll ecosystem has water temperatures for one or two consecutive month similar to the temperature projected for the highest emissions scenario (32-34ºC). However, the sustained rate of warming due to anthropogenic climate change is at least ten times faster than any climate shift that has occurred in the past 50 Myr (Pörtner et al. 2019), the time period over which reef fishes have evolved, diversified and acclimated (Bellwood et al. 2014; Bellwood et al. 2017). Moreover, tropical species that have evolved the greatest tolerance to high temperatures have done so at the expense of acclimation capacity, and it is these species that will be the most susceptible to the smallest increases in micro-habitat temperatures (Stillman 2003). Despite the fact that reef fishes had their origins in a geological time when temperatures were much higher than those in the current day, the projected and sustained increase of temperatures of just 1.5-3°C above current-day averages will likely exert negative effects on fish aerobic scope, swimming performance, growth and reproduction (Rummer and Munday 2017), leading to suffer population declines such as those observed in this study.

Another major consideration in predicting the potential risk for reef fishes to future climate change is their reliance on reef ecosystem (Komyakova et al. 2018; Samoilys et al. 2019). Corals, the builders of the reef matrix and providers of complex reef habitat, are highly susceptible to ocean warming (Hoegh-Guldberg et al. 2018; Schoepf et al. 2019). Up to 75% of reef fish species may decline in abundance following severe habitat degradation, with some species declining in abundance by 50% or more (Jones et al. 2004; Wilson et al. 2006). Importantly, ecological feedbacks can promote recovery of corals following disturbances: for example, grazing by herbivorous fish can prevent algal proliferation and allow successful coral recruitment and survival (Mumby and Steneck 2008; Burkepile and Hay 2008).The five herbivorous/detritivorous species that could do that in Rocas Atoll are living close to their thermal optima (26.5ºC). Biomass of these five herbivorous/detritivorous species is predicted to reduce and approach zero for three of them under the high emissions scenario. Therefore, we suggest that the predicted loss of herbivore/detritivore fish is likely to reinforce the substitution of corals by macroalgae, which may ultimately decrease ecosystem structural complexity intensifying the overall biodiversity loss already imposed by extinctions promoted by ocean warming.

The loss of primary and secondary consumers in reef ecosystems can cause shifts in the trophic structure, stability and even microbiome diversity, affecting ecosystem functioning (Wernberg et al. 2016; Booth 2020; Vanwonterghem and Webster 2020). Reefs that loose top predators and herbivores, tend to become increasingly dominated by autotrophs and bacterivores (Petchey et al. 1999). The microbiome of corals exposed to intense algal competition, showed a decline in bacterial metabolic pathways for photosynthesis, and an increase in metabolic pathways associated with virulence, such as bacterial invasion systems, bacterial motility, and secretion systems (Zaneveld et al. 2016; Vanwonterghem and Webster 2020). Increasing temperatures can also constrain productivity by enhancing cyanobacterial biomass and reducing energy flow to higher trophic levels, thus lowering energy transfer efficiency between producers and consumers (Ullah et al. 2018). These onset of alterations in the food web structure of reef ecosystems could increase the relative importance of certain biological pathways such as the sponge loop (Pawlik et al. 2016; Bell et al. 2018) and the microbial loop (Haas et al. 2016; Roach et al. 2017). On the other hand, it could also degrade reef ecosystems via increased hypoxia and greater CO2 release from the microbial respiration of dissolved organic matter (Haas et al. 2016; Hughes et al. 2020).

We hope our study may be considered the groundwork for several future research directions. Therefore, it is important to acknowledge the main assumptions and limitations in our modelling approach. First, we evaluated the influence of temperature on specie-specific consumption rates, but not on group production and respiration rates, or recruitment and species physiological adaptations. Reef fishes, the dominant marine vertebrate group for instance, have complex life histories a planktonic life-stage for many species in which habitat occupancy and prey use differs from adult life stages, resulting in different vulnerabilities to changes in seawater temperature (Sydeman et al. 2015). Second, biomass dynamics are also driven by the cumulative impact of numerous climate change effects not accounted in our models, such as ocean acidification and ocean deoxygenation (Gruber 2011; Gallo et al. 2017). Therefore, conclusions drawn from modelling of warming without the other parameters may differ from those that consider synergistic effects (Bopp et al. 2013; Guénette et al. 2014; Henson et al. 2017). Progress in the development of global species-specific datasets for environmental variables other than temperature would enable more comprehensive investigations in the future. Lastly, the use of food webs models has been criticized because of difficulties in accounting for model assumptions, uncertainty, and bias in post hoc analyses (Essington 2007; Essington and Plagányi 2014). Despite these assumptions and limitations, the modelling approach used in this study deals with uncertainty associated with the model basic estimates via Monte Carlo statistical routine. This procedure ascertains important trophic interactions through model fitted to time series data, which enhance our fundamental and quantitative understanding of the consequences of ocean warming on community biomass dynamics and trophic structure of reef ecosystems. Each of the assumptions explored here can be converted into testable hypotheses and then explored in empirical sensitivity analyses, which will provide insights into how much detail is needed and what can be ignored, reducing the uncertainty in the relationship between temperature and trophic interactions to predicting the biological impacts of climate change.

Our model predicted more severe changes and local extinctions to occur within 55 years. Considering that Rocas Atoll is a near-pristine ecosystem with no direct influence of other human related impacts, such as coastal pollution and fishing (Longo et al. 2015), the degradation of food webs and local extinctions are likely to occur much faster in tropical ecosystems facing multiple synergistic stressors (Trisos et al. 2020). Because local management has clearly limited power in promoting certain aspects of biodiversity such as trait diversity, international action on climate change will be crucial for ensuring a future for tropical reefs ecosystems (Williams et al. 2019; Jouffray et al. 2019).

**Conclusions**

Considering the projected decrease of over 44% of living biomass by ~2100, warming associated to the projected increases in the frequency and intensity of thermal stress events on tropical reef ecosystems will cause persistent changes in reef diversity, community structure and ecosystem functioning. Our projections suggest that tropical reef ecosystems will be severely impacted by increasing temperatures through biomass declines, mainly of reef fish and benthic suspension/deposit feeding invertebrates, which are predicted to occur gradually by the end of the 21st century both under the medium and high greenhouse gas emissions scenarios (RCP 4.5 and RCP 8.5). These changes will shift the trophic structure from a bottom-driven to a middle-driven shape, with the majority of fish biomass concentrated in mid-trophic position. Losing carnivorous and herbivorous fishes from the reefs, increases the relative abundance of macroalgae and algae turfs, which in turn may enhance the microbial loop, leading to a strong degrading to the food web and changing energetic pathways. These changes will affect the ecosystem functioning, leading to a less stable and diverse ecosystem, potentially hampering the services provided by these ecosystems. To the best of our knowledge, this is the first theoretical demonstration of community-level biomass shift for a tropical reef ecosystem under ocean warming. Ocean acidification, disturbance in nutrient cycles, pollution, and fisheries are also important threats to reef ecosystems that could be further explored within this general framework generalized model that we propose for tropical reef ecosystems.

**Materials and methods**

A brief description of our modelling approach and data is outlined below. Materials and methods are supplemented with tables, figures and appendices (Supplementary Materials 1-2), as well as all raw data and programming code to reproduce figures are publicly available at Git Hub public repository (<https://github.com/leomarameo7/Atoll_Rocas_project>). All analysis and figures were implemented in R software version 3.6.1 (R Core Team 2019).

**Study area**

Rocas atoll is located in the South Atlantic Ocean, approximately 230 km off the NE coast of Brazil (03°50’S, 33°49’W). Rocas is the only atoll formation in the South Atlantic and is part of a seamount chain in the E-W direction known as the fracture zone of Fernando de Noronha island. The atoll surface area is 7.5 km2 and average sea surface temperature is 27.3 ºC, varying between 19° and 34.5°C (Longo et al. 2015). The Rocas Atoll was established as a marine reserve in 1978, and effective enforcement was implemented in 1991 through the establishment of a permanent monitoring research station at the atoll. Nowadays, it is a no-take no-entry marine reserve, in which the Brazilian research scientific team (PELD-ILOC; <http://peldiloc.sites.ufsc.br/>), conduct monitoring efforts at least once a year (Figure 5). Being one of the few reef ecosystems in the western South Atlantic Ocean without direct human impacts (fishing, tourism, pollution), it can be considered as a natural laboratory where it is possible to test the current and future effects of climate change without the influence of local and direct anthropogenic impacts.

**Fig. 5** Study location Rocas Atoll ecosystem (3°50’S, 33°49’W), with the different reef habitats. The illustration was adapted from Longo et al. (2015) with permissions.

**The food web model**

The model was built in Ecopath with Ecosim (EwE) software version 6.6 (details of the EwE modeling approach can be obtained from www.ecopath.org). The Ecopath module comprises a series of linear equations that define a mass-balanced state of an aquatic food web (Polovina 1984). Individual species or groups of species are represented as functional groups which have approximately the same growth, consumption rates, diet composition, and predators. The functional groups are regulated by gains (consumption, production, and immigration) and losses (mortality, fishery and emigration), and are linked to each other by predatory relationships (Christensen and Walters 2004). The parameterization of an Ecopath model is based on satisfying two ‘master’ equations. The first equation describes how the production term for each functional group can be divided (1):

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| Production = predation + net migration + biomass accumulation + other mortality | (1) |

The second ‘master’ equation is based on the principle of conservation of matter within a functional group (2):

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| --- | --- |
| Consumption = production + respiration + unassimilated food | (2) |

In general, an Ecopath model requires input of three of the following four parameters: biomass (B), production/biomass ratio (or total mortality, P/B), consumption/biomass ratio (Q/B), and ecotrophic efficiency (EE) for each of the functional groups in a model. Here, the ecotrophic efficiency expresses the proportion of the production that is used in the system, (i.e., it incorporates all production terms apart from the ‘other mortality’). If all four basic parameters are available for a group the program can instead estimate either biomass accumulation or net migration. Ecopath sets up a series of linear equations to solve for unknown values establishing mass-balance in the same operation. The approach, its methods, capabilities and pitfalls are described in detail by Christensen and Walters (2004).

**Model parameterization**

The Rocas Atoll Ecopath model was parameterized using field observations and data from several sources (stock assessments, literature, FishBase (Froese and Pauly 2019), and existing ecosystem models; Supplementary materials\_1, Table S1). All data were converted to biomass per unit area of reef (g·m-2) using conversion factors from the literature for fish and most mobile invertebrates, and our own determinations of coral and algal biomass per unit surface area (Longo et al., 2015). Biomass estimates for single fish species groups were taken from underwater visual censuses (UVC) by the year 2012 until 2018, obtained from abundance-by-length data using length–weight relationships estimated with the local samples. UVC consisted of belt transects in which a diver identified, counted, and estimated the total length of fish species inside an area of 40 m2 (20·2 m). A total of 153 UVC were performed in March 2012 (the year of the baseline model), and the number of transects varied from 5 to 25, depending on the available area. It was generally acknowledged that counting fish that enter the survey boundaries after the census started could generate bias in the counts. We accounted for this general bias produced by fish speeds and survey procedures by standardizing observed fish abundances by relative biases values for different reef fish speeds. The biases for each combination of the survey parameters (fish speed, survey time, visibility, transect width, diver speed, fish turning angle) were taken in Ward-Paige et al. (2010). Underwater visual censuses for 2013-2018 had the same methodology and a very similar observation effort, and in several years, the same diver from 2012.

There are no biomass estimates for macro invertebrates and micro invertebrates in Rocas Atoll. Since these were not scientific field data for these functional groups in Rocas Atoll ecosystem, Ecotrophic Efficiency was used instead. The EE of macro invertebrate was set to 0.9, and for micro invertebrates EE was set to 0.85. The choice of EE values was made based on recommendations in the literature, especially in “best practices in Ecopath approach” by Heymans et al. (2016). For groups with multiple species, their biomasses were summed and then divided by the model area (7.5 km2). For species that only occupy part of the area, the biomass parameter was pro-rated by area.

**Diet composition**

The fish diet data came mainly from stomach contents analysis, stable isotopes analysis, and primary literature. Diet information for lower trophic levels was taken from primary literature (Supplementary materials, Table S1; Longo et al. 2015; Andrades 2018). Estimates of P/B and Q/B of fish were obtained from empirical equations (Pauly 1980; Palomares and Pauly 1998). For invertebrates, estimates for P/B and Q/B ratios were obtained from another South Atlantic Ecopath model (Araújo et al. 2017).

**Fish biomass accumulation**

Biomass accumulation of zero for all groups in the Ecopath model is the same as assuming steady-state with the same biomass at the start and at the end of the modeled year. In this study, biomass accumulation values for fish species were calculated as the biomass in one year minus previous biomass averaged over six years (2012-2018). The values of biomass accumulation are given in Table S3, Supplementary materials\_1.

**Development of temporal simulations using Ecosim module**

In this study, Ecosim module was used to create time dynamic simulations, as initially represented by the mass-balanced Ecopath model for 2012 year, in response to fish time series data (2012-2018) and ocean warming scenarios (2018-2100). The basics of Ecosim are described in detail by Walters et al. (1997, 2000), and will only be given a cursory treatment here, omitting details that have been previously published. In overview, Ecosim consists of biomass dynamics expressed through a series of coupled differential equations. The equations are derived from the Ecopath master Eq. (1), and take the form (3):

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|  | (3) |

where *d*Bi/d*t* represents the growth rate during the time interval d*t* of group *i* in terms of its biomass, *B*i, *gi* is the net growth efficiency estimated using the ratio between P/B and Q/B, *MO*i is the non-predation (‘other’) natural mortality rate estimated from the ecotrophic efficiency, *e*i is emigration rate, Ii is immigration rate (assumed constant over time, and hence independent of events in the ecosystem modeled). The two summations of the Eq. (3) estimate consumption rates, the first expressing the total consumption by group *i*, and the second the predation by all predators on the same group *i*. The consumption rates, Q*ji*, are calculated based on the ‘foraging arena’ concept, where Bi’s are divided into vulnerable and invulnerable components (Walters et al., 1997), and it is the transfer rate (v*ij*) between these two components that determines if control is top-down (i.e., Lotka-Volterra), bottom-up (i.e., donor-driven), or of an intermediate type. The set of differential equations is solved in Ecosim using an Adams-Basforth integration routine (Butcher 2000). For each predator-prey interaction, consumption rates were calculated as (4):

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|  | (4) |

where aij is the rate of effective search for prey (*i*) by predator (*j*), vij is the vulnerability parameter, Ti represents prey relative feeding time, Tj is the predator relative feeding time, Bi is prey biomass, Pj is the predator biomass, Mij is the mediation forcing effects, and Dj represents effects of handing time as a limit to consumption rate. Environmental response functions (*Envfunction, t*), which represent the tolerance relationship of a species to an environmental parameter (here defined with a minimum and maximum levels and the 5th and 90th percentiles), can be used to account for environmental drivers that change overtime, such as temperature. It has to be noted that non-living compartments (detritus) are set to be flow-based so their dynamic is almost insensitive to their initial biomass.

**Model fitting**

The Rocas Atoll Ecopath model for the reference year 2012 was fitted to the fish time series (14 species, period 2012-2018) by conducting vulnerability parameters searches for each predator/prey diet combination. Vulnerability parameters are estimated using an optimization search routine in Ecosim (i.e.*,* stepwise method), which reduces the sum of squares difference between the predicted and observed data (Scott et al. 2016). The best-fit model is found and determined by the minimum difference between model predictions to time-series observations using the weighted sum of squared differences (SS) and the Akaike Information Criterion (AIC) (Akaike 1974), which penalizes for fitting too many parameters based on the number of time series available for estimating the SS. The best-fitted model (called *status quo*) was able to reproduce the historical trends as we showed in Supplementary materials\_2, Table S1, and Fig. S1.

**Fish biomass dynamics projections under ocean warming scenarios**

Future sea surface temperature projections were extracted from the Royal Netherlands Meteorological Institute Climate Explorer portal (http://climexp.knmi.nl) within the study area rectangle from the climate changing multi-model ensemble means (RCP2.6, RCP4.5 and RCP8.5 scenarios, Fig. S2, Supplementary Materials\_2). Thirty-two model outputs, sourced from the Coupled Model Intercomparison Project phase 5 (CMIP5), were extracted for the study area with temperatures fluctuating around their mean.

Optimal temperatures and tolerances were defined for each species using estimates for minimum and maximum preferable and survivable temperatures from AquaMaps (Kaschner et al. 2019). Optimum temperatures were calculated by averaging 10th and 90th preferable temperature quantiles (Supplementary materials\_2, Fig. S3). For groups with multiple species, temperature parameters were averaged and weighted by biomass. In Ecosim, optimal temperatures and tolerances were included as species temperature Gaussian response functions, as has already been done in other research using the EwE approach in analyzing the temporal dynamics of fish biomass under increasing sea temperature (Bentley et al. 2017; Serpetti et al. 2017; Corrales et al. 2018). The Gaussian function has been used widely throughout optimality studies of thermal performance curves (Cheung et al. 2009; Sunday et al. 2012; Betini et al. 2019). The intercept between each specific response function and the annual water temperature were used to calculate a factor to modify the predator consumption rates with a maximum multiplier of 1 which declines as the water temperature deviates from the optimum at a rate determined by the function standard deviations (Bentley et al. 2017).

**Assessing uncertainty**

The Monte Carlo routine in Ecosim was used to perform sensitivity analyses for projections of biomass dynamics under ocean warming (Steenbeek et al. 2018). This routine tests the sensitivity of Ecosim's output to Ecopath input parameters by drawing input parameters from a uniform distribution centered on the base Ecopath value with the coefficients of variation 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 P/B, Q/B, and Biomass Accumulation parameters. Fish biomass coefficients of variation were defined as the ratio between the standard deviation and the mean of each fish time series (Supplementary materials\_2, Table S2). We ran 250 Monte Carlo simulations for each scenario based on coefficients of variation to determine the 95% confidence intervals.

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