

Trophic interactions across 61 degrees of latitude in the Western Atlantic

Guilherme O. Longo^{1,2,*}  | Mark E. Hay²  | Carlos E. L. Ferreira³  | Sergio R. Floeter¹ 

¹Marine Macroecology and Biogeography Laboratory, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, Brazil

²School of Biological Sciences and Aquatic Chemical Ecology Center, Georgia Institute of Technology, Atlanta, Georgia

³Reef Systems Ecology and Conservation Laboratory, Universidade Federal Fluminense, Niterói, Brazil

Correspondence

Guilherme O. Longo, Marine Ecology Laboratory, Department of Oceanography and Limnology, Universidade Federal do Rio Grande do Norte, Av. Via Costeira S/N, Natal, RN 59014-002, Brazil.
Email: guilherme.o.longo@gmail.com

Funding information

Teasley Endowment to MEH; Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: Jovem Pesquisadores #571295/2008-8 to SRF (PI), SISBIOTA #563276/2010-0 to SRF (PI) and Science Without borders to GOL; Serrapilheira Institute, Grant/Award Number: Serra-1708-15364 to GOL(PI); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: PhD Scholarship to GOL; National Council for Scientific and Technological Development; Brazilian Government

Editor: Amanda Bates

Abstract

Aim: The aim was to evaluate the hypothesis that biotic interactions are more intense in the tropics using reef fishes (from both functional and taxonomic perspectives), the crucial consumers on most reefs.

Location: Fifteen reef locations between 34°N and 27°S in the Western Atlantic.

Time period: 2011–2014.

Major taxa studied: Reef fishes.

Methods: We quantified fish feeding pressure on the benthos across 61° of latitude in the Western Atlantic via 1,038 10 min videos of 2 m² reef areas, where every fish feeding on the benthos was identified, had its total length estimated, and the number of bites on the reef substratum was counted. Fish were assigned to functional groups based on diet and feeding modes. Benthic cover estimates were also obtained through visual assessments from the videos.

Results: We documented feeding rates that were 2- to 22-fold higher in tropical versus extratropical locations. This pattern was driven mainly by an interaction between fish functional group and temperature, with herbivory dominating in tropical regions (c. 20-fold higher), shifting to omnivory in temperate regions of both Hemispheres. Feeding by invertivores was common across all latitudes. Consumer species composition differed between Northern and Southern Hemispheres, but functional groups were similar, and their feeding changed in a similar manner with temperature regardless of Hemisphere.

Main conclusions: Our results support the hypothesis that biotic interactions, especially plant-herbivore interactions, are more intense in the tropics. These findings help to explain the lower palatability of tropical versus extratropical seaweeds and suggest that herbivory is favoured in warm conditions but omnivory in colder waters. The functional approach indicated that factors associated with latitude or temperature have selected for similar feeding functions among the different species occupying these geographical regions. Understanding the shifting trophic interactions across latitudes might help to predict the impacts of global changes on ecosystem function as tropical species move polewards and contact temperate systems.

KEYWORDS

biotic interactions, fish–benthos interaction, herbivory, latitudinal gradient, marine biogeography, reef fish

*Present address: Marine Ecology Laboratory, Department of Oceanography and Limnology, Universidade Federal do Rio Grande do Norte, Av. Via Costeira S/N, Natal, RN 59014-002, Brazil.

1 | INTRODUCTION

Trophic interactions commonly determine ecosystem structure and function, but consumers are being depleted worldwide, producing dramatic changes in processes as diverse as biogeochemical cycles, biodiversity maintenance, carbon sequestration, disease dynamics and the stability of ecosystem services (Estes et al., 2011; McCauley et al., 2015; Ripple et al., 2014). To enhance our understanding of trophic interactions, their consequences and drivers, it is necessary to combine macroecology and biogeography; this may be achieved via comparisons across large geographical scales using consistent methods (Pennings & Silliman, 2005; Pennings et al., 2009; Roslin et al., 2017).

There is a common perception that biotic interactions are intense in the tropics and decrease towards higher latitudes (Freestone, Osman, Ruiz, & Torchin, 2011; Roslin et al., 2017; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009), but this notion has been challenged by meta-analyses that question the occurrence of higher herbivory in the tropics (Moles, Bonser, Poore, Wallis, & Foley, 2011; Poore et al., 2012). In contrast to these meta-analyses, several direct measures of herbivory across latitudes have indicated higher rates of herbivory at lower latitudes (Bennett & Bellwood, 2011; Longo, Ferreira, & Floeter, 2014; Pennings et al., 2009), in addition to increased defenses and lower palatability among more tropical versus more temperate plants (Bolser & Hay, 1996; Coley & Aide, 1991; Morrison & Hay, 2012; Siska, Pennings, Buck, & Hanisak, 2002). These conflicting findings have fuelled debate, leading some authors to address the notion of greater herbivory in the tropics as a “zombie hypothesis” that persists despite adequate data to refute it (Moles & Ollerton, 2016). In contrast, a recent review identifies methodological flaws in previous studies of biotic interactions across latitudes, particularly regarding the latitudinal herbivory–defense hypothesis, and suggests that more uniform approaches are needed (Anstett, Nunes, Baskett, & Kotanen, 2016).

The controversy and the apparently divergent findings regarding latitudinal trends in trophic interactions might be related to the following difficulties: consistently measuring feeding pressures across large spatial scales; measuring actual feeding versus indicators of feeding (e.g., holes in leaves) that may not be reliable (e.g., if entire leaves or plants are consumed, evidence is lost); adequately resolving the relative importance of the different consumers involved; or assessing rates of consumption relative to rates of replenishment owing to productivity. The assessment of feeding by reef fishes avoids many of these issues. Fish taxonomy and biogeography are well resolved, their trophic interactions, particularly herbivory, are known and crucial to the function of reef ecosystems, and their feeding can be well quantified (Floeter et al., 2008; Hay, 1981; Poore et al., 2012), allowing estimates of consumption rates per area of reef matrix (Longo et al., 2014) across latitudes where annual net primary productivity varies minimally (Behrenfeld et al., 2001; Steinarcher et al., 2010), diminishing the need to correct herbivory for differences in production.

Fishes, like insects and other ectothermic herbivores, have a thermo-dependent metabolism (Clarke & Johnston, 1999); therefore, their feeding may be expected to vary with temperature. Grazing rates of herbivorous fishes at a site are positively correlated with water temperature (Carpenter, 1986; Ferreira, Peret, & Coutinho, 1998), and recent increases in the temperatures of western boundary currents have resulted in tropical herbivorous fishes extending their range polewards, resulting in increased herbivory and fundamental alterations in community structure and ecosystem function in some regions (Vergés et al., 2014, 2016). Reef fishes also use a wide variety of feeding modes, diets and nutritional strategies (Bellwood, Hoey, Bellwood, & Goatley, 2014; Clements, German, Piché, Tribollet, & Choat, 2017; Clements, Raubenheimer, & Choat, 2009; Harmelin-Vivien, 2002), and fishes of different trophic categories can exert different feeding pressure on the benthos. Thus, reef fishes are a good model to investigate large-scale variation in trophic interactions and how these may vary with latitude, temperature and feeding guilds.

We addressed latitudinal variation in feeding by reef fishes in terms of intensity and functional and taxonomic composition in 15 locations distributed between latitudes 34°N and 27°S in the Western Atlantic (mid-Atlantic of the U.S.A. to southern Brazil). We evaluated latitudinal gradients in biotic interactions by assessing size-scaled bite rates per area of reef matrix as a metric of consumption by reef fishes (total fish feeding pressure; *sensu* Longo et al., 2014). We hypothesized that because fish have a thermo-dependent metabolism, feeding pressure would be higher in warmer tropical regions than in cooler extratropical regions, a response that would be symmetrical in both Hemispheres. Apart from temperature, the abundance of benthic foods and the identity of feeding fishes could be important drivers. Additionally, if the cost-benefit ratio of some feeding strategies (herbivory on relatively lower-quality foods) varies more with temperature than other strategies (invertivory on relatively higher quality foods), then we anticipated seeing different latitudinal patterns in feeding rates on these differing foods (Harmelin-Vivien, 2002) and that this should occur in both Hemispheres. Our goal was to describe and test the notion of latitudinal trends in biotic interactions from the functional and taxonomic perspectives in the context of ecological drivers and the biogeography of reef fishes, the crucial consumers on most reefs.

2 | MATERIALS AND METHODS

2.1 | Field procedures

We assessed fish feeding pressure on the benthos in 15 locations across 61° of latitude (from 34°N to 27°S) comprising tropical and extratropical sites in both Hemispheres of the Western Atlantic (Figure 1; see Supporting Information Appendix S1 Table S1.1). All fieldwork was conducted during the summer of each Hemisphere between 2011 and 2014. At each of the 15 locations, we sampled

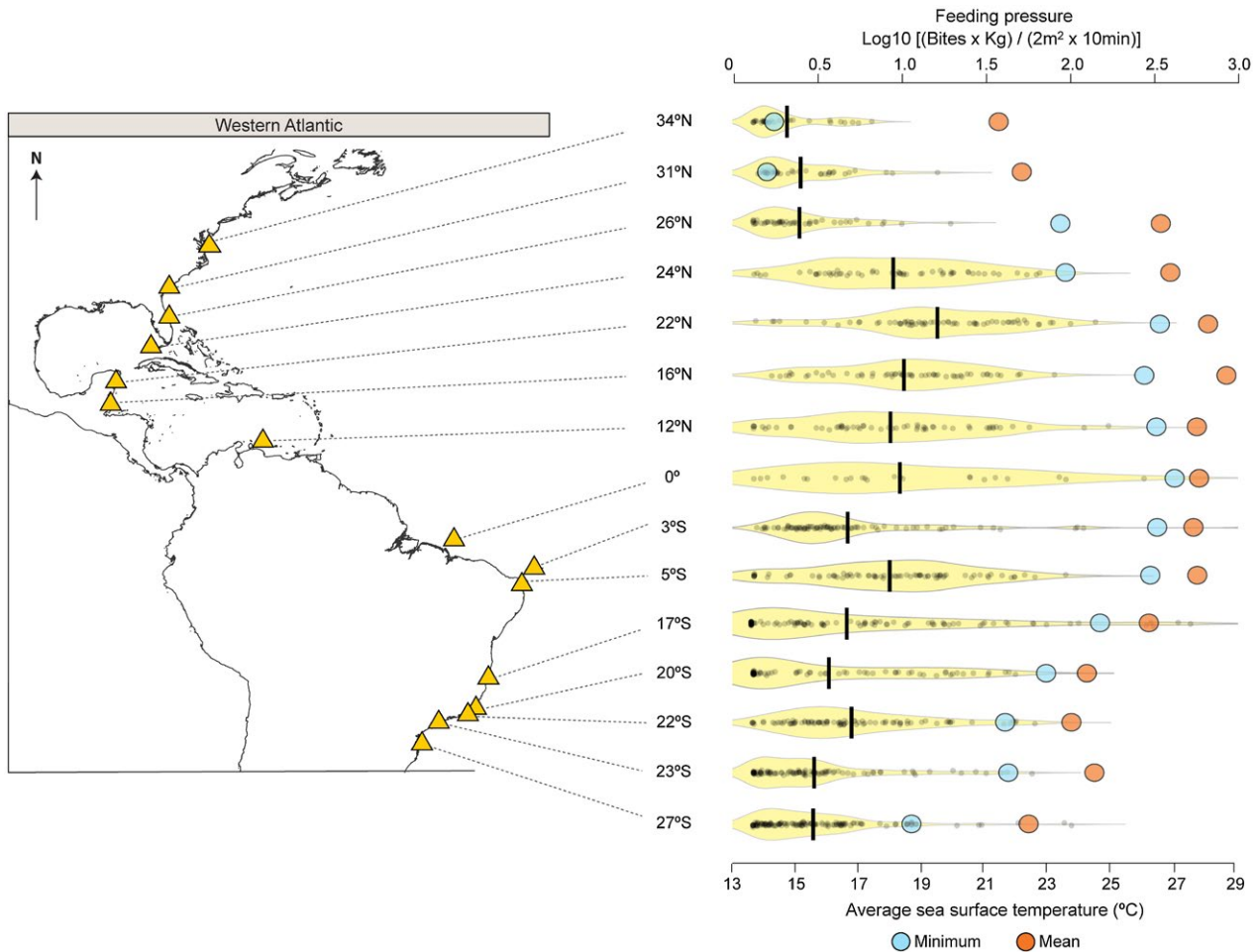


FIGURE 1 Latitudinal trend of benthic fish feeding pressure (logarithmic scale) in the Western Atlantic and its relationship to average minimum and mean sea surface temperature. Shapes represent the density of data points (i.e., thicker areas indicate a higher density of points). Black vertical lines indicate the mean feeding pressure [Colour figure can be viewed at wileyonlinelibrary.com]

between two and six hard-substrate sites separated by 0.5–90 km and at depths ranging from 1 to 25 m (but most in the 3–12 m range). At each site, we videoed replicated 2 m × 1 m areas positioned haphazardly on the reefs (5–40 samples per site) and separated from its nearest neighbour by 5–10 m. We evaluated 1,038 10 min videos, with a mean of c. 17 videos per site and approximately four sites per location (Supporting Information Appendix S1 Table S1.1). In each video, every fish feeding on the benthos was identified and had its total length estimated, and the number of bites on the reef substratum was counted (Longo et al., 2014). Feeding pressure was estimated as the product of the number of bites taken and the body mass (in kilograms) of the fish, obtained through length–weight relationships from the literature (Froese & Pauly, 2016). The inclusion of fish biomass accounts for body size variation, per unit time and area [(Bites × kg)/(2 m² × 10 min)]. Benthic cover estimates for each 2 m² area videoed were obtained through visual assessments from the videos in association with five detailed pictures of the videoed area. This strategy allowed us to assess benthic cover in detail, factoring out the aspect issue of the video and serving as a calibration for the estimates for the videoed area. Given that the lack of resolution

could be a problem for these estimates, the substratum of the recorded area was classified in broad and identifiable groups, such as algal turf, upright macroalgae, crustose coralline algae, scleractinian corals, other anthozoans, sponges, sand and rubble, or other. The percentage cover of each category was estimated in classes of 5%.

Reef fishes were assigned to functional groups based on diet and feeding modes (*sensu* Ferreira, Floeter, Gasparini, Ferreira, & Joyeux, 2004; Longo et al., 2014; Supporting Information Appendix S1 Table S1.2). Fishes that feed on macroalgae, filamentous algae and associated detritus and microorganisms were categorized as “herbivores” even in the cases when the species ingests algae but most of its nutrition comes from detritus, cyanobacteria or other autotrophic organisms (Clements et al., 2017, 2009). Herbivores were separated into functional groups based on feeding modes and behaviour (scrapers, excavators, fine browsers, rough browsers and territorial herbivores; see Longo et al., 2014 for a detailed definition of each group). Invertivores were separated into those feeding on mobile invertebrates (e.g., crustaceans or molluscs; Haemulidae) or on sessile invertebrates (e.g., corals, gorgonians or sponges; Chaetodontidae). Species with diversified diets, including plankton, benthic animals

Parametric terms	Estimates	<i>t</i>	<i>p</i> -value	Adjusted R^2	Deviance explained (%)
Intercept	0.34	7.83	<0.001	0.64	64.7
Smooth terms	edf	<i>F</i>	<i>p</i> -value		
Fish	5.69	8.31	<0.001		
Temperature	8.40	4.03	<0.001		
Fish × Temperature	14.01	7.77	<0.001		

Note. In this table, “Fish” is an abbreviation for composition of fish functional groupings. Abbreviation: edf = estimated degrees of freedom.

and plants, were grouped as omnivores (Supporting Information Appendix S1 Table S1.2).

2.2 | Data analyses

Given that mass-standardized bites and non-mass-standardized bite rates were correlated ($r = 0.75$), all analyses were based on mass-standardized bites (feeding pressure), because this allows a better comparison within individuals of the same species and among different functional groups (Longo et al., 2014; see Supporting Information Appendix S1 Figure S1.1). A linear mixed effect model was used to evaluate whether the pattern of total feeding pressure was symmetrical between Northern and Southern Hemispheres. Feeding pressure (response variable) was modelled as a function of absolute latitude and Hemisphere (predictors), allowing for interactions and with sites within locations as a random factor to account for the hierarchical sampling design. Generalized additive mixed models (GAMMs) assessed factors explaining the variation in feeding pressure across locations. Feeding pressure (response variable) was modelled as a function of mean sea surface temperature, depth, benthic cover and the composition of fish functional groups (explanatory variables). Average mean sea surface temperatures were obtained for each location from the online Bio-ORACLE database (2005–2010; c. 9 km spatial resolution; Tyberghein et al., 2012) using the bilinear method with the “raster” package (Hijmans & vanEtten, 2012) in R software (R Development Core Team, 2016). Separate principal components analyses (PCAs) were performed on benthic community composition and on the composition of fish functional groups feeding. The principal component 1 (PC1) obtained from each of these analyses were included as explanatory variables in the model (see Supporting Information Appendix S2). Sites within locations were included in the model as a random factor to account for the hierarchical sampling design. The best-fitted model was obtained through a forward selection procedure, by building models with one single term at a time and comparing the percentage of deviance explained by each variable alone, followed by models that combined the most explanatory variables and accounted for their interaction (see Supporting Information Appendix S3). We also used GAMMs to assess the effect of temperature (predictor) on feeding pressure by each functional group (response variable), accounting for the hierarchical sampling design as described above (see Supporting Information Appendix

TABLE 1 Summary of the selected general additive mixed model (GAMM) relating the variation in total feeding pressure along the studied locations and explanatory variables (mean sea surface temperature, benthic cover and composition of fish functional groupings; see Supporting Information Appendix S2 and S3)

S3). Compositional changes in feeding pressure across locations, from both the functional and the taxonomic perspectives, were evaluated using cluster analyses [Bray–Curtis similarity; unweighted pair-group method using arithmetic averages (UPGMA)] with a profile similarity analysis to evaluate the significance of the observed groups (SIMPROF; Clarke, Somerfield, & Gorley, 2008). A distance-based linear model was used to assess the effect of temperature on the composition of feeding pressure by functional group across latitudes. Data analyses were performed in R software (R Development Core Team, 2016) using the packages “FactoMinR” (Le, Josse, & Husson, 2008), “gamm4” (Wood & Scheipl, 2013), “yarr” (Phillips, 2016) “lme4” (Bates, Maechler, Bolker, & Walker, 2015) and “vegan” (Oksanen et al., 2018).

3 | RESULTS

Fish feeding pressure on the benthos was variable, but was 2- to 22-fold higher in tropical (24°N–22°S) than in extratropical reefs in both the Northern (24–34°N) and Southern (23–27°S) Hemispheres (Figure 1). Mean feeding pressure in tropical areas varied from 10 to 22 [(bites × kg)/(2 m² × 10 min)], whereas in extratropical areas it varied from c. 1 to 6 [(bites × kg)/(2 m² × 10 min)] (Supporting Information Appendix S1 Figure S1.1). Total feeding pressure was negatively affected by latitude (linear mixed effect model; estimate = −0.12, $t = -3.63$, $p < 0.001$) and varied between the Hemispheres (estimate = −2.54, $t = -2.95$, $p = 0.003$), but with no interaction between them (estimate = −0.06, $t = 1.59$, $p = 0.112$). This indicates that feeding pressure decreases with increasing latitudes in both Hemispheres, but the magnitude of the decrease is variable between Hemispheres. Indeed, feeding pressure declined more steeply in the Northern (26–31°N) versus the Southern Hemisphere, following the more pronounced decline in minimum temperatures between latitudes 26 and 31°N (minimum average temperature 24 and 14°C, respectively). About 65% of the variation in mean feeding pressure was explained by an interaction between temperature and the composition of fish functional groups feeding on the benthos (Table 1). Benthic cover (within the videoed areas) explained little of the variation in feeding pressure and was excluded from the best-fitted model (see Supporting Information Appendix S3). Scraping herbivores, which remove small amounts of reef substratum when

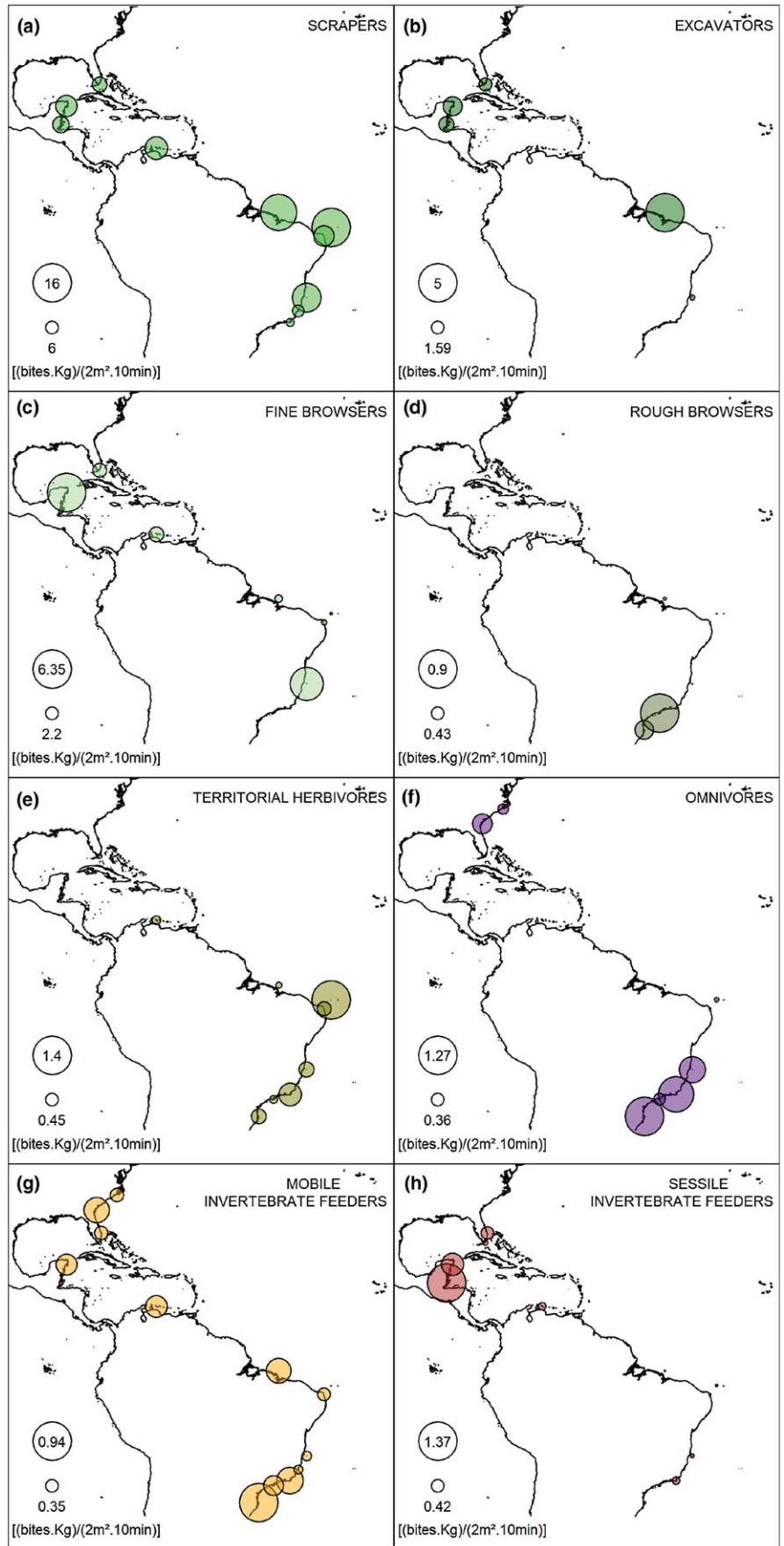


FIGURE 2 Benthic feeding pressure by reef fish functional groups: (a) scrapers, (b) excavators, (c) fine browsers, (d) rough browsers, (e) territorial herbivores, (f) omnivores, (g) mobile invertebrate feeders, and (h) sessile invertebrate feeders. Indications of scales are in the bottom left corner of each panel [Colour figure can be viewed at wileyonlinelibrary.com]

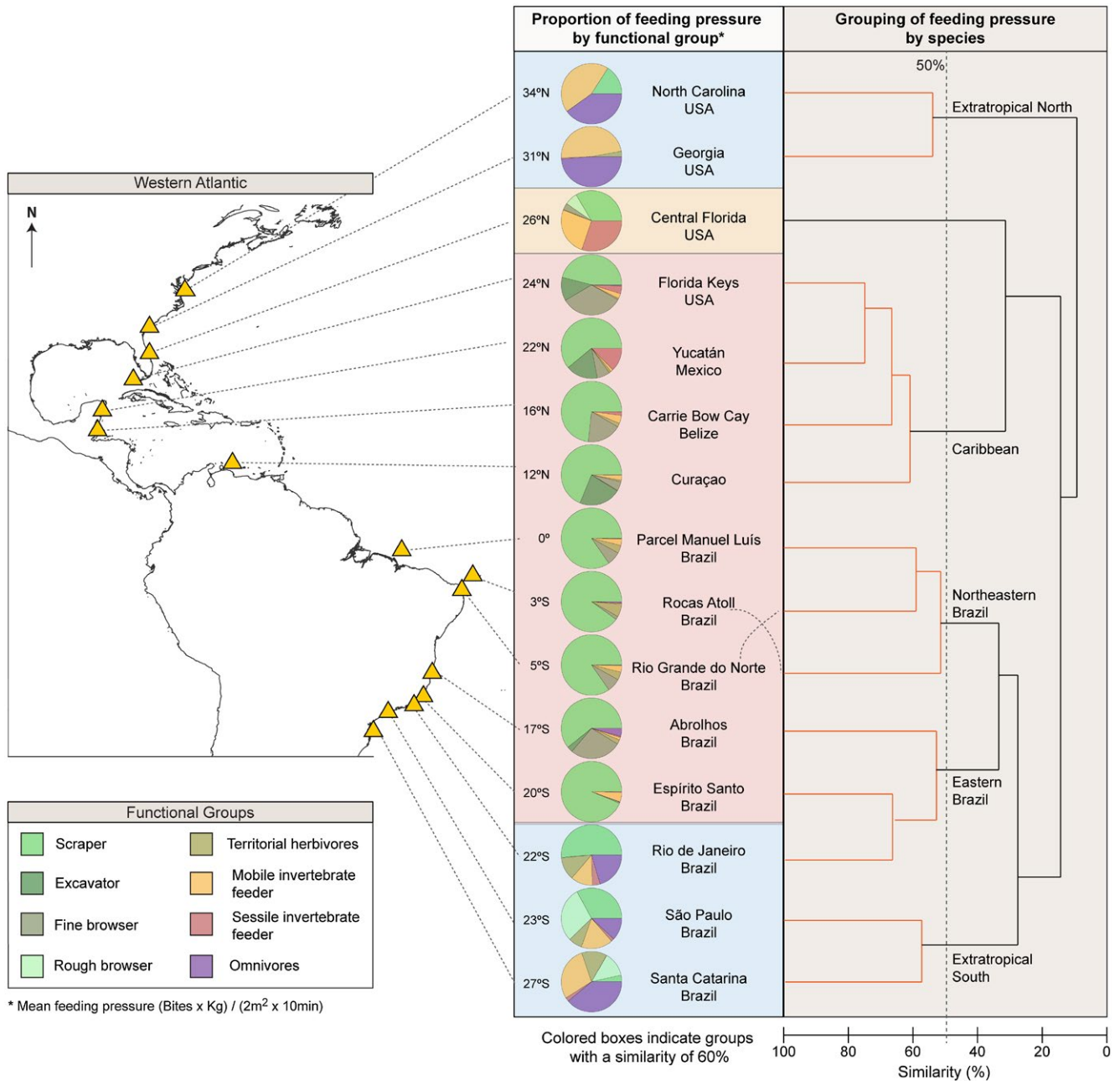


FIGURE 3 The composition of reef fish feeding pressure by functional group, and a cluster analysis of feeding pressure composition by species [Bray–Curtis; unweighted pair-group method using arithmetic averages (UPGMA)]. Similar-coloured boxes around the pie charts indicate locations showing 60% similarity when analysed by functional group (Bray–Curtis; UPGMA; Supporting Information Appendix S1 Figure S3). The dendrogram on the right depicts results from analyses using species (instead of functional groups); clusters in red represent those with significant results in the profile similarity analysis (SIMPROF test) to evaluate the significance of the observed groups; the grey dashed line indicates clusters with 50% similarity. Note the dashed lines indicating a shift in the relationship between the pie charts and cluster branch for Rocas Atoll (3°S) and Rio Grande do Norte (5°S) [Colour figure can be viewed at wileyonlinelibrary.com]

feeding on macroalgae or the epilithic algal matrix (Longo et al., 2014), presented the highest correlation with the principal component that represented the composition of fish functional group in the model (76%), indicating that much of the highest feeding pressure in tropical areas was attributable to scrapers (see Supporting Information Appendix S2). This was corroborated by modelling the feeding pressure by scrapers as a function of temperature alone. This model explained 26% of the deviance and indicated a positive

relationship between feeding pressure by scrapers and temperature (see Supporting Information Appendix S3).

Feeding pressure from herbivores in the tropics (24°N–20°S) was 10- to 25-fold higher than from all the other functional groups combined; this was not the case in extratropical areas (Supporting Information Appendix S1 Figure S1.2). Among the herbivorous groups, feeding by scrapers dominated, particularly in the tropical regions (Figure 2), but there was no clear latitudinal trend for

excavating herbivores (which remove considerable amounts of reef substrata while feeding) and fine browsers (which crop small pieces of algae). Although feeding pressure by scrapers, excavators and fine browsers was variable, it increased with temperature (see Supporting Information Appendix S3). Feeding pressure of rough browsers (which crop large pieces of algae) and omnivores

was mostly recorded in extratropical reefs and tended to decrease with higher temperatures (Figure 2; see Supporting Information Appendix S3). Feeding by territorial herbivores (which farm, defend and feed on the epilithic algal matrix within a territory) was higher along the Brazilian coast in comparison to the Caribbean. Feeding by consumers of mobile invertebrates (which target mostly crustaceans

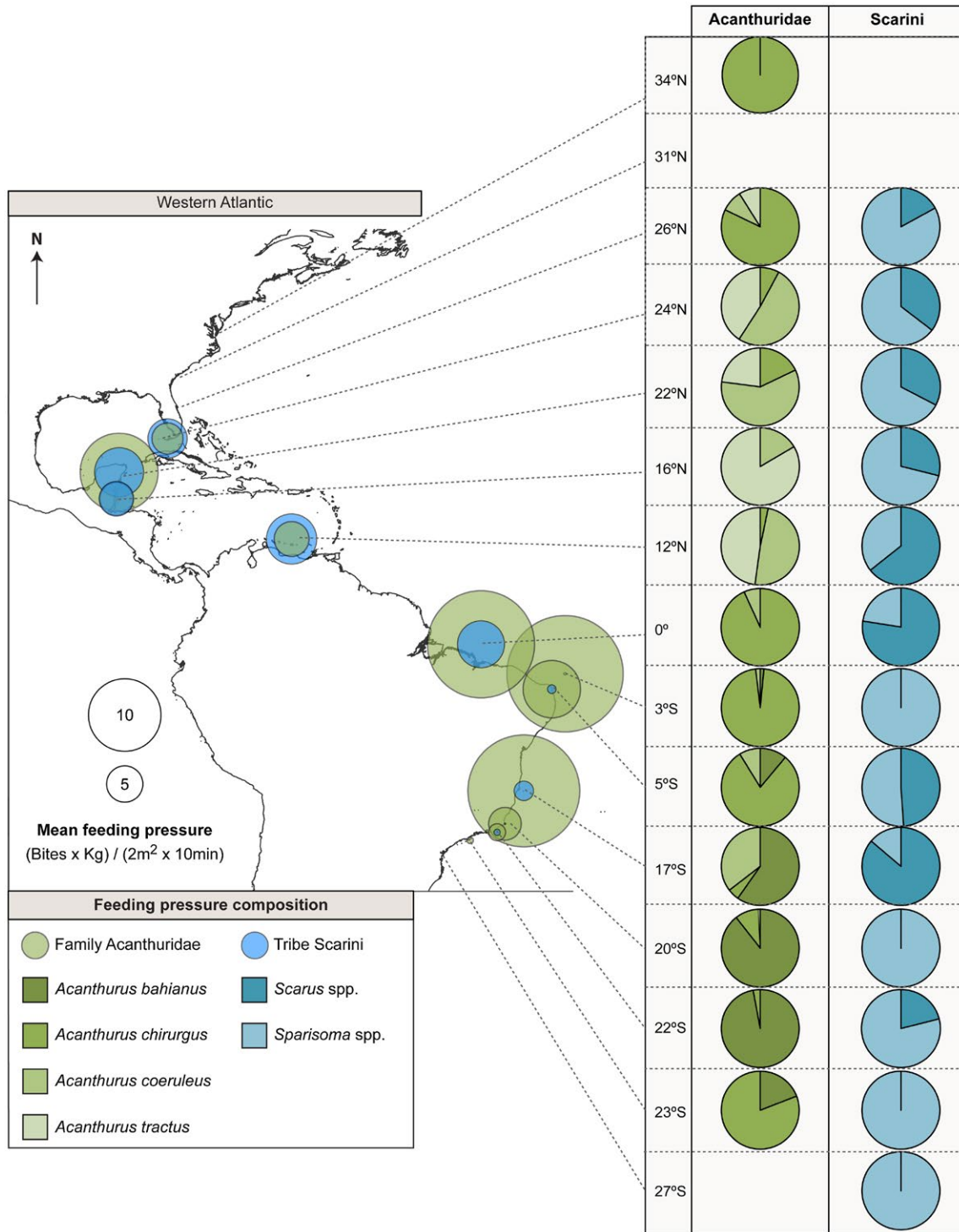


FIGURE 4 Feeding pressure of the two most representative herbivorous groups in the Western Atlantic (the family Acanthuridae and the Tribe Scarini). Pie charts on the right indicate relative feeding pressure for species or genera in that group. The absence of pie charts indicates that the group was not recorded in that location [Colour figure can be viewed at wileyonlinelibrary.com]

and worms) was similar throughout the latitudinal range; and the contribution of sessile invertebrate feeders (which target cnidarians and sponges) was higher in the Caribbean (Figure 2).

The composition of feeding pressure by functional groups varied with latitude, particularly between tropical and extratropical areas. Temperature explained 56% of the variation (distance-based linear model; pseudo- $F = 16.42$; $p = 0.001$), and the cluster analysis revealed three different groups: tropical reefs (24°N–20°S), extratropical reefs (34 and 31°N and 22–27°S) and Central Florida (26°N), which clustered more closely with the tropical reefs despite being outside the tropics (Figure 3; Supporting Information Appendix S1 Figure S1.3). Therefore, the composition of feeding pressure by functional group was similar within regions having comparable temperature conditions, irrespective of their biogeographical history or geographical distance. In contrast, the cluster analysis on feeding pressure by species (Figure 3) revealed six different groups with $\geq 50\%$ similarity: extratropical reefs of the Northern Hemisphere (34 and 31°N), Central Florida (26°N), Caribbean reefs (24–12°N), Northeastern Brazil (0–5°S), Eastern Brazil (17–22°N) and extratropical reefs of the Southern Hemisphere (23 and 27°S).

The combined results from the cluster analyses on feeding pressure by functional groups and species indicate that within the tropical region of both Hemispheres, the same function could be performed by different species (Figure 3). For example, some species from both the Acanthuridae family and the Labridae family, Tribe Scarini, can be classified as scrapers (see Longo et al., 2014). However, feeding pressure by scrapers in the Brazilian province was mostly represented by Acanthuridae, whereas the scrapers in the Caribbean were mostly Scarini (Figure 4). Within Acanthuridae, the sister species pair *Acanthurus tractus* in the Northern Hemisphere and *Acanthurus bahianus* in the Southern Hemisphere were frequently among the most actively feeding species along with *Acanthurus chirurgus* and *Acanthurus coeruleus*, which were common to both Hemispheres. Within Scarini, feeding pressure in most sites was dominated by *Sparisoma* spp. except for Curaçao (12°N), Parcel do Manoel Luis (0°) and Abrolhos (17°S), where *Scarus* spp. prevailed. Likewise, feeding pressure by omnivores in the extratropical regions of both Hemispheres was performed by different species within the same genus (*Diplodus*), with *Diplodus holbrooki* occurring in the Northern Hemisphere and *Diplodus argenteus* in the Southern Hemisphere.

4 | DISCUSSION

We documented the latitudinal variation in the intensity of feeding pressure and remarkable compositional changes in terms of fish functional groups and species across 61° of latitude in the Western Atlantic. We found a higher intensity of biotic interaction in the tropics (Roslin et al., 2017; Schemske et al., 2009), especially herbivory, and documented how feeding by different functional groups varies with latitude. Human impacts, such as overfishing, are probably altering the magnitude and variation of feeding pressures we measured, but despite this interference,

which is high in the tropics and often suppresses herbivory (Jackson, Donovan, Cramer, & Lam, 2014), we still documented latitudinal patterns.

Feeding pressure was c. 2- to 22-fold higher at tropical versus extratropical locations, as a combined result of temperature and herbivory, with herbivory being c. 20-fold higher in tropical than extratropical sites. This pattern was consistent in both Hemispheres, contrary to recent findings for herbivory in terrestrial systems (Zhang, Zhang, & Ma, 2016). If productivity scaled with herbivory, this might not result in increased selective pressure on algal prey; however, productivity throughout this region appears to vary by 1-fold, or less (Behrenfeld et al., 2001; Steinacher et al., 2010), not 20-fold; thus, selection attributable to herbivory should be high in the tropics and much lower in temperate areas. Increased herbivory was driven mostly by scraping herbivores. At lower temperatures, herbivorous fishes have lower bite rates (Carpenter, 1986; Ferreira et al., 1998) and remove less macroalgae (Bennett & Bellwood, 2011). Omnivores demonstrated an opposing trend, with higher feeding pressure towards higher latitudes. This switch from herbivory to omnivory with polewards movement in both Hemispheres suggests that herbivory is favoured in warm conditions but less so in colder or more temperature-variable waters. Given that animals are protein rich compared with plants, there would be more nitrogen available to the consumer in an animal prey than in a plant, and nitrogen can be limiting to herbivores (Harmelin-Vivien, 2002; Mattson, 1980). This could be reflected in species' bite rates, because those using lower-quality food would need to compensate by ingesting larger amounts of food or mixing in foods of different quality (Carpenter, 1986; Cruz-Rivera & Hay, 2000; Floeter, Behrens, Ferreira, Paddock, & Horn, 2005; Floeter, Ferreira, Dominici-Arosemena, & Zalmon, 2004). If complementing the algal diet with higher proportions of non-algal materials is metabolically necessary at lower temperatures (Lobato et al., 2014), this could select for higher omnivory in the extratropics. Also, if warmer and more stable temperatures in the tropics enhance the ability of species to use low-quality food sources, this could aid diversification of important reef fish families and alter the trophic structure of reef fish assemblages across latitudes (Lobato et al., 2014).

An important caveat to this hypothesis is that the relative value of a food item will depend on the proportion and nutrient composition of other foods in the diet, the consumer's ability to digest and assimilate the nutrients, and the fact that tropical herbivores often rely on nutrients from organic detritus, microorganisms (both epilithic and endolithic) and seaweeds (Clements et al., 2017, 2009). The key to shifts from herbivory to omnivory in tropical versus extratropical areas could be driven by changes in the abundance or nutritional quality of these microorganisms and detritus, which might grow more rapidly and be more enriched or more abundant in warmer tropical waters. The ability to complement plant-based diets with organic detritus or microorganisms might play an important role in determining feeding pressure among and within functional groups across geographical scales.

We did not quantify the effects of feeding pressure on prey or prey defenses, but our documentation of higher herbivory in the

tropics supports previous findings of lower palatability and greater chemical defenses in tropical versus extratropical marine and aquatic plants (Bolser & Hay, 1996; Morrison & Hay, 2012; Siska et al., 2002). The weak relationship between macroalgal cover and herbivory (Supporting Information Appendix S3) might also indicate that high herbivory selects for well-defended plants that are less affected by herbivory. Thus, reefs with high herbivory may support similar macroalgal cover to reefs with less herbivory, but with the defenses of the algae on each differing considerably (Bolser & Hay, 1996; Hay, 1981; Pennings et al., 2009). Some herbivore-deterrent secondary metabolites also deter fouling (Schmitt, Hay, & Lindquist, 1995). If this is a general trend for tropical seaweeds, then the recent findings that parrotfish are nutritionally targeting cyanobacteria and other microorganisms living on seaweeds, on the reef matrix or within the reef (Clements et al., 2017) could translate into herbivorous fishes contributing in additional ways to selection for better-defended seaweeds in the tropics by selectively feeding on fouled seaweeds, therefore further strengthening selection for antifouling compounds (Wahl & Hay, 1995). The nuances of fish nutritional targets interacting with prey defenses need to be better understood before a conclusive evolutionary framework can be drawn. Both seaweeds and terrestrial plants are attacked by a host of consumers, and it is crucial that important biotic forces, such as consumer–prey interactions, be studied from a multispecies perspective to understand latitudinal patterns.

The composition of feeding pressure by functional groups was related to temperature in both Hemispheres, but with a slight latitudinal disparity between them. In the Northern Hemisphere, the warmer currents coming up from the Caribbean reach Central Florida (26°N), keep the average minimum temperature at c. 22°C and preclude the steep decline to 14°C that occurs northwards (see Figure 1). In contrast, the warmer currents in the Southern Hemisphere reach down to 20°S, where there is less variation between higher and lower temperatures in comparison to the reefs southwards, which experience a stronger influence of cold currents. Therefore, the average minimum temperature declines more steeply only between 23 and 27°S (see Figure 1). Despite these particularities, overall the herbivorous groups were well represented in warmer areas, whereas omnivores were more prevalent in colder areas of both Hemispheres. These similarities in function occurred despite shifts in major species both within and across latitudes. Therefore, conditions associated with latitudes seem to be selecting for similar feeding modes within different species pools. In the tropical region, for instance, different species within the family Acanthuridae marked the differences between locations, with the regional endemics *A. tractus* characterizing the Caribbean, *A. bahianus* (sister species of *A. tractus*) Eastern Brazil, and the widely distributed *A. chirurgus* characterizing Northeastern Brazil (Figure 4; Supporting Information Appendix S1 Table S1.2). The predominance of feeding pressure of the tribe Scarini over the family Acanthuridae in the Caribbean in comparison to Brazil agrees with patterns of density and biomass, and can be associated with a greater degree of reef complexity in the Caribbean (Floeter et al., 2005). These shifts in Acanthuridae-to-Scarini ratios and species within these groups

between the Caribbean and Brazil suggest that the same functional groups are composed of different species as a combined result of biogeographical (e.g., regional endemics) and ecological factors (e.g., tolerance to different conditions). This could have profound effects for functional redundancy for the following reasons: (a) there might be different levels of complementarity and redundancy within and between genera, with functions of species from different genera sometimes being more similar than functions of congeneric species (Burkepile & Hay, 2011); (b) species of the same group might explore different microhabitats (Fox & Bellwood, 2013) or present different capacities of nutrient assimilation (Dromard, Bouchon-Navaro, Harmelin-Vivien, & Bouchon, 2015); and (c) species within a functional group might perform functions unevenly (Duffy, 2002; Longo et al., 2014). Likewise, in the extratropical areas of both Hemispheres feeding pressure by omnivores was by the congeneric species *D. holbrooki* in the Northern Hemisphere and *D. argenteus* in the Southern Hemisphere. Therefore, the effects of feeding pressure might depend not only on the identity of functional groups but also on the identity of species in these groups.

As a result of ocean warming, tropical herbivores are expanding into the extratropics, particularly where western boundary currents foster greater rates of warming. These regions have experienced increased herbivory and a shift from palatable to less palatable seaweeds or even from macroalgae to coral reefs (Vergés et al., 2014; 2016). As examples, when tropical herbivorous fishes moved into extratropical parts of Japan and Australia dominated by kelps, these herbivores removed the kelps, and in Japan, the former kelp beds became dominated by corals (Vergés et al., 2014; 2016). Such shifts have not occurred in the Western Atlantic, but as oceans warm it is likely that tropical herbivores will expand into transitional and extratropical areas, potentially removing less-defended seaweeds and facilitating the establishment of better-defended tropical organisms. Such changes could significantly impact ecosystem structure and function.

We demonstrate latitudinal variation in the intensity and composition of trophic interactions using a standardized method across a broad geographical scale encompassing both Northern and Southern Hemispheres of the Western Atlantic. Our results support the hypothesis that biotic interactions are more intense in the tropics, especially plant–herbivore interactions. The functional approach was consistent between the different biogeographical regions despite large shifts in species identity and their relative contribution within functional groups. This suggests that factors associated to latitude such as temperature have selected for similar feeding functions among the different species occupying these geographical regions. Understanding the patterns and drivers of biotic interactions across broad geographical scales is crucial for predicting shifts in ecosystem function as climate changes and waters warm in temperate seas (Vergés et al., 2014, 2016).

DATA ACCESSIBILITY STATEMENT

The data in this manuscript will be available at the Zenodo platform DOI: 10.5281/zenodo.1345159.

ACKNOWLEDGMENTS

We thank the Marine Biodiversity Network (SISBIOTA–Mar) team for logistical and fieldwork support, and M. G. Pennino for statistical advice. Funding was provided by CNPq through the grants MCT Jovens Pesquisadores (#571295/2008–8) and SISBIOTA–Mar (CNPq 563276/2010–0; FAPESC 6308/2011–8) to S.R.F.; by the Teasley Endowment to M.E.H., and scholarships from CAPES, Brazilian Ministry Educational Council and the National Council for Scientific and Technological Development (CNPq) of the Brazilian Government's program "Science Without Borders" to G.O.L. This work was also supported by the Serrapilheira Institute (grant number Serra-1708-15364) awarded to G.O.L.

ORCID

Guilherme O. Longo  <https://orcid.org/0000-0003-2033-7439>

Mark E. Hay  <https://orcid.org/0000-0002-6130-9349>

Carlos E. L. Ferreira  <https://orcid.org/0000-0002-4311-0491>

Sergio R. Floeter  <https://orcid.org/0000-0002-3201-6504>

REFERENCES

- Anstett, D. N., Nunes, K. A., Baskett, C., & Kotanen, P. M. (2016). Sources of controversy surrounding latitudinal patterns in herbivory and defense. *Trends in Ecology and Evolution*, 31(10), 789–802. <https://doi.org/10.1016/j.tree.2016.07.011>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). *lme4: Linear mixed-effects models using Eigen and S4*. R package version 1.1-8. Retrieved from <http://CRAN.R-project.org/package=lme4>
- Behrenfeld, M. J., Randerson, J. T., McClain, C. R., Feldman, G. C., Los, S. O., Tucker, C. J., ... Kolber, D. D. (2001). Biospheric primary production during an ENSO transition. *Science*, 291(5513), 2594–2597.
- Bellwood, D. R., Hoey, A. S., Bellwood, O., & Goatley, C. H. R. (2014). Evolution of long-toothed fishes and the changing nature of fish–benthos interactions on coral reefs. *Nature Communications*, 5, 3144. <https://doi.org/10.1038/ncomms4144>
- Bennett, S., & Bellwood, D. R. (2011). Latitudinal variation in macroalgal consumption by fishes on the Great Barrier Reef. *Marine Ecology Progress Series*, 426, 241–252. <https://doi.org/10.3354/meps09016>
- Bolser, R. C., & Hay, M. E. (1996). Are tropical plants better defended? Palatability and defenses of temperate versus tropical seaweeds. *Ecology*, 77, 2269–2286.
- Burkpile, D. E., & Hay, M. E. (2011). Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs*, 30, 351–362. <https://doi.org/10.1007/s00338-011-0726-6>
- Carpenter, R. C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs*, 56, 345–363. <https://doi.org/10.2307/1942551>
- Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68(5), 893–905. <https://doi.org/10.1046/j.1365-2656.1999.00337.x>
- Clarke, K. R., Somerfield, P. J., & Gorley, R. N. (2008). Testing null hypotheses in exploratory community analyses: Similarity profiles and biota–environmental linkage. *Journal of Experimental Marine Biology and Ecology*, 366, 56–69.
- Clements, K. D., German, D. P., Piché, J., Tribollet, A., & Choat, J. H. (2017). Integrating ecological roles and trophic diversification on coral reefs: Multiple lines of evidence identify parrotfishes as microphages. *Biological Journal of the Linnean Society of London*, 120, 729–751.
- Clements, K. D., Raubenheimer, D., & Choat, J. H. (2009). Nutritional ecology of marine herbivorous fishes: Ten years on. *Functional Ecology*, 23, 79–92. <https://doi.org/10.1111/j.1365-2435.2008.01524.x>
- Coley, P. D., & Aide, T. M. (1991). Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In P. W. Price, T. M. Lewinsohn, G. W. Fernandes, & W. W. Benson (Eds.), *Plant–animal interactions; Evolutionary ecology in tropical and temperate regions* (pp. 25–49). New York, NY: John Wiley and Sons Inc.
- Cruz-Rivera, E., & Hay, M. E. (2000). The effects of diet mixing on consumer fitness: Macroalgae, epiphytes, and animal matter as food for marine amphipods. *Oecologia*, 123(2), 252–264. <https://doi.org/10.1007/s004420051012>
- R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved from www.R-project.org/
- Dromard, C. R., Bouchon-Navaro, Y., Harmelin-Vivien, M., & Bouchon, C. (2015). Diversity of trophic niches among herbivorous fishes on a Caribbean reef (Guadeloupe, Lesser Antilles), evidenced by stable isotope and gut content analyses. *Journal of Sea Research*, 95, 124–131. <https://doi.org/10.1016/j.seares.2014.07.014>
- Duffy, J. E. (2002). Biodiversity and ecosystem function: The consumer connection. *Oikos*, 99, 201–219. <https://doi.org/10.1034/j.1600-0706.2002.990201.x>
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... Marquis, R. J. (2011). Trophic downgrading of planet Earth. *Science*, 333(6040), 301–306.
- Ferreira, C. E. L., Floeter, S. R., Gasparini, J. L., Ferreira, B. P., & Joyeux, J. C. (2004). Trophic structure patterns of Brazilian reef fishes: A latitudinal comparison. *Journal of Biogeography*, 31(7), 1093–1106. <https://doi.org/10.1111/j.1365-2699.2004.01044.x>
- Ferreira, C. E. L., Peret, A. C., & Coutinho, R. (1998). Seasonal grazing rates and food processing by tropical herbivorous fishes. *Journal of Fish Biology*, 53, 222–235.
- Floeter, S. R., Behrens, M. D., Ferreira, C. E. L., Paddock, M. J., & Horn, M. H. (2005). Geographical gradients of marine herbivorous fishes: Patterns and processes. *Marine Biology*, 147, 1435–1447. <https://doi.org/10.1007/s00227-005-0027-0>
- Floeter, S. R., Ferreira, C. E. L., Dominici-Arosemena, A., & Zalmon, I. (2004). Latitudinal gradients in Atlantic reef fish communities: Trophic structure and spatial use patterns. *Journal of Fish Biology*, 64, 1680–1699. <https://doi.org/10.1111/j.0022-1112.2004.00428.x>
- Floeter, S. R., Rocha, L. A., Robertson, D. R., Joyeux, J. C., Smith-Vaniz, W. F., Wirtz, P., ... Bernardi, G. (2008). Atlantic reef fish biogeography and evolution. *Journal of Biogeography*, 35(1), 22–47.
- Fox, R. J., & Bellwood, D. R. (2013). Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. *Coral Reefs*, 32(1), 13–23. <https://doi.org/10.1007/s00338-012-0945-5>
- Freestone, A. L., Osman, R. W., Ruiz, G. M., & Torchin, M. E. (2011). Stronger predation in the tropics shapes species richness patterns in marine communities. *Ecology*, 92(4), 983–993. <https://doi.org/10.1890/09-2379.1>
- Froese, R., & Pauly, D. (2016). *FishBase*. Retrieved from www.fishbase.org
- Harmelin-Vivien, M. L. (2002). Energetics and fish diversity on coral reefs. In P. F. Sale (Ed.), *Coral reef fishes: Dynamics and diversity in a complex ecosystem* (pp. 265–274). San Diego, CA: Academic Press.
- Hay, M. E. (1981). Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. *The American Naturalist*, 118, 520–540. <https://doi.org/10.1086/283845>
- Jackson, J., Donovan, M., Cramer, K., & Lam, V. (2014). *Status and trends of Caribbean coral reefs: 1970–2012*. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland.

- Le, S., Josse, J., & Husson, F. (2008). FactoMineR: An R package for multi-variate analysis. *Journal of Statistics Software*, 25(1), 1–18.
- Lobato, F. L., Barneche, D. R., Siqueira, A. C., Liedke, A. M., Lindner, A., Pie, M. R., & Floeter, S. R. (2014). Diet and diversification in the evolution of coral reef fishes. *PLoS One*, 9(7), e102094. <https://doi.org/10.1371/journal.pone.0102094>
- Longo, G. O., Ferreira, C. E. L., & Floeter, S. R. (2014). Herbivory drives large-scale spatial variation in reef fish trophic interactions. *Ecology and Evolution*, 4(23), 4553–4566. <https://doi.org/10.1002/ece3.1310>
- Mattson, W. J., Jr. (1980). Herbivory in relation to plant nitrogen content. *Annual Review in Ecology and Systematics*, 11(1), 119–161. <https://doi.org/10.1146/annurev.es.11.110180.001003>
- McCaughey, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R. (2015). Marine defaunation: Animal loss in the global ocean. *Science*, 347(6219), 1255641. <https://doi.org/10.1126/science.1255641>
- Moles, A. T., Bonser, S. P., Poore, A. G., Wallis, I. R., & Foley, W. J. (2011). Assessing the evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology*, 25(2), 380–388. <https://doi.org/10.1111/j.1365-2435.2010.01814.x>
- Moles, A. T., & Ollerton, J. (2016). Is the notion that species interactions are stronger and more specialized in the tropics a zombie idea? *Biotropica*, 48, 141–145. <https://doi.org/10.1111/btp.12281>
- Morrison, W. E., & Hay, M. E. (2012). Are lower-latitude plants better defended? Palatability of freshwater macrophytes. *Ecology*, 93(1), 65–74. <https://doi.org/10.1890/11-0725.1>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, ... Oksanen, M. J. (2018). Package 'vegan'. *Community ecology package, R package version 2.5-2*. Retrieved from <https://CRAN.R-project.org/package=vegan>
- Pennings, S. C., Ho, C. K., Salgado, C. S., Więski, K., Davé, N., Kunza, A. E., & Wason, E. L. (2009). Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology*, 90(1), 183–195. <https://doi.org/10.1890/08-0222.1>
- Pennings, S. C., & Silliman, B. R. (2005). Linking biogeography and community ecology: Latitudinal variation in plant-herbivore interaction strength. *Ecology*, 86(9), 2310–2319. <https://doi.org/10.1890/04-1022>
- Phillips, N. (2016). *yarr: A companion to the e-Book "YaRrr!: The pirate's guide to R"*. R package version 0.1.2. Retrieved from <https://CRAN.R-project.org/package=yarr>
- Poore, A. G., Campbell, A. H., Coleman, R. A., Edgar, G. J., Jormalainen, V., Reynolds, P. L., & Emmett Duffy, J. (2012). Global patterns in the impact of marine herbivores on benthic primary producers. *Ecology Letters*, 15(8), 912–922. <https://doi.org/10.1111/j.1461-0248.2012.01804.x>
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., & Schmitz, O. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343(6167), 1241484. <https://doi.org/10.1126/science.1241484>
- Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., ... Cameron, E. K. (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356(6339), 742–744.
- Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M., & Roy, K. (2009). Is there a latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology Evolution and Systematics*, 40, 245–269. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173430>
- Schmitt, T. M., Hay, M. E., & Lindquist, N. (1995). Constraints on chemically mediated coevolution: Multiple functions for seaweed secondary metabolites. *Ecology*, 76(1), 107–123. <https://doi.org/10.2307/1940635>
- Siska, E. L., Pennings, S. C., Buck, T. L., & Hanisak, M. D. (2002). Latitudinal variation in palatability of salt-marsh plants: Which traits are responsible? *Ecology*, 83, 3369–3381. [https://doi.org/10.1890/0012-9658\(2002\)083\[3369:LVIPOS\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[3369:LVIPOS]2.0.CO;2)
- Steinacher, M., Joos, F., Frolicher, T. L., Bopp, L., Cadule, P., Cocco, V., ... Segsneider, J. (2010). Projected 21st century decrease in marine productivity: A multi-model analysis. *Biogeosciences*, 7, 979–1005. <https://doi.org/10.5194/bg-7-979-2010>
- Tyberghein, L., Verbruggen, H., Pauly, K., Troupin, C., Mineur, F., & De Clerck, O. (2012). Bio-ORACLE: A global environmental dataset for marine species distribution modelling. *Global Ecology and Biogeography*, 21, 272–281. <https://doi.org/10.1111/j.1466-8238.2011.00656.x>
- Hijmans, R. J., & vanEtten, J. (2012). *raster: Geographic analysis and modeling with raster data. R package version 2.0-12*. Retrieved from <https://cran.r-project.org/web/packages/raster/index.html>
- Vergés, A., Doropoulos, C., Malcolm, H. A., Skye, M., Garcia-Pizá, M., Marzinelli, E. M., & Bozec, Y. M. (2016). Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proceedings of the National Academy of Sciences of the USA*, 113(48), 13791–13796. <https://doi.org/10.1073/pnas.1610725113>
- Vergés, A., Steinberg, P. D., Hay, M. E., Poore, A. G., Campbell, A. H., Ballesteros, E., ... Figueira, W. (2014). The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. *Proceedings of the Royal Society Bulletin*, 281(1789), 20140846.
- Wahl, M., & Hay, M. E. (1995). Associational resistance and shared doom: Effects of epibiosis on herbivory. *Oecologia*, 102, 329–340. <https://doi.org/10.1007/BF00329800>
- Wood, S., & Scheipl, F. (2013). *gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.2-2*. Retrieved from <http://CRAN.R-project.org/package=gamm4>
- Zhang, S., Zhang, Y., & Ma, K. (2016). Latitudinal variation in herbivory: Hemispheric asymmetries and the role of climatic drivers. *Journal of Ecology*, 104(4), 1089–1095. <https://doi.org/10.1111/1365-2745.12588>

GUILHERME LONGO is an early-career professor at Universidade Federal do Rio Grande do Norte in Northeast Brazil (<https://longolab.weebly.com>). His research interests relate to the importance of ecological interactions in reef ecosystem functioning and how these interactions may change as a result of human impacts across multiple spatial scales. He is also interested in unravelling the potential effects of global changes on Brazilian reefs.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Longo GO, Hay ME, Ferreira CEL, Floeter SR. Trophic interactions across 61 degrees of latitude in the Western Atlantic. *Global Ecol Biogeogr*. 2019;28: 107–117. <https://doi.org/10.1111/geb.12806>