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Regional variability in the sensitivity of Caribbean reef fish assemblages to ocean warming

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ABSTRACT: Ocean warming is expected to impact biodiversity and fisheries in the tropics through shifts in species' distributions, leading to local extinctions and changes in species composition of catches. However, regional-scale patterns may differ from global trends due to the influence of important environmental factors such as ocean warming, fishing and habitat availability. Here, we used the mean temperature of the catch to test the hypothesis that, for the period of 1971 to 2010, regional variation in species-turnover of exploited reef fish assemblages among 9 Caribbean countries can be explained by differences in the rate of warming, species' thermal preferences, changes in trophic structure due to fishing and potential reef habitat across the region. Sea surface temperature and the mean temperature of the catch displayed rates of increase of 0.14 and 0.19°C decade^{-1} respectively, on par with the global average and higher when compared to the global average for all tropical fisheries. These rates also varied across the 9 Caribbean countries, ranging from 0.04 to 0.18°C decade^{-1} for sea surface temperature and 0.10 to 0.62°C decade^{-1} for the mean temperature of the catch. The negative interaction between potential reef habitats in each country and sea surface temperature in relation to the mean temperature of the catch suggests possible moderating effects of available habitats on the sensitivity of fish communities to warming. In addition, the negative relationship of trophic level with the mean temperature of the catch suggests that fishing increases their vulnerability. Findings from this study can help elucidate factors driving variations in the sensitivity of exploited fish communities to warming, and have implications for the management of living marine resources in the Caribbean region.

KEY WORDS: Ocean climate · Coral reef · Fish community · Caribbean · Fisheries · Habitat · Ecosystem indicator

INTRODUCTION

Many tropical developing countries benefit from the wide array of ecological goods and services provided by coral reef ecosystems including nutrition, economic security, coastal protection and recreation (Moberg & Folke 1999, Brander et al. 2007, Seenprachawong 2016). Previous studies suggest that ocean warming could drive large-scale shifts in the distribution of fish species, with the potential to alter the composition, dynamics and productivity of local fish assemblages as well as their dependent fisheries (Cheung et al. 2013a, Jones et al. 2015). However, making predictions about the future state of local communities in the context of climate change requires a better understanding of the role that small-scale heterogeneity in the broader ecosystem may play in shaping these impacts (Sherman 2014). Here, we investigated the role played by 2 factors considered very influential in shaping reef fish assemblages: thermal exposure and habitat availability.

The relationship between thermal exposure and metabolic functioning across marine fishes through oxygen limitation is well established (Pörtner &

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Knust 2007, Pauly 2010, Pauly & Cheung 2018), as are the implications for their distribution and abundance (Dulvy et al. 2008, Cheung et al. 2011, Fernandes et al. 2013). Because thermal tolerance varies across fish assemblages, the distribution of some species will be affected before others, making shifts in the composition of fish assemblages likely. In addition, the rate at which these changes occur may differ across ecosystems depending on species' degree of thermal exposure. Cheung et al. (2013b) illustrated this using an ecological indicator, the mean temperature of the catch (MTC), to demonstrate that more thermophilous species (species with higher thermal tolerances) were increasing in dominance in fisheries catch across the large marine ecosystems (LMEs) of the globe in accordance with rates of sea surface temperature (SST) increase (Cheung et al. 2013b).

The impact of external environmental stressors has been shown to scale negatively with habitat size across a variety of spatial scales in terrestrial (Amundrud & Srivastava 2015) and marine realms (Nagelkerken et al. 2015). While mechanisms seem to be specific to each system, they generally relate to the provision of habitat resources, which are understood to be more abundant on larger habitat tracts. In the case of coral reefs, most of the prominent literature focuses on the importance of the number and density of refuge spaces (Messmer et al. 2011, Graham 2014, Rogers et al. 2014) in mediating key ecological processes such as species coexistence (Holt 1984), recruitment (Gilinsky 1984, Almany 2004) and predation (Gilinsky 1984, Gotceitas & Colgan 1989, Hixon & Beets 1993, Beukers & Jones 1998). In essence, more complex and extensive reef habitat will have greater numbers of fish refuge spaces, and as a result, more diverse and abundant fish assemblages. Ultimately, it is possible that the persistence of these assemblages under climate stress is more likely with a greater availability of habitat resources, illustrated by smaller changes in MTC (ΔMTC) through time.

Fishing may exacerbate the sensitivity of marine populations and communities to climate change (Perry et al. 2010). Specifically, it has been shown to increase the variability of population size, as the surplus production typically targeted by fisheries acts as a buffer against environmental variability (Hsieh et al. 2006). In addition, temperature may reduce the reproductive output of fish populations, and as such, their regenerative capacity (Rijnsdorp et al. 2010). Given the importance of reef fisheries to the region, it is likely that such impacts are affecting the resilience of reef species against the effects of ocean warming.

In this study, we built on the findings of Cheung et al. (2013b) by assessing the strength of the relationship between SST and MTC trends, focusing on the Caribbean LME and the associated coral reef fisheries. Furthermore, we assessed the influence of habitat resources across this LME in shaping the impact of ocean warming on coral reef assemblages, with consideration of potential effects of fishing-induced changes in assemblages. Given the previously mentioned theoretical basis, we established our main assumptions regarding the interaction of climate with the mediating effects of habitat and fishing as follows:

Habitat effects:

(1) For 2 coral reefs A and B, with A being the larger of the 2, reef A will have a greater quantity of habitat resources;

(2) Habitat resources are important for various fish life history processes and increase the resilience of fish populations, particularly for less thermophilous species;

(3) Because of assumptions 1 and 2, changes in community structure in reef A in response to ocean warming are more likely to be slower than in reef B, resulting in smaller values for ΔMTC.

Fishing effects:

(1) Reef fisheries tend to target large, high trophic level species over smaller, lower trophic level species;

(2) Larger, higher trophic level species are slower growing, making them less sensitive to ocean warming compared to smaller, faster-growing species;

(3) Because of assumptions 1 and 2, for 2 fish communities A and B, with A being the less fished of the 2, changes in community A will show a smaller decrease in mean trophic level and as such, a lower sensitivity to the impacts of ocean warming.

MATERIALS AND METHODS

Site description

The Caribbean large marine ecosystem (CLME) is an area of 3.2 million km^2 situated in the tropical western hemisphere, bounded by North America (south Florida), Central and South America and the Caribbean archipelago (Fig. 1). Since the formation of the Isthmus of Panama some 5 to 3 million years ago (Mya), species and ecosystems within the Caribbean basin have taken on evolutionary pathways distinct from those of other, similar regions of the world and as a result, it contains numerous endemic species (Kuffner & Toth 2016). Coral reef complexes within

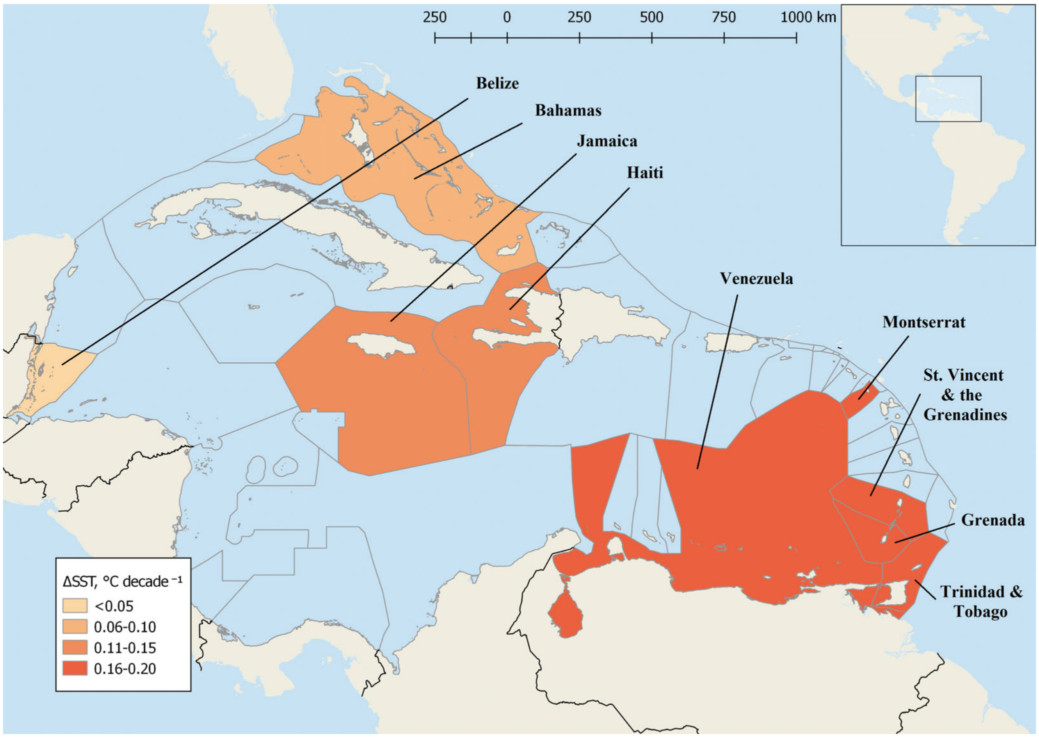

Fig. 1. The Caribbean large marine ecosystem; the exclusive economic zones (EEZs) of the 9 countries considered here are highlighted, with colors reflecting the strength of ocean warming (change in sea surface temperature (ΔSST) from 1971–2010)

the region, which in total constitute ~7% of global coral cover, are distributed throughout the region, intimately associated with islands of the Caribbean archipelago. They range in size from smaller fringing reefs (e.g. the Buccoo reef complex off the southwestern coast of Trinidad and Tobago) to larger barrier reefs (e.g. the Meso-American barrier reef associated with the Yucatan Peninsula of Central America) (Cortés 2003). Since the 1980s, many of these reefs have experienced significant declines in structural complexity, overall coverage and shifts to community dominance by macroalgae species (Alvarez-Filip et al. 2009, Jackson et al. 2014).

The CLME has also experienced significant increases in ocean temperature (Hayes & Goreau 2008, Jury & Winter 2010), with negative consequences already observed for coral reef ecosystems across the region. The CLME is located within the geographically complex Caribbean basin, the circulation patterns of which result in substantial spatial heterogeneity in the observed warming trend (Hayes & Goreau 2008) (Fig. 1).

Fisheries in the CLME target a wide range of ecosystems from shallow reefs to open water pelagic systems, with coral reefs being the most socioeconomically important, supplementing the income and nutrition of many local communities. More specifically, reef fisheries focus on a variety of species spanning the entire breadth of taxa represented in coral reef ecosystems. While these fisheries are generally considered overfished, fish landings and effort levels are thought to have stabilized in the early 1980s (Mahon 2002). In this study, 9 countries were selected to represent the region (Table 1). We outline the criteria for their selection in the following sections.

Table 1. Countries selected for the analyses, their potential reef habitat (PRH) in km^2 and the number of coral fish taxa present within the processed catch record (n Taxa)

Country	PRH (km^2)	n Taxa
Bahamas	2869	8
Belize	1552	13
Jamaica	958	10
Venezuela	670	8
St. Vincent and the Grenadines	225	8
Grenada	213	7
Haiti	197	6
Montserrat	94	14
Trinidad and Tobago	40	6

Fisheries and environmental data

Fisheries landings were obtained through the Sea Around Us catch reconstructions database (Pauly & Zeller 2016). This database complements the Food and Agriculture Organization records of global fisheries landings (which is based on self-reports by member countries), using a variety of sources ranging from national archives to field reports to correct official estimates, and increases the resolution of data around catch composition and fisheries sector. The resulting catch estimates were aggregated by each country's exclusive economic zone (EEZ) (Fig. 1). In this analysis, we obtained a subset of the catch from 1971 to 2010 containing only species with estimates of thermal preference and a non-zero value of coral affinity. Catch data were then processed further by removing taxa across the catch record that fulfilled at least 1 of 3 criteria: (1) the taxon comprised >20% of a single country's catch record; (2) was not included in FishBase (not a fish species); or (3) was classified as 'pelagic–oceanic' according to FishBase.

Criterion 1 was implemented to remove a single taxa that may dominate the catch record, thus MTC can be more representative of species assemblages and avoid trends that are disproportionately affected by one species. Criterion 2 was meant to remove non-fish taxa that, due to different anatomical constraints, may display different responses to the metabolic constraints of temperature and oxygen limitation. Criterion 3, on the other hand, excludes coastal–migratory species that may have a non-zero value for coral affinity, but have abundance trends that are heavily influenced by the productivity of small pelagic fishes. Species fulfilling these criteria are documented in Tables S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m590p201_supp.pdf. Following this, only countries with 5 or more taxa remaining in their respective catch records were selected for the study (Table 1).

Temperature and coral reef area data were obtained from published databases. SSTs were provided by the Hadley Center. This SST data set is constructed by interpolating annual average SSTs onto a 0.5 × 0.5° grid using the nearest neighbor method, then averaging the SST of spatial cells within the EEZ boundary. Ideally, the availability of habitat resources would be best represented using an index of habitat complexity collected through the study period. However, such data only exist for a small subset of Caribbean countries included in the analysis (Alvarez-Filip et al. 2009, 2011a,b), precluding its use for our analysis. As such, we utilized data for coral reef area extracted from the UNEP World Conservation Monitoring Center's (UNEP-WCMC) database for the global distribution of coral reefs (UNEP-WCMC et al. 2010). While this database does not explicitly represent live coral cover, the authors assume that the area of the polygons is proportional to the likelihood that reef habitat exists. Furthermore, that database represents one of the best available databases for coral cover, especially considering its spatial coverage and the consistency of methods applied in its construction. Henceforth, we refer to this predictor as 'potential reef habitat' (PRH). PRH for each EEZ was estimated by first rasterizing WCMC shapefiles of potential coral distribution into a 0.5 × 0.5° spatial grid, determining the proportion of each cell covered by coral. This proportion was then multiplied by the estimated area of each cell, which were finally summed by EEZ and are presented in Table 1.

The habitat preference index obtained from the Sea Around Us was based on qualitative descriptions of the species' degree of association with coral reef in published literature and databases (Pauly & Zeller 2015) (see also Table S1). It scales between 0 and 1, with 0 and 1 denoting no evidence of association and obligatory association with coral reef, respectively.

Thermal preference was estimated using the same method described in Cheung et al. (2013b), which combines the estimated relative abundance of each species with the climatology (averaged from 1971 to 2000) of SST data. Briefly, first the present (1971 to 2000) distribution of relative abundance of each species was estimated on a 0.5° latitude × 0.5° longitude grid of the world ocean. Temperature was not used in predicting species distribution to avoid circularity in subsequent analyses, in which SST is an important component (Palomares et al. 2016). Second, each modelled species distribution was normalized and overlaid on the SST climatology from the Hadley Centre SST data set for 1971 to 2010. The temperature preference profile at SST bin i (p_i) of each species was calculated from the total relative abundance, K_i, and range area, A_i:

$$p_i = \frac{(K_i / A_i)}{\sum_i (K_i / A_i)} \quad (1)$$

The median value of the temperature preference profile was used as thermal preference of the species (Table S1).

Calculating MTC by EEZ

We calculated annual MTC for each EEZ and the region as a whole from 1971 to 2010 as the weighted average of temperature preference for taxa in the country's annual catch record:

$$\mathrm{MTC}_{yr} = \frac{\sum_i^n T_i . C_{i,yr}}{\sum_i^n C_{i,yr}} \quad (2)$$

where MTC_{yr} is the mean temperature of the catch for year *yr*, T_i is the estimated thermal preference for species *i*, $C_{i,yr}$ is the catch for species *i* in year *yr*, and *n* is the number of species in the catch record.

We calculated changes in SST (ΔSST) and MTC (ΔMTC) between 1975 and 2005 for each EEZ and the entire region by taking the difference between the average of 1971 to 1980 and 2001 to 2010. The formulations are as follows:

$$\Delta\mathrm{SST} = \left(\frac{\sum_{t=2001}^{2010} \mathrm{SST}_t}{10} - \frac{\sum_{t=1971}^{1980} \mathrm{SST}_t}{10} \right)$$
$$\Delta\mathrm{MTC} = \left(\frac{\sum_{t=2001}^{2010} \mathrm{MTC}_t}{10} - \frac{\sum_{t=1971}^{1980} \mathrm{MTC}_t}{10} \right) \quad (3)$$

Testing the relationship between SST, MTC, PRH and mean trophic level

We examined the relationship between SST, PRH, mean trophic level (MTL) and MTC using a linear mixed-effects model. Specifically, we tested the hypothesis that SST is directly related to MTC while the available reef fish habitat, indicated by PRH, will reduce the positive relationship between SST and MTC, with country's EEZ being a random effect. Prior to its inclusion in the analyses, PRH values were rescaled to units of 1000 km^2 to increase the visibility of its associated regression parameters in the model statistics. The trends of catches may be influenced by the effects of fishing through the modification of species' population structure and their representation in the catch. We accounted for such potential effects by including changes in MTL (ΔMTL) in the model, an indicator that can be used to demonstrate the impact of fishing on fish assemblages (Pauly et al. 1998, Graham et al. 2017). MTL was calculated using the same formulation for MTC, by taking the weighted average of the estimated trophic level for taxa in the annual catch record of the country:

$$\mathrm{MTL}_{yr} = \frac{\sum_i^n \mathrm{TL}_i . C_{i,yr}}{\sum_i^n C_{i,yr}} \quad (4)$$

where MTL_{yr} is the mean trophic level for year *yr*, TL_i is the estimated trophic level for species *i* obtained from FishBase (www.fishbase.org), $C_{i,yr}$ is the catch for species *i* in year *yr*, and *n* is the number of species in the catch record.

We used the R package 'nlme' and function 'lme', with the full model taking the following form:

$$\mathrm{MTC} \sim \boldsymbol{A} \times \mathrm{SST} + \boldsymbol{B} \times \mathrm{PRH} + \boldsymbol{C} \times \mathrm{SST} \times \mathrm{PRH} + \boldsymbol{D} \times \mathrm{MTL} + z \times \mathrm{country} \quad (5)$$

where ***A***, ***B***, ***C*** and ***D*** are matrices representing the fixed effects of SST, PRH and their interactions, while *z* is the random effect of different country's EEZs. Since we did not have any sub-sample of PRH for each country, the random effect of a country's EEZs were specified for the intercept only.

We used a backward elimination approach to explore the alternative hypotheses of simpler models. For each method, we sequentially removed non-significant predictors until we obtained the most parsimonious model. We also compared the goodness-of-fit and model performance based on R^2 and Akaike's information criterion (AIC) from alternative models.

RESULTS

Trends in SST, MTC and MTL

For the period from 1971 to 2010, the regional average of ΔSST of 0.13°C decade^{-1} was found to be similar, to the global average for tropical LMEs of 0.14°C decade^{-1}. MTC for coral reef catch across the Caribbean showed linear rates of increase of 0.19°C decade^{-1}, on par with the global average of 0.19°C decade^{-1} and higher than the global estimate of 0.14°C decade^{-1} for tropical catches from all fisheries. Across EEZs, ΔSST ranged from 0.04°C decade^{-1} to 0.18°C decade^{-1} (Belize and Trinidad & Tobago, respectively), while ΔMTC ranged from −0.10°C to 0.62°C decade^{-1} (Bahamas and Trinidad & Tobago, respectively). More than half of the countries assessed produced estimates for ΔMTC exceeding the global mean for tropical ecosystems. Also, 8 out of 10 countries showed a decrease in MTL, Trinidad & Tobago having no change and Venezuela an increase in MTL. Table 2 provides a summary of these values. ΔSST and ΔMTC are seen to be significantly correlated with each other, with a glm (R function 'glm') returning an R^2 of 0.6. (Fig. 2). Countries with smaller PRH seem to be underestimated by the simple linear relationship between ΔMTC and ΔSST.

The relationship between SST, PRH, MTC and MTL

Based on the results of the mixed effects modeling and backward elimination, the full model (with SST, PRH and their interactions, as well as MTL) was

Table 2. Estimates of changes in sea surface temperature (ΔSST), the mean temperature of the catch (ΔMTC) and mean trophic level (ΔMTL) for the 9 countries assessed, along with corresponding regional and global tropical averages

Country	ΔSST	ΔMTC	ΔMTL
Trinidad & Tobago	0.18	0.62	0.00
Venezuela	0.17	0.16	0.05
Grenada	0.17	0.48	–0.08
Montserrat	0.16	0.49	–0.15
St. Vincent & the Grenadines	0.16	0.57	–0.11
Jamaica	0.13	0.04	–0.01
Haiti	0.11	0.00	–0.01
Bahamas	0.06	–0.10	–0.02
Belize	0.04	0.04	–0.01
Regional average	0.14	0.19	0.01
Global tropical average[a]	0.14	0.14	–

[a]Values estimated by Cheung et al. (2013b)

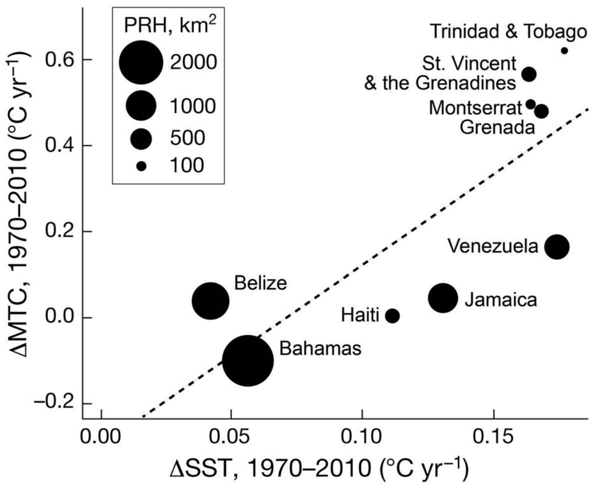

Fig. 2. Positive correlation between changes in the mean temperature of the catch (ΔMTC) and sea surface temperatures (ΔSST). Potential reef habitat (PRH) for each country is represented by the size of each data point while the dotted line represents the linear relationship between ΔSST and ΔMTC

selected as the most parsimonious (Table 3). This suggests that SST is positively related to MTC and explains most of the variance. Though PRH explains a much smaller component of the variance in MTC, the interaction between SST and PRH is significant, and has a negative relationship with MTC which agrees with our *a priori* expectation. We sequentially removed the term representing the interaction between PRH and SST, and the PRH term altogether to test whether these would improve the performance of the model. The simpler models resulted in slight decreases in R^2 values and increases in AIC (Table 3). The predictor indicating fishing effect (MTL) was also significantly and negatively related to MTC, suggesting that the targeted removal of higher trophic level species may be increasing the vulnerability of reef fish assemblages to ocean warming.

Models without PRH and their interactions with SST in the model had a lower R^2 and higher AIC compared to the full model (Table 3). As PRH explained the smallest component of the variance in MTC, we sequentially removed the term representing the interaction between PRH and SST, and the PRH term altogether to test whether these would improve the performance of the model. The simpler models resulted in slight decreases in R^2 values and increases in AIC.

Table 3. Statistics obtained from mixed effects modeling for our full model. MTC: mean temperature of the catch; SST: sea surface temperature; PRH: potential reef habitat; MTL: mean trophic level; AIC: Akaike's information criterion

Model specification	Predictors	Coefficient	p-value	R^2	AIC
MTC ~ SST × PRH + MTL	SST	0.687	<0.001	0.901	308
	PRH	11.780	0.0023		
	SST × PRH	–0.422	<0.001		
	MTL	–3.200	<0.001		
MTC ~ SST + PRH + MTL	SST	0.430	<0.001	0.898	324
	PRH	0.232	0.4715		
	MTL	–3.272	<0.001		
MTC ~ SST + MTL	SST	0.438	<0.001	0.894	321
	MTL	–3.271	<0.001		

DISCUSSION

Marine species are shifting their distribution ranges around the world in response to ocean warming, leading to changes in community structure (Poloczanska et al. 2016), and our study confirms that such a signature of ocean warming is robust, even at the regional and sectoral scale of Caribbean reef fisheries. It also suggest that the vulnerability of reef fisheries to ocean warming varies substantially across the region and is, for some countries, greater than previously estimated at the global scale (Cheung et al. 2013b). In addition, the negative relationship between MTL and MTC suggests that changes in trophic structure because of fishing and/or other human and natural drivers may exacerbate warming-induced changes in reef fish community structure (Hsieh et al. 2006, Rijnsdorp et al. 2010). Our findings highlight that the interactions between climate and non-climatic drivers of reef fish assemblages warrant further exploration in future studies. Finally, while this analysis is limited by the use of a habitat proxy (i.e. PRH) and a relatively small sample size, the results support our main hypothesis that available habitat might play an important role in reducing the impact of ocean warming on reef fish communities. These findings add to the growing body of evidence of the important role benthic habitat and vegetation play in moderating climate impacts on marine communities (Leonard 2000, Mellin et al. 2010, Mantyka-pringle et al. 2012).

While mechanisms underlying the combined effect of habitat and climate on biodiversity are better established on land than in the ocean (Mantyka-pringle et al. 2012), thermal acclimation may serve as a possible point of intersection in the marine realm. Evidence suggests that while adults of some damselfish species show little to no capacity for acclimation (Nilsson et al. 2010, Donelson et al. 2011), juveniles display acclimation based upon the environmental conditions of their early developmental stages (Grenchik et al. 2013). This suggests that recruitment success, which complex habitat is known to facilitate (Almany 2004), may be key to increasing the thermal resilience of reef fish across generational time scales. On the contrary, our results suggest that even if such adaptive responses exist in some reef fishes, they may not be sufficient to fully counter the effects of warming across fish assemblages in these time scales. Finally, with the decline of corals in recent years, some scientists suggest that new configurations of reef habitat consisting of sponges, macroalgae, soft corals and smaller amounts of slow-growing but stress-tolerant hard corals may arise in the future and continue to provide refuge spaces in some capacity (Done 1992, Cruz et al. 2015). Due to the novel nature of such benthic configurations (Norström et al. 2009), their relative effects on the productivity of fisheries is yet to be properly understood.

Data availability and resolution were the main limiting factors in this study, affecting the number of countries included, our indices for the effect of fishing and reef habitat and finally the interpretation of our results. First, our analyses were limited to 9 EEZs since the taxonomic resolution of other countries' catch records did not fit the demands of our analysis. We repeated our analyses with a larger sample size by relaxing the threshold of taxonomic diversity required of a country's catch record (from 5 taxa to 3), but our conclusions remained unchanged (see Tables S4 & S5 in the Supplement at www.int-res.com/articles/suppl/m590p201_supp.pdf). Second, the limited sample size and the use of a habitat proxy in PRH introduced some uncertainty in our statistical analyses. For example, we could have potentially avoided the apparent co-variance between exposure to ocean warming and reef habitat size if other Caribbean nations were included to increase our sample size. Furthermore, because PRH is ultimately a proxy for coral cover, it may not have properly represented the available habitat resources use by reef fish (Alvarez-Filip et al. 2011a). In addition, tropical reefs are part of a much larger coastal seascape that includes vast tracts of mangrove and seagrass habitat. Both of these play a significant role in the early life histories and survival of many of the species included in this analysis (Nagelkerken et al. 2000, 2017, Jones et al. 2010). As such, our analyses may have grossly underestimated the buffering effect of habitat through our limited sample size and use of PRH. Third, while MTL is a widely accepted indicator for detecting the influence of fishing on assemblages (Pauly et al. 1998, Pauly & Watson 2005, Graham et al. 2017), its use is not an adequate replacement for effort data, which lacks spatiotemporal consistency across the CLME. Future studies should expand the current analysis to test whether the effects of available reef habitat are robust when more sample EEZs from coral reefs in different parts of the world are included. If the effect of available habitat area is real, it should also apply to other, non-Caribbean reef fish assemblages, such as those in the Pacific and Indian Oceans. It would also be useful to use more direct observations of habitat area, as the remote sensing-based estimates of PRH used in this study may not represent habitat resources actually utilized by reef fish (Alvarez-Filip et al. 2011a). Other additional habitat-related variables that could be included in future studies include an index of reef complexity, such as rugosity (Almany 2004, Graham 2014, Newman et al. 2015), as well as variables representing other components of the larger seascape within which corals exist. The findings from this study may help inform the design of field experiments to identify the mechanisms through which habitat availability may affect the sensitivity of reef fish communities to warming.

In conclusion, our study agrees with the growing consensus that climate change has affected, and will continue to affect, marine biodiversity, further underscoring the importance of slowing human impact on the myriad biological systems supporting important human activities. There is a dire need for effective traditional management mechanisms in the Caribbean region (Mahon 2002), and other studies suggest that interactions between climate impacts and unmanaged fisheries are likely to weaken the resilience of fish populations (Hsieh et al. 2006, Rijnsdorp et al. 2010). Our results also agree with a growing consensus that increasing the resilience of fish populations to climate impacts will involve management of the broader ecosystem (Levin & Lubchenco 2008, Sherman 2014), particularly through the designation and enforcement of marine protected areas (Agardy 1994, Hyrenbach et al. 2000). The implementation of such plans though will also need to consider the impacts of climate change on the distribution of critical reef fish habitats (Edgar et al. 2014), which have already experienced, and will undoubtedly continue to experience, the greatest impacts from climate change (Hoegh-Guldberg 2000, Orth et al. 2006, Gilman et al. 2008). It is only after measures such as those previously mentioned are considered that reef fisheries will begin to receive thorough protection against the present and future impacts of climate change.

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