



Ocean Warming Will Reduce Standing Biomass in a Tropical Western Atlantic Reef Ecosystem

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ABSTRACT

Ocean warming is altering life on Earth from individuals to ecosystems. The impacts on standing biomass and food webs functioning are less evident due to the paucity of data and difficulty to generate reliable models. We modeled the food web of a tropical near-pristine reef ecosystem and analyzed changes on living biomass across trophic levels as a response to ocean warming over the twenty-first century. By the end of the century, total standing biomass will decrease by 1%, 8% and 44% under different ocean warming scenarios (from reduced RCP 2.6 emission scenario to business-as-usual RCP 8.5 scenario). As total biomass decreases, the ecosystem structure shifts favoring invertivorous fishes, suspension feeding zooplankton, and algal

turfs while corals collapse. The mean trophic transfer efficiency is expected to decrease by ~ 2% between 2012 and 2100 under the RCP 8.5, while biomass residence time (mean time that a unit of biomass remains in the ecosystem) will decrease by ~ 10%. Such food web degradation can alter the dominant biomass flow jeopardizing biomass replenishment, resulting in a less productive ecosystem with increasing dependency on pelagic energy subsidies, reducing the resilience of tropical reef ecosystems.

Key words: Ecopath with Ecosim; Marine ecosystem; Warming; Climate change; Food web simulations; Atoll.

INTRODUCTION

Human-induced warming is affecting ecosystems in all oceans (McCauley and others 2015; Lotze and others 2019). Rising temperatures will transform marine ecosystems into new configurations, toward more homogeneous and less stable biological communities (Sydeman and others 2015; Nolan and others 2018). The predicted ocean warming under high greenhouse-gas emissions scenarios will severely affect species distribution, abundance and extinction rates (Bryndum-Buchholz and

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Author Contribution: LC, RA and GOL conceived the idea. LC, RA and JNA developed the Ecopath food web model and implement functional groups-specific temperature response functions. EV designed the figures. LC led the writing of the manuscript. All authors contributed critically to the draft and gave the final approval for publication. RA and GOL equally share the senior authorship of this study.

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58 others 2019; Pörtner and others 2019). Ocean
59 warming will also affect trophic interactions and
60 entire food webs that control the dynamics and
61 stability of biological communities, as well as en-
62 ergy and matter flow within and across ecosystems
63 (Zhang and others 2017; Gibert 2019; Inagaki and
64 others 2020). Despite overlooked due to lack of
65 data and difficulties in generating reliable models,
66 predicting changes in food webs can help us
67 understand the structure and dynamics of these
68 novel and simplified ecosystems that are likely to
69 emerge under ocean warming scenarios (Blanchard
70 and others 2012).

71 Coral reefs are among the most diverse and
72 sensitive ecosystems on the planet, with multiple
73 reports of severe impacts by ocean warming
74 (Hughes and others 2017; Williams and others
75 2019). Major impacts on these ecosystems include
76 coral bleaching leading to loss of structural com-
77 plexity and diversity (Magel and others 2019),
78 shifts in species distribution (Robinson and others
79 2019) and changes in the ecosystem trophic struc-
80 ture with increasing algal cover leading to an in-
81 crease in the importance of microbes in the energy
82 flow (that is, microbialization; Haas and others
83 2016). Such deleterious impacts of ocean warming
84 on ectotherms will be amplified if food intake is
85 reduced, either because warming reduces standing
86 food resources or because it restricts foraging time
87 (Huey and Kingsolver 2019). Besides ecosystem
88 functioning, the degradation of coral reefs threat-
89 ens important services, including fisheries and
90 tourism, on which millions of humans rely (Rogers
91 and others 2018; Curnock and others 2019).

92 To understand the impacts of ocean warming on
93 reef ecosystems, we investigated the potential fu-
94 ture effects of human-induced ocean warming on
95 standing biomass in reef food webs using a near-
96 pristine tropical reef ecosystem in the Southwest-
97 ern Atlantic Ocean as a model. Specifically, we
98 hypothesize that local increases or decreases in the
99 standing biomass of species during warming can be
100 predicted by their thermal range (TR). We expect
101 that the species with a reduced TR (that is, less than
102 2 °C) will be the ones that will have their standing
103 biomass most impacted when compared to those
104 species that have a wide TR (> 2 °C) (Burrows and
105 others 2020; Fredston-Hermann and others 2020).
106 We constructed and fitted a food web model based
107 on primary data obtained in the field along a seven-
108 year time series complemented with data from the
109 literature. Then, we explored the temporal evolu-
110 tion of the ecosystem trophic structure through
111 comparisons of standing biomass and transfer effi-
112 ciency indicators. In the food web model, we

incorporated species-specific thermal ranges and 113
functional responses to test the impact of ocean 114
warming under three projected scenarios predicted 115
by the Intergovernmental Panel on Climate 116
Change until 2100 (IPCC; Pörtner and others 117
2019). Finally, we calculated biomass' transfer 118
efficiency indicators to assess the modifications in 119
the structure and functioning of the tropical reef 120
ecosystem under future ocean warming. 121

METHODS 122

Study Area 123

Rocas atoll is the only atoll formation in South 124
Atlantic Ocean, laying approximately 230 km off 125
the NE coast of Brazil (03°50'S, 33°49'W) as part of 126
a seamount chain in the E-W direction known as 127
the fracture zone of Fernando de Noronha. It has a 128
surface area of 7.5 km² with large and shallow in- 129
ner lagoon and reef flat areas (Supplementary 130
Material, Figure S1; Longo and others 2015). The 131
Rocas Atoll was established as a marine reserve in 132
1978 and effectively enforced since 1991 and is one 133
of the few reef ecosystems in the western South 134
Atlantic Ocean in a near-pristine condition (no 135
local fishing, tourism or pollution). Since 2013, 136
Rocas Atoll is annually monitored through the 137
Brazilian Long-Term Ecological Research program 138
(PELD-ILOC; <http://peldiloc.sites.ufsc.br/>) and is 139
considered a natural laboratory to assess ocean 140
warming impacts with minimal local direct 141
anthropogenic impact. Our food web model in- 142
cludes the entire reef flat and pools that are formed 143
during high and low tide (Supplementary Material, 144
Figure S1). 145

Food Web Modeling 146

The model was built on the Ecopath with Ecosim 147
(EwE) software version 6.6 (Christensen and Pauly 148
1993; Walters and others 1997, 2000). The equa- 149
tions and algorithms underlying the EwE frame- 150
work are documented in Supplementary materials 151
and extensively in the scientific literature (Chris- 152
tensen and Walters 2004; Heymans and others 153
2016). The model consisted of 28 functional 154
groups: ranging from primary producers to herbi- 155
vores and carnivores, but with the 13 fish species 156
considered as individual model species. We in- 157
cluded one non-living group (detritus). All func- 158
tional groups were defined as adult ontogenetic 159
phase. We aggregated several species into func- 160
tional groups with other species of similar life his- 161
tory traits, diet composition and shared predators in 162
the interest of keeping the model results easy to 163



164 deal (Supplementary Material, Table S1). The
165 functional groups are regulated by gains (con-
166 sumption, production, and immigration) and losses
167 (natural mortality and emigration), which are
168 linked to each other by trophic interactions (Sup-
169 plementary Material, Table S2).

170 Model Parameterization

171 We used the following input parameters for each
172 functional group to build the food web model:
173 biomass (B), production per unit of biomass that
174 must be consumed by predators, or exported out of
175 the ecosystem, or converted into detritus (P/B),
176 consumption per unit of biomass on preys from the
177 ecosystem or from outside in the form of imports
178 (Q/B), diet matrix (DC), biomass accumulation
179 (BA) and the model-estimated ecotrophic effi-
180 ciency (EE). EE describes the fraction of the pro-
181 ductivity that is used in the system. Ecopath sets up
182 a series of linear equations to solve for unknown
183 values establishing mass-balance in the same
184 operation.

185 All data were converted to biomass per unit area
186 of reef ($\text{g}\cdot\text{m}^{-2}$) using conversion factors from the
187 literature for fish and most mobile invertebrates,
188 and our own determinations of coral and algal
189 biomass per unit surface area (Longo and others
190 2015). Abundance-by-length estimates for fish
191 species were taken from underwater visual cen-
192 suses (UVC) between 2012 and 2018 and converted
193 to standing biomass using length–weight relation-
194 ships estimated with the local samples. Because
195 there are no biomass estimates for benthic macro
196 invertebrates and micro invertebrates in Rocas
197 Atoll, we used the Ecotrophic Efficiency parameter
198 (EE), based on Heymans and others (2016), set to
199 0.9 and 0.85 for macro and micro invertebrates,
200 respectively. For functional groups with multiple
201 species, their biomasses were summed and then
202 divided by the ecosystem area (7.5 km^2). For spe-
203 cies that only occupy part of the area, the biomass
204 parameter was pro-rated by area. Estimates of P/B
205 and Q/B of fish were obtained from empirical
206 equations (Pauly 1980; Palomares and Pauly 1998).
207 For invertebrates, estimates for P/B and Q/B ratios
208 were obtained from another South Atlantic Eco-
209 path model (Araújo and others 2017). The non-
210 assimilated biomass (detritus) of all functional
211 groups was assumed to be exported outside from
212 the Rocas Atoll reef ecosystem. Biomass accumu-
213 lation values for fish species were calculated as the
214 biomass in one year minus previous biomass
215 averaged over six years (2012–2018) (Supplemen-
216 tary Material, Table S3).

Trophic Relationships

218 Data on diet were obtained from stomach contents
219 analysis, stable isotopes analysis, and primary lit-
220 erature (Supplementary Material, Tables S1 and
221 Table S2). To help visualize the results, fish species
222 were assigned to trophic guilds based on their diet
223 and feeding behavior, including the way they
224 capture, store, and transfer energy across trophic
225 levels (Madin and others 2016). We have defined
226 four trophic guilds: reef sharks, generalist fish
227 predators, invertivorous fish, herbivorous and
228 detritivorous fish.

Model Fitting

229 The Rocas Atoll food web model for the reference
230 year 2012 was fitted to the time series data on fish
231 biomass (14 species, period 2012–2018) using the
232 temporal dynamic module of the Ecopath, named
233 Ecosim (Walters and others 1997). Vulnerability
234 parameters, for each predator/prey diet combina-
235 tion, are estimated using an optimization search
236 routine in Ecosim (that is, stepwise method), which
237 reduces the sum of squares difference between the
238 predicted and observed data (Scott and others
239 2016). The best-fit model is found and determined
240 by the minimum difference between model pre-
241 dictions to time-series observations using the
242 weighted sum of squared differences (SS) and the
243 Akaike Information Criterion (AIC) (Akaike 1974),
244 which penalizes for fitting too many parameters
245 based on the number of time series available for
246 estimating the SS . The best-fitted model (*status quo*)
247 was able to reproduce the historical trends (Sup-
248 plementary Material, Table S4 and Figure S3).
249

Biomass Dynamics Projections Under Ocean Warming Scenarios

252 We ran simulations (using the Ecosim module) on
253 biomass dynamics based on fish time-series data
254 and using temperature projections from 2018 to
255 2100. We present species-specific biomass dynam-
256 ics and compare each ocean warming scenario
257 relative to a hypothetical future with no changes in
258 sea temperature by 2100 (*status quo* scenario)
259 using the average percent variation of the relative
260 biomass.

261 Three Representative Concentration Pathways
262 (RCP 2.6, RCP 4.5, and RCP 8.5) were used for
263 projections of the future ocean warming in the
264 Coupled Model Intercomparison Project Phase 5
265 (Taylor and others 2012). They are identified by
266 their approximate anthropogenic radiative forcing
267 (in $\text{W}\cdot\text{m}^{-2}$, relative to 1750) by 2100 (Pörtner and



268 others 2019). Future sea surface temperature val- 323
 269 ues were extracted from the Royal Netherlands 324
 270 Meteorological Institute Climate Explorer portal (h 325
 271 ttp://climexp.knmi.nl) within the study area loca- 326
 272 tion. Thirty-two model outputs were extracted for 327
 273 the study area with temperatures fluctuating 328
 274 around their mean. Current average seawater 329
 275 temperature in Rocas Atoll's is 27.3 °C, which by
 276 2100, is expected to rise 0.5 °C, 1.3 °C and 3 °C
 277 under the low (RCP 2.6), medium (RCP 4.5) and
 278 high (RCP 8.5) ocean warming scenarios, respec-
 279 tively (Supplementary Material, Figure S2).

280 Optimal temperatures and thermal ranges were
 281 defined for each modeled functional group using
 282 5th and 95th percentiles estimates for minimum
 283 and maximum preferable and survivable tempera-
 284 tures from AquaMaps (Kaschner and others 2019)
 285 (Figure 1). We checked the reliability of the
 286 AquaMaps data based on expert knowledge about
 287 species-specific thermal ranges and habitat usage.
 288 We performed a scrupulous check of each thermal
 289 range, comparing it with the maximum and mini-
 290 mum temperature values observed in the western
 291 Atlantic Ocean, using NOAA Optimum Interpolat-
 292 ion 1/4 Degree Daily Sea Surface Temperature
 293 model data as reference (Reynolds and Banzon
 294 2008), which demonstrated a good level of agree-
 295 ment.

296 For functional groups with multiple species,
 297 temperature ranges were averaged and weighted
 298 by biomass. In Ecosim, optimal temperatures and
 299 temperature ranges were included as species tem-
 300 perature Gaussian response functions, following
 301 similar methodology using the EwE approach in
 302 analyzing the temporal dynamics of fish biomass
 303 under increasing seawater temperature (Bentley
 304 and others 2017; Serpetti and others 2017; Corrales
 305 and others 2018). Species thermal performance
 306 followed the classic bell shape supported by field
 307 data (Payne and others 2016; Childress and Letcher
 308 2017; Waldock and others 2019) and physiological
 309 models (Angilletta 2009; Neubauer and Andersen
 310 2020). The thermal performance curves were then
 311 used to modify the feeding rate of each functional
 312 group within the model, where the maximum
 313 feeding rate occurred at the optimum temperature,
 314 and feeding rates declined as temperature departed
 315 from the optimum. It follows that reduced feeding
 316 rates would lead to reduced biomass. The intercept
 317 between each species-specific thermal performance
 318 curves and the annual average sea water temper-
 319 ature were used to calculate a factor to modify the
 320 predator consumption rates with a maximum
 321 multiplier of 1 for optimum temperature (Bentley
 322 and others 2017). The multiplier declines as the

average sea water temperature deviates from the
 optimum at a rate determined by the thermal
 performance curve standard deviations (Bentley
 and others 2017; Serpetti and others 2017; Corrales
 and others 2018).

Therefore, for each predator-prey interaction,
 consumption rates were calculated as (1):

$$Q_{ij} = \frac{a_{ij} \times v_{ij} \times B_i \times P_j \times T_j \times M_{ij}/D_j}{v_{ij} + (v_{ij} \times T_i \times M_{ij}) + (a_{ij} \times M_{ij} P_i \times T_j/D_j)} \times f(\text{Env}_{\text{function}}, t) \quad (1)$$

where a_{ij} is the rate of effective search for prey (i)
 by predator (j), v_{ij} is the vulnerability parameter, T_i
 represents prey relative feeding time, T_j is the
 predator relative feeding time, B_i is prey biomass, P_j
 is the predator biomass, M_{ij} is the mediation forcing
 effects, and D_j represents effects of handling time as
 a limit to consumption rate. Environmental re-
 sponse functions ($\text{Env}_{\text{function}}, t$) represent the tol-
 erance of a species to an environmental parameter
 (here based on the minimum and maximum levels
 and on the 5th and 95th percentiles; Figure 1). We
 used the Environmental response function to ac-
 count for changes in sea surface temperature over
 time.

Assessing Uncertainty

The Monte Carlo routine in Ecosim was used to
 perform sensitivity analyses for projections of bio-
 mass dynamics under ocean warming (Steenbeek
 and others 2018). This routine tests the sensitivity
 of Ecosim's output to Ecopath input parameters by
 drawing input parameters from a uniform distri-
 bution centered on the baseline Ecopath values
 with the coefficients of variation (CV) set to default
 0.1 (Christensen and Walters 2004; Steenbeek and
 others 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/Bio-
 mass), and Biomass Accumulation parameters for
 the functional groups of which we do not have
 detailed information over at least three years of
 local sampling. For the functional groups of which
 we had time series observed data, we defined the
 CV as the ratio between the standard deviation and
 the mean value of each fish standing biomass time
 series (Supplementary Material, Table S5). We ran
 250 Monte Carlo simulations for each scenario
 based on coefficients of variation to determine the
 95% confidence intervals.



Author Proof

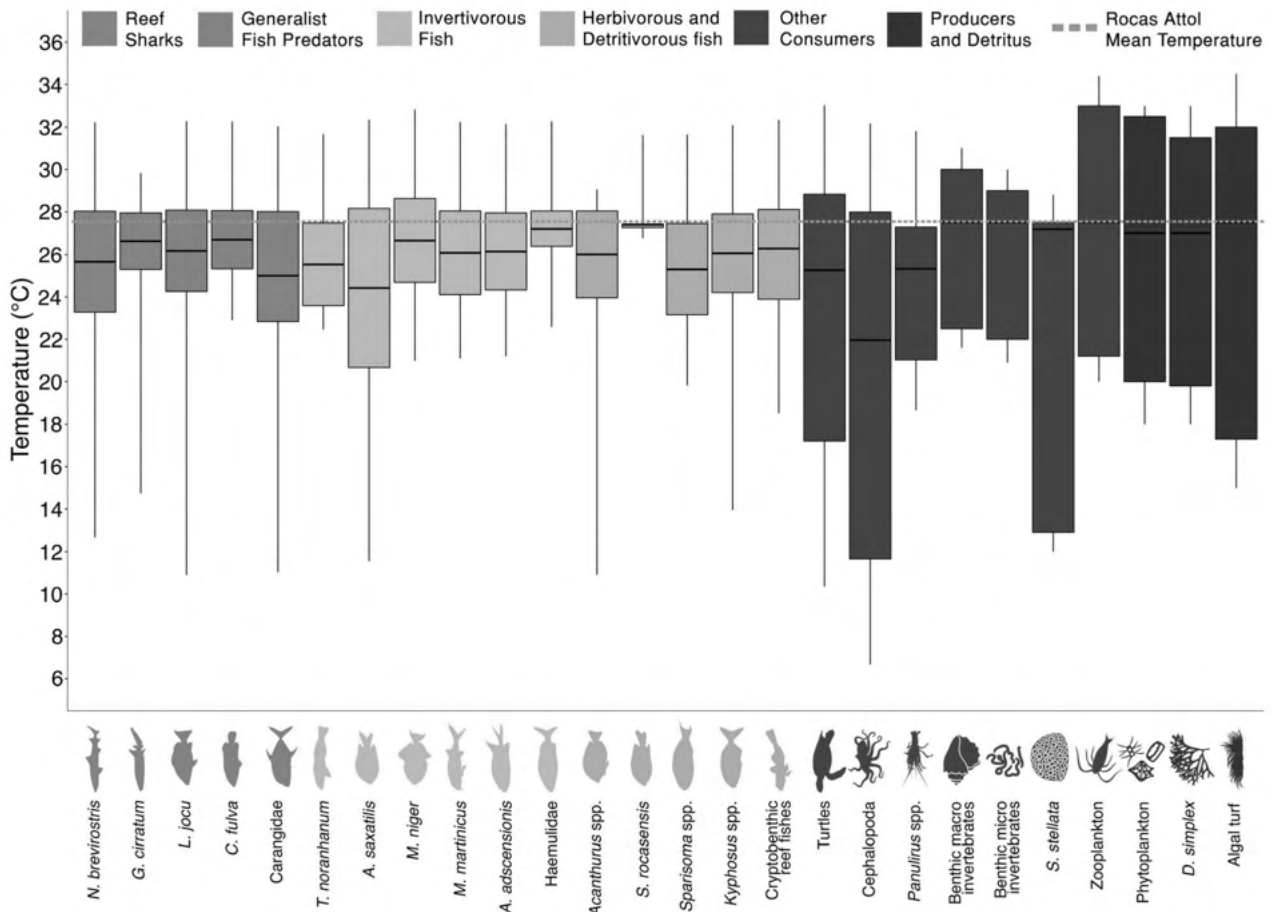


Figure 1. Water temperature ranges for functional groups in the Rocas Atoll reef ecosystem food web model. Box plots represent optimum temperature (bold black line), the lower and upper hinges correspond to the 5th and 95th percentiles and the end of the whiskers as maximum and minimum temperatures for each functional group.

370 Trophic Transfer Efficiency (TTE)
371 and Biomass Residence Time (BRT)
372 Indicators

373 To describe the overall impacts of ocean warming
374 on the Rocas Atoll's reef ecosystem structure, we
375 used two time-dependent indicators that summa-
376 rize biomass transfer efficiency through the food
377 web and are expected to change in a warming
378 ocean: the trophic transfer efficiency (TTE) and the
379 Biomass Residence Time (BRT) (Pontavice and
380 others 2020). The TTE indicator (%) is the fraction
381 of biomass production transferred from one trophic
382 level (TL) to the next and summarizes all the food
383 web losses at each TL. The BRT indicator (years) is
384 the average amount of time that a biomass unit
385 spends at a given TL before trophic transfer to
386 higher TLs in the food web through predation. The
387 BRT is inversely proportional to the speed of bio-
388 mass transfer across TLs. Five input parameters
389 were used to estimate the TTE and the BRT indi-

cators: P/B (Production to Biomass), P/Q (Produ- 390
tion to Consumption), Q/B (Consumption to 391
Biomass), BA (Biomass accumulation rate) and EE 392
(Ecotrophic Efficiency). For each functional group, 393
the parameters P/B , Q/B , P/Q , BA and EE were 394
extracted from the deterministic dynamic simula- 395
tions of Ecosim every 10 years, from 2012 to 2100 396
for each RCP scenario. Then, for each functional 397
group the parameters P/B , Q/B and P/Q were dis- 398
tributed over a range of trophic classes (following a 399
lognormal distribution and using classes with a 400
width of 0.1 TL) according to an established 401
methodology implemented in the R package Eco- 402
Troph (Coll ter and others 2015). In our analysis, 403
we estimated TTE and BRT indicators from trophic 404
level TL = 2 to TL = 4. Thus, the values of TTE and 405
BRT reflect mean estimates from trophic levels 2–3 406
and from trophic levels 3–4, every 10 years of 407
ocean warming simulation scenarios. We refer to 408
the detailed description on how to calculate the 409
TTE and BRT indicators in the publication of Pon- 410

411 tative and others 2020 and the specific R code
412 associated with the repository of this study [https://g](https://github.com/leomarameo7/Atoll_Rocas_project)
413 [ithub.com/leomarameo7/Atoll_Rocas_project](https://github.com/leomarameo7/Atoll_Rocas_project).

414 RESULTS

415 Simulated Biomass Changes Under 416 Ocean Warming Scenarios

417 Total standing biomass through the food web was
418 severely reduced under the warming scenarios
419 (Figures 2 and 3a). Qualitative visual food web
420 analysis suggests that ocean warming weakened
421 many trophic interactions, especially in trophic le-
422 vel 2 due to the severe reduction of macro and
423 micro invertebrates and cryptobenthic reef fishes
424 (Figure 2b). Total ecosystem standing biomass
425 ($1090 \text{ g}\cdot\text{m}^{-2}$), is expected to decrease by 1% under
426 RCP 2.6, by 8% under RCP 4.5, and by 44% under
427 RCP 8.5 (Figure 3a).

428 Regarding the biomass dynamics, the RCP 4.5
429 and RCP 8.5 scenarios began to diverge from RCP
430 2.6 and status quo scenarios in 2040 (Figure 3a).
431 There was a continuous overlap of the confidence
432 intervals of total biomass dynamics among all sce-
433 narios until 2075, when a steep decline started to
434 occur under the RCP 8.5, which deviated from the
435 other scenarios (Figure 3a). Under RCP 8.5, we
436 projected a severe loss of Trophic Transfer Effi-
437 ciency, from 4% to 2.4% (Figure 3b) and a
438 0.3 year decrease in Biomass Residence Time, from
439 2.1 to 1.8 years (Figure 3c) over the period 2012–
440 2100. After 2030, TTE and BRT remain stable in
441 scenario RCP 2.6. For the RCP 4.5 scenario, there is
442 no clear trend for TTE, and the initial (4.07%) and
443 final (4.08%) mean values are practically the same.

444 Under the status quo scenario, total fish biomass
445 reached an average of $27.2 \text{ g}\cdot\text{m}^{-2}$ by 2100, which
446 was close to that predicted under the RCP 2.6 sce-
447 nario (Figure 4). The RCP 4.5 scenario predicted an
448 average decrease of 17.3%, and the RCP 8.5 pre-
449 dicted an 86% decrease in total fish biomass which
450 is estimated to reach $3.7 \text{ g}\cdot\text{m}^{-2}$ (Figure 4b). In
451 addition to declines in biomass, model simulations
452 also predict alterations on the trophic structure of
453 the fish assemblage in 2100 (Figure 4c). Herbivores
454 and detritivores (currently $\sim 49\%$ of total fish
455 biomass) will experience the major declines under
456 RCP 8.5 reaching about 19% of fish total biomass
457 (Figure 4c). Invertivorous fishes (currently repre-
458 senting 22.5% of total fish biomass) increased their
459 relative proportion to about 51% under RCP 8.5,
460 despite the decrease in their standing biomass
461 (Figures 4 and 5). Under the RCP 8.5 scenario, the
462 trophic composition of the reef fish assemblages

463 changed from an herbivorous/detritivorous-domi-
464 nated assemblage to an invertivorous-dominated
465 assemblage by 2100 (Figure 4c).

466 Generalist predators and reef sharks maintained
467 similar biomass proportions under all scenarios
468 (Figure 4c) but also with a reduction in their
469 standing biomass (Figure 5). Under RCP 4.5 and
470 RCP 8.5, respectively, standing biomass decreased
471 by 28% and 88% for reef sharks, 15% and 8.5% for
472 generalist predators, 7% and 74% for invertivorous
473 fish, 23% and 94% for herbivorous/detritivorous
474 fishes (Figure 5, but see also Figure S4 and Fig-
475 ure S6 in Supplementary Materials).

476 Standing biomass of almost all non-fish func-
477 tional groups also decreased under RCP 4.5 and
478 RCP 8.5 scenarios, but with variable magnitudes
479 (Figure 6; but see also Figure S5 and Figure S7 in
480 Supplementary Materials). For instance, *Siderastrea*
481 *stellata* corals decreased by 61% under RCP 4.5
482 scenario, with prevision to be ecologically extinct
483 by 2075 under high emission scenarios. The bio-
484 mass of primary producers, lobsters, sea turtles,
485 seabirds, and invertebrates also declined in all sce-
486 narios (Figure 6). Conversely, zooplankton stand-
487 ing biomass remained unchanged under the RCP
488 2.6 but experienced a 37% increase under RCP 4.5
489 and 111% increase under RCP 8.5.

490 DISCUSSION

491 We found that most taxa are likely to experience
492 dramatic declines in standing biomass under the
493 most extreme ocean warming scenario (RCP 8.5).
494 Ecosystem trophic composition will shift by 2100,
495 affecting energy flow through the entire food web
496 by declining the trophic transfer efficiency (TTE)
497 and the biomass residence time (BTE). This change
498 may lead to a general degradation of the food web,
499 reducing the resilience of tropical reefs. Moreover,
500 the most dramatic changes predicted in our pro-
501 jections will occur by 2075, when climate condi-
502 tions exceed the current thermal niche of most
503 functional groups. These modifications will jeop-
504 ardize biomass replenishment resulting in a less
505 productive ecosystem with increasing dependency
506 on pelagic energy subsidies given the severe decli-
507 nes in benthic producers (algal turfs and seaweeds).
508 Our findings are consonant with recent studies
509 indicating that marine food webs are at risk of
510 collapse due to ocean warming (Blowes and others
511 2019; Bryndum-Buchholz and others 2019), par-
512 ticularly in reef ecosystems where synergistic hu-
513 man impacts have caused drastic changes (Hughes
514 and others 2017; Beyer and others 2018).



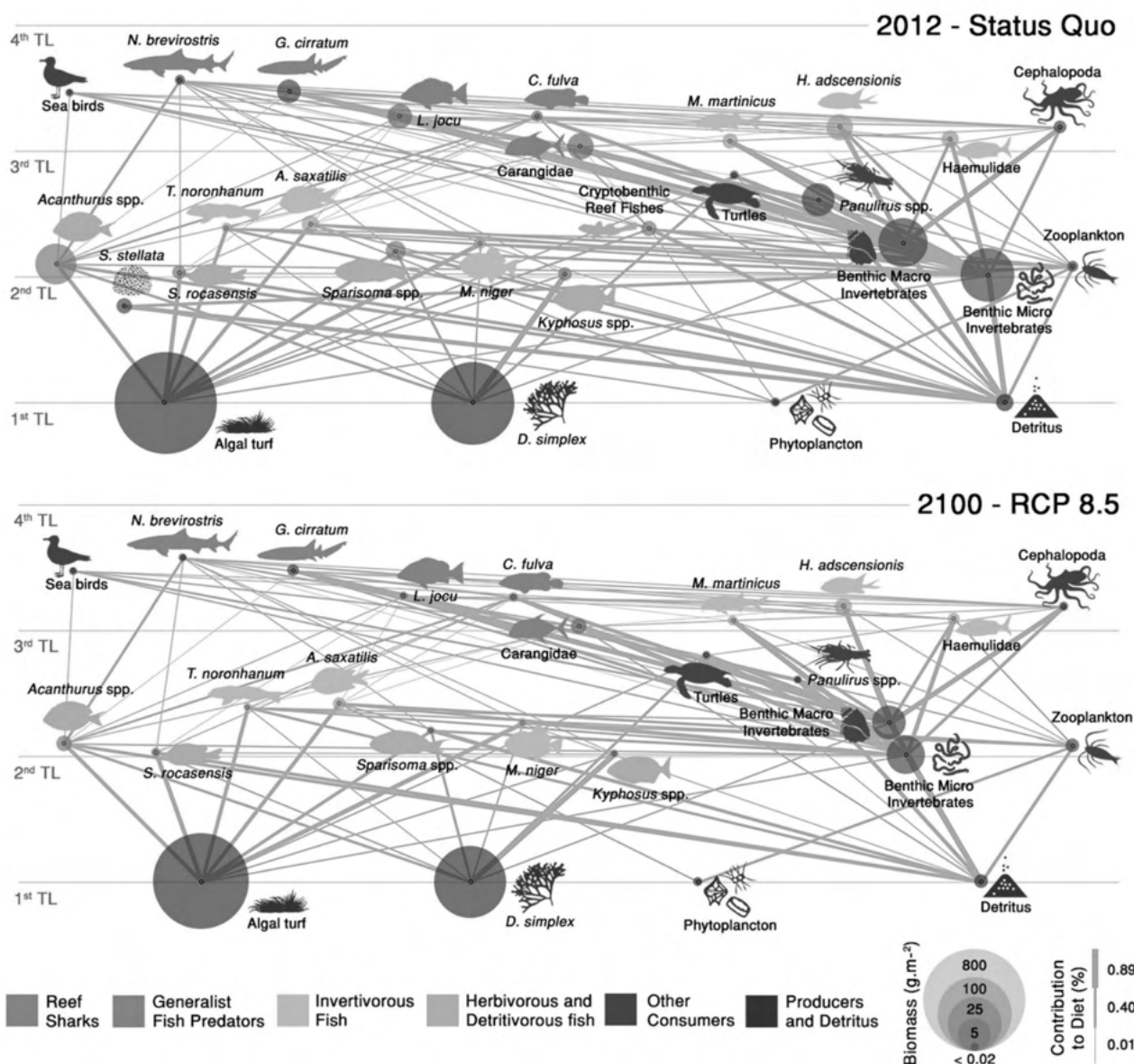


Figure 2. Alteration of standing biomass and trophic flows within the Rocas Atoll's food web under ocean warming. **a** Food web of the Rocas Atoll ecosystem (year 2012). **b** Food web of the Rocas Atoll ecosystem under RCP 8.5 ocean warming scenario (year 2100). Each functional group is shown as a 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.

515 Our results may have broader implications for
516 tropical reefs worldwide because many of the key
517 components of change (for example decrease in
518 nominally herbivorous fishes, decline of corals and
519 algal turfs) are congruent with previous studies
520 across the Pacific and South Atlantic Oceans
521 (Pratchett and others 2011; Richardson and others
522 2018; Inagaki and others 2020; Morais and others
523 2020). Herbivorous fishes transfer nutrients as
524 excreta, gametes, or somatic tissue to contribute to
525 food chains elsewhere on the reef, including

526 detrital food chains in back reef or lagoon envi-
527 ronments (Vermeij and others 2013; Bellwood and
528 others 2018). Grazing fish stimulate algal turfs'
529 productivity by selecting for fast-growing species
530 and growth forms, removing senescent material,
531 reducing self-shading effects, and enhancing the
532 availability of nutrients (Carpenter 1986; Klumpp
533 and Mckinnon 1992; Marshall and Mumby 2015).
534 Increased nutrient load and reduced herbivory
535 have resulted in long sediment-laden turfs as an
536 alternative and stable community state in degraded

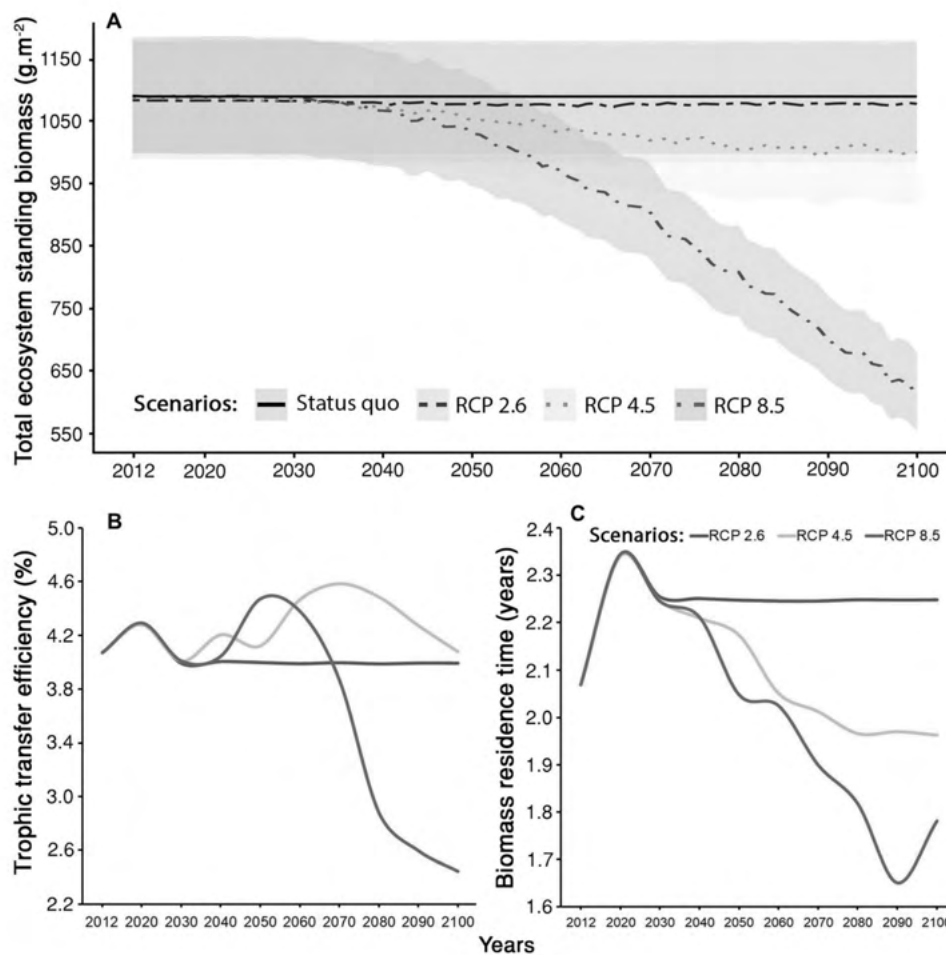


Figure 3. Response of total fish standing biomass to ocean warming. **a** Projections of the total fish standing biomass under ocean warming scenarios, low (RCP 2.6) medium (RCP 4.5) and high (RCP 8.5). 95% confidence intervals around the mean are shown for trend lines. **b** Projections of trophic transfer efficiency (TTE) and **c** projections of biomass residence time (BRT) between 2012 and 2100 under three ocean warming scenarios, RCP 2.6, RCP 4.5 and RCP 8.5 in blue, yellow and red, respectively. The lines are the mean values of both biomass' transfer efficiency indicators.

reefs (Goatley and others 2016). Therefore, the projected simultaneous decline of algal turfs and herbivore fish standing biomass may trigger a severe disruption of the major reef energetic pathway that supports higher-level food chains of the reef ecosystem, leading to novel states in these reefs (Inagaki and others 2020).

Shifts in the ecosystem trophic structure such as that generated by the loss of secondary consumers can alter primary production and, potentially, the functioning of reef ecosystems (Dulvy and others 2004; Inagaki and others 2020). Sea turtles, sea birds, and reef sharks can connect open oceans and reefs by vectoring organic matter and nutrients between them (Bouchard and Bjorndal 2000; Otero and others 2018; Williams and others 2019). Research has shown that, in reef environments, sharks and fish are a vital nutrient reservoir; pri-

mary production is enhanced by fish storing nutrients (in biomass) and egesting them (Allgeier and others 2014; Mourier and others 2016). Fishing on high trophic levels reduces nearly half of reef fish communities' capacity to store and recycle nutrients (Allgeier and others 2016). The loss of sea bird colonies as those present in the Rocas Atoll would severely affect biogeochemical cycles. Sea-birds are important global drivers in the nitrogen and phosphorus cycles, enhancing islands' primary production (Graham and others 2018). Therefore, the expected loss of secondary consumers such as sea birds, sharks, and sea turtles are likely to indicate lower fish production in future reef state with repercussions for the functioning of the entire reef ecosystem.

Ocean warming this century is likely to lead to a decline in tropical phytoplankton diversity and

Author Proof

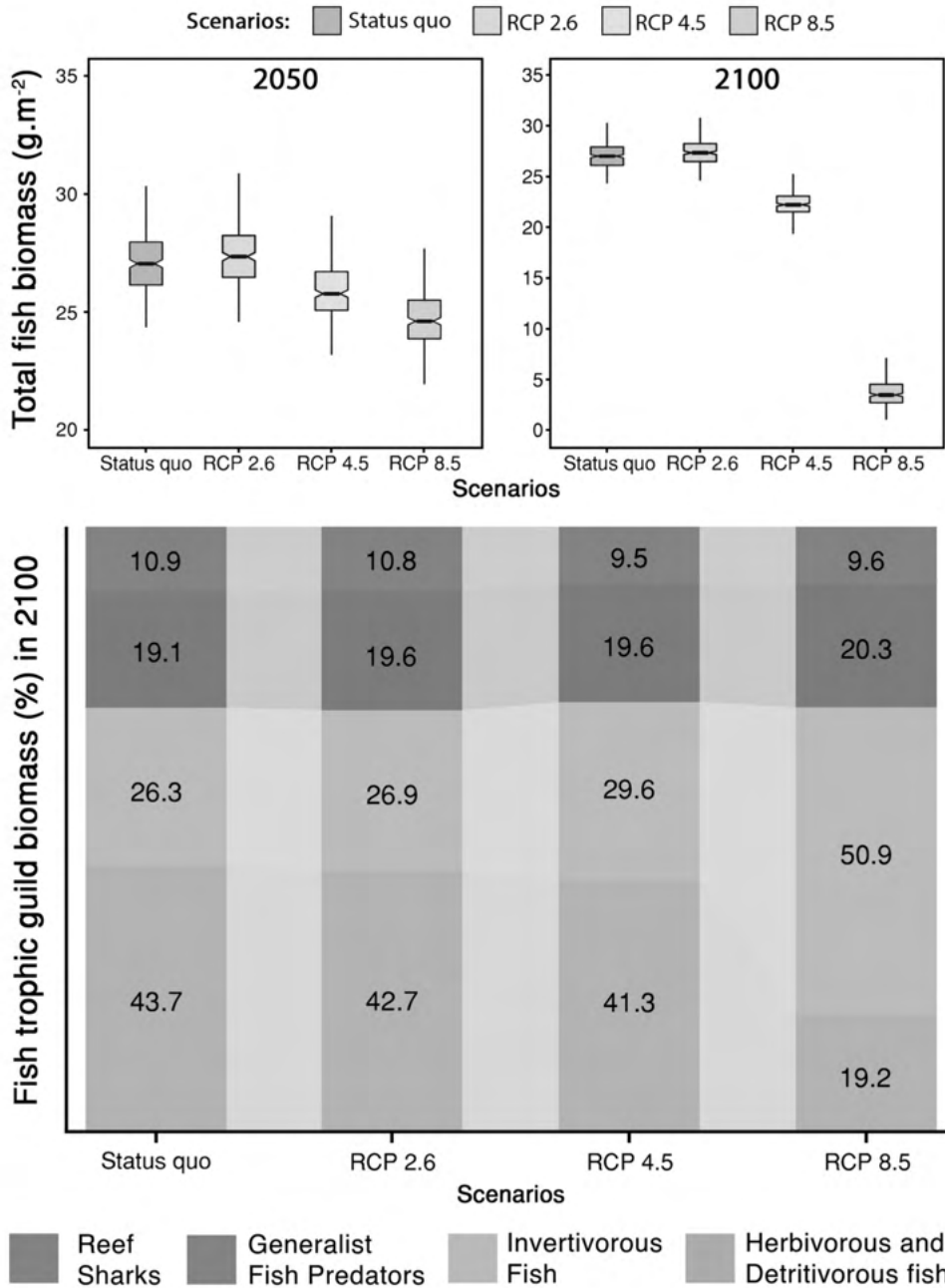


Figure 4. Projected ocean warming effect (RCP 2.6, RCP 4.5, RCP 8.5) vs. Status quo scenario in **a** 2050 and **b** 2100 for fish functional group standing biomass. Box plots display the median (horizontal line), the lower and upper hinges correspond to the first and third quartiles (the 25th and 75th percentiles). The lower whisker extends from the hinge to the smallest value at most 1.5 * interquartile range of the hinge. The red dotted line represents the Status quo scenario median value for reference. **c** Bar graphics represent trophic guild mean percent contribution for total fish biomass under ocean warming scenarios by 2100 year.

573 biomass (Thomas and others 2012; Lotze and others
 574 others 2019). This general trend can be explained by
 575 warming causing increased ocean stratification,
 576 which reduces nutrient availability in the upper
 577 ocean, leading to decreased primary production
 578 and lower energy supply for higher trophic levels

(Bopp and others 2013; Kwiatkowski and others 579
 580 2019). In oligotrophic systems of circulating ocean
 581 currents, islands and atolls can enhance phyto-
 582 plankton biomass and create hotspots of produc-
 583 tivity and biodiversity (for example, island mass
 584 effect, IME) (Gove and others 2016; James and

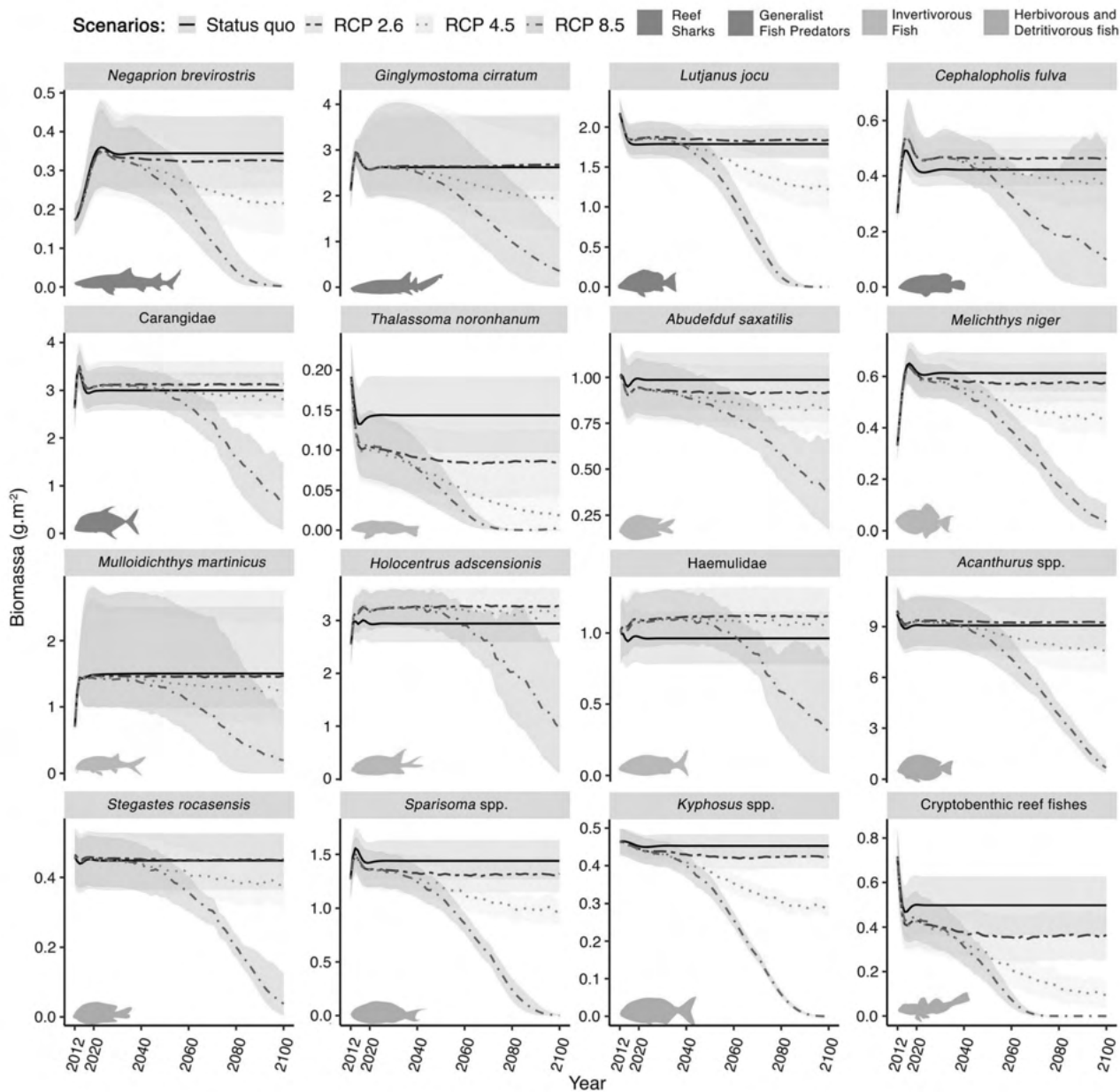


Figure 5. Projections of fish functional group biomass dynamics in the Rocas Atoll reef ecosystem under ocean warming scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

585 others 2020). For example, phytoplankton
 586 enhancement is a long-term, near-ubiquitous fea-
 587 ture among Pacific coral reef islands and atolls.
 588 Similarly, in Rocas Atoll, the increase in phyto-
 589 plankton biomass is also caused by the IME and not
 590 by upwelling (Jales and others 2015). We argue
 591 that reef biota may be constrained by ocean
 592 warming due to decreases in their primary trophic
 593 resources caused by bottom-up forcing and strati-
 594 fication in the water column, which changes the
 595 mixed layer depth resulting in lower nutrients and
 596 primary production. Also, our model indicated that

zooplankton functional group shall experience
 597 notable biomass increase because of decreasing
 598 predation pressure by invertivorous fish which
 599 would contribute to phytoplankton decline. Fur-
 600 thermore, zooplankton functional group has a
 601 strong trophic dependence on pelagic subsidies of
 602 (35%). As a result, we predict that tropical reef
 603 ecosystems such as Rocas Atoll will be severely
 604 threaded, mainly if there are no energetic subsidies
 605 in the form of plankton or inorganic nutrients
 606 provided by upwelling of pelagic deeper waters to
 607

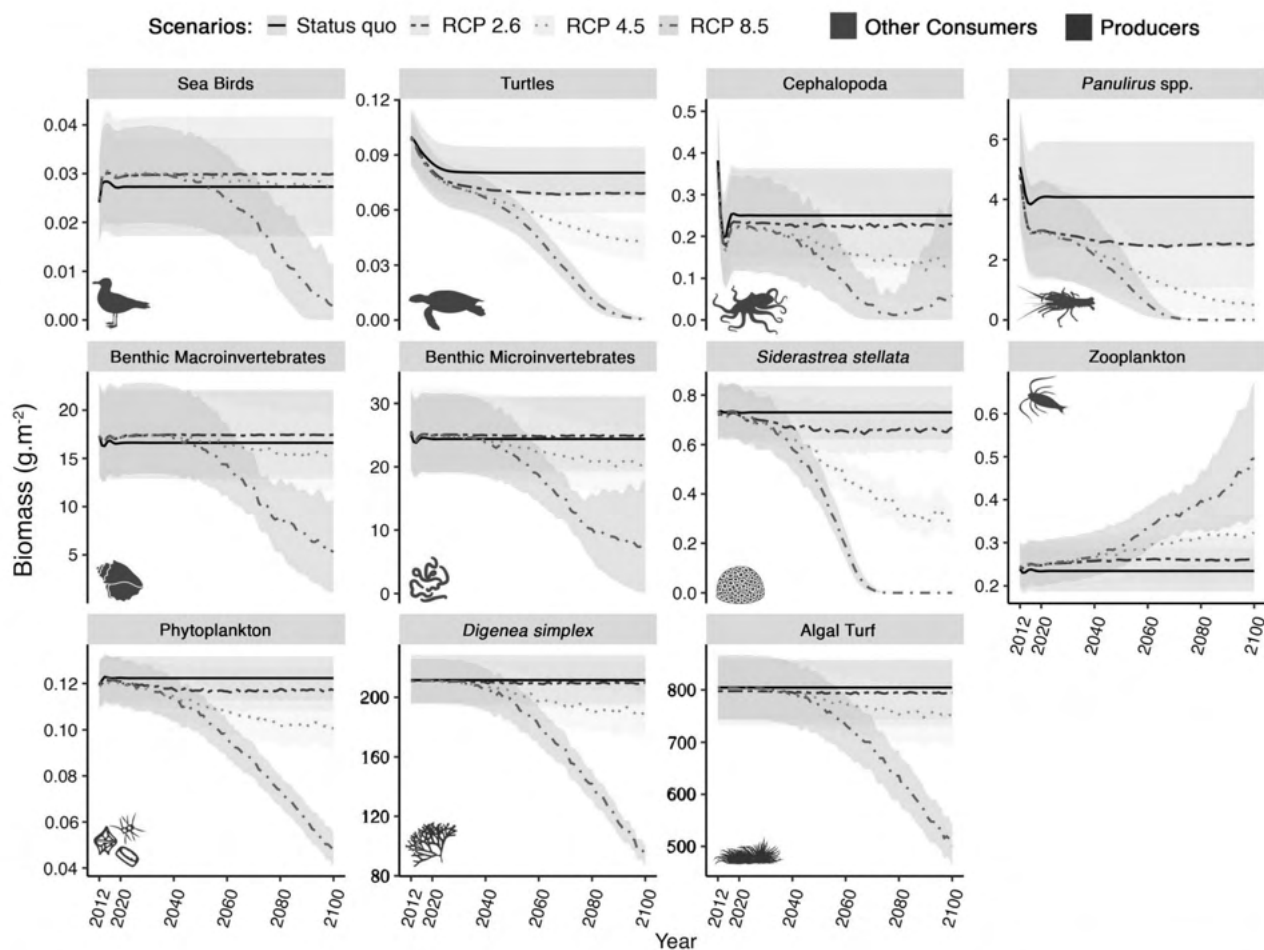


Figure 6. Projections of non-fish functional group biomass dynamics in the Rocas Atoll reef ecosystem under ocean warming scenarios. Shadows represent the 5% and 95% percentiles obtained using the Monte Carlo routine.

608 support the standing biomass of primary consumers
609 such as zooplankton.

610 Sea water temperature drives biomass transfers
611 through the food web in tropical marine ecosys-
612 tems (Pontavice and others 2020), which are
613 characterized by lower trophic transfer efficiency
614 and fast biomass transfers (lower BRT) in compar-
615 ison to temperate and polar ecosystems (Eddy and
616 others 2021). The projected decrease in transfer
617 efficiency at the global scale over the twenty-first
618 century is expected to amplify impacts at higher
619 trophic levels, leading to a 21% decrease in abun-
620 dance of marine predators (Pontavice and others
621 2021). Our study indicates that the Rocas Atoll's
622 reef ecosystem will experience a decline in trophic
623 transfer efficiency and biomass residence time
624 indicators under the most extreme ocean warming
625 scenario. This fact may be related to a severe de-
626 cline in fish standing biomass, especially at high
627 trophic levels and a species composition defined by
628 less efficient and fast-growing species (Maureaud

and others 2017). Thus, we expect that in the next 629
50 years the sustained increase in ocean tempera- 630
ture will alter the Rocas Atoll's reef ecosystem 631
functioning toward a faster and less efficient state. 632

633 Our approach also comprises caveats that need to
634 be acknowledged. Despite the robust direction of
635 change, the substantial spread in our projections'
636 magnitude illustrate considerable uncertainty in
637 functional groups' parameters estimates (for
638 example, micro and macro invertebrate's biomass,
639 production and consumption). We strictly checked
640 for thermodynamic and ecological principles for
641 balancing a food web model (sensu Heymans and
642 others 2016). Moreover, we dealt with the uncer-
643 tainty associated with the model parameters esti-
644 mates via Monte Carlo statistical routine
645 (Steenbeek and others 2018). This procedure
646 ascertains important trophic interactions through
647 model fitted to time series data, which provides a
648 good idea of the range of outputs available based on
649 the uncertainty surrounding the input data, as seen



650 by the 5th and 95th percentile values plotted.
 651 Additionally, we evaluated the influence of tem-
 652 perature on functional group-specific consumption
 653 rates but not on functional groups' production rate
 654 and functional groups physiological adaptations.
 655 Marine vertebrates with slow growth, late matu-
 656 rity, and low annual fecundity, such as sea birds,
 657 sea turtles, and sharks, are expected to be evolu-
 658 tionarily less resilient to rapid ocean warming, al-
 659 though they have substantial adaptive plasticity
 660 (Sydeman and others 2015). Adaptation could be
 661 impeded if there were negative genetic correlations
 662 between performance in warmer conditions and
 663 changes in other environmental parameters
 664 (Munday and others 2013; Sunday and others
 665 2014). One of the model's assumption is that
 666 detritus produced into the system and not con-
 667 sumed by the detritivorous species is exported
 668 outside the reef ecosystem to the adjacent pelagic
 669 system. We believe that our assumption is valid:
 670 That is that unconsumed detritus is likely fre-
 671 quently exported from the reef, consistent with the
 672 reef's isolated oceanic location and frequent expo-
 673 sure to strong waves and currents (Pereira and
 674 others 2013, and Figure S1 in Supplementary
 675 Materials). An alternative hypothesis would be that
 676 at least some of the detritus is accumulated into the
 677 system, which could magnify the influence of
 678 detritus on the reef's food-web structure and
 679 function. If both scenarios with export and accu-
 680 mulation of detritus occurring in variable propor-
 681 tions in space and time, then we could expect
 682 differences in the structure and function of food
 683 webs that could translate into different changes in
 684 standing biomass. Although predicting winners and
 685 losers can be challenging (Libralato and others
 686 2015) such changes could favor the increase in
 687 biomass of lower trophic levels and detritus due to
 688 reduced energy transfer efficiencies to higher
 689 trophic levels (Ullah and others 2018).

690 Thus, our results can be considered conservative
 691 in the magnitude of the projected impacts on
 692 functional groups biomass dynamics but assertive
 693 in the direction of changes. Progress in the devel-
 694 opment of global species-specific datasets for envi-
 695 ronmental variables other than the temperature
 696 would enable more comprehensive investigations
 697 in future. Each of the assumptions explored here
 698 can be converted into testable hypotheses and then
 699 examined in model sensitivity analyses. It would
 700 provide insights into how much detail is needed
 701 and what can be ignored, reducing the uncertainty
 702 in the relationship between temperature and
 703 trophic interactions to predict the biological im-
 704 pacts of ocean warming.

CONCLUSIONS

706 Considering the projected decrease of up to 44% of
 707 standing biomass by 2100 under the high ocean
 708 warming scenario, we consider that ocean warming
 709 on tropical reef ecosystems will cause synchronous
 710 and severe changes in reef biodiversity, ecosystem
 711 structure and functioning. Our projections suggest
 712 that tropical reef ecosystems will be severely im-
 713 pacted by increasing temperatures through standing
 714 biomass declines, mainly of reef fish and inverte-
 715 brates, which are predicted to occur by the end of
 716 the twenty-first century both under the RCP 4.5
 717 and the RCP 8.5 scenarios. These changes will lead
 718 to a less productive and diverse ecosystem, poten-
 719 tially hampering the services provided by reef
 720 ecosystems worldwide. Delaying the crossing of this
 721 ecological reef state scenario may be possible but
 722 requires rapid reductions in greenhouse-gas emis-
 723 sions. Our results also highlight the urgency of
 724 including monitoring sites in tropical marine re-
 725 gions and investigating the potential of migration
 726 and adaptation in marine biota. Ocean acidifica-
 727 tion, disturbance in nutrient cycles, pollution, and
 728 fisheries are also important threats that could be
 729 further explored to improve predictions of the fu-
 730 ture of tropical reef ecosystems.

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 750
 751

DATA AVAILABILITY

753 The raw data and the R code for data analysis that
 754 support the findings of this study are freely avail-
 755 able in the GitHub repository: https://github.com/leomarameo7/Atoll_Rocas_project.
 756 Biological



757 parameters can be consulted in Fishbase website (h
758 ttps://www.fishbase.org) and AquaMaps (https://
759 www.aquamaps.org/). Ecopath model file is avail-
760 able on request to the corresponding author.
761

762 Declarations

763 Conflict of interests The authors declare
764 that they have no conflict of interests.

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