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Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects

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On coral reefs, herbivorous fishes consume benthic primary producers and regulate competition between fleshy algae and reef-building corals. Many of these species are also important fishery targets, yet little is known about their global status. Using a large-scale synthesis of peer-reviewed and unpublished data, we examine variability in abundance and biomass of herbivorous reef fishes and explore evidence for fishing impacts globally and within regions. We show that biomass is more than twice as high in locations not accessible to fisheries relative to fisheries-accessible locations. Although there are large biogeographic differences in total biomass, the effects of fishing are consistent in nearly all regions. We also show that exposure to fishing alters the structure of the herbivore community by disproportionately reducing biomass of large-bodied functional groups (scraper/excavators, browsers, grazer/detritivores), while increasing biomass and abundance of territorial algal-farming damselfishes (Pomacentridae). The browser functional group that consumes macroalgae and can help to prevent coral–macroalgal phase shifts appears to be most susceptible to fishing. This fishing down the herbivore guild probably alters the effectiveness of these fishes in regulating algal abundance on reefs. Finally, data from remote and unfished locations provide important baselines for setting management and conservation targets for this important group of fishes.

1. Introduction

Understanding the causes and consequences of phase shifts from coral to algal dominance on tropical reefs has been a central theme in reef research for several decades [1–3]. Coral reef degradation generally results in a reduction in or loss of key ecosystem services including fisheries productivity, coastal protection and economic revenue associated with tourism. Primary drivers of system-wide shifts include anthropogenic disturbances occurring on both global and local scales [1,4,5]. Globally, anthropogenic carbon emissions have led to ocean warming and acidification that can profoundly reduce the growth and fitness of stony corals and other calcifiers [6]. Locally, and at the scale most relevant to resource managers, overfishing of herbivores, disease and declines in water quality can alter benthic competitive dynamics to favour fleshy algae over corals and other reef-building organisms [3,7–11]. However, we still lack comprehensive and necessary first-order knowledge of the magnitude and patterning of individual

disturbances around the tropics. Here, we conduct a global synthesis of the status of coral reef herbivorous fish populations, and investigate the potential impacts of fishing on the abundance, biomass and community composition of these fishes.

As consumers of benthic algae, coral reef herbivores directly affect the structure and composition of benthic communities. Numerous experimental studies have shown that herbivore exclusion quickly and consistently leads to dominance by fleshy turf or macroalgae across many marine ecosystems [10]. Similarly, observational studies in the Caribbean and the Pacific have found negative correlations between herbivorous fish biomass and macroalgal cover, suggesting that herbivores can exert top-down control on macroalgal abundance [12,13], but the magnitude of these effects may vary by system [14]. Other studies have shown that coral recruitment and the abundance of crustose coralline algae (CCA) are positively associated with grazing intensity [15] or the presence of grazers [7,8], suggesting that herbivores directly facilitate reef-building taxa. Further, some herbivores may regulate coral–algal competition by consuming seaweeds that produce allelopathic chemicals that cause coral mortality [16]. But because not all herbivores consume the same types of algae, at the same rates or in the same way, functional diversity within the guild should be considered and has been shown to increase resilience following bleaching events [17] and crown-of-thorns (*Acanthaster planci*) outbreaks [18]. Although herbivorous fishes are clearly important for regulating reef community structure and function, critical information is lacking about the status of this group of fishes globally.

Accurately characterizing the distribution and ecological roles of herbivorous fishes at broad spatial scales is challenging due to species-specific variability in feeding mode and biogeographic limits on species ranges [19]. Pooling species into higher taxonomic groups, such as major families or sub-families, is a common solution. However, because feeding behaviour can vary among species, even within families, examining how individual species feed may be more informative. Distinct herbivore feeding sub-guilds have been identified that are largely decoupled from taxonomy and instead defined by the feeding mechanism and behaviour of a given species [20,21]. However, dietary flexibility within some species is expected and precise functional designations of all species can be difficult without context-specific data [16,21–23]. Despite these limitations, functional group designations are useful for describing community-level feeding patterns, allow for broad biogeographic comparisons and provide an important characterization of how the herbivore guild as a whole may influence the reef benthos [23,24].

Coral reef fish assemblage structure has been examined over large spatial scales and across gradients of human population density (as a proxy for fishing intensity), latitude and across reserve boundaries [25–28]. These large-scale studies show clear declines in fish biomass and more equivocal patterns in numerical abundance with fishing pressure (although see [29]). Discrepancies between these biomass and abundance metrics probably arise from the fact that fishing disproportionately removes larger-bodied species and individuals, leaving many smaller individuals in heavily fished locations (high abundance, low biomass [25,30,31]). Several regional studies have shown negative effects of human populations on higher trophic-level reef fishes or fish assemblages as a whole, but much less is known about the impacts on the abundance, biomass or

composition of herbivorous fishes. Recently, Bellwood *et al.* [11] documented strong evidence of fishing effects on functional roles of parrotfishes (Scaridae) in the Pacific and Indian Oceans (e.g. corallivory, bioerosion), suggesting that fishing can systematically affect at least some functional characteristics of the herbivore community.

To more accurately characterize the role of herbivores in structuring coral reef benthic environments, comprehensive baseline knowledge of the abundance, biomass and composition of herbivorous fish assemblages across the tropics is needed. Further, before effective conservation strategies can be designed, there is a need to determine the direction and magnitude of the effects of fishing on this important group of coral reef fishes. Here, using a broad geographical approach, we collate and synthesize data from peer-reviewed publications and from rigorous monitoring programmes to establish comprehensive ‘current-condition’ levels of herbivorous fishes around the world and to assess the extent to which fishing alters their abundance, biomass and the structure of the assemblage.

2. Material and methods

(a) Database

We used ISI (now Thomson Reuters) Web of Knowledge to identify peer-reviewed studies that reported coral reef herbivorous fish abundance and biomass using the following search strings: coral reef and herb*; graz*; biomass; abundance; density; fish*. We only used studies that included metadata on reef zone/habitat (e.g. fore- versus back-reef), depth, year, description of sampling methods and survey effort (e.g. number of survey stations). We also used original data collected using underwater visual census (UVC) methods from 1989 to 2009. To enhance comparability between areas, only data from fore-reef sites between 5 and 20 m were included as this habitat type is available in most reef areas, it supports a high diversity and abundance of herbivorous reef fishes [32–34] and encompasses a depth range that includes the home ranges of many of the species of interest.

We limited our analyses to data collected using either of two standardized UVC methods—stationary point count (SPC) or belt transect (BLT) [35,36]. Although the relative efficacy of these methods is debated [37], they each sample roughly the same area (150–175 m²) and several studies have demonstrated that for most mobile non-cryptic mid-sized fishes there is little effect of method on estimates of density [28]. However, in order to ensure comparability between methods here, we conducted analyses explicitly testing the effects of sampling method on herbivore biomass. Given that we found little evidence of differences between methods (see electronic supplementary material, table S1), we pooled data collected using both methods for our regional and global analyses. Owing to the nature of our dataset (spanning across multiple years), we were unable to examine the effects of a variety of physical (exposure, temperature), chemical (nutrient availability) or biological (predator abundance, food availability) factors on herbivore populations and instead focused specifically on the probable effects of fishing on this important group of fishes.

(b) Accessibility by fisheries

All sites were classified as either ‘not fisheries accessible’ (NFA) or ‘fisheries accessible’ (FA) based upon human habitation, isolation and level of protection. Sites were classified as NFA if they were located on remote and uninhabited islands where fishing is formally banned or severely limited by remoteness (e.g. *de facto* marine reserves *sensu* Williams *et al.* [28]) or inside protected areas on

inhabited islands or coastlines. Because the efficacy of protected areas is a function of compliance, enforcement and reserve age [38,39], we identified sites within protected areas as NFA only if they had been protected from fishing for a minimum of six years, received institutional enforcement and lacked evidence of non-compliance. FA sites were the remainder of locations, which due to accessibility and regulations are likely to experience fishing.

Data varied in level of resolution, especially in terms of sampling design and taxonomic detail. While the majority of studies reported estimates of biomass and abundance (per unit area), approximately 31% of studies only reported abundance. Additionally in some regions only data from NFA locations, or alternatively FA locations, were available. Sample sizes of analyses reflect the availability of data specific to the question addressed (see below).

(c) Statistical analyses

(i) Total herbivore assemblage

Global assessment

The global mean for herbivore biomass and abundance across NFA and FA locations was calculated using all data compiled. The basic sampling unit was the 'site', the position where surveys were conducted. Site estimates were pooled to calculate 'location'-specific means. Locations were defined as continuous continental or bank areas, or islands and atolls; in some cases provinces or groups of many small islands (e.g. the Solomon Islands) were considered a location. To maintain sufficient statistical power, only locations with more than four sites were included in the analysis. Some of the data were reported only at the location level. When multiple estimates were available for a single location (e.g. separate studies or years), we calculated a single mean for that location. When comparing estimates of mean biomass and abundance worldwide, we pooled location estimates to compute global NFA and FA means. A two-sample *t*-test was used to determine whether significant differences existed in the abundance and biomass of herbivorous fishes between all NFA and FA locations.

Regional assessments

Where raw site-level data were available (see electronic supplementary material, table S2), we explored regional differences in herbivore biomass and abundance between NFA and FA locations. Here, regions were designated as a group of locations and usually represented individual archipelagos (e.g. the Hawaiian Islands); in some cases, due to a lack of adequate data, we pooled locations at higher levels based on natural geographical breaks (e.g. the Caribbean basin).

For some regions, data were non-normal, even after transformations, making use of parametric statistics inappropriate. Because comparisons of back-transformed values are often uninterpretable and data were not evenly available across study regions, a non-parametric bootstrapping procedure was used to calculate regional differences between NFA and FA locations. A repeated random resampling of site means with replacement was used to generate new location-level estimates [40]. These bootstrapped estimates of mean biomass and abundance from NFA and FA locations were then used to calculate regional means. By repeating this process 10 000 times, we estimated the distribution of probable differences between the means for NFA and FA locations within regions. We consider differences between NFA and FA means to be statistically significant if the 95% quantile range (QR) of bootstrapped differences does not overlap zero [28].

(ii) Functional groups

Using studies with full species lists and site-level data, we subdivided herbivorous fish assemblages into functional groups based broadly on the studies of Steneck [41] and Green & Bellwood [20]

and analysed the effects of fisheries accessibility on each group separately. Four herbivore functional groups were considered: (i) scraper/excavators, (ii) grazer/detritivores, (iii) browsers and (iv) territorial damselfishes (see electronic supplementary material, figure S1; electronic supplementary material, table S3 for designations). Deviations in previous designations were adopted because we were unable to separate the large versus small scraper/excavators groups due to lack of size data from published studies and lack of fine-resolution feeding behaviour for some non Indo-Pacific species. Additionally, we designated *Ctenochaetus* spp. as grazer/detritivores as they have been shown to consume significant amounts of turf algae [42]. Finally, we included territorial damselfishes as they are herbivores and we were interested in examining the entire herbivorous fish assemblage.

Scraper/excavators graze primarily on turf algae but often remove portions of the underlying carbonate substratum as they feed. Grazer/detritivores intensely graze turf algae but rarely alter the underlying substratum; some species also obtain portions of their diets by feeding on organic material in sediments. Browsers feed almost exclusively on macroalgae and associated epiphytic material, removing only the algae without directly affecting the underlying substratum. Finally, territorial damselfishes comprise the only group whose unique behaviour is linked by taxonomy; they employ a grazer/detritivore feeding method but also aggressively repel competitors and selectively cultivate algal farms that can differ markedly from outside territories [43,44]. When available, species were categorized based on previously published designations; the remainder were categorized based on the best available dietary and behavioural information.

To test whether fisheries accessibility altered the structure of the herbivorous fish guild globally, a non-parametric bootstrapping procedure was used. However, instead of calculating mean differences, we generated a distribution of scale-independent ratios between the biomass means for NFA and FA locations for each of the four functional groups. Statistically significant differences were reported if the 95% QR of the biomass ratio did not overlap 1.

Analyses were performed using the program R version 2.9.2 (<http://www.r-project.org>).

3. Results

(a) Effects of fishing on total herbivore assemblage

We collected 2706 site-level estimates of biomass and abundance from 145 locations across the globe (figure 1). Biomass values varied among regions and across locations, ranging from 2.5 g m⁻² at the FA sites of Santa Rosa, Mariana Islands, to 175.1 g m⁻² at NFA sites in the Seychelles (figure 2). The grand mean biomass of herbivores in NFA locations was 56.4 g m⁻² (± 7.9 s.e.) which was significantly greater than at FA locations with only 20.5 g m⁻² (± 1.6 s.e.; $T = 9.5$, $p < 0.001$). There was no significant difference in numerical abundance of herbivores across levels of fisheries accessibility ($T = 0.4$, $p > 0.10$; electronic supplementary material, table S4 and figure S2), with an average of 0.48 individuals (ind.) m⁻² (± 0.13 s.e.) at NFA locations and 0.55 ind. m⁻² (± 0.54 s.e.) at FA locations.

Biomass varied considerably within and among regions (figure 2) but overall NFA locations tended to support higher biomass values than FA locations (see electronic supplementary material, table S4). For all regions where raw site-level data were available, the estimated difference in biomass between NFA and FA locations ranged

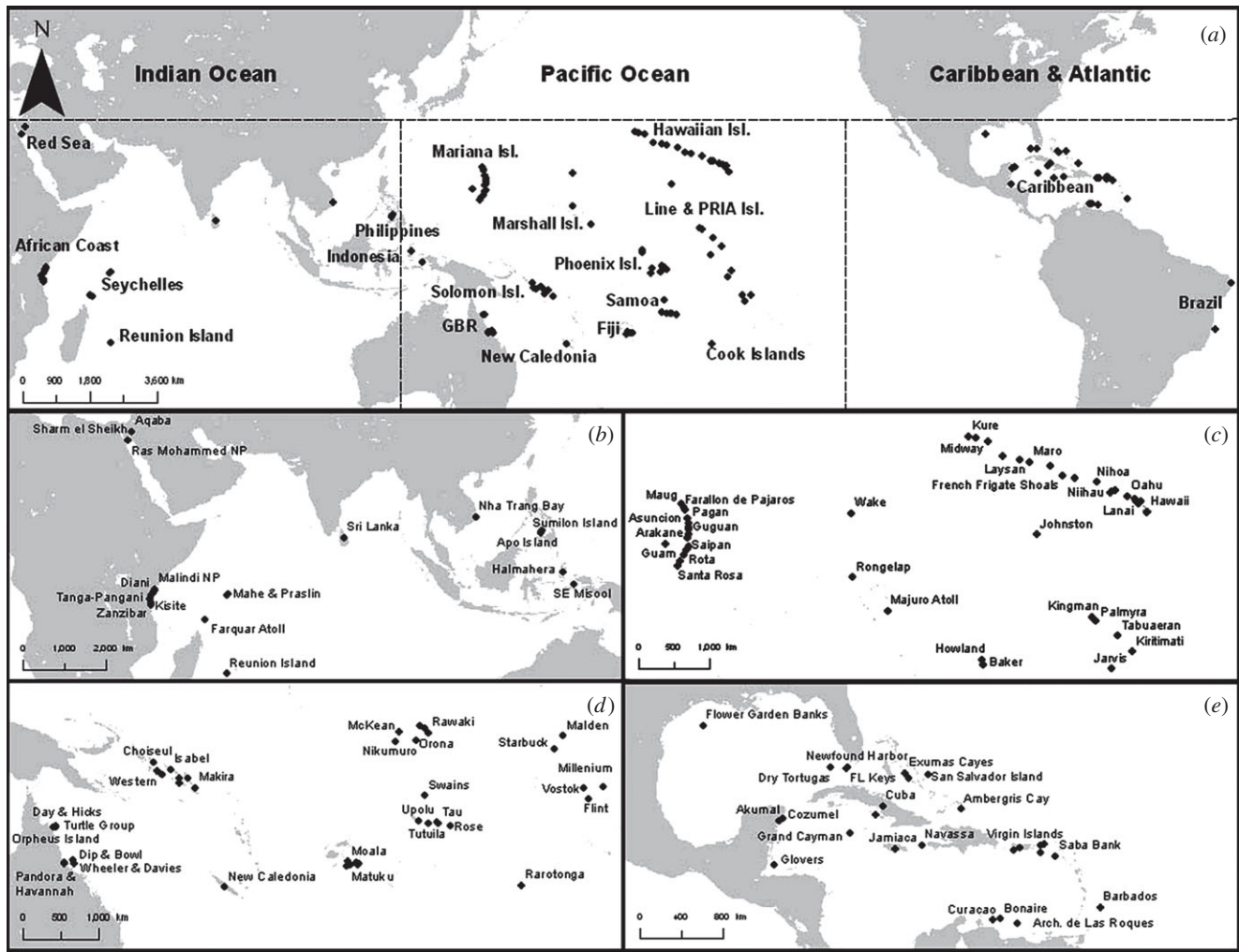


Figure 1. (a) Distribution of locations included in the database. Dotted lines delineate ocean basins and inset maps (b–e) are provided for detail. The number of survey sites ($n > 4$) and the types of data (abundance versus biomass) for each sampling location are variable (see electronic supplementary material, table S2). Some location names have been excluded from inset maps for ease of display. Identification of locations as FA or NFA is shown in electronic supplementary material, table S2.

between 6.6 and 25.4 g m^{-2} (95% QR) with a median of 15.6 (figure 3a), indicating moderate-to-strong declines in biomass in fisheries-accessible locations. By contrast, the 95% QR of the mean difference in abundance between NFA and FA locations included zero, with some regions having higher abundance and others having lower abundance or demonstrating no difference (figure 3b; electronic supplementary material, figure S3 and tables S3 and S4).

(b) Effects of fishing on herbivore functional groups

We analysed the effects of fisheries accessibility on herbivore functional groups for 109 locations around the globe. None of the functional group response ratios (between the NFA and FA locations) overlapped 1, indicating significant differences for all groups (figure 4). Specifically, three functional groups (scraper/excavators, browsers and grazer/detritivores) showed significantly lower biomass at locations accessible to fishing. However, these three groups showed no difference in abundance between NFA and FA locations. By contrast, both biomass and abundance for territorial damselfish were greater at FA locations.

Biomass of scraper/excavators was 14.4 g m^{-2} (± 1.0 s.e.) and 9.5 g m^{-2} (± 0.4 s.e.) at NFA and FA locations, respectively, or 33% (95% QR: 8–57) lower biomass at FA locations. Browser biomass was 21.9 (± 11.1 s.e.) and 2.0 g m^{-2} (± 0.4

s.e.) at NFA and FA locations, respectively, or more than 80% lower biomass at FA locations (95% QR: 70–88). Biomass of the grazer/detritivores was 17.5 (± 1.6 s.e.) and 8.4 g m^{-2} (± 1.1 s.e.) at NFA and FA locations, respectively, amounting to more than 50% (95% QR: 48–61) lower biomass at FA locations. Territorial damselfish made the smallest contribution to total biomass with 1.0 (± 1.7 s.e.) and 1.3 (± 1.7 s.e.) g m^{-2} or 2 and 6% of total herbivore biomass at NFA and FA locations, respectively. Territorial damselfishes were the only group with higher biomass at FA locations (45% higher; 95% QR: 4–85) and were the only group that showed a significant difference in numerical abundance, with 0.9 (± 0.2 s.e.) and 1.2 (± 0.1 s.e.) ind. m^{-2} at NFA and FA locations, respectively ($T = -2.5$, $p = 0.05$).

4. Discussion

The locations included in this analysis span a range of environmental and oceanographic parameters (e.g. temperature, productivity, exposure, depth) known to influence the structure of local fish stocks. Despite such variability, our results show that globally, herbivorous fish assemblages at locations not accessible to fisheries supported on average more than twice the total biomass, relative to those accessible to fisheries. Although other studies have noted similar trends

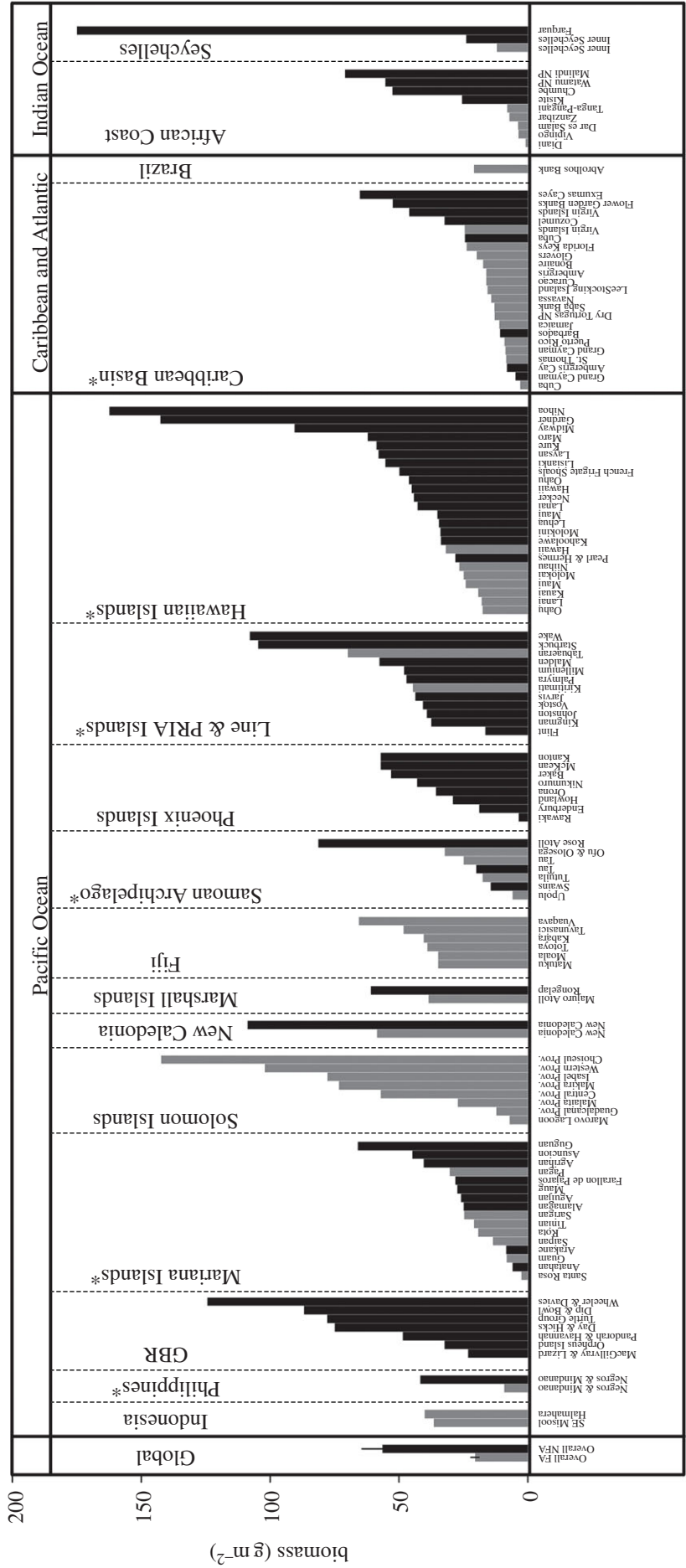


Figure 2. Mean herbivore biomass (g m^{-2}) for NFA (black bars; $n = 86$) and FA (grey bars; $n = 74$) across the globe ($n > 4$ sites per location) organized by ocean basin and geographical region (dashed lines). Regions are arranged longitudinally. The grand mean (± 1 s.e.) of herbivore biomass at NFA and FA locations is shown on the far left. Asterisks indicate regions where raw site-level data were available to conduct more detailed regional comparisons (figure 3). GBR, Great Barrier Reef; PIRIA, Pacific Remote Island Areas.

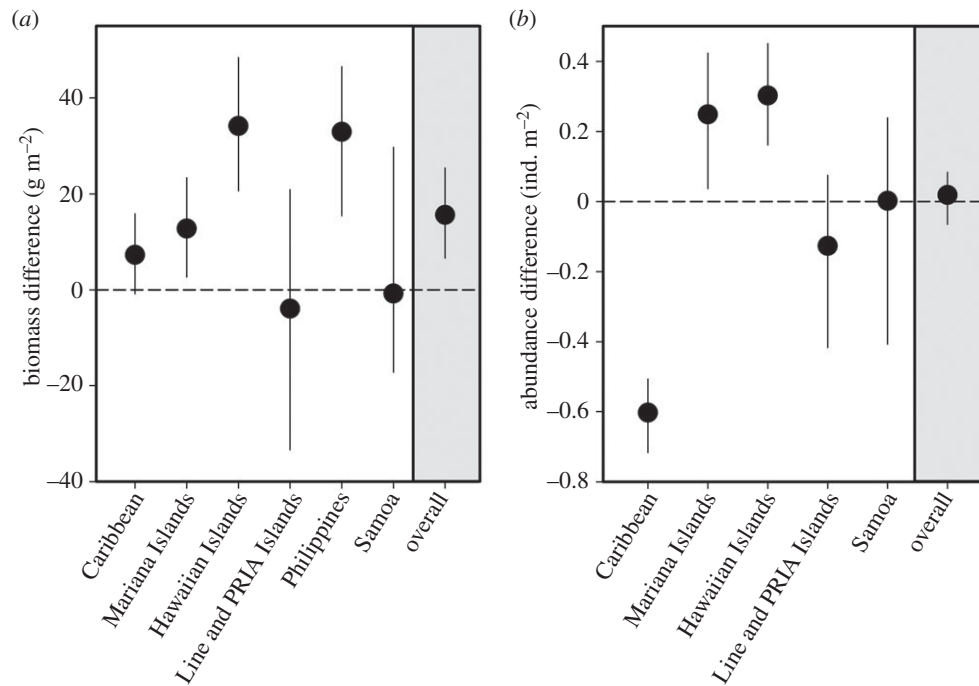


Figure 3. Distribution of mean bootstrapped differences between NFA and FA locations among regions around the world (see asterisks in figure 2) for: (a) herbivorous fish biomass (g m^{-2}) and (b) abundance (ind. m^{-2}). Circles are median differences within regions; vertical lines are 95% quantile ranges of differences. Dashed lines represent mean differences of 0 indicating no significant difference between FA and NFA locations within regions.

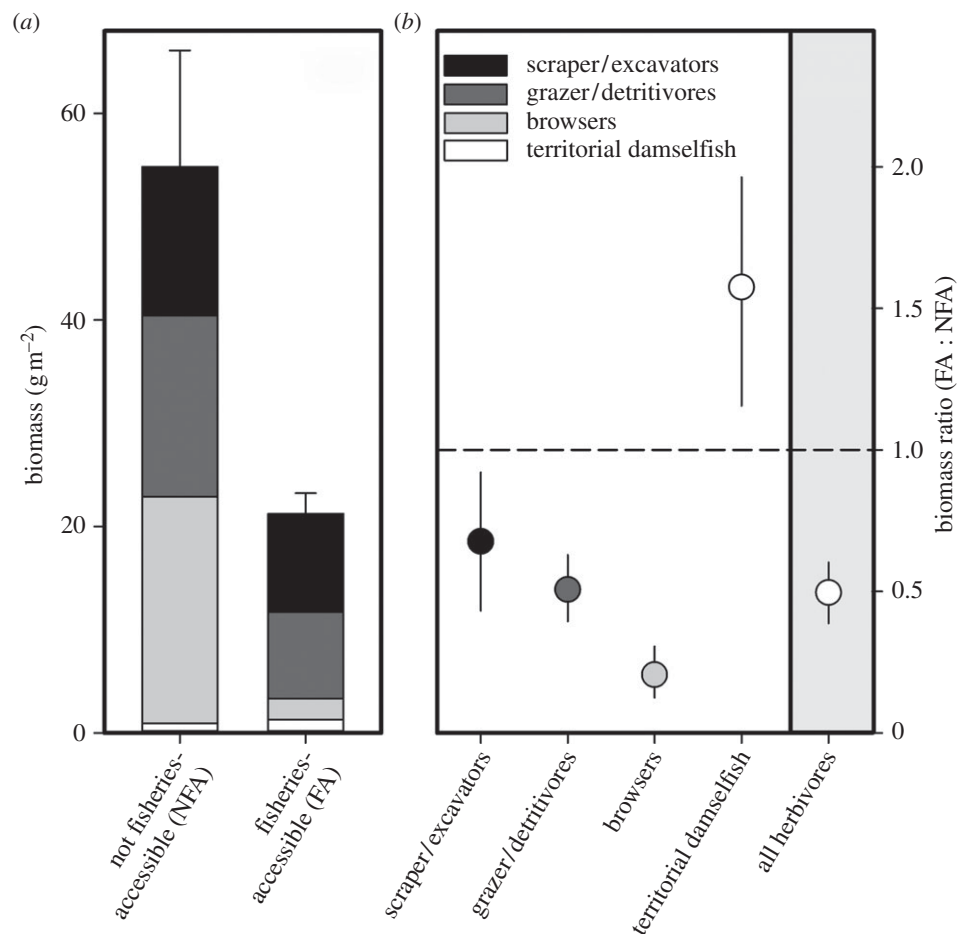


Figure 4. Bootstrapped functional group biomass at NFA and FA locations around the world. (a) The bar on the left is the mean of NFA locations ($n = 57$) and the bar on the right is the mean of FA locations ($n = 52$). Vertical lines are ± 1 s.e. for the entire herbivore assemblage and data are broken down into the respective feeding guilds. (b) Bootstrapped biomass ratios of overall herbivore and functional group biomass (g m^{-2}) between NFA and FA locations around the world; circles are medians and vertical lines are 95% quantile ranges of ratios. The dashed line indicates a ratio of 1 (no significant difference in biomass between FA and NFA locations).

in herbivore biomass across regional gradients in fishing pressure [11,28,45], this is the first study to demonstrate this pattern globally.

Despite strong evidence of fishing impacts on herbivorous fish biomass, there was no clear pattern in numerical abundance between NFA and FA locations. These contrasting patterns between biomass and abundance suggest an alteration in the size structure of the herbivorous fish assemblage, as has been observed in other regional studies investigating fishing effects on all reef fishes [25,46]. In our study, the more than twofold decline in herbivore biomass, but no difference in abundance, indicate that FA locations are dominated by a relatively higher number of smaller-bodied fish. Shifts in the overall size structure can result from within-species reductions in size or among-species shifts in relative abundance favouring smaller-bodied species [46]. Both have important consequences for the emergent foraging capacity of the herbivore guild, as there are size-dependent effects, within and among species and functional groups, on algal consumption and feeding impacts. Larger individuals generally consume more algae and expose larger areas of substratum [22,47]. A shift to smaller-bodied fishes may also result in a loss of key ecological functions provided by the largest species, such as bioerosion and coral predation by scraper/excavators [11] and the targeted removal of macroalgae, including many allelopathic taxa, by browsers [16]. Thus, reductions in total herbivore biomass and a shift to smaller-bodied fishes may lead to multiplicative declines in herbivory potential—less herbivore biomass with lower foraging capacity per unit biomass with less breadth of potential algal prey.

Our most striking finding was the extreme range of herbivore biomass values observed across study locations, in particular the high values reported from some remote, protected NFA locations. Several NFA locations across the Pacific (Nihoa and Gardner: Northwestern Hawaiian Islands, Wake: central Pacific, Starbuck: Line Islands and Wheeler and Davies Reefs: Great Barrier Reef) and the Indian Ocean (Farquar: Seychelles) have herbivore biomass values exceeding 100 g m^{-2} (figure 2). These trends still hold even after removing the largest-bodied species (e.g. *Bolbometopon muricatum* and *Chlorurus* spp.) from the analysis. The biomass potential of the herbivore assemblage is highlighted when comparing these values to total fish biomass from some FA locations. Our global mean herbivore biomass from NFA locations was 56.4 g m^{-2} , while a recent study estimated the total reef fish biomass from inhabited islands in Hawaii, the Marianas and American Samoa to be 33.2 g m^{-2} [28]. Herbivores clearly play an important trophic role on coral reefs, and our findings show that their contribution to total fish biomass and fisheries potential should not be undervalued.

There are notable differences in the biomass of the herbivorous fish guild across the globe, with the Caribbean having particularly low values (see electronic supplementary material, table S2). The highest values reported from the Caribbean were from a protected area in the Bahamas with approximately 65 g m^{-2} ; however, many locations have much lower values (figure 2). These low biomass values may be due to reduced regional species richness or complete absence of many of the largest-bodied herbivore taxa, including large parrotfishes and many browsers (e.g. *Naso* spp.). Alternatively, lower herbivore biomass may be the result of a longer history and greater impact of fishing in the Caribbean, including poaching in NFA locations; thus, our results

may not reflect the true biomass potential in this region. Large differences in herbivore biomass between Pacific and Caribbean reefs have been previously noted (Pacific: 29.0 and Caribbean: 9.25 g m^{-2}) and may possibly explain why the Caribbean seems more susceptible to macroalgal blooms than the Pacific [14]. However, with a larger dataset, we show a wider range of values across basins and, importantly, demonstrate a much higher biomass potential for both the Pacific and the Caribbean (mean herbivore biomass in NFA sites: $59.9 (\pm 2.2)$ and $29.2 (\pm 6.2) \text{ g m}^{-2}$, respectively). If management strategies are to be effective at increasing the feeding capacity of the herbivore guild, restoration targets should not be based on limited data from highly exploited areas. Rather, they should consider the maximum potential biomass of locations not accessible to fishing within and among regions.

The binary evaluation of sites as NFA/FA allows for a straightforward examination of the effects of fishing on fish populations. Because this approach does not quantify levels of fishing our results are probably conservative, underestimating the true differences in herbivore biomass between the most remote locations and the most heavily fished ones [28]. For example, unprotected sites in Jamaica with a human population density of 23 people per square kilometre were classified as FA and had a mean biomass of 16 g m^{-2} . However, the Western Province of the Solomon Islands, with only 5.2 people per square kilometre but also classified as FA, supports some of the highest biomass values observed (102.1 g m^{-2}). Similarly, NFA locations include areas near large population centres such as protected areas on densely populated islands (e.g. Oahu, Hawaii), where active or inadvertent reductions of herbivores are probable, as well as isolated locations, such as in the Line and Northwestern Hawaiian Islands, hundreds of kilometres away from any direct human disturbance. Without standardized measures of fishing intensity, it is difficult to move beyond simple designations of fisheries accessibility. However, despite the crudeness of our designations, mean herbivore biomass values in NFA locations were still more than double those in FA locations.

Alterations of consumer communities due to anthropogenic activities have been linked to myriad dramatic shifts in structure and functioning of ecosystems worldwide [48]. Although many of these shifts are caused by reductions in the abundance (or biomass) of key consumers, it is also important to consider functional transitions within trophic groups. For example, disproportionate reductions of large-bodied herbivores due to exploitation by Late Pleistocene humans of the Beringia tundra have been implicated in broad-scale transitions of the biome from domination by grasses to mosses [49]. Herbivorous megafauna on land maintained more open and heterogeneous vegetative assemblages due to their physical impacts on plants. With the extinction of many of these large herbivores, there is consistent evidence of the emergence of more dense and homogeneous vegetative landscapes [50]. Because of the ecosystem services conferred disproportionately by large-bodied herbivores, some scientists and conservationists have proposed the so-called 'Pleistocene re-wilding' of landscapes to restore the critical ecosystem services provided by large animals.

A parallel pattern of anthropogenic downsizing of herbivores is evident in our study where there is significantly lower biomass of all feeding guilds of herbivorous fishes, aside from the smallest-bodied taxa, in areas accessible to

fishing. The preferential removal of larger-bodied fish species has been well documented [30], but this is the first study to show this globally for the herbivore guild. While the magnitude of the effects of fishing varied by functional group—the biggest reductions occurred in the large-bodied browser group, followed by the grazer/detritivores and scraper/excavators. By contrast, the biomass and numerical abundance of territorial damselfishes were greater at FA locations. Because of the vastly different and complementary roles that different herbivore functional groups play on reefs [23], it is probable that declines in biomass and changes in community structure associated with fishing are altering the capacity of the group as a whole to control algal communities on reefs around the world.

Here, we show a 33% reduction in the biomass of the largest-bodied functional group, the scraper/excavators, on fisheries-accessible reefs globally. The largest-bodied taxa within this group, such as *Bolbometopon*, *Chlorurus* and some *Scarus* species, are highly prized in many artisanal fisheries. As such, in 2007, due to high levels of exploitation and declining populations throughout most of its range, *Bolbometopon muricatum* was listed as ‘vulnerable’ on the IUCN Red List. Declining scraper/excavator populations may significantly threaten reef health as these fish perform a variety of ecosystem functions in addition to algal grazing, including sediment removal, bioerosion and coral predation, the latter two of which have been shown to be highly vulnerable to fishing in some locations [11]. Some species of parrotfish also consume macroalgae and thus may functionally overlap with the browser group described below [16,23]. Fishing-induced declines in parrotfish populations are known to result in the loss of vital ecosystem services that are key components of reef resilience [11]. Though we show only moderate declines in this group relative to others, our results highlight a need to protect and restore declining scraper/excavator populations if we are to maintain the important ecological services that they provide.

The browser functional group appears to be most susceptible to fishing (figure 4), with a biomass decline of approximately 80% at fished locations worldwide. This group consists of a diverse assemblage of fishes from a number of different families (e.g. Acanthuridae-Nasiinae, Labridae-Scariinae, Kyphosidae and Siganidae) and is particularly important for reef health and resilience as they feed almost exclusively on macroalgae. Further, some browser species specifically consume macroalgae that directly compete with corals, cause coral mortality via the production of toxic allelochemicals and lower coral recruitment and growth rates [16,51,52]. Thus, browser diversity and feeding complementarity are important for controlling the abundance of a suite of macroalgal taxa [23]. A recent study on the GBR following a bleaching event found that the only reef out of several examined that suffered a coral-to-macroalgal phase shift had extremely low browser diversity and abundance [17], highlighting the importance of this group for resilience. The massive global depletion of browsers probably indicates a diminished capacity of fished reefs to recover following disturbance events and to defend against phase shifts to macroalgal dominance.

The fishes in the grazer/detritivores group (mostly Acanthurids) feed almost exclusively on organic matter/detritus or turf algae, which directly compete with corals for space, prevent coral recruitment, directly overgrow corals and trap sediments [53]. Species in this mid-sized functional

group tend to have the highest bite rates and probably are major contributors to the cropping of turf algae, often the first benthic functional group to increase in abundance following coral mortality [53]. Despite their clear importance, grazer/detritivores comprise a larger proportion of total herbivore biomass at FA areas relative to NFA areas, suggesting an overrepresentation of a functional group that neither specializes in removing large macroalgae nor directly creates space for coral and CCA recruitment. Nonetheless, this group clearly plays an important role in keeping algal turfs cropped and clearing organic matter from the reef benthos; thus, the large impacts we observe on this group are probably affecting reef health to some degree in fished locations.

Territorial damselfishes are not common fishery targets so were not expected to vary across FA and NFA locations; thus, our finding of greater biomass and numerical abundance of this group at FA locations was interesting. The causes of damselfish population increases in fished locations are probably indirect and associated with a reduction in both predation and competition due to general overfishing [46,54]. These fishes are active algal farmers and aggressively defend territories against competing herbivores. Inside territories, CCA, coral colony and recruit density tend to be reduced, while turf, macroalgae and cyanobacteria increase, and may represent a cumulative decline in reef health within territories [43,44,55]. Given that territoriality is more effective against smaller schools of fish, the interaction of increased density of this functional group and reduced density of other groups may exacerbate the negative effects of these fish on the benthos [54]. Further, the reduction in biomass of all other herbivore functional groups and an increase in the biomass and abundance of territorial damselfish at FA locations suggest that fishing not only reduces the capacity of the herbivore guild to consume algae but may also enhance algal growth and abundance by promoting algal farming.

5. Conclusion

This study represents the first global assessment of the status of herbivorous fishes on coral reefs. We show that herbivore biomass is reduced by more than 50% in locations accessible to fishing, and provide important baselines for the structure of herbivore communities in remote, uninhabited islands and protected areas. While biomass is clearly impacted by fishing, numerical density of herbivores shows no difference between FA and NFA reefs. These contrasting patterns indicate that fishing has disproportionately removed larger-bodied species and/or functional groups. This ‘fishing down the herbivore guild’ leads to a reduction in biomass of all herbivore feeding groups other than small territorial damselfishes, which show the opposite pattern. Territorial damselfishes, through aggressive defense of algal farms, can negatively affect coral growth and recruitment. Thus, our results demonstrate that fishing probably reduces the ability of herbivore communities to maintain top-down control on coral reef algal communities.

Because of global declines in coral cover, benthic reef communities today probably have much more algae present than they did in the past. Thus, a much greater area needs to be grazed to maintain low algal standing stock and allow coral recruitment, survival and growth. Resource managers may therefore need to manage herbivore populations to be much

larger than they ever were naturally, in order to effectively control algal abundance on degraded reefs. Moreover, because of the complementarity among herbivore functional groups, it is important to ensure that members of each group are represented if the full suite of ecological services they provide is to be preserved. Even within a given functional group, diversity, complementarity and redundancy of different taxa will probably help to ensure the stability and resilience of reefs to disturbance events. Most management strategies today focus on restoring overall fish populations to levels comparable to unfished reefs, without specific focus on herbivore assemblages. Given that this is impractical in many locations, we believe that more effort should be directed towards managing both the biomass and composition of key groups of fishes, such as the herbivores. Finally, our results from unfished locations provide important templates that can be used for setting

management priorities for herbivorous fish populations, both regionally and around the globe.

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