Natural bounds on herbivorous coral reef fishes

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14

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16   **Abstract**
17
18   Humans are an increasingly dominant driver of Earth's biological communities,
19   but differentiating human impacts from natural drivers of ecosystem state is
20   crucial. Herbivorous fish play a key role in maintaining coral dominance on coral
21   reefs, and are widely affected by human activities, principally fishing. We assess
22   the relative importance of human and biophysical (habitat and oceanographic)
23   drivers on the biomass of five herbivorous functional groups among 33 islands in
24   the central and western Pacific Ocean. Human impacts were clear for some, but
25   not all, herbivore groups. Biomass of browsers, large excavators and of all
26   herbivores combined declined rapidly with increasing human population
27   density, whereas grazers, scrapers and detritivores displayed no relationship.
28   Sea-surface temperature had significant but opposing effects on the biomass of
29   detritivores (positive) and browsers (negative). Similarly, the biomass of
30   scrapers, grazers and detritivores correlated with habitat structural complexity,
31   however relationships were group-specific. Finally, the biomass of browsers and
32   large excavators was related to island geo-morphology, both peaking on low-
33   lying islands and atolls. The substantial variability in herbivore populations
34   explained by natural biophysical drivers highlights the need for locally-
35   appropriate management targets on coral reefs.
36
37   **Keywords:** fish biomass; functional group; herbivore; human drivers; natural
38   drivers, Pacific Ocean
39
40

Introduction

Humans are increasingly a dominant global force influencing the structure and function of ecosystems through the removal of key species and functional groups, habitat modification, and the effects of pollution and climate change [1–3]. Coral reef ecosystems are especially vulnerable to such human-forcing [4], and while anthropogenic impacts are globally pervasive, they occur against a backdrop of high natural variability in reef systems caused by differences in the environment and bio-geographic context. Oceanic productivity, water temperature, habitat area, reef geomorphology and larval connectivity can have substantial impacts on coral reef fish assemblages [5–10]. For example, the natural fish carrying capacity of a coral reef has been shown to double along a gradient of increasing oceanic productivity [11]. Understanding the relative influence of human versus natural drivers is key to assessing the current status of these ecosystems.

Here we focus on one component of coral reef systems, namely herbivorous fishes in the Pacific Ocean. Despite some uncertainty, particularly in the Indo-Pacific, about the relative importance of herbivory in mediating coral-algal dynamics [12–16], herbivorous fishes are widely recognised to play an important role in maintaining the competitive dominance of reef calcifiers (e.g. hard corals and crustose coralline algae), over other benthic components (e.g. fleshy macroalgae) [17–20]. For example, following climate-induced coral bleaching, fished reefs with reduced herbivore populations have a greater propensity to become dominated by macroalgae [21]. For that reason, some coral reef management strategies now focus specifically on protecting or restoring herbivorous fish populations [22,23]. There is a need, therefore, to better understand the role of the natural environment in determining distribution patterns of herbivorous fishes [8,24–26] independent of local human impacts on coral reefs. Indeed, the upper bounds of herbivore biomass will be determined by a reef's local biophysical setting, and once identified, will allow for realistic fisheries management strategies to address the widespread effect of fishing on this trophic group [7,8,11,27–30].

Herbivorous reef fish assemblages vary with local environmental factors. For instance, parrotfish tend to be more abundant and species-rich on barrier reefs compared to atoll, fringing or low coral cover reefs [31]. Intra-island variation in herbivore species composition and behavior is also evident among different reef habitats. Typically, the abundance and feeding activity of grazing surgeonfishes and large parrotfishes is lower on near-shore coastal reefs compared to wave exposed offshore reefs [32,33]. Conversely, browsing herbivores are often more abundant on wave protected back reef habitats, as compared to exposed fore-reef areas [32,34,35]. Furthermore, herbivore biomass and rates of herbivory tend to be greatest on the reef crest, and both decrease across the reef flat and down the reef slope [35–38]. These patterns in herbivorous fishes are variously attributed to the availability and quality of food and shelter, in addition to the wave energy, and sedimentation regimes experienced [34,38–40]. The implication of this localised among- and within-habitat variation is that the need

89   for, and potential effectiveness of, fishery management interventions are highly
90   dependent on natural bounds set by the location's biophysical setting [41].
91
92   Here we make use of a consistent monitoring dataset from 33 islands and atolls
93   across the central and western Pacific to better understand the relative role of
94   anthropogenic impacts and biophysical drivers (habitat and physical
95   environmental conditions) in structuring herbivore populations on coral reefs.
96   These islands span large gradients of human population density (0-27 people per
97   hectare of reef) [11,42] and biophysical condition [43], allowing us to separate
98   the relative effect of those in driving variation in herbivore biomass.
99
100 **Methods**
101
102 **Fish assemblage and reef habitat surveys**
103
104 We used coral reef monitoring data collected between 2010 and 2015 across 33
105 Pacific islands and atolls (electronic supplementary material table S1). The
106 surveys were performed for the National Oceanic and Atmospheric
107 Administration (NOAA) Pacific Reef Assessment and Monitoring Program
108 (Pacific RAMP), a long-term ecosystem monitoring effort focused on United
109 States and United States-affiliated coral reefs [44]. Data from two underwater
110 visual census techniques were used, the stationary point count (SPC) and the
111 towed-diver (tow) survey method [45,46]. The SPC was used to estimate the
112 biomass of herbivorous fishes, whilst the latter was used to estimate biomass of
113 large (>50 cm in total length) piscivores. Piscivore biomass was used to
114 investigate what effect, if any piscivores may have in exerting top-down control
115 on herbivore populations [47]. The tow estimates of piscivore biomass was used
116 in preference to the SPC due to the concern that small-scale surveys can
117 overestimate the biomass of large roving predators, such as sharks and jacks
118 [48].
119
120 A total of 3309 SPC surveys were conducted by experienced surveyors. Survey
121 site locations were selected per sampling unit (typically an island / atoll,
122 occasionally a cluster of small islands, or for large islands, island sub-section) by
123 means of a randomised stratified design [49]. The target sampling domain of
124 Pacific RAMP is hard bottom habitat in depths less than 30 m, and site allocation
125 is stratified by reef-zone (fore-reef; back reef; lagoon) and depth (0-6 m; 6-18 m;
126 18-30 m). Only data from the fore-reef habitat were used to remove any biases
127 associated with inter-habitat differences on herbivorous fish assemblages; the
128 fore-reef is the most comparable reef habitat present across all islands. At each
129 survey site, a pair of divers conducted simultaneous adjacent counts in which
130 they first compiled lists of all fish species present within their survey area (7.5 m
131 radius cylinder) during a 5-minute interval. After the timed interval, divers
132 proceeded to count and size all fishes from the species list within their survey
133 area. Divers then visually estimated benthic cover and reef complexity, the mean
134 vertical substrate height from the reef plane in the survey cylinder.
135
136 A total of 861 tow surveys were analysed. Surveys were haphazardly located on
137 reef areas at a depth of 10-20 m, with the broad goal of spreading sites as widely

138   as possible around each island; circumnavigating the island where practical. A
139   pair of divers (one fish, one benthic surveyor) were towed behind a small boat
140   travelling ~2 km for each 50-minute survey. During each tow, the fish diver
141   recorded the number and size of all species > 50 cm in total length within a belt-
142   transect extending 5 m on either side and 10 m in front of the diver, from the
143   seafloor to the surface. Full details on the tow survey method are available in
144   [48].
145

146   **Data processing**

147

148   The weight per individual fish was calculated using length-to-weight
149   relationships from FishBase and other sources [50,51]. To date, much of the
150   evidence of human impacts on herbivore populations relative to regional
151   biophysical variation considers these herbivorous fishes as a single trophic guild
152   or broad taxonomic groups [8], although see [24]. Collectively these studies point
153   to differences in the expected richness and biomass of herbivorous fishes, either
154   *in toto* or of specific families, based on habitat, island type, and biogeographic
155   region [7,8]. There is, however, increasing evidence that different herbivore
156   functional groups perform complimentary roles in reef processes [52], have
157   different dietary and habitat requirements [8,53,54], and are likely to respond
158   differently to local biophysical settings. Therefore, we classified herbivores
159   functionally (*sensu* [55]) and incorporated new dietary data specific to the study
160   area. Five groups resulted: 'browsers', 'grazers', 'detritivores', 'large
161   excavators/bioeroders' and 'scrapers/small excavators' (electronic
162   supplementary material S2).

163

164   For the SPC surveys, site-level herbivorous fish biomass (g m^{-2}), hard coral cover
165   and reef complexity were calculated by averaging the two diver replicates
166   conducted at each site location. Data were inspected for site-level outliers, site
167   level observations of any of the fish metrics that were > 97.5% the inter-quartile
168   range, were capped at that 97.5% value (electronic supplementary material S3).
169   Island-scale averages of the site level metrics were calculated, first by averaging
170   values within each depth stratum per island, and then weighting the mean
171   estimates by the total area of each stratum per island [56,57]. Island-level tow
172   estimates of piscivore biomass were calculated as equally weighted means of
173   each tow per island across years. Species richness per functional group was
174   estimated by generating species accumulation curves for each island using the
175   rarefaction method in the R package *vegan* [58].

176

177   **Quantifying human and biophysical predictors**

178

179   We used published estimates of the following human and biophysical covariates,
180   derived at the island level: human population density, chlorophyll-a (mg m^{-3}) as
181   a proxy for phytoplankton biomass and oceanic productivity, total area of reef
182   habitat, sea-surface temperature (SST °C), wave energy (kW m^{-1}) and island type
183   (electronic supplementary material table S3.1). Island types were based on
184   geomorphology, and classed as either high (e.g. basalt island) or low-lying (e.g.
185   carbonate island or atoll). Islands were also grouped by region (Hawaii, Central

186   Polynesia, Gilbert, Ellis and Marshall Islands and Tropical Northwest Pacific
187   [59]).
188
189   To determine anthropogenic impacts on herbivorous fishes, we used human
190   population density (the number of people resident per island (from the 2010 US
191   census) divided by the area of fore-reef habitat per island from GIS habitat layers
192   maintained by Pacific RAMP (electronic supplementary material S3.1). For the
193   remote-sensing data, we used the lower climatological mean of sea-surface
194   temperature from the Pathfinder v5.0 dataset, and the climatological mean of
195   chlorophyll-a derived from the Moderate Resolution Imaging Spectroradiometer
196   (MODIS). The wave energy metric used was the climatological mean from
197   NOAA's Wave Watch III wave model. Details on the methods used to generate
198   island specific biophysical metrics are described in full in [43].
199
200   **Modeling**
201
202   We fitted generalised additive mixed-effects models (GAMM) of island-level
203   herbivore biomass (electronic supplementary material S3) in R (ww.r-
204   project.org), using the *gamm4* package [60]. All models included region as a
205   random effect to account for autocorrelation amongst islands within regions
206   [61]. Wake is the only replicate in the Marshall, Gilbert and Ellis Islands region,
207   therefore we report summary fish metrics for Wake (biomass and richness) but
208   excluded it from the statistical modeling (total number of island replicates = 33).
209   For total fish biomass and functional group biomass separately, we fitted GAMMs
210   for all possible combinations of the predictor variables using the *UGamm*
211   wrapper function, in combination with the *dredge* function in the *MuMIn* package
212   [62].
213
214   We calculated Akaike's Information Criterion, corrected for small sample size
215   (AICc) and the AICc-based relative importance weights (w_i) to assess the
216   conditional probability of each model. We report the model-average estimates
217   for each predictor term based on the top-ranked models for each fish metric, top-
218   ranked models being those with > 0.05 Akaike weight. To test for influential data
219   points and to check for model stability, we performed a jack-knife sensitivity test,
220   calculating the percentage of times sequentially deleting single response variable
221   data points produced the same top-ranking model structure (*sensu* [63]).
222   Finally, to visualise the effect of predictor terms on the herbivorous fish
223   responses, we used the coefficients from the top-ranked models for each
224   response variable separately to generate a predicted dataset. We set all other
225   predictors terms to their median value then generated smoother terms for the
226   predictor of interest and plotted these against the untransformed, un-scaled fish
227   metrics [11].
228
229   **Results**
230
231   Across the western central Pacific, a large degree of variability exists in the
232   biomass and composition of herbivorous fish assemblages, including the species
233   richness within functional groups. Generally, there is greater biomass and
234   richness of detritivores in Central Polynesia, and a greater biomass of browsers

235   in the unpopulated northerly latitudes (figure 1, electronic supplementary
236   materials S4). Functional group biomass and richness was positively related in
237   large excavators/bioeroders, scrapers/small excavators and detritivores (Figure
238   S4, Table S4).
239
240   Major drivers of this spatial variation in total herbivorous fish biomass were
241   identified as reef complexity, hard coral cover and human population density
242   (electronic supplementary material table S5). The original smoothers fitted to
243   the functional group and total herbivore biomass values are in electronic
244   supplementary material figure S5. Total herbivore biomass plateaued at
245   intermediate complexity, decreased at highest coral cover, and continually
246   decreased with human population density (electronic supplementary material
247   figure S5). The best-fit model that contained these three biological variables had
248   high explanatory power and stability (~69% variability explained in total
249   herbivore biomass, 94% jack-knife stability; electronic supplementary material
250   table S5). When functional groups were modeled individually, the top candidate
251   models showed similar stability. Specifically, the dominant predictors identified
252   from the variable importance (vi) estimates from the top candidate model of the
253   entire dataset matched those identified from the jack-knifing method (electronic
254   supplementary material table S5). The amount of variance explained by the top-
255   ranking models of herbivore biomass for each functional group (figure 2) was as
256   follows: browsers (84%); detritivores (84%); grazers (73%); scrapers/small
257   excavators (36%) and; large excavators/bioeroders (59%) (electronic
258   supplementary material figure S5).
259
260   The relationship between the top predictor terms and herbivore biomass were
261   distinct for different functional groups. Biomass of large excavators/bioeroders
262   (all parrotfishes > 35 cm in total length) and browsers was significantly greater
263   at low islands/atolls as compared to high islands (figure 3, electronic
264   supplementary material table S5). These were also the only functional groups for
265   which human population density was a strong predictor of biomass (figure 3,
266   electronic supplementary material table S5), with both groups declining rapidly
267   from low to mid human population density.
268
269   The dominant drivers of variability in browsers, detritivores and grazers and
270   scrapers/small excavators were biophysical. These data showed that reefs in
271   warmer waters have lower browser biomass and greater detritivore biomass
272   and species richness (figure 3, electronic supplementary material table S5).
273   Increased detritivore, grazer and scraper/small excavator biomass was evident
274   from low to mid habitat complexity. The biomass of grazers continued to
275   increase at high complexity locations, whereas for detritivores and
276   scrapers/small excavators the biomass either plateaued or was reduced at high
277   complexity (figure 3). Locations with a larger amount of fore-reef habitat had
278   greater biomass of detritivores, while areas with intermediate wave-energy and
279   high chlorophyll-a had increased grazer biomass (figure 3, electronic
280   supplementary material table S5).
281
282   **Discussion**
283

284   Our results are consistent with the growing understanding that regional
285   variability in the biophysical attributes of coral reef ecosystems acts to
286   determine ecological state independent of local human impacts [11,63,64].
287   Specifically, our findings confirm clear anthropogenic impacts to herbivorous
288   fishes across the Pacific, but importantly also show that; i) effects are functional-
289   group specific and; ii) the biophysical attributes of reefs, especially sea-surface
290   temperature (SST) and large-scale geo-morphological habitat complexity also
291   drive herbivorous coral reef fish assemblage states. Prior to this study,
292   quantitative evidence for anthropogenic impacts on herbivorous fishes, while
293   simultaneously accounting for large-scale natural variability in fish assemblages,
294   has been sparse [8,30,31]. To our knowledge, this is the first ocean basin-scale
295   study quantifying the relative effects of human versus natural biophysical
296   drivers of herbivorous fish functional group biomass.
297
298   In the absence of fisheries dependent data on subsistence, recreational and
299   commercial take, human density and distance to market have proven to be useful
300   proxies for the influence of humans on coral reef fishes [11,65,66]. Our results
301   show a steep and rapid decline in the biomass of large excavators and browsers
302   with increasing human population density. This pattern is consistent with other
303   global and regional assessments documenting the negative effect of fishing on
304   herbivores [27,28]. Herbivorous fishes, in particular large excavating
305   parrotfishes, and browsing surgeonfishes, are highly desired fisheries targets in
306   the Pacific [67–70]. Our results demonstrate the sensitivity of populations of
307   these large herbivores to fishing mortality, presumably due to their large
308   maximum body size and for some species, late age at maturity and the
309   disproportion contribution of large old females to population replenishment
310   [67,71–74]. The vulnerability of these two functional groups to human impacts is
311   particularly important as they contribute disproportionately to reef processes
312   [52,75,76].
313
314   Herbivores vary in richness, abundance and biomass by island geomorphology
315   [8,31]. Our results show ~ 24-45% greater biomass of large-excavating and
316   browsing fishes at low-lying islands (carbonate) and atolls, compared to high
317   islands (basalt). There was no evidence for an island type effect for the
318   remaining functional groups, although consistent with a previous study [8], we
319   found that the biomass of detritivores (all acanthurids) was positively associated
320   with reef area. It may be that this island type difference in biomass is driven by
321   differential species-specific habitat requirements. For example, lagoonal habitat
322   for settlement or nursery areas [77] is only present within atoll systems. The
323   implications of our analyses are that large-scale habitat differences should be
324   considered before comparing herbivorous fish assemblages across different
325   island types.
326
327   Here we found no consistent relationship between the biomass of different
328   herbivore functional groups and the cover of hard corals, but still an overall
329   relationship between coral cover and total herbivore biomass. Our results
330   suggest that in areas of coral cover greater than 22-24% the total herbivore
331   assemblage will tend to be reduced in biomass, whilst the biomass of grazers,
332   detritivores and scrapers/small excavators increases with habitat complexity,

333   with peak biomass for scrapers and detritivores at intermediate complexity.
334   Previously, a non-linear association between coral species richness and fish
335   community abundance has been shown [78], as has a reduction in abundances of
336   small and medium sized herbivores at low habitat complexity [79]. Taking these
337   effects of complexity and coral cover together it seems plausible that this reflects
338   the opposing changes in the availability of refugia and food with coral cover. In
339   general, high coral cover, and associated structural complexity, reduces the
340   foraging efficiency of predators [79–81]. Furthermore, the availability of shelter
341   reduces the energy that fishes must allocate to swimming in high flow water
342   environments [34], giving them an energetic advantage. As such, more complex
343   environments support higher fish abundances [82]. However, increases in coral
344   cover are accompanied by concomitant decreases in cover of other benthic
345   organisms, such as turf, endolithic, and macroalgae [83]. These algal
346   assemblages, and associated detritus, are the primary food sources for
347   herbivores, and as such food availability may limit population size in areas of
348   high coral cover. This notion is supported by several studies that have
349   documented increases in the abundance and biomass of herbivorous fishes
350   following extensive coral mortality and reduced structural complexity [84–86].
351
352   The increased biomass of grazers in areas of moderate wave exposure and
353   increased oceanic productivity could also be related to food availability. Both
354   algal and detrital mass tends to decrease with increasing wave energy and the
355   highest edible algal mass occurs at moderately exposed reefs [87]. The positive
356   association between chlorophyll-a and grazer biomass could be due to greater
357   food availability for grazing fishes, specifically nutrients and sinking detrital
358   particles like phytodetritus, feces or dead planktonic material [79]. If this were
359   the case, one might expect to see a similar effect on detritivore biomass,
360   however, we did not. Instead, the dominant biophysical driver of variability in
361   detritivore biomass was sea surface temperature (SST).
362
363   Notably, detritivores and browsers showed opposing responses to SST, with
364   browser biomass being negatively and detritivore biomass positively related to
365   SST. Similar decreases in the biomass of browsing fishes with decreasing
366   latitude, and hence SST, are evident in both the Atlantic [25] and southern Pacific
367   Ocean [88]. Temperature fundamentally constrains the metabolic processes of
368   ectotherms and various hypotheses have been proposed to explain how
369   temperature might impact the performance and fitness of individuals [89]. For
370   instance, the temperature-size rule predicts ectotherms to be smaller in warmer
371   waters, due to reduced mean body size, earlier maturation and increased initial
372   growth rates [90–92]. While the temperature-constraint hypothesis relates to
373   the interacting effects of temperature and food quality on fish physiology
374   [25,93]. Here we found increased browser biomass in cooler waters and
375   increased detritivore biomass in warmer waters. Whether these trends in the
376   standing stock of these functional groups relates to larger individuals and/or
377   intra-specific variability in life history characteristics across the temperature
378   gradients surveyed would require location specific age-based studies on
379   individual species.
380

381   The different effect of temperature on these functional groups could also be a
382   response to the very different dietary strategies of these fishes. Browsing
383   acanthurids, such as *Naso unicornis,* and kyphosids, are the only functional group
384   that hindgut ferment, which allows these fish to gain energy from refractory
385   fleshy macroalgal carbohydrates, including mannitol [94–97]. Macroalgae, the
386   preferred food of browsers is more abundant on reefs in cooler climes in the
387   Pacific [63] and thus browser biomass may be tracking the availability of their
388   target resource. It is difficult to ascertain the primary nutrient sources of
389   detritivores which feed on the epilithic algal matrix (EAM) [98]. The EAM
390   contains a mixture of filamentous algal turfs, cyanobacteria, macroalgal spores,
391   microalgae (diatoms and dinoflagelletes), heterotrophic bacteria, sediment and
392   organic detritus [99]. Stomach content analyses of the detritivore *Ctenochaetus*
393   *striatus* reveal large amounts of loose plant cells, sediment and algal filaments
394   while the composition of short-chain fatty acids in *Ctenochaetus striatus* and
395   *Ctenochaetus strigosus* guts are indicative of a diet of diatoms and bacteria
396   [53,100]. Whether detritivorous fish biomass tracks spatial variability in the
397   abundance and production of their target resource remains to be established.
398
399   ## Conclusions
400
401   Our findings highlight that coral reefs' biophysical setting strongly determine
402   their carrying capacity and community composition of herbivorous reef fishes.
403   Human impacts are superimposed over the back-drop of these naturally
404   occurring drivers. Herbivore-focused management interventions are likely to
405   become more widely implemented due to the perception that greater herbivore
406   biomass promotes reef resilience. Our results show large natural differences in
407   the capacity of individual reefs to support herbivore populations and therefore it
408   is unlikely that all reefs will respond similarly to particular interventions, such as
409   prohibition of fishing. Moreover, our results show that herbivore functional
410   groups respond in different ways along gradients of those natural biophysical
411   drivers. Locally-appropriate management targets for herbivore functional group
412   biomass must therefore factor in the natural bounds set by the reef's biophysical
413   setting.
414

420   **Author contributions**
421   AH, IDW and ASH conceived and designed the analysis; AH and GJW performed
422   the analysis; all authors wrote the paper.
423

429   **Competing interests**

430   We have no competing interests.
431
440

441   **Figure captions**
442
443   **Figure 1. Herbivorous fish biomass by functional group per region**. B =
444   browsers (red), D = Detritivores (green), G = Grazers (yellow), S = scrapers and
445   small excavators (blue), E = Large excavators and bioeroders (dark blue).
446   Trop.NW.Pacific = Tropical Northwest Pacific, C. Polynesia = Central Polynesia,
447   M. = Marshall Islands. AGS = Alamagan, Guguan and Sarigan, FDP = Farallon de
448   Pajaros, O&O = Ofu and Olosega, FFS = French Frigate Shoals, P&H = Pearl and
449   Hermes. Islands within region are ordered by Latitude.
450
451   **Figure 2: Model performance of generalised additive mixed effects models**
452   (GAMMs). T = total herbivores (grey), for remaining letter and colour codes see
453   figure 1. Rows represent separate model fits, colored bars indicate that the
454   predictor was included in a particular model and the height of each row adjusted
455   to the cumulative Akaike weight, expressed as a proportion of all fitted models. I
456   = model intercept term, ISL.TYPE = island type, CHL = chlorophyll-a, COMP = reef
457   complexity, CORAL = hard coral cover, HUM = human population density, PISC. =
458   piscivore biomass, TEMP = sea surface temperature, AREA = area of habitat,
459   WAVES = wave energy.
460
461   **Figure 3: Predicted biomass and 95% confidence limits of functional**
462   **groups by island type and along human and biophysical gradients:** human
463   population density; sea surface temperature, habitat complexity; wave energy,
464   area of fore-reef and chlorophyll-a. Functional groups are indicated by color code
465   and letter (see figure 1).
466

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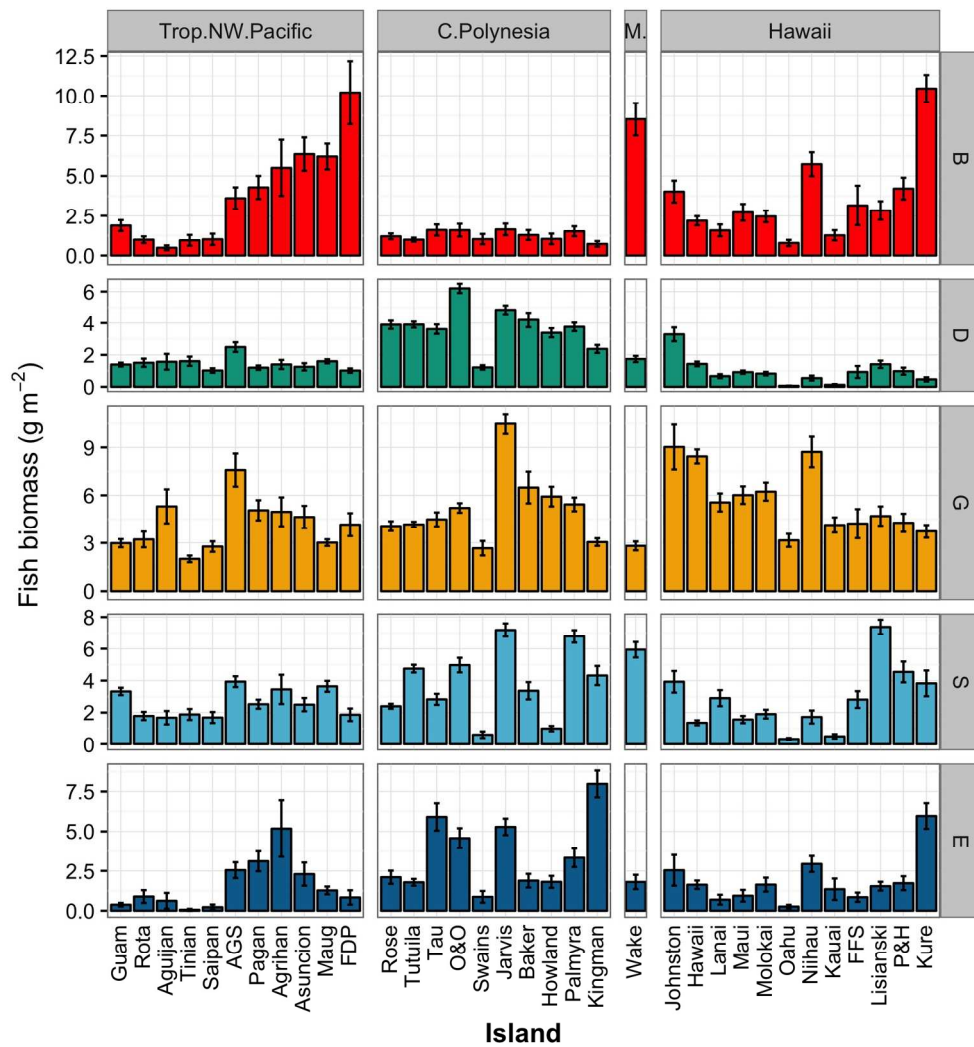
Herbivorous fish biomass by functional group per region. B = browsers (red), D = Detritivores (green), G = Grazers (yellow), S = scrapers and small excavators (blue), E = Large excavators and bioeroders (dark blue). Trop.NW.Pacific = Tropical Northwest Pacific, C. Polynesia = Central Polynesia, M. = Marshall Islands. AGS = Alamagan, Guguan and Sarigan, FDP = Farallon de Pajaros, O&O = Ofu and Olosega, FFS = French Frigate Shoals, P&H = Pearl and Hermes. Islands within region are ordered by Latitude.

figure 1
666x708mm (72 x 72 DPI)