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GLOBAL ASSESSMENT OF THE STATUS OF CORAL REEF HERBIVOROUS FISHES:
EVIDENCE FOR FISHING EFFECTS

A Thesis submitted in partial satisfaction of the requirements for the degree

Master of Science

in

Biology

by

Clinton Brook Edwards

Committee in charge:

Professor Jennifer Smith, Chair
Professor Jonathan Shurin, Co-Chair
Professor Joshua Kohn
Professor Stuart Sandin

2013

The Thesis of Clinton Brook Edwards is approved and it is acceptable in quality and form for publication on microfilm and electronically:

Co-Chair

Chair

University of California, San Diego

2013

Dedication

To my sister Katee, who never had the opportunity to grow old and define new dreams as old ones were reached. I will carry your purple spirit with me wherever I go.

To my sister Shannon...nobody makes me more mad or proud!!!! I love you!!

To Brandon.....my co-conspirator, brother and best friend. You taught me to be proud of being smart, to be bold in my opinions and to truly love people. Thank you.

To Seamus, Nagy, Neil, Pete, Pat, Mikey B and Spence dog. Learning to surf with you guys has been one of the true honors of my life.

To the madmen, Ed, Sean, Garth, Pig Dog and Theo. Not sure if thanking you guys is necessarily the most appropriate course of action but I am certain that I would not be here without you guys....

To my parents and Rozy.....this is as much your thesis as it is mine.

Epigraph

No man is an island, Entire of itself.

Each is a piece of the continent, A part of the main.

If a clod be washed away by the sea, Europe is the less.

As well as if a promontory were. As well as if a manor of thine own, Or of thine friend's were.

Each man's death diminishes me, For I am involved in mankind.

Therefore, send not to know For whom the bell tolls,

It tolls for thee.

-John Donne

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ABSTRACT OF THE THESIS

GLOBAL ASSESSMENT OF THE STATUS OF CORAL REEF HERBIVOROUS FISHES:
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by

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Professor Jennifer Smith, Chair

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Herbivores provide important ecological services across ecosystems where they influence productivity and plant community composition. 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 worldwide synthesis of herbivorous reef fishes we show that biomass is more than

twice as high at sites not accessible to fishing relative to fished sites. Further, while there are large biogeographic differences, the effects of fishing on herbivorous fish biomass are independent of regional effects. Further, fishing alters community structure by disproportionately reducing biomass of larger-bodied functional groups, while increasing both biomass and abundance of smaller territorial damselfishes. This fishing down the herbivore guild likely alters the effectiveness of these fishes to regulate algal abundance on reefs. Our study reveals that herbivores are systematically affected by fishing and provides insights and baselines for herbivore assemblages which can be used for developing informed management targets globally.

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 over the past decades (1-3). Coral reef degradation generally results in a reduction in or loss of key ecosystem services including fisheries productivity, biodiversity conservation, coastal protection and economic revenue associated with tourism (4). Primary drivers of system-wide shifts include anthropogenic disturbances occurring on both global and local scales (1, 5, 6). Globally, anthropogenic carbon emissions have led to ocean warming and acidification which can profoundly reduce the fitness of stony corals and other calcifiers (7). Locally, and at the scale most relevant to resource managers, nutrient pollution, disease and reductions in herbivory caused by fishing can alter benthic competitive dynamics to favor fleshy algae over corals and other reef builders (1, 3, 8, 9). Despite the need to understand the interactions among anthropogenic stressors, we still lack comprehensive knowledge of the magnitude and patterning of individual disturbances around the tropics. Here we provide 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 important reef fish.

As consumers of benthic algae, coral reef herbivores directly affect the structure and composition of benthic communities. Experimental removal of herbivores quickly and consistently leads to dominance by fleshy turf or macroalgae

across many marine ecosystems (10). Field studies in the Caribbean and the Pacific have found negative correlations between herbivorous fish biomass and macroalgal cover, suggesting that herbivores can exert strong top down control on macroalgal abundance (11) but the magnitude of these effects may vary by system (12). Other studies have shown that coral recruitment and the abundance of crustose coralline algae (CCA) are positively associated with grazing intensity (13, 14) suggesting that herbivores directly facilitate growth of calcifying taxa. In addition to their ability to intensely graze algae, scraping and excavating herbivores (e.g. parrotfishes) are particularly important for coral reef resilience and recovery by exposing bare substrata that opens space for CCA and coral recruitment (9, 13, 15). While herbivorous fishes are clearly important for regulating reef community structure and therefore function, little is known about their status globally.

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 (11, 16-22). These large-scale studies show clear declines in fish biomass and more equivocal patterns in numerical abundance with fishing pressure (although see: (23)). Discrepancies between metrics likely arise from the fact that fishing disproportionately removes larger bodied species and individuals, leaving many small individuals in heavily fished locations (high abundance, low biomass (17, 22, 24)). Many regional studies have shown large scale 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 and biomass of herbivorous fishes.

It is challenging to accurately characterize the distribution and ecological roles of herbivorous fish assemblages at broad spatial scales due to species-specific variability in feeding mode and biogeographic limits on species ranges. One solution is to pool species into higher taxonomic groups, for example considering densities of fish from major families or subfamilies. However, due to variation in feeding behaviors among species, even within families, it may not be appropriate to focus on taxonomic groupings, but instead on how individual species feed. Distinct feeding groups/functional groups, have been identified among herbivorous reef fishes that are largely decoupled from taxonomy and are defined instead by the feeding mechanism and behavior of given species (25). Considering the distributions of fishes based on these functional-groups can provide a more informative characterization of how the herbivore guild as a whole can influence the benthos (26, 27).

A first step toward identifying the role of herbivores in structuring coral reef benthic environments is to establish comprehensive baseline knowledge of the abundance, biomass and composition of herbivorous fish assemblages across the tropics. Further, in order to build effective conservation strategies, there is need to determine the direction and magnitude of the effects of fishing on coral reef herbivorous fish assemblages. Here, using a broad geographical approach, we collate and synthesize peer-reviewed literature and data from rigorous monitoring programs

to establish comprehensive 'current-condition' levels of herbivorous fishes around the world and to assess the extent to which fishing alters the structure of herbivorous fish assemblages.

Methods and Materials

Database

We searched the peer-reviewed literature using ISI Web of Knowledge database to identify 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 detailed metadata on reef zone/habitat (e.g. fore vs. back reef), depth, year of survey, description of sampling methods and survey effort (e.g. number of survey stations). We also include original data collected by the authors using underwater visual census (UVC) methods from 1989-2009. To enhance comparability between areas, only data from fore-reef sites between 2-20 m are included as this habitat type is consistently available in most reef areas, and supports a high diversity and abundance of herbivorous reef fishes (42-44).

We limited our analysis to data collected using either of two standardized UVC methods- stationary point count (SPC) or belt transect (BLT) (19, 45). While there is debate regarding the biases of these methods (46, 47), several studies have suggested that for many mobile non cryptic mid-sized fishes this bias is negligible and prior studies have made use of combined estimates from these two methods (29, 48). We pooled estimates from both methods when computing regional and global means.

Accessibility by Fisheries

All sites were categorized into distinct levels of fisheries accessibility based upon human habitation, isolation and level of protection. We designated two levels – “not fisheries accessible” (NFA) and “fisheries accessible” (FA). NFA sites were located on remote and uninhabited islands where fishing is formally banned or severely limited by remoteness (e.g., de facto marine reserves) or they were on inhabited islands or coastlines but inside protected areas (as per Williams et al. 2011). Because the efficacy of protected areas is a function of compliance, enforcement, and reserve age (21, 49), we identified sites within protected areas as NFA if they had been protected from fishing for a minimum of 6 years, enforcement and evidence of 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 the herbivorous fish assemblage in units of biomass and abundance (both estimated per unit area), ~ 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).

Statistical Analyses

Total Herbivore Assemblage

(i) 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 and/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 >4 sites were included in the analysis. Some of the data extracted from the literature 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.

(ii) Regional Assessments: Using the subset of data where raw site-level data were available (Table S1), 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 geographic breaks (e.g. the Caribbean basin).

For some regions data were non-normal, even after transformations, making use of parametric statistics inappropriate. Also, because comparisons of backtransformed values are often un-interpretable and data were not evenly available across study regions leading to an unbalanced design, a rigorous 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 (50). These bootstrapped estimates of mean biomass and abundance from NFA and FA locations were then used to calculate regional level means. By repeating this process 10,000 times, we estimated the distribution of likely 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 0 (29).

Functional Groups

Using studies which provided full species lists and site level data, we subdivided herbivorous fish assemblages into functional groups/feeding sub-guilds based broadly on Green & Bellwood (2009) and analyzed the effects of fisheries accessibility on each group separately. Four herbivore functional groups were

considered: 1) scrapers/excavators, 2) grazer/detritivores, 3) browsers and, 4) territorial damselfishes (see Table S2 for designations). Deviations from Green and Bellwood (2009) 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 behavior for some non Indo-Pacific species.

Additionally, we included *Ctenochaetus* spp. as grazer/detritivore as they have been shown to consume significant amounts of turf algae (51). Finally, we included territorial damselfishes as they are herbivores and we were interested in examining the entire herbivorous fish assemblage.

Scrapers/excavators graze primarily on turf algae but they often remove portions of the underlying carbonate substratum as they feed. Grazers/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. Territorial damselfishes comprise the final group whose unique behavior 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 (39, 40). When available, species were categorized based on previously published designations; the remainder were categorized based on the best available dietary and behavioral information.

To test whether fishery accessibility altered the structure of the herbivorous fish guild globally, a non-parametric bootstrapping procedure was again used. However, instead of calculating mean differences, we generated a distribution of ratios between the biomass means for NFA and FA locations for each of the four functional groups. Application of ratios provides a scale-independent means of quantifying the impact of fisheries accessibility on each of the herbivore functional groups. A statistically significant difference in means was 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>).

Results

Effects of Fishing on Total Herbivore Assemblage

We collected 2706 site level estimates of biomass and abundance from 145 locations distributed 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 areas was 56.4 g m⁻² (± 7.9 SE) which was significantly greater than at FA locations with only 20.5 g m⁻² (± 1.6 SE; $T = -9.5$, $p < 0.001$). There was no significant difference in numerical abundance of herbivores across levels of fisheries accessibility ($T = 0.4$, $p > 0.10$; Table S3; Figure S1), with an average of 0.48 individuals m⁻² (± 0.13 SE) at NFA locations and 0.55 individuals m⁻² (± 0.54 SE) at FA locations.

There was considerable variability in biomass within and among regions (Figure 2) but there was an overall tendency for NFA locations to support higher herbivorous fish biomass than FA locations (Table S3). When considering all regions where raw site level data were available, the estimated difference in biomass between NFA and FA locations ranged between 6.6-25.4 g m⁻² (95 % QR) with a median of 15.6 (Figure 3a), indicating moderate to strong declines in biomass in areas accessible to fishing pressure. In contrast, the 95% QR of the mean difference in abundance between NFA and FA locations included 0, with some regions having

higher numerical abundance and others having lower abundance or demonstrating no difference (Table S3, Figures 3b and S2).

Effects of Fishing on Functional Group Variation

Analysis of the effects of fishing accessibility on herbivore functional groups was completed from 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 guilds (Figure 4). Specifically, three functional groups (scraper/excavators, browsers and grazers) showed significantly lower biomass at locations accessible to fishing. However, these three groups showed no difference in abundance between NFA and FA locations, indicating a reduction in the mean body size of these fishes within individual groups. In contrast, both biomass and abundance for territorial damselfish were greater at FA locations.

Biomass of scraping/excavating herbivores was 14.4 g m^{-2} ($\pm 1.0 \text{ SE}$) and 9.5 g m^{-2} ($\pm 0.4 \text{ SE}$) at NFA and FA locations, respectively, amounting to 33% (95% QR: 8-57) lower biomass at FA locations. The scraper/excavators contributed to just over 25 and 45 % of the overall guild biomass at NFA and FA locations, respectively. Browser biomass was 21.9 ($\pm 11.1 \text{ SE}$) and 2.0 g m^{-2} ($\pm 0.4 \text{ SE}$) at NFA and FA locations, respectively, amounting to > 80 % lower biomass at locations with fishing (95% QR: 70-88). The proportional contribution to the overall guild biomass of browsing herbivores was 40 and 9.5% at NFA and FA locations, respectively. The biomass of the

grazer/detritivore functional group was $17.5 (\pm 1.6 \text{ SE})$ and $8.4 \text{ g m}^{-2} (\pm 1.1 \text{ SE})$ at NFA and FA locations, respectively. This represents $> 50\%$ (95% QR: 48-61) lower biomass of grazer/detritivores at FA locations. Overall the grazer/detritivore group made up 31 and 40% of total herbivore biomass at NFA and FA locations, respectively.

Territorial damselfish comprised the smallest portion of the overall guild biomass with $1.0 (\pm 1.7 \text{ SE})$ and $1.3 (\pm 1.7 \text{ SE}) \text{ g m}^{-2}$ amounting to 2 and 6% of total herbivore biomass at NFA and FA locations, respectively. In contrast to other functional groups, territorial damselfishes were the only group with higher biomass at FA locations (45% higher; 95%QR: 4-85). Additionally, territorial damselfishes were the only group for which there was a significant difference in numerical abundance with $0.9 (\pm 0.2 \text{ SE})$ and $1.2 (\pm 0.1 \text{ SE})$ individuals m^{-2} , at NFA and FA locations respectively ($T=-2.5$, $p=0.05$).

Discussion

The locations included in this analysis span a range of environmental and oceanographic parameters known to influence the structure of local fish stocks (e.g. reef type, zone, exposure, depth). Despite such variability, our results show that herbivorous fish assemblages in locations not accessible to fisheries consistently supported more than twice the total biomass, relative to those accessible to fisheries. While other regional studies have noted similar patterns between areas under high and light exploitation levels (8, 28, 29), this is the first study to show the global generality of this pattern.

Despite consistent patterns in biomass, there was no clear pattern in numerical herbivore abundance between NFA and FA locations. Similar patterns have been observed in other regional studies investigating fishing impacts on all reef fishes. Contrasting patterns between biomass and abundance suggest alteration of the size structure of the total fish assemblage and herbivores specifically, in fisheries accessible locations around the world. In our study, the more than two-fold decline in herbivore biomass, but no difference in abundance, indicates that FA locations are dominated by a relatively higher number of smaller-bodied fish. Shifts in the overall size-structure could have emerged due to within-species reductions in size and/or among-species shifts in relative abundance favoring smaller-bodied species (16). Both types of shifts 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, both overall and per unit biomass, expose larger areas of substratum and have the capacity to consume more heavily defended seaweeds (30). These shifts may result in a loss of key ecological services provided by the largest species within the scraper/excavator functional group such as bioerosion and coral predation (8). Thus, reductions in total herbivore biomass and a shift to smaller-bodied fishes will likely lead to multiplicative declines in herbivory potential – less herbivore biomass to consume algae with less foraging capacity per unit biomass.

Our most striking finding was the extreme range of herbivore biomass values across study locations, in particular the high values reported from some remote, protected NFA locations. Several NFA locations across the Pacific (Nihoa and Gardner: NWHI, 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 spectacular values were observed across regions and sampling methodologies and represent means of many sites per location. Further, though fish assemblages at many of these locations include the largest bodied species of coral reef herbivores (e.g. *Bolbometopon muricatum* and *Chlorurus* spp.), after removing these species from the analysis, biomass values remain among the highest observed around the globe. The biomass potential of the herbivore assemblage is highlighted when comparing these values to

the total fish biomass from some FA coral reefs. 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} (29). Herbivores clearly play an important trophic role on coral reefs, and our findings show that their contribution to total fish biomass and likely fisheries potential should not be undervalued.

There are notable differences in the biomass of the herbivorous fish guild across the globe, with the Caribbean basin having particularly low biomass values (Table S2). The highest values reported from the Caribbean were from a protected area in the Bahamas with $\sim 65 \text{ g m}^{-2}$, however many locations feature much lower values (Figure 2). These low biomass values may be due to reduced species richness or complete absence of many of the largest bodied herbivore taxa including large parrotfishes and many browsers (e.g. *Naso* spp.) in the Caribbean region. Alternatively, lower herbivore biomass may be the result of a longer history and greater impacts of fishing, potentially including poaching in NFA locations thus our results may not reflect the true biomass potential in this region. It has been suggested that the large differences in herbivore biomass between Pacific and Caribbean reefs (Roff and Mumby (12); Pacific: 29.0 and Caribbean: 9.25 g m^{-2}) may partially explain why the Caribbean appears to be more susceptible to macroalgal blooms than the Pacific. Our results show similar trends but suggest that when considering a comprehensive set of data from NFA locations the biomass potential

for both regions is actually much higher (Pacific: 59.9 (± 2.2) and Caribbean: 29.2 g m⁻² (± 6.2)). 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 as evidenced by 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 likely conservative, underestimating the true differences in herbivore biomass between the most remote, pristine locations and the most heavily fished ones (29). For example, unprotected sites in Jamaica with a human population density of 23 people km⁻² were classified as FA with a reported mean biomass of 16 g m⁻². However, the FA location of the Western Province of the Solomon Islands had only 5.2 people km⁻², yet supports some of the highest biomass values observed (102.1 g m⁻²). Similarly, NFA locations include areas near large population centers such as protected areas on densely populated islands (e.g. O'ahu, Hawai'i) where active or inadvertent reductions of herbivores are likely, as well as isolated locations, such as in the Line Islands and NWHI, hundreds of kilometers from any direct human disturbance. In the absence of comparable measures of fishing intensity, it is difficult to move beyond simple designations based on fisheries accessibility. However, despite the crudeness of our binary designations, mean

herbivore biomass value in NFA locations was still more than twice as high as that from FA locations.

Alterations of consumer communities due to anthropogenic activities have been linked to a myriad of dramatic shifts in structure and functioning of ecosystems worldwide (31). While 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 (32). 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 (33). Because of the ecosystem services conferred disproportionately by large-bodied herbivores, some scientists and conservationists have proposed 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. In marine fisheries, the preferential removal of larger bodied fish species has been well

documented (24) but this is the first study to show this for herbivores. While the magnitude of the effect varied by functional group, there was lower biomass for the scraper/excavator, browser, and grazer/detritivore groups at FA sites. In contrast, there was greater biomass and numerical abundance of territorial damselfishes at FA locations. Declines in biomass and alteration of functional-group structure suggest that herbivore communities at FA sites likely have a diminished capacity to graze algae and have experienced shifts in their influence on benthic community structure.

Changes in the structure of the herbivore guild are important because of the unique roles played by the different functional groups. The largest bodied feeding guild, the scraper/excavators perform a variety of ecosystem functions such as bioerosion, coral predation, sediment removal and algal grazing. These fish consume a diversity of benthic organisms and actively expose bare substrata, acting as biological disturbances that facilitate coral recruitment and enhance biodiversity. The largest bodied taxa in this group such as *Bolbometopon*, *Chlorurus* and *Scarus* are highly vulnerable to fishing as they are 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 (34). The decline of large parrotfishes due to exploitation is known to result in the loss of vital ecosystem services which are key components of reef resilience (8). The browsers, which directly consume macroalgae and consist of a number of fishes from different families (e.g. Acanthuridae-Nasiinae, Labridae-Scarinae, Kyphosidae and

Siganidae), appear to be most susceptible to fishing (Figure 4). All regions in our study show nearly three-fold lower browser biomass in FA areas. Such depletion will likely impair the ability of affected reefs to defend against or cope with increases in macroalgae (35). The fishes in the grazer/detritivore 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 sediment (36). Species in this mid-sized group tend to have the highest bite rates and likely make the greatest contribution to cropping of algal turfs (37). Despite their clear importance, grazer/detritivores make up a larger proportion of the overall herbivore guild at FA areas relative to NFA areas, suggesting overrepresentation of a functional group that neither specializes in removing large macroalgae nor directly creates space for coral and CCA recruitment. Finally, while our study was entirely focused on examining how accessibility to fisheries influences coral reef herbivorous fishes around the world, given the magnitude of our results it is likely that fishing is causing significant direct and indirect effects on the reef benthos as well.

Territorial damselfishes are not common fishery targets so were not expected to vary across FA and NFA locations. Therefore, our finding of greater biomass and numerical abundance of this group at FA locations was surprising. The causes of damselfish population increases in fished locations are likely indirect and associated with a reduction in predation and/or competition due to general overfishing in these areas (16, 38). These fishes are active algae farmers and aggressively defend

territories against competing herbivores. Inside territories, CCA, coral colony, and recruit density tend to be reduced, while there is an increase in turf, macroalgae, and cyanobacteria which may contribute to a cumulative decline in reef health within territories (39-41). The increase in numerical density suggests an increased influence of this group on the benthos in FA areas. Given that territoriality is more effective against smaller schools of approaching fish, the interaction of increased density of this group and reduced density of other functional groups may exacerbate the negative impacts of territorial damselfish on the benthos (38). Greater territorial damselfish biomass and abundance in FA locations indicates that impacts to the herbivore guild due to fishing will extend beyond reductions in grazing capacity.

Conclusions

This study represents the first global assessment of the status of herbivorous coral reef fishes. Our results show that herbivorous fish biomass is >50% lower in locations accessible to fishing, while also providing important baselines for the structure of herbivore communities in remote, uninhabited islands and protected areas. Furthermore, while herbivore biomass is clearly impacted by fishing activity, herbivore abundance shows no difference between fishery accessible and not-accessible reefs. Collectively, lower biomass but no change in abundance indicates that fishing disproportionately removes larger bodied species and/or functional groups. This 'fishing down the herbivore guild' leads to a reduction in biomass of all herbivore feeding groups in fished areas, 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 likely 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 likely have much more algae present than they did in the past. Thus, a much greater area that needs to be grazed to maintain low algal standing stock and allow coral recruitment, survival and growth. Given these trends, resource managers may need to manage herbivore populations to be much larger than they ever were naturally, in order to be effective at controlling algal abundance on degraded reefs. Moreover, because of the complementarity among herbivore functional groups, it is important to ensure 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 or redundancy of different taxa will likely help to ensure stability of these ecological functions over time. Most management strategies today focus on restoring overall fish populations to levels comparable with healthy reefs, without specific focus on herbivore assemblages. However, given the numerous ecological services that are provided by the different herbivore feeding guilds attention should be directed towards managing not just biomass, but also the composition of this highly important group of fishes.

Figures

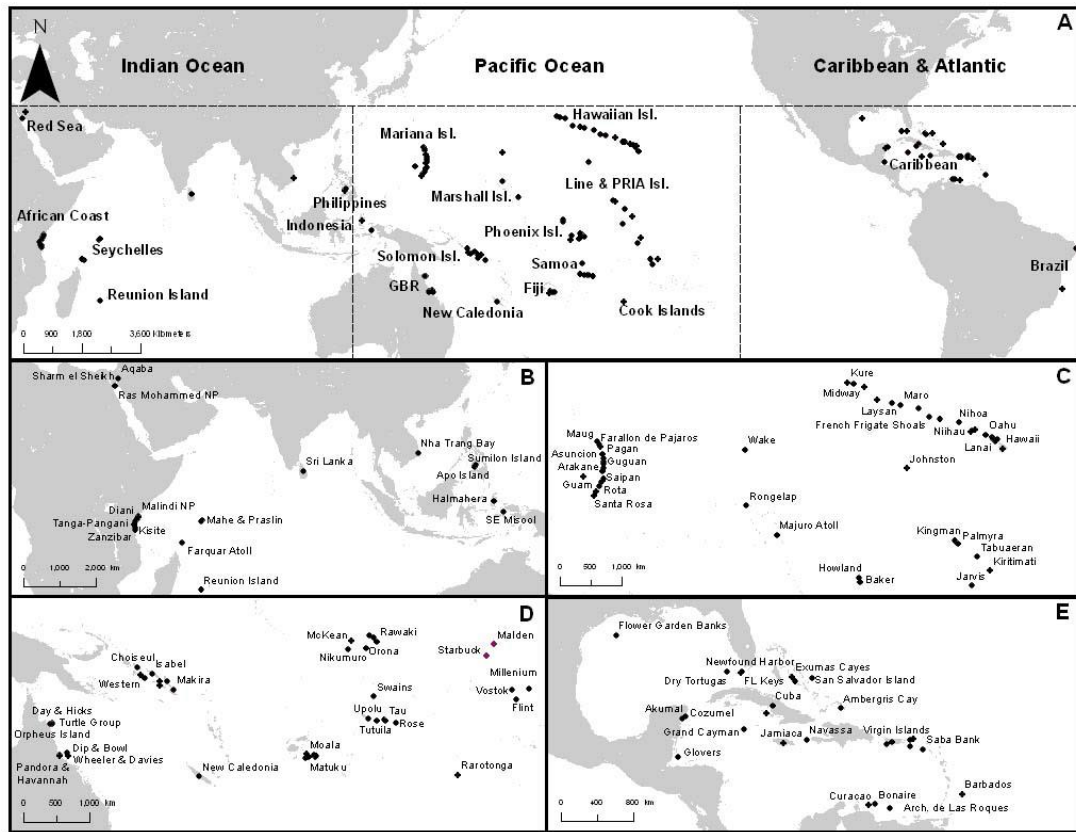


Figure 1. A) Map showing the distribution of sampling locations included in the database. Dotted lines correspond to ocean basins and inset maps are provided for detail, (B-E) arranged top-bottom, left-right. The number of survey sites ($n > 4$) and the types of data (abundance vs. biomass) for each sampling location is variable (Table S2). Some location names have been excluded from inset maps for ease of display.

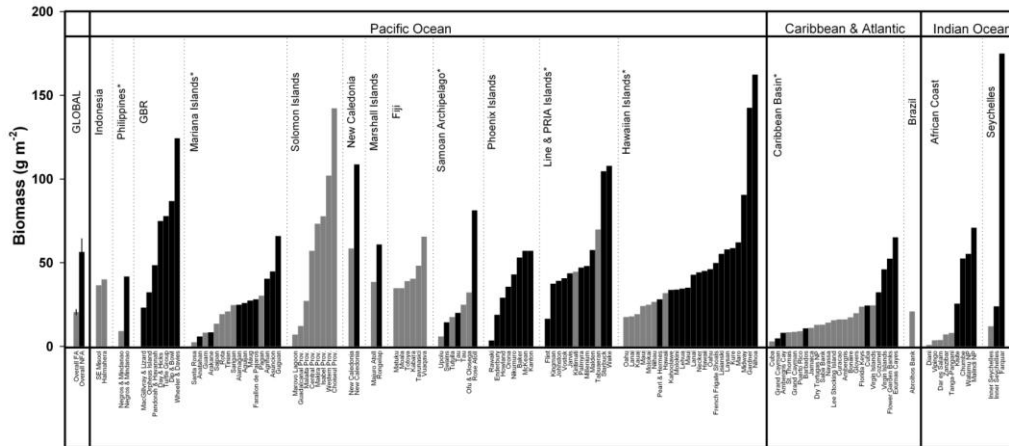


Figure 2. Mean herbivorous fish biomass ($g\ m^{-2}$) values for locations not fisheries accessible (NFA; black bars; $n=86$) and fisheries accessible (FA; grey bars; $n=74$) across the globe ($n > 4$ sites per location) organized into ocean basins and geographic regions (separated by dashed lines). Regions are arranged longitudinally. The grand mean (± 1 SE) of herbivore biomass at NFA and FA locations is shown on the far left. Regions with asterisks indicate areas where raw site level data were available to conduct more detailed regional comparisons (see Figure 3).

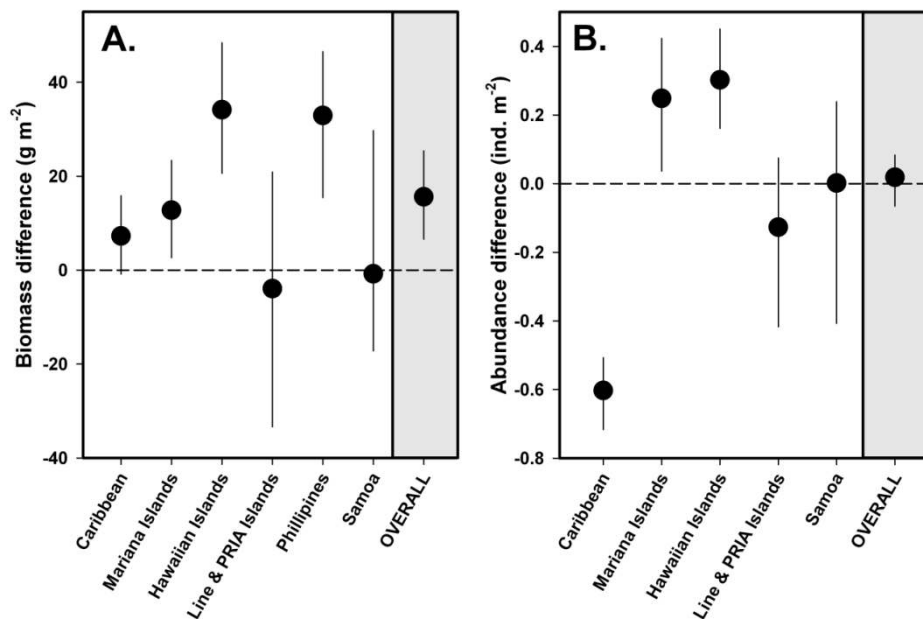


Figure 3. Analysis of the subset of data where raw site level data were available to assess differences among regions for: A) herbivorous fish biomass (g m^{-2}) and, B) abundance (ind. m^{-2}) between NFA and FA locations around the world (see asterisks in Figure 2). Circles are the median difference within regions and vertical lines are the 95 % quantile-range of differences. Dashed lines represent a mean difference of 0 indicating no significant difference in biomass between FA and NFA locations.

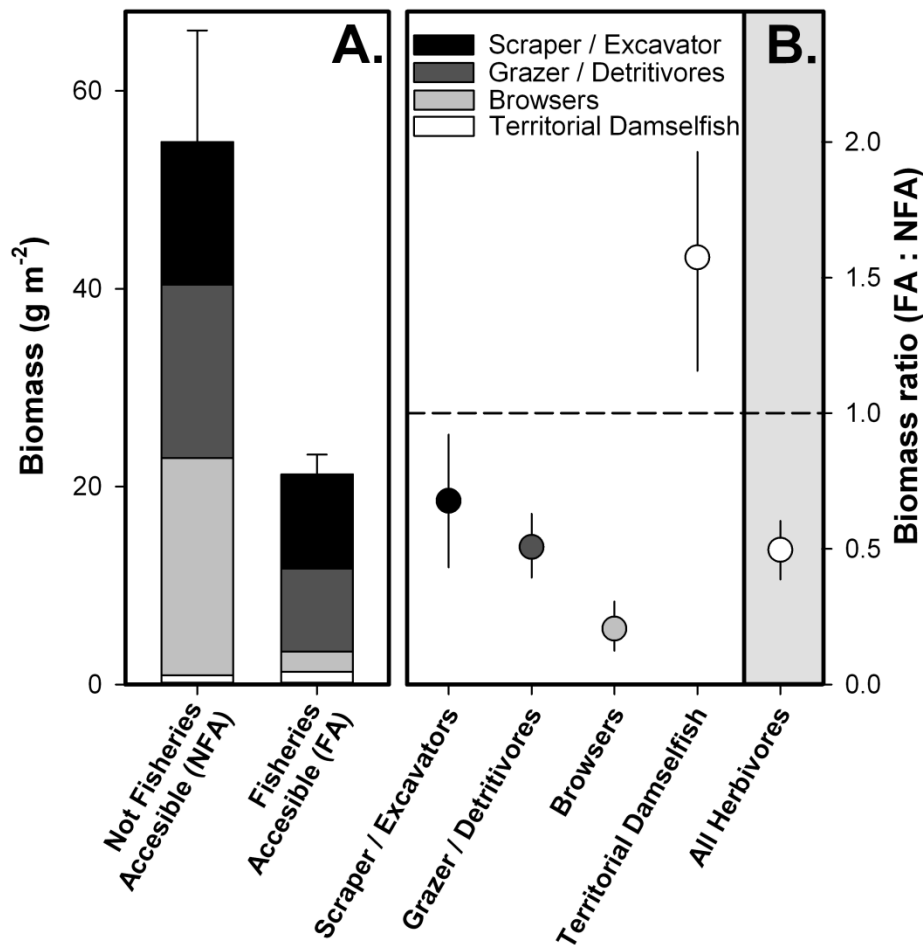


Figure 4. Analysis of the subset of data where raw species level biomass data (g m^{-2}) were available at the site level to assess differences in feeding guild structure at NFA and FA locations worldwide. A) The bar on left is the mean of NFA locations ($n=57$) and the bar on right is the mean of FA locations ($n=52$) \pm 1 SE in total 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 the median and vertical lines are the 95% quantile-range of ratios. The dashed line represents a ratio of 1 (no significant difference in biomass between fished and NFA locations).

Appendix

Table A1. Site level effort for all locations not fisheries accessible (NFA) and fisheries accessible (FA) included in the analysis. Sites are defined as the positions where surveys were conducted. As site estimates were pooled to calculate location specific means, sample sizes here reflect the total number of sites surveyed for a given location.

Accessibility	Region	Location	n (stations)
FA	Indonesia	SE Misool	36
FA	Indonesia	Halmahera	45
NFA	Philippines	Negros & Mindanao	9
FA	Philippines	Negros & Mindanao	6
NFA	GBR	N. Inner GBR	7
NFA	GBR	S. Inner GBR	3
NFA	GBR	N. Middle GBR	25
NFA	GBR	S. Middle GBR	27
NFA	GBR	N. Outer GBR	12
NFA	GBR	S. Outer GBR	18
NFA	GBR	Day & Hicks	4
NFA	GBR	Dip & Bowl	4
NFA	GBR	Macgillvray & Lizard	4
NFA	GBR	Pandora & Havannah	4
NFA	GBR	Turtle Group	4
NFA	GBR	Wheeler & Davies	4
NFA	GBR	Orpheus Island	24
NFA	Mariana Isl.	Agrihan	18
NFA	Mariana Isl.	Aguijan	8
NFA	Mariana Isl.	Alamagan	11
NFA	Mariana Isl.	Anatahan	3
NFA	Mariana Isl.	Arakane	3
NFA	Mariana Isl.	Asuncion	14
NFA	Mariana Isl.	Farallon de Pajaros	13
FA	Mariana Isl.	Guam	39
NFA	Mariana Isl.	Guguan	11
NFA	Mariana Isl.	Maug	34
FA	Mariana Isl.	Pagan	33
FA	Mariana Isl.	Rota	23
FA	Mariana Isl.	Saipan	30
FA	Mariana Isl.	Santa Rosa	3
FA	Mariana Isl.	Sarigan	13

Table A1. (continued)

FA	Hawaiian Isl.	Niihau	28
NFA	Hawaiian Isl.	Pearl & Hermes	43
FA	Hawaiian Isl.	Hawaii	69
NFA	Hawaiian Isl.	Kahoolawe	8
NFA	Hawaiian Isl.	Molokini	3
NFA	Hawaiian Isl.	Lehua	8
NFA	Hawaiian Isl.	Maui	10
NFA	Hawaiian Isl.	Lanai	3
NFA	Hawaiian Isl.	Necker	20
NFA	Hawaiian Isl.	Hawaii	14
NFA	Hawaiian Isl.	Oahu	8
NFA	Hawaiian Isl.	French Frigate Shoals	42
NFA	Hawaiian Isl.	Lisianski	55
NFA	Hawaiian Isl.	Laysan	34
NFA	Hawaiian Isl.	Kure	40
NFA	Hawaiian Isl.	Maro	59
NFA	Hawaiian Isl.	Midway	21
NFA	Hawaiian Isl.	Gardner	16
NFA	Hawaiian Isl.	Nihoa	11
FA	African Coast	Diani	10
FA	African Coast	Vipingo	10
FA	African Coast	Dar es Salam	8
FA	African Coast	Zanzibar	4
FA	African Coast	Tanga-Pangani	8
NFA	African Coast	Kisite	6
NFA	African Coast	Chumbe	4
NFA	African Coast	Watamu NP	10
NFA	African Coast	Malindi NP	10
NFA	Seychelles	Farquar	20
FA	Seychelles	Mahe & St. Anne	21
FA	Seychelles	Praslin & Cousin	21
NFA	Line & PRIA Isl.	Flint	14
NFA	Line & PRIA Isl.	Kingman	38
FA	Line & PRIA Isl.	Kiritimati	25
NFA	Line & PRIA Isl.	Palmyra	65
FA	Line & PRIA Isl.	Tabuaeran	25
NFA	Line & PRIA Isl.	Johnston	7
NFA	Line & PRIA Isl.	Wake	36
NFA	Line & PRIA Isl.	Jarvis	29

Table A1. (continued)

NFA	Line & PRIA Isl.	Malden	25
NFA	Line & PRIA Isl.	Millenium	25
NFA	Line & PRIA Isl.	Starbuck	20
NFA	Line & PRIA Isl.	Vostok	10
FA	Caribbean	Cuba	18
NFA	Caribbean	Grand Cayman	24
NFA	Caribbean	Ambergris	21
FA	Caribbean	Grand Cayman	12
FA	Caribbean	Puerto Rico	45
NFA	Caribbean	Barbados	5
FA	Caribbean	Jamiaca	27
FA	Caribbean	Dry Tortugas NP	6
FA	Caribbean	Saba Bank	8
FA	Caribbean	Navassa	8
FA	Caribbean	Lee Stocking Island	6
FA	Caribbean	Curacao	9
NFA	Caribbean	Ambergris Cay	6
FA	Caribbean	Bonaire	6
FA	Caribbean	Virgin Islands	32
FA	Caribbean	Glovers	3
FA	Caribbean	Florida Keys	20
NFA	Caribbean	Cuba	15
NFA	Caribbean	Cozumel	3
FA	Caribbean	Virgin Islands	18
NFA	Caribbean	Flower Garden Banks	12
NFA	Caribbean	Exumas Cayes	6
FA	Brazil	Abrolhos Bank	76

Table A2. Herbivore functional group designations used for the functional group analysis. Herbivore functional groups/feeding sub-guilds are based broadly on Green & Bellwood (2009) and analyzed for the effects of accessibility to fishing on these groups separately. Four herbivore functional groups were considered here: 1) scrapers/excavators (SE), 2) grazer/detritivores (GD), 3) browsers (BR) and, 4) territorial damselfishes (TERR). Deviations from Green and Bellwood (2009) were adopted because we were unable to separate out the large versus small scraper/excavators groups due to the lack of size data from published studies and lack of finer resolution in feeding behavior for some non Indo-pacific species. When available, species were categorized based on previously published designations; the remainder were categorized based on the best available dietary and behavioral information (see Supplemental references).

Family	Species	Functional Group	Source
Acanthuridae	<i>Acanthurus achilles</i>	GD	(1)
Acanthuridae	<i>Acanthurus bahianus</i>	GD	(2); (3)
Acanthuridae	<i>Acanthurus bariene</i>	GD	(1)
Acanthuridae	<i>Acanthurus blochii</i>	GD	(1)
Acanthuridae	<i>Acanthurus chirurgus</i>	GD	(2); (3)
Acanthuridae	<i>Acanthurus coeruleus</i>	GD	(2); (3)
Acanthuridae	<i>Acanthurus dussumieri</i>	GD	(1)
Acanthuridae	<i>Acanthurus guttatus</i>	GD	(1)
Acanthuridae	<i>Acanthurus leucocheilus</i>	GD	(1)
Acanthuridae	<i>Acanthurus leucochilus</i>	GD	(1)
Acanthuridae	<i>Acanthurus leucopareius</i>	GD	(1)
Acanthuridae	<i>Acanthurus leucosternon</i>	GD	(1)
Acanthuridae	<i>Acanthurus lineatus</i>	GD	(1)
Acanthuridae	<i>Acanthurus maculiceps</i>	GD	(1)
Acanthuridae	<i>Acanthurus nigricans</i>	GD	(1)
Acanthuridae	<i>Acanthurus nigricauda</i>	GD	(1)
Acanthuridae	<i>Acanthurus nigrofuscus</i>	GD	(1)
Acanthuridae	<i>Acanthurus nigroris</i>	GD	(1)
Acanthuridae	<i>Acanthurus olivaceus</i>	GD	(1)
Acanthuridae	<i>Acanthurus olivaceus x nigricans</i>	GD	Parents are grazer / detritivore
Acanthuridae	<i>Acanthurus pyroferus</i>	GD	(1)

Table A2. (continued)

Acanthuridae	<i>Acanthurus achilles</i> X <i>nigricans</i> hybrid= <i>rackliffei</i>	GD	Parents are grazer / detritivore
Acanthuridae	<i>Acanthurus sp. (ringtail)</i>	GD	(1); (4)
Acanthuridae	<i>Acanthurus spp. (ringtail)</i>	GD	(1); (4)
Acanthuridae	<i>Acanthurus strigosus</i>	GD	(2)
Acanthuridae	<i>Acanthurus tennenti</i>	GD	(1)
Acanthuridae	<i>Acanthurus tennentii</i>	GD	(1)
Acanthuridae	<i>Acanthurus triostegus</i>	GD	(1)
Acanthuridae	<i>Acanthurus xanthopterus</i>	GD	(1)
Acanthuridae	<i>Ctenochaetus binotatus</i>	GD	(2); (5)
Acanthuridae	<i>Ctenochaetus cyanocheilus</i>	GD	(2); (5)
Acanthuridae	<i>Ctenochaetus flavicauda</i>	GD	(2); (5)
Acanthuridae	<i>Ctenochaetus hawaiiensis</i>	GD	(2); (5)
Acanthuridae	<i>Ctenochaetus marginatus</i>	GD	(2); (5)
Acanthuridae	<i>Ctenochaetus sp</i>	GD	(2); (5)
Acanthuridae	<i>Ctenochaetus striatus</i>	GD	(2); (5)
Acanthuridae	<i>Ctenochaetus strigosus</i>	GD	(2); (5)
Acanthuridae	<i>Naso annulatus</i>	BR	(1)
Acanthuridae	<i>Naso brachycentron</i>	BR	(1)
Acanthuridae	<i>Naso brevirostris</i>	BR	(1)
Acanthuridae	<i>Naso lituratus</i>	BR	(1)
Acanthuridae	<i>Naso tonganus</i>	BR	(1)
Acanthuridae	<i>Naso unicornis</i>	BR	(1)
Acanthuridae	<i>Zebrasoma desjardinii</i>	GD	(1)
Acanthuridae	<i>Zebrasoma flavescens</i>	GD	(1)
Acanthuridae	<i>Zebrasoma rostratum</i>	GD	(1)
Acanthuridae	<i>Zebrasoma scopas</i>	GD	(1)
Acanthuridae	<i>Zebrasoma veliferum</i>	GD	(1)
Acanthuridae	<i>Prionurus laticlavus</i>	GD	(2)
Balistidae	<i>Melichthys vidua</i>	GD	(2); (5)
Blenniidae	<i>Cirripectes auritus</i>	GD	(2); (5)
Blenniidae	<i>Cirripectes castaneus</i>	GD	(2); (5)
Blenniidae	<i>Cirripectes filamentosus</i>	GD	(2); (5)
Blenniidae	<i>Cirripectes obscurus</i>	GD	(2); (6)
Blenniidae	<i>Cirripectes polyzona</i>	GD	(2); (5)
Blenniidae	<i>Cirripectes sebae</i>	GD	(2); (6)
Blenniidae	<i>Cirripectes sp</i>	GD	(2); (6)

Table A2. (continued)

Blenniidae	<i>Cirripectes springeri</i>	GD	(2); (5)
Blenniidae	<i>Cirripectes stigmaticus</i>	GD	(2); (5)
Blenniidae	<i>Cirripectes vanderbilti</i>	GD	(2); (5)
Blenniidae	<i>Cirripectes variolosus</i>	GD	(2); (5)
Blenniidae	<i>Scartella cristata</i>	GD	(2)
Blenniidae	<i>Atrosalarias fuscus</i>	GD	(2)
Blenniidae	<i>Ecsenius monoculus</i>	GD	(2); (5)
Blenniidae	<i>Entomacrodus marmoratus</i>	GD	(2)
Blenniidae	<i>Omobranchus rotundiceps</i>	GD	(2)
Blenniidae	<i>Ophioblennius atlanticus</i>	GD	(2)
Blenniidae	<i>Ophioblennius macclurei</i>	GD	(2)
Blenniidae	<i>Parablennius marmoratus</i>	GD	(2)
Chaetodontidae	<i>Chaetodon mertensii</i>	GD	(7)
Chaetodontidae	<i>Chaetodon semeion</i>	GD	(7)
Ephippidae	<i>Platax boersi</i>	BR	(1); (4)
Ephippidae	<i>Platax spp.</i>	BR	(1); (4)
Ephippidae	<i>Platax teira</i>	BR	(1); (4)
Ephippidae	<i>Platax batavianus</i>	BR	(1); (4)
Ephippidae	<i>Platax pinnatus</i>	BR	(1); (4)
Ephippidae	<i>Platax orbicularis</i>	BR	(1)
Gobidae	<i>Amblygobius phalaena</i>	GD	(2); (6)
Gobidae	<i>Gnatholepis thompsoni</i>	GD	(2)
Kyphosidae	<i>Kyphosidae sp</i>	BR	(1)
Kyphosidae	<i>Kyphosus bigibbus</i>	BR	(1)
Kyphosidae	<i>Kyphosus cinerascens</i>	BR	(1)
Kyphosidae	<i>Kyphosus hawaiiensis</i>	BR	(1)
Kyphosidae	<i>Kyphosus incisor</i>	BR	(1)
Kyphosidae	<i>Kyphosus pacificus</i>	BR	(1)
Kyphosidae	<i>Kyphosus sandwicensis</i>	BR	(1)
Kyphosidae	<i>Kyphosus sectator</i>	BR	(1)
Kyphosidae	<i>Kyphosus sectatrix</i>	BR	(1)
Kyphosidae	<i>Kyphosus sp</i>	BR	(1)
Kyphosidae	<i>Kyphosus species</i>	BR	(1)
Kyphosidae	<i>Kyphosus vaigiensis</i>	BR	(1)
Kyphosidae	<i>Sectator ocyurus</i>	BR	(1)
Monacanthidae	<i>Cantherhines sandwichiensis</i>	GD	(2); (6)
Monacanthidae	<i>Pervagor spilosoma</i>	GD	(2)
Pomacanthidae	<i>Centropyge acanthops</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge argi</i>	GD	(2); (1)

Table A2. (continued)

Pomacanthidae	<i>Centropyge bicolor</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge bispinosa</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge bispinosus</i>	GD	(1); (4)
Pomacanthidae	<i>Centropyge fisheri</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge flavicauda</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge flavissima</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge flavissima x vroliki hybrid</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge heraldi</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge loricula</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge loriculus</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge multicolor</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge multifaciata</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge multispinis</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge nigriocellus</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge potteri</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge shepardi</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge sp</i>	GD	(2); (1)
Pomacanthidae	<i>Centropyge tibicens</i>	GD	(1); (4)
Pomacanthidae	<i>Centropyge vroliki</i>	GD	(1); (4)
Pomacanthidae	<i>Centropyge vrolikii</i>	GD	(2); (1)
Pomcentridae	<i>Plectroglyphidodon dickii</i>	TERR	(1)
Pomcentridae	<i>Plectroglyphidodon flaviventris</i>	TERR	(1)
Pomcentridae	<i>Plectroglyphidodon imparipennis</i>	TERR	(1)
Pomcentridae	<i>Plectroglyphidodon johnstoninaus</i>	TERR	(1)
Pomcentridae	<i>Plectroglyphidodon lacrymatus</i>	TERR	(1)
Pomcentridae	<i>Plectroglyphidodon leucozonus</i>	TERR	(1)
Pomcentridae	<i>Plectroglyphidodon phoenixensis</i>	TERR	(1)
Pomcentridae	<i>Plectroglyphidodon sindonis</i>	TERR	(1)
Pomcentridae	<i>Stegastes adustus</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes albifasciatus</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes apicalis</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes aureus</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes diencaeus</i>	TERR	(2); (1)

Table A2. (continued)

Pomcentridae	<i>Stegastes dorsopunicans</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes fasciolatus</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes gascoyni</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes leucostictus</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes lividus</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes nigricans</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes partitus</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes planifrons</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes sp</i>	TERR	(2); (1)
Pomcentridae	<i>Stegastes variabilis</i>	TERR	(2); (1)
Pomcentridae	<i>Abudefduf sordidus</i>	TERR	(2)
Pomcentridae	<i>Dischistodus melannotus</i>	TERR	(2); (1)
Pomcentridae	<i>Dischistodus perspicillatus</i>	TERR	(2); (1)
Pomcentridae	<i>Dischistodus prosopotaenia</i>	TERR	(2); (1)
Pomcentridae	<i>Dischistodus pseudochrysopoecilus</i>	TERR	(2); (1)
Pomcentridae	<i>Abudefduf taurus</i>	TERR	(2)
Pomcentridae	<i>Microspathodon chrysurus</i>	TERR	(2)
Scaridae	<i>Bolbometopon muricatum</i>	SE	(1)
Scaridae	<i>Calotomus carolinus</i>	BR	(1)
Scaridae	<i>Calotomus zonarchus</i>	BR	(1)
Scaridae	<i>Cetoscarus bicolor</i>	SE	(1)
Scaridae	<i>Cetoscarus ocellatus</i>	SE	(1)
Scaridae	<i>Chlorurus bleekeri</i>	SE	(1); (4)
Scaridae	<i>Chlorurus bowersi</i>	SE	(1); (4)
Scaridae	<i>Chlorurus capistratoides</i>	SE	(1)
Scaridae	<i>Chlorurus frontalis</i>	SE	(1)
Scaridae	<i>Chlorurus japonensis</i>	SE	(1)
Scaridae	<i>Chlorurus microrhinos</i>	SE	(1)
Scaridae	<i>Chlorurus microrhinos</i>	SE	(1); (4)
Scaridae	<i>Chlorurus perspicillatus</i>	SE	(1)
Scaridae	<i>Chlorurus sordidus</i>	SE	(1)
Scaridae	<i>Chlorurus sp</i>	SE	(2); (1)
Scaridae	<i>Chlorurus sp.</i>	SE	(1); (4)
Scaridae	<i>Chlorurus strongylocephalus</i>	SE	(1)
Scaridae	<i>Hipposcarus harid</i>	SE	(1)
Scaridae	<i>Hipposcarus longiceps</i>	SE	(1)
Scaridae	<i>Leptoscarus vaigiensis</i>	BR	(1)
Scaridae	<i>Scarus chameleon</i>	SE	(1); (4)

Table A2. (continued)

Scaridae	<i>Scarus coeruleus</i>	SE	(3)
Scaridae	<i>Scarus dimidatus</i>	SE	(1); (4)
Scaridae	<i>Scarus dimidiatus</i>	SE	(1)
Scaridae	<i>Scarus dubius</i>	SE	(1)
Scaridae	<i>Scarus flavipectoralis</i>	SE	(1)
Scaridae	<i>Scarus forsteni</i>	SE	(1)
Scaridae	<i>Scarus frenatus</i>	SE	(1)
Scaridae	<i>Scarus fuscocaudalis</i>	SE	(1)
Scaridae	<i>Scarus ghobban</i>	SE	(1)
Scaridae	<i>Scarus globiceps</i>	SE	(1)
Scaridae	<i>Scarus globiceps</i>	SE	(1); (4)
Scaridae	<i>Scarus niger</i>	SE	(1)
Scaridae	<i>Scarus oviceps</i>	SE	(1)
Scaridae	<i>Scarus prasiognathos</i>	SE	(1)
Scaridae	<i>Scarus psittacus</i>	SE	(1)
Scaridae	<i>Scarus quoyi</i>	SE	(1); (4)
Scaridae	<i>Scarus rivulatus</i>	SE	(1); (4)
Scaridae	<i>Scarus rubroviolaceus</i>	SE	(1)
Scaridae	<i>Scarus scaber</i>	SE	(1)
Scaridae	<i>Scarus schlegeli</i>	SE	(1)
Scaridae	<i>Scarus sp.</i>	SE	(1); (4)
Scaridae	<i>Scarus sp. juvenile</i>	SE	(1)
Scaridae	<i>Scarus spinus</i>	SE	(1)
Scaridae	<i>Scarus tricolor</i>	SE	(1)
Scaridae	<i>Scarus trispinosus</i>	SE	(3)
Scaridae	<i>Scarus xanthopleura</i>	SE	(1)
Scaridae	<i>Sparisoma amplum</i>	SE	(3)
Scaridae	<i>Sparisoma viride</i>	SE	(8); (9)
Scaridae	<i>Chlorurus gibbus</i>	SE	(1); (2)
Scaridae	<i>Sparisoma atomarium</i>	SE	(2); (10); (9); (11)
Scaridae	<i>Sparisoma aurofrenatum</i>	SE	(2); (10); (9)
Scaridae	<i>Sparisoma chrysopterum</i>	SE	(2); (10); (9)
Scaridae	<i>Sparisoma radians</i>	BR	(2); (10); (9)
Scaridae	<i>Sparisoma rubripinne</i>	SE	(2); (10); (9)
Scaridae	<i>Scarus altipinnis</i>	SE	(1)
Scaridae	<i>Scarus vetula</i>	SE	(2); (9)
Scaridae	<i>Scarus taeniopterus</i>	SE	(2); (12); (10)
Scaridae	<i>Scarus ferrugineus</i>	SE	(2)

Table A2. (continued)

Scaridae	<i>Cryptotomus roseus</i>	GD	(2)
Scaridae	<i>Scarus festivus</i>	SE	(2)
Scaridae	<i>Scarus gibbus</i>	SE	(2); (13)
Scaridae	<i>Scarus guacamaia</i>	SE	(2); (10)
Scaridae	<i>Scarus iseri / criocensis</i>	SE	(2); (10); (9)
Scaridae	<i>Scarus sordidus</i>	SE	(2)
Siganidae	<i>Siganus argenteus</i>	GD	(1)
Siganidae	<i>Siganus corallinus</i>	GD	(1); (4)
Siganidae	<i>Siganus corallinus</i>	GD	(1); (4)
Siganidae	<i>Siganus doliatus</i>	GD	(1)
Siganidae	<i>Siganus doliatus/virgatus</i>	GD	(1); (4)
Siganidae	<i>Siganus fuscescens</i>	GD	(1)
Siganidae	<i>Siganus fuscescens?</i>	GD	(1); (4)
Siganidae	<i>Siganus fuscescens?</i>	GD	(1); (4)
Siganidae	<i>Siganus guttatus</i>	GD	(1); (4)
Siganidae	<i>Siganus lineatus</i>	GD	(1)
Siganidae	<i>Siganus lineatus/guttatus</i>	GD	(1); (4)
Siganidae	<i>Siganus puellus</i>	GD	(1)
Siganidae	<i>Siganus punctatissimus</i>	GD	(1), (4)
Siganidae	<i>Siganus punctatus</i>	GD	(1)
Siganidae	<i>Siganus sp</i>	GD	(1)
Siganidae	<i>Siganus spinus</i>	GD	(1)
Siganidae	<i>Siganus spp.</i>	GD	(1); (4)
Siganidae	<i>Siganus spp.</i>	GD	(1); (4)
Siganidae	<i>Siganus stellatus</i>	GD	(1)
Siganidae	<i>Siganus vermiculatus</i>	GD	(1)
Siganidae	<i>Siganus virgatus</i>	GD	(1); (4)
Siganidae	<i>Siganus vulpinus</i>	GD	(1)
Tetradontidae	<i>Canthigaster coronata</i>	GD	(2); (6); (5)
Tetradontidae	<i>Canthigaster epilampra</i>	GD	(2); (6); (5)
Tetradontidae	<i>Canthigaster jactator</i>	GD	(2); (6); (5)
Tetradontidae	<i>Canthigaster janthinoptera</i>	GD	(2); (6); (5)
Tetradontidae	<i>Canthigaster rivulata</i>	GD	(2); (6); (5)
Tetradontidae	<i>Canthigaster rostrata</i>	GD	(2); (6); (5)
Tetradontidae	<i>Canthigaster solandri</i>	GD	(2); (6); (5)
Tetradontidae	<i>Canthigaster valentini</i>	GD	(2); (6); (5)
Tetradontidae	<i>Canthigaster amboinensis</i>	GD	(2)
Tetradontidae	<i>Canthigaster bennetti</i>	GD	(2)

Table A3. Regional mean herbivore biomass ($\text{g m}^{-2} \pm 1 \text{ SE}$) values calculated from the means of survey sites within a location and the mean of locations within a region (FA: Fisheries Accessible; NFA: Not Fisheries Accessible). Standard errors were calculated from means of locations, except when only one location was available where site level variability is shown (Table S2). The minimum number of sites used to calculate means by location was 4. Regions are arranged longitudinally.

Region	Accessibility	Biomass (g m^{-2})	Abundance (ind. m^{-2})	n (locations)
Indonesia	FA	38.25 (± 1.45)	0.13 (± 0.04)	3
Philippines	NFA	41.77 (± 2.01)	0.23 (± 0.12)	1
Philippines	FA	9.17 (± 5.06)	0.29 (± 0.15)	1
GBR	NFA	68.36 (± 18.53)	0.13 (± 0.02)	5
Mariana Islands	NFA	30.21 (± 6.15)	0.65 (± 0.13)	9
Mariana Islands	FA	17.08 (± 3.41)	0.44 (± 0.08)	8
Solomon Islands	FA	62.4 (± 9.02)	0.38 (± 0.05)	7
New Caledonia	NFA	108.8* (± 9.01)	1.36 (± 0.10)	1
New Caledonia	FA	58.6* (± 4.43)	0.7 (± 0.01)	1
Marshall Islands	NFA	38.46 (± 1.90)	-	1
Marshall Islands	FA	61 (± 2.40)	-	1
Fiji	FA	43.8 (± 4.80)	-	6
Samoan Archipelago	NFA	50.16 (± 13.32)	0.53 (± 0.09)	7
Samoan Archipelago	FA	27.31 (± 8.08)	0.43 (± 0.11)	8
Phoenix Isl.	NFA	37.19 (± 6.83)	0.44 (± 0.09)	8
Line & PRIA Isl.	NFA	52.29 (± 8.08)	0.6 (± 0.08)	12
Line & PRIA Isl.	FA	57.29 (± 12.68)	0.73 (± 0.07)	2
Hawaiian Isl.	NFA	59.91 (± 7.08)	0.56 (± 0.06)	26
Hawaiian Isl.	FA	22.08 (± 2.15)	0.25 (± 0.02)	25
Caribbean Basin	NFA	29.19 (± 6.17)	0.29 (± 0.05)	11
Caribbean Basin	FA	17.62 (± 1.72)	0.84 (± 0.14)	27

Table A3. (continued)

Brazil	FA	20.90* (\pm 1.25)	0.66 [†] (\pm 0.08)	1
Red Sea	NFA	-	0.12 [†] (\pm 0.02)	1
Red Sea	FA	-	0.16 [†] (\pm 0.02)	1
Seychelles	NFA	99.88 (\pm 75.17)	0.38 (\pm 0.19)	2
Seychelles	FA	12.02 (\pm 0.25)	-	1
African Continent	NFA	51.10 (\pm 9.43)	0.31 (\pm 0.20)	4
African Continent	FA	4.71 (\pm 1.30)	0.52 (\pm 0.17)	5

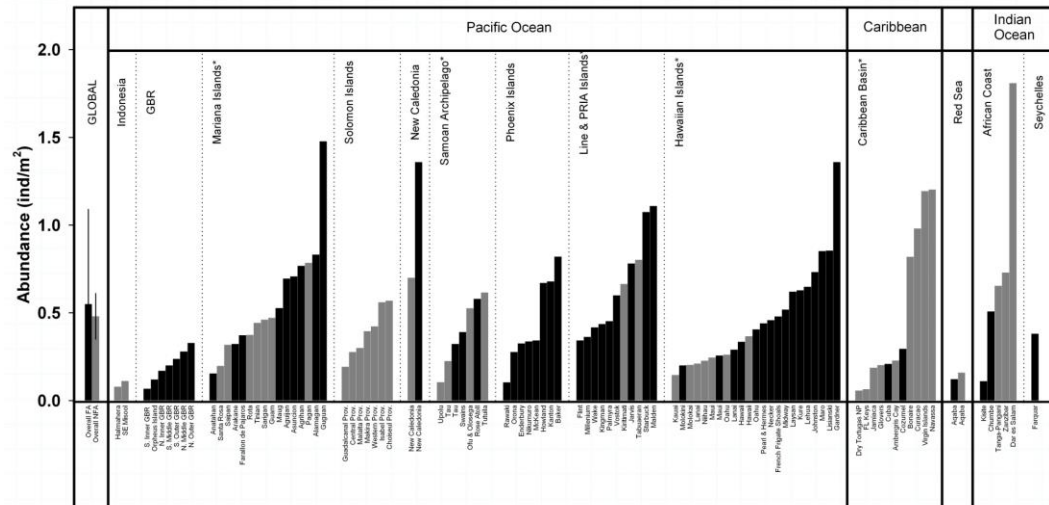


Figure S1. Mean values of herbivorous fish abundance (ind m⁻²) for locations not fisheries accessible (NFA; black bars; n=59) and fisheries accessible (FA; gray bars; n=64) at all locations (n > 4 sites per location) across the globe organized into ocean basins and geographic regions (separated by dashed lines). Regions are arranged longitudinally. The grand mean (± 1 SE) of herbivore abundance at NFA and FA locations is shown on the far left. Regions with asterisks indicate areas where raw site level data were available to conduct more detailed regional comparisons (see Fig 3)

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