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Trophic interactions will expand geographically but be less intense as oceans warm

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Abstract

Interactions among species are likely to change geographically due to climate-driven species range shifts and in intensity due to physiological responses to increasing temperatures. Marine ectotherms experience temperatures closer to their upper thermal limits due to the paucity of temporary thermal refugia compared to those available to terrestrial organisms. Thermal limits of marine ectotherms also vary among species and trophic levels, making their trophic interactions more prone to changes as oceans warm. We assessed how temperature affects reef fish trophic interactions in the Western Atlantic and modeled projections of changes in fish occurrence, biomass, and feeding intensity across latitudes due to climate change. Under ocean warming, tropical reefs will experience diminished trophic interactions, particularly herbivory and invertivory, potentially reinforcing algal dominance in this region. Tropicalization events are more likely to occur in the northern hemisphere, where feeding by tropical herbivores is predicted to expand from the northern Caribbean to extratropical reefs. Conversely, feeding by omnivores is predicted to decrease in this area with minor increases in the Caribbean and southern Brazil. Feeding by invertivores declines across all latitudes in future predictions, jeopardizing a critical trophic link. Most changes are predicted to occur by 2050 and can significantly affect ecosystem functioning, causing dominance shifts and the rise of novel ecosystems.

KEYWORDS
Bayesian models, feeding pressure, future projections, latitudinal patterns, temperature, tropicalization, Western Atlantic

1 | INTRODUCTION

Tropical ecosystems commonly harbor higher diversity and more intense biotic interactions than extratropical regions (Longo et al., 2019; Roslin et al., 2017; Schemske et al., 2009). Global climate change is altering biodiversity patterns at an alarming pace, threatening not only species, but altering their interactions, which mediate critical ecosystem processes (IPPC et al., 2019; Romero et al., 2018). Predictions of shifts in biotic interactions under climate change are challenging and restricted to terrestrial ecosystems (Romero et al., 2018), but are critical to

inform how changes in biodiversity will scale up to affect ecosystem function.

Biotic interactions depend on species co-occurrence, and are influenced by temperature, trophic categories, abundance, the size of individuals, and environmental conditions, all of which can affect the physiology and ecological performance of species (Clarke & Johnston, 1999; Englund et al., 2011; Longo et al., 2014). Theory predicts that organisms reach their highest performance (e.g., feeding, growing, and reproducing) under an optimal range of temperature, but become less efficient when temperatures are above or below this optimal range (Poloczanska et al., 2013).

Increasing temperatures can enhance or reduce interactions rates and constrain or expand species' geographic distributions (Sunday et al., 2015). Tropical marine ectotherms are especially affected by increasing temperatures, because they live near the upper limit of their optimal temperature range (Pinsky et al., 2019) and have been moving poleward as temperatures warm. Tropical herbivorous reef fishes, for instance, are expanding their distribution and changing the ecosystem structure in extratropical reefs by feeding on and suppressing seaweeds, and by facilitating invasions by species that are more resistant to feeding by these herbivores (Vergés et al., 2019). Therefore, predicting shifts in biotic interactions due to ocean warming requires integrating information on species occurrence, including probabilities of range shifts, changes in abundance and interaction rates, and how these factors vary with temperature.

We combined projections of reef fish occurrence, biomass, and feeding pressure under future climate change scenarios (RCP8.5 scenario) to predict changes in distribution and intensity of trophic interactions on nearshore reefs in the Western Atlantic Ocean by 2050 and 2100, in comparison to current projections. Fishes are critical consumers in reef ecosystems, so we modeled three trophic categories comprising four families: (a) the herbivorous–detritivorous Acanthuridae and Labridae-Scarini, (b) the invertivorous Haemulidae, and (c) the omnivorous Sparidae. We reasoned that these trophic categories are among the most critical trophic interactions in reefs and might respond differently to warming because physiology and thermal tolerance varies among these groups (Longo et al., 2019). We used the differences between future and current projections to analyze the changes in geographic extension and intensity of trophic interactions under climate change. As mathematical modeling is getting more accurate and congruent for large spatial scales (Parmesan & Yohe, 2003), projections of future intensity and distribution of interactions can be useful tools to understand the impacts of climate change on ecosystem functioning.

2 | MATERIALS AND METHODS

To evaluate how trophic interactions will respond to increasing temperatures, we used reef fishes as models, data on their abundance and feeding behavior collected along 61° of latitude including both hemispheres in the Western Atlantic (see Longo et al., 2019), and the natural temperature gradients extending from tropical regions into both temperate regions (Spalding et al., 2007). Tropical areas occur between 23°N (Mexico) and 23°S (Brazil), with extratropical areas extending poleward from northern Mexico (>23°N), and from southeast Brazil (>23°S). The Western Atlantic has an interesting biogeographic history where the Caribbean province is the main center of biodiversity and the Amazon River acts as a biogeographic barrier between the Caribbean and the Brazilian province (Floeter et al., 2008). The long and continuous coastline, latitudinal pattern, and biodiversity gradient makes the Western Atlantic a good model to study the effects of climate change and tropicalization of

ecological interactions (Vergés, Steinberg, et al., 2014). Additionally, an extensive data set is available on reef fish-benthos trophic interactions, fish abundance, and fish biomass for 15 locations along the latitudinal gradient of the Western Atlantic between North Carolina, United States (34°N) and Santa Catarina, Brazil (27°S; Longo et al., 2019).

We used data on reef fish occurrence, biomass, and feeding pressure on shallow reefs distributed across 61° of latitude in the Western Atlantic (Longo et al., 2019; see Supplementary Materials 1.1 and 1.2). Species occurrence and biomass data were obtained from underwater visual census of fishes on replicated 20 × 2 m transects (Longo et al., 2019) and complemented with data from Floeter et al. (2008). Fish biomass was calculated by applying length–weight relationships available in the literature (Froese & Pauly, 2019; see details in Supplementary Material 1.2). Fish feeding pressure on the benthos (sensu Longo et al., 2019) is expressed as the product of the number of bites and the individual biomass of each fish (kg) in a 2 m^2 reef area during 10 min videos of the natural reef benthos (see Longo et al., 2014). Data were derived from 1,038 separate 10 min videos, with a mean of ~4 sites/location and ~17 videos per site for 15 locations scattered between Santa Catarina, Brazil (27°S) in the South and North Carolina, United States (34°N) in the North (Supplementary Material 1.2).

In this study, we selected four reef fish families: Acanthuridae (surgeonfishes), Labridae-Scarini (parrotfishes), Haemulidae (grunts) and Sparidae (porgies), due to their wide distribution, variety of trophic categories and functional importance in Atlantic reefs (Floeter et al., 2008; Longo et al., 2019). For each family, we selected species playing important functional roles in the studied areas (see details in Supplementary Material 1.1). Surgeonfishes and parrotfishes are herbivorous–detritivorous and responsible for the majority of trophic interactions on the benthos in the Western Atlantic (Longo et al., 2019). Haemulidae are invertivores and the intensity of their trophic interactions is homogeneous across latitudes in the Western Atlantic (Longo et al., 2019). Some Sparidae are omnivores and have greater affinity to colder waters in the Western Atlantic (e.g. genus *Diplodus*; Floeter et al., 2008), being more abundant in extratropical regions. Their feeding has a greater relative impact in temperate than in tropical areas (Longo et al., 2019), indicating that this family may be affected differently by climate change relative to others.

We used Bayesian hierarchical spatial models to predict, separately, the probability of occurrence, biomass, and fish feeding pressure independently for the four families combined and for each family under each scenario—current, 2050 and 2100, totalizing 45 models. The Bayesian approach provides better estimates of uncertainty when compared to traditional methods (frequentist methods; Fonseca et al., 2017) and includes data and model parameters as random variables providing a more realistic prediction (Fonseca et al., 2017). To calibrate each model, we selected eight environmental variables (bathymetry, rugosity, turbidity measured as diffuse attenuation coefficient, dissolved molecular oxygen, pH, primary productivity, sea surface salinity, and sea surface temperature) that can affect the occurrence and intensity of trophic interactions,

we then checked their correlation and colinearity (see details in Supplementary Materials 1.3 and 2.2).

Bayesian parameters and estimates were computed using the Integrated Laplace Approximations (INLA) approach and the package INLA (Rue et al., 2009) in the R software (Team, 2019). This procedure relates predictors as a condition for response variables (occurrence, biomass, and fish feeding pressure) and also implements the Stochastic Partial Differential Equations (SPDE) approach for the spatial effect (Lindgren & Rue, 2011; Martínez-Minayayet al., 2018; see details in Supplementary Material 1.4). The best-fitted models were selected based on Watanabe Information Criterion (WAIC; Watanabe, 2010) and the averaged logarithmic score of the Conditional Predictive Ordinate (LCPO; Roos & Held, 2011), also considering ecological validation of models (Supplementary Material 1.5). Based on the selected model, we projected occurrence, biomass and feeding pressure in the current scenario and used IPCC projections of sea surface temperature to project trophic interactions for 2050 and 2100 (see detail in Supplementary Material 1.6)—assuming no adaptation or acclimation during this period.

This process resulted in one spatial effect and one prediction for fish occurrence, biomass, and feeding pressure for each fish family in each scenario. Because fish feeding pressure is dependent on fish occurrence and influenced by fish biomass (Longo et al., 2014), we overlapped the spatial maps multiplying the maps from each family in each scenario (see details in Supplementary Material 1.6). This overlap aggregates the information of each model to avoid, for example, that a probability of feeding pressure is being predicted where fish do not occur (Kaschner et al., 2016). It generates a final map of probabilities of trophic interaction index for each family in each scenario (see details in Supplementary Materials 1.5 and 2.3). We extracted the values from the final maps using *raster* package (Hijmans, 2019) and plotted the differences between future and current scenarios using *ggplot2* package (Wickham, 2016), to visualize the changes in intensity and distribution of trophic interactions and compared scenarios (see details in Supplementary Material 1.6). The values in these graphs vary between −1 and 1, where −1 indicates the maximum decrease in the intensity of trophic interaction probabilities and 1 indicates the maximum increases.

To compare information about thermal ranges and optimal temperatures with our results from Bayesian models, we plotted the density of temperatures (frequency) for each scenario (Tyberghein et al., 2012) using *ggplot2* package (Wickham, 2016). We also obtained species-specific data of minimum, preferred minimum, preferred maximum, and maximum temperatures from Aquamaps (Kaschner et al., 2016; see Supplementary Material 1.1), assuming temperatures between preferred minimum and preferred maximum temperatures for each specie as the optimal range. Temperatures obtained for species within the same family were averaged to estimate the mean optimal value for each family, plotted with *ggplot2* package (Wickham, 2016) and used in the discussion, but not as model parameters. We acknowledge that thermal tolerance alone is not enough to explain performance (Brandl et al., 2020) and the potential constrains in Aquamaps assumptions to determine the thermal

tolerance envelopes (see details in Kaschner et al., 2016). However, optimal ranges obtained in this current approach corroborated relationships between feeding intensity and temperature of these trophic groups in the Atlantic (see appendix S3 in Longo et al., 2019). All scripts and codes are available in the GitHub repository (https://github.com/KellyInagaki/Inagaki_etal_trophicinteractions).

3 | RESULTS

Trophic interactions of herbivores, invertivores, and omnivores combined (all interactions) will expand poleward in the northern hemisphere but will decrease in intensity along most of the Western Atlantic (Figure 1a). Each trophic category displayed a variable response. Trophic interactions by herbivores were responsible for the tropicalization in the northern hemisphere, where we observed

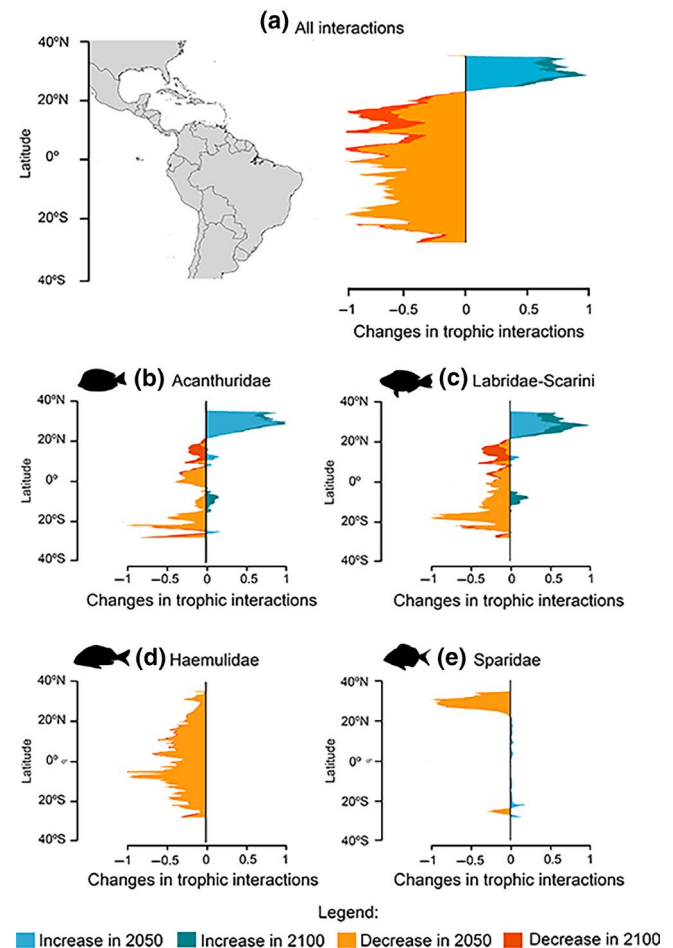Differences between future and current scenarios of trophic interactions

FIGURE 1 Changes in trophic interactions of reef fish families together (a) and one-by-one (b–e) projected for future dates. Scales vary from −1 to 1 unity of change, where −1 and 1 values represent the maximum values of change (decrease/increase, respectively). Blue colors present increase in trophic interactions and orange/red colors represent decrease in trophic interactions. Predicted changes for 2050 are superimposed on the predictions for 2100 to highlight the earlier changes

an abrupt increase of their interactions between the northern Caribbean and North Carolina (USA). Minor increases were observed in the Caribbean and in tropical and southeast Brazil, while interactions will decrease in intensity from Caribbean to southern Brazil (Figure 1b,c). Interactions by invertivores consistently decreased across all latitudes (Figure 1d) and interaction intensity of omnivores decreased from the northern Caribbean to the extratropics, with small increases in the Caribbean and in eastern and part of southern Brazil (Figure 1e). There was little variation between the 2050 and 2100 projections, but temperature was an important predictor in all models, while species occurrence was also influenced by bathymetry, turbidity (diffuse attenuation coefficient), pH, and rugosity. Although temperature, turbidity, and pH influenced fish biomass and feeding pressure under the current scenario, the relationship between response and independent variables varied among families (Supplementary Materials 2.1 and 2.2).

Temperatures are predicted to increase in the 2050 and 2100 scenarios, with the most prominent temperature for the present being about 27°C, while predictions for 2050 and 2100 are 28 and 31°C, respectively (Figure 2). Minimum temperatures for all three scenarios are about 16°C (Figure 2). Thermal ranges and optimal range temperatures varied among reef fish families. Although temperature range is within projected temperatures, the average temperature exceeds the optimal temperature range of some reef fish families. Surgeonfishes in the Acanthuridae family live between 18.2 and 32.2°C, with optimal temperature range between 24.5 and 28°C (Figure 2; Supplementary

Material 1.1). Parrotfishes Labridae-Scarini presented the narrowest thermal range, varying between 22 and 32.2°C, and having an optimal temperature range between 25.1 and 28°C. Haemulidae live between 21.6 and 32.3°C, and present an optimal temperature range of 25.2–28.1°C; and Sparidae have the widest thermal range, from 16.6 to 30.7°C, with an optimal temperature range between 22.5 and 27.2°C (Figure 2; Supplementary Material 1.1).

4 | DISCUSSION

We projected reef fish trophic interactions under climate change scenario in the South Western Atlantic Ocean and found that tropicalization of interactions is predicted to occur mainly in the northern hemisphere, but also in southern Brazil at a lower intensity. Trophic interactions will be less intense in tropical areas, with decreases varying among trophic categories of reef fishes. Most changes predicted in our projections will occur by 2050, potentially affecting ecosystem functioning and prompting the rise of novel ecosystems.

Temperature was an important factor in the projections and it strongly relates to fishes' physiology, thermal tolerance, and geographic distribution. In higher temperatures, ectothermic organisms, such as reef fishes, are expected to be more active and demand more energy, often resulting in higher feeding rates (Clarke & Johnston, 1999). However, feeding rates reach a peak and decrease above an optimal temperature as temperature becomes detrimental and exceeds the fish's thermal limits (Barneche et al., 2014; Englund et al., 2011). Because modern tropical fishes live closer to their upper thermal limits than extratropical fishes (Pinsky et al., 2019), most trophic interactions of fishes feeding on the benthos in their present ranges are likely to decline across latitudes as temperature increases (Figure 1). This was particularly true for herbivores (Acanthuridae, Labridae: Scarini) and invertivores (Haemulidae) that share similar ranges of optimal and maximum temperatures (Figure 2), and whose interactions tend to decline mostly in the tropics where future temperatures will exceed their optimal ranges. Trophic interactions by omnivores (Sparidae), which are currently more intense in extratropical regions of both hemispheres (Longo et al., 2019), are predicted to experience a severe decline in the northern Caribbean toward the extratropical area, where warming and tropicalization events will be more intense and exceed their optimal temperature range (Kaschner et al., 2016; Miller & Stillman, 2012; Supplementary Material 1.1; Table S1). Not only mean and maximum temperature, but also the frequency, duration, and intensity of extreme temperatures influence fish physiology (Barneche et al., 2014). Maximum temperatures predicted for 2050 (Figure 2), for instance, fall within the range of maximum temperature tolerated by the four families used in the projections and are above the current average temperature. Being above the average optimal range temperature for these groups may explain the decrease in trophic interactions, even though future temperatures are within the tolerance limits of these fishes.

Each trophic category has different behavior and physiology linked to their food sources and functional roles in the reefs (Ferreira
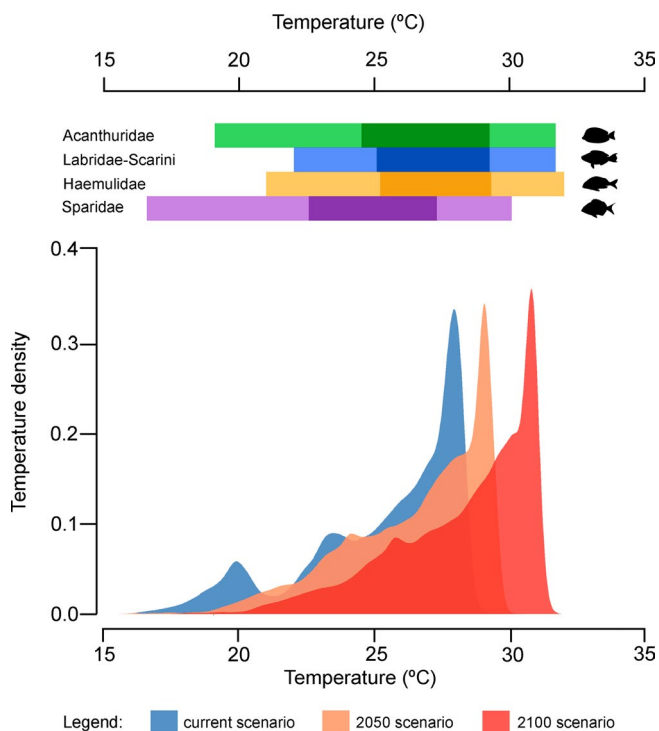

FIGURE 2 Thermal ranges of each family and densities of temperature in current, 2050, and 2100 scenarios. Above, colors represent different families and shadow boxes indicate the range of optimal temperature of each family (Kaschner et al., 2016). Below, colors represent different IPCC scenarios, according to the legend

et al., 2004). We expected that tropical herbivorous and invertivorous fishes (surgeonfishes and parrotfishes, and grunts) would increase their trophic interactions up to their optimal temperatures and migrate poleward, while omnivores (porgies) would maintain the intensity of their trophic interactions and likely expand poleward because increasing temperatures would make these habitats more suitable. However, trophic interactions by herbivorous fishes that are currently more intense in tropical regions are projected to decline by 2050 and 2100 (Figure 1b,c). A 3–4°C increase in temperature (IPPC et al., 2019), which should be achieved by 2100, will be sufficient to overtake the range of optimal temperature of most herbivores long enough to affect their physiology (Figure 2), potentially causing a decline of their feeding and likely their abundance.

Less herbivory in the Caribbean may reinforce the ongoing phase shift, favoring macroalgal abundance and negatively affecting coral health, diversity, and the associated ecological functions and ecological services, such as fishing and tourism (Figueira & Booth, 2010; Nakamura et al., 2013; Williams et al., 2016). Alternatively, in Brazilian reefs that are already dominated by algal turfs and macroalgae (Aued et al., 2018), declines in herbivory can maintain a stable state of algal dominance (Dell et al., 2016), likely sustained by a feedback cycle where less herbivory leads to more algae (Bellwood et al., 2012; Hoey & Bellwood, 2011). Declines in trophic interactions can lead tropical coral reefs in the Atlantic to a stable and resistant, but less diverse environment (Mumby, 2006; Mumby et al., 2005).

The poleward expansion of tropical herbivorous fishes that allows extratropical ecosystems to become more similar to tropical ones (Stuart-Smith et al., 2015) can cause phase shifts from algal-dominated to coral- or turf-dominated reefs due to increase in algal consumption, as already recorded in Australia and Japan (Vergés et al., 2016; Vergés, Tomas, et al., 2014; Yamano et al., 2011). We expected that both hemispheres in the Atlantic could face tropicalization events, but the projections showed a much more pronounced tropicalization in the northern hemisphere. This was possibly because ocean warming will be more intense in this region (Pinsky et al., 2019) due to the intensification of warm currents flowing northwards from the Caribbean (Kumagai et al., 2018), and leading to abrupt shifts in regional reef ecosystem as occurred in the northern Caribbean (Figure 1a–c). While in the southern hemisphere, tropicalization is projected to occur less intensely through the increase in interactions by herbivorous acanthurids and scarinis on reefs between São Paulo and Santa Catarina (24°S and 26°S), possibly related to a cold water current flowing northwards from southern Brazil, which could soften warming effects in this region.

The overall decline of trophic interactions by invertivores indicates that this group will be more sensitive to future temperatures, which will exceed their range of optimal temperature (Figures 1d and 2). Invertivores are critical trophic links between low level consumers (invertebrates) and higher trophic levels (predatory fish; Kramer et al., 2015). The suppression of this link in a food web may not necessarily cause severe damage to the trophic structure of the system (Solé & Montoya, 2001), but it can affect community structure and split the food web into smaller and less connected compartments,

jeopardizing community stability (Solé & Montoya, 2001). These changes may diminish the functional redundancy of species, making the community food web less complex, less resilient, and more prone to extinctions (Solé & Montoya, 2001).

Predicted trophic interactions by omnivores changed modestly across most of the Western Atlantic, but it had a steep decline from the northern Caribbean poleward, likely due to the higher warming expected in this area resulting from northbound warm Caribbean currents (Philander, 2001; Rocha et al., 2008). In contrast to our expectations, we observed a modest increase in the trophic interactions of omnivores in some tropical areas. Omnivores have been shown to alter diet according to temperature, shifting from a predominantly animal-based diet under cold waters to a plant-based diet in warmer waters (Behrens & Lafferty, 2007; Zhang et al., 2020). Therefore, if trophic interactions by omnivores increase substantially in the tropics and they consume primarily macroalgae, then omnivore feeding in tropical regions could lessen the effects of decreased feeding by herbivores. Additionally, once invertivores are feeding less in the tropics, populations of herbivorous invertebrates (mesograzers) could increase and generate considerable feeding on algae (Davenport & Anderson, 2007; Duffy & Hay, 2000; Lewis & Anderson, 2012). The combined effects of greater trophic interactions by omnivores (assuming a substantial increase in feeding intensity) and prey release of grazing invertebrates (caused by the reduced feeding of invertivorous fishes) might assuage the impacts of the projected decline in herbivory.

Alternatively, organisms could also acclimate and adapt to new conditions (Narum et al., 2013). Some corals, for instance, have adapted to the higher temperatures and bleaching events that have increased in the past 20 years (Sully et al., 2019). Similarly, experiments have demonstrated that fishes can acclimate to warmer waters (Donelson et al., 2011), even if it results in lower performance (Munday, 2014). Even though our projections indicated decreases in trophic interactions, it did not account for the possibility of organisms acclimating and adapting, which could lead to unknown responses to these environmental changes. Acclimating and adapting rates are important but difficult to include into the model projections because they would require many variables accounting for phylogeny, life-history traits, and fish biology and ocean warming, potentially leading to confused results (Bruno et al., 2018). Because the ocean is a tridimensional space and warming intensity will vary with depth, populations could also adjust their depth ranges toward more favorable thermal conditions modulating potential latitudinal shifts (Bates et al., 2014). Despite including bathymetry as a model parameter, our projections do not include these potential depth adjustments. Additionally, we did not account for changes in food sources, but some groups (algae, crustaceans, arthropods, and mollusks) are prone to be affected by ocean warming in variable directions (Pinsky et al., 2019) including changes in algal palatability to herbivores (Poore et al., 2013). Temperature changes could either benefit consumers and attenuate the impacts of temperature or jeopardize them even more, depending on whether resources will be abundant, scarce, or change in nutritional value due to future conditions.

Climate warming can dramatically impact not only consumer distribution (Romero et al., 2018; Vergés et al., 2016, 2019; Vergés, Steinberg, et al., 2014) but also trophic interactions of critical consumers in reef ecosystems. While the tropics will experience diminished trophic interactions possibly reinforcing dominance shifts that are already underway, tropicalization events are more likely to occur in the northern hemisphere, possibly creating novel dynamics in extratropical reef ecosystems. Predicting how climate change will affect trophic interactions may help predict and adapt to ecosystem shifts and changes in the services they provide.

AUTHOR CONTRIBUTION

G.O.L. conceived the idea and developed it with all co-authors; G.O.L., M.E.H., and S.R.F. provided the database; M.G.P. and K.Y.I. performed the statistical analyses; K.Y.I. and G.O.L. drafted the manuscript with inputs from all co-authors; K.Y.I. designed and created the figures. All authors contributed with text revision and the final format of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study, scripts, and codes are available in the GitHub repository (https://github.com/Kelly Inagaki/Inagaki_etal_trophicinteractions).

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SUPPORTING INFORMATION

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