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#### Frontiers in Marine Science

DOI:

10.3389/fmars.2020.571115

Published: 21/10/2020

Peer reviewed version

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA): Ford, A., Jouffray, J.-B., Norstrom, A. V., Moore, B., Nugues, M., Williams, G. J., Bejarano, S., Magron, F., Wild, C., & Ferse, S. (2020). Local human impacts disrupt relationships between benthic reef assemblages and environmental predictors. *Frontiers in Marine Science*, 7, Article 571115. https://doi.org/10.3389/fmars.2020.571115

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# Local human impacts disrupt relationships between benthic reef assemblages and environmental predictors

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#### **Abstract**

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Human activities are changing ecosystems at an unprecedented rate, yet large-scale studies into how local human impacts alter natural systems and interact with other aspects of global change are still lacking. Here we provide empirical evidence that local human impacts fundamentally alter relationships between ecological communities and environmental drivers. Using tropical coral reefs as a study system, we investigated the influence of contrasting levels of local human impact using a spatially extensive dataset spanning 62 outer reefs around inhabited Pacific islands. We tested how local human impacts (low versus high determined using a threshold of 25 people km<sup>-2</sup> reef) affected benthic community (i) structure, and (ii) relationships with environmental predictors using pre-defined models and model selection tools. Data on reef depth, benthic assemblages, and herbivorous fish communities were collected from field surveys. Additional data on thermal stress, storm exposure, and market gravity (a function of human population size and reef accessibility) were extracted from public repositories. Findings revealed that reefs subject to high local human impact were characterised by relatively more turf algae (>10% higher mean absolute coverage) and lower live coral cover (9% less mean absolute coverage) than reefs subject to low local human impact, but had similar macroalgal cover and coral morphological composition. Models based on spatio-physical predictors were significantly more accurate in explaining the variation of benthic assemblages at sites with low (mean adjusted- $R^2 = 0.35$ ) rather than high local human impact, where relationships became much weaker (mean adjusted- $R^2 = 0.10$ ). Model selection procedures also identified a distinct shift in the relative importance of different herbivorous fish functional groups in explaining benthic communities depending on the local human impact level. These results demonstrate that local human impacts alter natural systems and indicate that projecting climate change impacts may be particularly challenging at reefs close to higher human populations, where dependency and pressure on ecosystem services is highest. 

#### 94 **1** Introduction

95

Humans have become a dominant force of planetary change (Steffen et al., 2007). 96 Ecosystems worldwide are being fundamentally altered by climate change impacts 97 against a diverse backdrop of local anthropogenic stressors. Our ability to reliably 98 predict the future configuration of affected ecosystems requires a thorough 99 understanding of interactions between these different stressor types (Williams et al., 100 101 2019). Increasing evidence indicates that ecosystems are being reorganised, or homogenised, into stress-tolerant or opportunistic communities, leading to novel 102 systems that differ from their previous state in terms of their dominant constituents 103 (Graham et al., 2014; Morse et al., 2014). Quantifying ecological reorganisation over 104 broad scales remains challenging due to coarse taxonomic resolution inherent to 105 large datasets that are necessary to address this topic. Nonetheless, this 106 phenomenon may significantly alter a system's relationship with various 107 environmental and climate change-related drivers (Côté and Darling, 2010; Williams 108 et al., 2015a). Understanding what role local human impacts play in driving 109 ecological reorganisation and changing a system's relationship with its biophysical 110 environment is thus pivotal to improving predictive models and informing local 111 management (Robinson et al., 2018; Jouffray et al., 2019; Henderson et al., 2020). 112 113 114 Inherent high biodiversity and the presence of multiple stressors acting at local and global scales make tropical coral reefs a unique system to examine how local human 115 impacts drive ecological states (Hoegh-Guldberg et al., 2007; Ban et al., 2014; 116 Norström et al., 2016; Darling et al., 2019). Locally, rapidly expanding coastal 117 development, sewage input, and agricultural practices are reducing water quality, 118 whilst the modernisation of fishing gear and expedited market access are facilitating 119 120 overexploitation of coastal fisheries resources (Fabricius et al., 2005; Brewer et al., 2012; Hamilton et al., 2012). Globally, the intensity and frequency of thermal 121 anomalies, unusual weather patterns, and destructive storm events are increasing 122 (Gattuso et al., 2015; van Hooidonk et al., 2016; IPCC, 2019), and recovery windows 123 between stress events are narrowing (Riegl et al., 2013; Hughes et al., 2018). The 124 productivity and provision of ecosystem services (e.g. Woodhead et al., 2019) of 125 coral reef benthic communities differ depending on their composition (Ferrario et al., 126 2014; Rogers et al., 2018), underlining the importance of quantifying how 127 communities are affected by global change. The widespread negative effects of 128 climate change-related stressors are relatively well-understood. However, despite 129 more than half the world's coral reefs being located within 30 minutes travel time 130 from human populations (Maire et al., 2016), the role of local stressors remains 131 somewhat contested. These local stressors can range greatly in their intensity 132 depending on inherent factors such as human population density and the level of 133 exploitation, such as reliance on marine resources. 134 135 Higher human population densities have been linked to reductions in reef fish 136

biomass and coral cover, and to increases in fleshy (turf and macro-) algal cover

138 (Sandin et al., 2008; Williams et al., 2015b; Heenan et al., 2016; Smith et al., 2016).

139 However, coarse taxonomic resolution (inherent to large-scale datasets) can lead to

140 the conclusion that there is no link between local stressors and reef condition (e.g.

- Bruno and Valdivia, 2016). This may be a particular issue in regions such as the
- tropical Pacific where species diversity is exceptionally high and fleshy macroalgae,

frequently stated as principal alternative organisms on degraded reefs, do not play 143 such a dominant role in benthic dynamics compared, for instance, to the Caribbean 144 region (Roff and Mumby, 2012). Furthermore, reefs are increasingly existing in a 145 partially degraded condition between distinct regimes (Mumby, 2017), likely having 146 undergone ecological homogenisation resulting from the non-random removal of 147 species with particular traits in response to environmental factors (McWilliam et al., 148 2020). In this case, coral cover can remain moderate but comprises a less diverse 149 community of stress-tolerant and opportunistic types (Côté and Darling, 2010; van 150 Woesik et al., 2011; Riegl et al., 2013). Ecological homogenisation is visible across 151 reef habitat types, with inshore reefs that are naturally exposed to a more 152 challenging environment (e.g. in terms of light, temperature, and sediment input) 153 favouring a smaller species pool of stress-resistant corals compared to nearby outer 154 reef habitats (Rogers, 1990; Browne et al., 2013; Williams et al., 2013; Schoepf et 155 al., 2015; Morgan et al., 2016). 156

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A recent study demonstrated that whilst sea surface temperature (SST), chlorophyll 158 159 concentration, and wave energy have strong power in predicting benthic assemblages at remote reefs, this predictive power is lost or the relationships 160 fundamentally altered at reefs closer to human populations (Williams et al., 2015a). 161 Considering the dominant role of humans in shaping ecosystems, factors associated 162 with local anthropogenic impacts may have overtaken biophysical drivers in 163 structuring these altered reefs. It has also been postulated that reorganisation 164 towards a stress-tolerant coral community could increase resilience to climate 165 change, assuming co-tolerance between local and climate change-related stressors 166 (Côté and Darling, 2010), in line with the concept of 'intrinsic resistance' (Darling and 167 Côté, 2018). Indeed, coral richness does not translate into higher resilience to 168 disturbances (Zhang et al., 2014). Better understanding and accounting for the role 169 that local human impacts play in shaping benthic communities and their relationships 170 with environmental drivers is important for developing theories, designing 171 experiments, setting baselines, informing management, as well as optimising large-172 scale spatial predictive models for coral reef futures. 173

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Here, we investigate how local human impacts affect coral reef benthic communities 175 in the tropical Pacific. We start by classifying 62 island sites into two levels of local 176 human impact (low versus high) using a set threshold of human population density 177 informed by previous work (i.e. D'agata et al., 2014). We then ask whether the level 178 179 of local human impact influences benthic community structure or the relationship between benthic community structure and spatio-physical explanatory drivers. Lastly, 180 we examine the relative roles of ten biophysical parameters as drivers of benthic 181 community structure under low versus high local human impacts. We hypothesised 182 that spatio-physical drivers would be more related to benthic community structure on 183 reefs exposed to low local human impacts compared to those with high local human 184 impacts, where we expect human-associated factors to have become more 185 dominant. This approach allowed us to develop on the findings of Williams et al. 186 (2015a) by testing whether decoupling between reefs and biophysical drivers in the 187 presence of humans was also detectable between different levels of local human 188 impact. 189 190

192 193

### 2 Material and methods

#### 194 2.1 Study area and sampling design

This study intended to build on work from Williams et al. (2015a) by assessing in 195 more detail how local population density, rather than human presence/absence, 196 197 potentially decouples the relationship between reef benthos and larger-scale environmental drivers. To do so, we utilised a large-scale dataset that is unique in 198 having both site-level ecological (fish and benthic) and socio-economic data (in 199 200 particular human density per reef area at the site level), which is missing from other datasets that rely on global socioeconomic estimates for human population density. 201 or in some cases district-level surveys. Fish and benthic communities at 62 reefs 202 203 within 17 different Pacific Island countries and territories were surveyed once between 2003–2008 (see Supplementary Figure 1 for map) as part of the Pacific 204 Regional Oceanic and Coastal Fisheries Development Programme 205 (PROCFish/C/CoFish) under the auspices of the Pacific Community. Importantly, all 206 reefs were in close vicinity to, and used by, coastal human communities across a 207 large range of intensities (e.g. relative human density ranged from 1.3–1705 humans 208 km<sup>-2</sup> reef). For site disturbance history, sampling dates and detailed sampling 209 methodology, refer to Supplementary Table 1 and Pinca et al. (2010). Though it is 210 important to acknowledge that the sampling program was not originally designed in a 211 way to address macroecological questions or aggregate beyond the state/territory 212 213 level, we did our best to account for the shortcomings in the design by including additional information such as observer bias (see section 2.3 for details on 214 215 environmental parameters included). Furthermore, while data may not be 216 representative of the current-day scenario, it is the trends that are important for this study. Accordingly, we are confident that despite some inevitable compromising, this 217

gave us the best possible dataset to look at the effects of site-specific human density.

#### 220

#### 221 2.2 Field surveys

Underwater surveys covered outer (fore-) reefs, with on average nine (n = 3-47) joint 222 fish-benthic 50 m transects measured at each site. Transect data were pooled within 223 each site. Reef fish communities were measured using the variable distance-224 sampling underwater visual census method along transects (described in Labrosse 225 et al., 2002). Data on abundance and size were recorded to species-level for 226 herbivorous fish. Counts were converted to biomass (g m<sup>-2</sup>) from established length-227 weight relationships (Kulbicki et al., 2005). Benthic cover data was obtained using 228 the medium-scale approach described by Clua et al., (2006). This method is based 229 on a semi-quantitative description of ten  $25 \text{ m}^2$  (5 x 5 m) quadrats laid down on each 230 side of the 50 m transect (i.e. 20 replicate quadrats / 500 m<sup>2</sup> per transect). Surveyors 231 first recorded abiotic and live coral substrates, i.e. sand, rubble, rocky slab, boulders, 232 and hard coral - live, bleached, and long dead, with live coral divided into broad 233 234 morphologies (e.g. branching, encrusting, massive). Each component was quickly estimated using a semi-guantitative scale ranging from 0 to 100% per guadrat, in 235 units of 5%. Secondly, benthic groups (e.g. macroalgae - inclusive of calcified and 236 fleshy types, turf algae, crustose coralline algae [CCA], sponges, cyanobacteria) 237 238 growing over abiotic substrate such as long dead coral were recorded using the same semi-quantitative scale (Table 1). 239

Fishing grounds were initially delineated from information given by local fishers and 241 quantified from satellite interpretations (similar to methods in Close and Hall, 2006; 242 Léopold et al., 2014). Total reef area (km<sup>2</sup>) within each fishing ground was then 243 derived from reef areas guantified by the Millennium Coral Reef Mapping Project 244 from satellite images (Andréfouët et al., 2006). Socioeconomic assessments 245 determined total population within communities with access to the fishing ground, 246 allowing subsequent calculation of human population relative to reef area (referred to 247 as 'relative human density'). Finfish landings for each site, determined from 248 interviews with fishers, were extrapolated to total finfish catch per year per reef area 249 250 ('relative fishing pressure') (see Pinca et al., 2010).

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#### **Table 1** Benthic variables included in the models and their ranges.

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Variable	Description	Range (%)
live hard coral	mean cover (%) of live hard coral	6.1–65.1
dead hard coral	mean cover (%) of dead hard coral; including rubble, boulders, and pavement. Dead hard coral may also include biotic groups (i.e. growing over the dead coral), which are further classified as additional categories below*	5.5–61.2
branching morphologies	proportion (%) of branching coral morphologies within live hard coral community	0.1–85.6
encrusting morphologies	proportion (%) of encrusting coral morphologies within live hard coral community	2.8–72.9
massive morphologies	proportion (%) of massive coral morphologies within live hard coral community	0.1–60.6
CCA	mean cover (%) of crustose coralline algae	0.2–43.5
macroalgae	mean cover (%) of macroalgae; inclusive of calcified and fleshy types	0.0–31.2
turf algae	mean cover (%) of turf algae	0.0–45.6

254

\*not all categories are mutually exclusive – abiotic (e.g. dead coral, sand) and live
 coral substrates were recorded up to 100%, and biotic cover (e.g. algal groups) was
 recorded separately up to 100% (i.e. sum of substrate and biotic cover ≠100%).

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### 259260 **2.3**

### 260 **2.3 Data analyses** 261

#### 262 **2.3.1 Response variables**

As response variables, we selected the main benthic groups (i.e. those with a mean composition >10% of benthic community): dead coral (incorporating long dead coral, rubble, boulders, and pavement), live hard coral, and algal groups (differentiating turf algae, macroalgae, and CCA). We also assessed the proportional representation (within the live hard coral community) of the three most commonly observed morphological groups: branching, encrusting and massive morphologies. Pairwise relationship tests (*corvif* function – Zuur et al., 2009) established no collinearity among the response variables (correlation;  $R^2 < 0.5$ ). Table 1 provides an overview of the benthic variables and their ranges.

272

#### 273 2.3.2 Model predictors

274 We had to make a feasible choice of how to determine low versus high impact sites. Rather than choosing a completely arbitrary threshold, we selected one that was 275 informed by previous findings by D'agata et al., (2014) – using boosted regression 276 trees for the same dataset, the authors identified 25 people km<sup>-2</sup> reef to be the 277 threshold after which taxonomic diversity of parrotfishes significantly declined. We 278 then ran a sensitivity analysis to demonstrate how robust our findings were (see 279 section 2.3.4). To compare reefs exposed to different disturbance regimes, we thus 280 categorised all sites into those subject to low (i.e. < 25 people  $\text{km}^{-2}$  reef; n = 29) and 281 high (i.e. > 25 people km<sup>-2</sup> reef; n = 33) local human impact. Relative human density 282 correlates with relative exploitation – i.e. relative human density was collinear ( $R^2$  = 283 0.8) with fishing pressure (tonnes fish km<sup>-2</sup> reef year<sup>-1</sup>; Table 2). This threshold was 284 also a median point and allowed similar sample sizes in each impact level (see 285 Supplementary Figure 2). Relative human density also showed weak positive 286 correlation with market gravity – an index combining the population size of nearby 287 human settlements and their accessibility to reefs (Cinner and Maire, 2018; Cinner et 288 al., 2018). However, we decided to base our study on relative human density as we 289 290 had unique site-level data and we see this metric to be more directly linked to benthic communities in terms of human density-dependent sewage and agricultural 291 run-off in addition to subsistence and artisanal fishing. 292

293

The selected biophysical predictors included a variety of factors that were either 294 collected during field surveys or extracted from public data repositories (Table 2). 295 Due to inherent differences in coral reefs across latitudinal scales (e.g. Hughes et al., 296 1999; Harriott and Banks, 2002), latitude was represented by degree distance from 297 the equator without differentiating between north and south (0-23.9°). Degree 298 heating weeks (DHW) data were extracted from the NOAA Coral Reef Thermal 299 Anomaly Database (CoRTAD version 4 - Casey et al., 2012)). Storm exposure was 300 quantified from the NOAA IBTrACS-WMO data (Knapp et al., 2010a, 2010b) within 301 ArcMAP 10.4 (ESRI, 2011), where the number of storms (categories 1-5 on the 302 303 Saffir-Simpson Hurricane Scale) passing within a 50 km radius of each site (Behrmann projection) was extracted. Storm exposure and DHW data were confined 304 to 12 years prior to each respective site's survey date based on the premise that 305 remote reefs can recover from acute disturbances within this timeframe (Sheppard et 306 al., 2008; Gilmour et al., 2013). Reef depth, estimated during field surveys, was 307 averaged over all transects at each site. Island relief refers to each site's 308 309 geomorphology, and was classified into three categories; atoll, low-lying island, and high island based on available information (see Supplementary Table 1 for 310 references), and authors' knowledge. Island relief was included as a predictor due to 311 312 its known influence on coral reef benthic and fish communities (Donaldson, 2002; Houk et al., 2015). Herbivorous fish from selected families (e.g. excluding 313

herbivorous damselfish) encountered during visual surveys were classified into
functional groups according to Heenan et al. (2016) (see Supplementary Table 2).
Biomasses (g m<sup>-2</sup>) of the following functional groups were then incorporated as
predictors: browsers, grazers, detritivores, scrapers and small excavators, and large
excavators and bioeroders. Market gravity (Cinner and Maire, 2018) was extracted
for each site in QGIS (QGIS Development Team, 2019) and was incorporated as a
continuous predictor.

Prior to model fitting, paired plots were assessed for collinearity between model 322 terms. Strong collinearity ( $R^2 > -0.9$ ) between latitude and DHW precluded their joint 323 inclusion in subsequent models, and consequently latitude was selected because of 324 its complete reef-specific dataset (DHW data limited to n = 55 sites). Multi-collinearity 325 was also then tested using the generalised variance inflation factor (GVIF) function 326 (car package - Fox and Weisberg, 2019) where values >3 suggest collinearity – as a 327 result longitude was excluded from all models and the joint inclusion of browsers and 328 scrapers was prohibited (i.e. individual best-fit models were constrained to contain 329 330 only one or the other).

#### 332 2.3.3 Statistical models

333 All statistical analyses were performed in R version 3.6.1 (R Development Core Team, 2019). Differences in benthic community structure between reefs exposed to 334 low *versus* high local human impact level were tested using *t*-tests with appropriate 335 variance structures depending on homogeneity of variance test outcomes. Due to 336 surveyor discrepancies in recording turf algal cover, we created a random effect 337 (bias score) to be incorporated within turf algae models (see Supplementary Figure 338 339 3 for details). No surveyor-related discrepancies were evident for other benthic groups (see Supplementary Figure 3). To test how turf algal cover differed across 340 the two local human impact levels we thus used a linear mixed effects model 341 incorporating bias score as a random effect. All hereon described models were run 342 separately for sites predetermined to be exposed to either low or high local human 343 impacts to explicitly test for decoupling of abiotic and biotic predictors under different 344 disturbance regimes. 345

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331

To test whether the level of local human impact influences the relationship between 347 benthic community structure and spatio-physical explanatory drivers, we developed 348 349 a 'spatio-physical' model (i.e. focusing on spatial and physical predictors only) that included storm exposure, reef depth, latitude, and island relief. To account for non-350 linear relationships between response variables and predictors, we applied 351 generalised additive mixed effects models (GAMM) using the (Wood and Scheipl, 352 2014) and Ime4 packages. To account for possible spatial autocorrelation, ten 353 unique island clusters (*cluster*) were identified and incorporated into models as a 354 random effect (for details see Supplementary Figure 4). For turf algae models, 355 bias score was additionally included as a random effect. To avoid overfitting, the 356 number of knots within models was limited to four. We retained the adjusted-R<sup>2</sup> (Adj-357  $R^{2}$ ) values from the model output to quantify each model's explanatory power. Adj- $R^{2}$ 358 values for each response variable were then compared (by paired *t*-tests) to test 359 overall differences in model performance in explaining benthic community structure 360 361 under the two local human impact levels. 362

Table 2 Predictor descriptions and ranges at outer reefs. <sup>a</sup> predictor incorporated in
 'spatio-physical' models; <sup>b</sup> predictor used in model selection procedures. For sources
 of data, see main text.

Predictor	Description	Range
reef depth <sup>a,b</sup>	mean depth (m) of transects	3.9–10.5
degree heating weeks (DHW)	measure of cumulative thermal stress – sum of previous 12 weeks where thermal stress anomaly $\ge$ 1°C; value averaged over 12 years preceding survey; negatively collinear (R <sup>2</sup> = -0.9) with latitude; only available for n = 55 sites	0.6–3.5
latitude <sup>a,b</sup>	degrees (°) distance from equator (absolute value). Negatively collinear (R <sup>2</sup> = -0.9) with DHW	0.0–23.9
longitude	degrees (°) longitude on continuous scale (i.e175 counted as 185), included to account for distance from the Coral Triangle biodiversity hotspot	134.3–214.2 (i.e 145.8)
storm exposure <sup>a,b</sup>	sure <sup>a,b</sup> total number of storms (cat. 1 to 5 on the Saffir-Simpson Hurricane Scale) passing within 50 km of site within previous 12 years	
relief <sup>a.b</sup>	3 classifications: 1 = atoll; 2 = low-lying island; 3 = high island	
browser biomass <sup>b</sup>	biomass (g m <sup>-2</sup> ) of browsers	0.1–58.5
detritivore biomass <sup>b</sup>	biomass (g m <sup>-2</sup> ) of detritivores	0.5–62.8
excavator biomass <sup>b</sup>	biomass (g m <sup>-2</sup> ) of large excavators and bioeroders	0.0–369.1
grazer biomass <sup>b</sup>	biomass (g m <sup>-2</sup> ) of grazers	1.1–161.0
scraper biomass <sup>b</sup>	biomass (g m <sup>-2</sup> ) of scrapers and small excavators	1.9–134.3
relative human density	number of people within communities of the primary/customary resource users (living adjacent to/accessing fishing grounds within the reef area) related to total reef area (people km <sup>-2</sup> reef), positively collinear ( $R^2 = 0.7$ ) with relative fishing pressure. Used to determine local human impact level	1.3–1705
relative fishing pressure	annual reef finfish catch (tonnes) km <sup>-2</sup> reef year <sup>-1</sup> ; positively collinear (R <sup>2</sup> = 0.8) with relative human density	0.1–78.2

montrat analytity b	index that combines human population	0–1140
market gravity	size and reef accessibility	

367

Lastly, to examine the relative roles of ten biophysical parameters as predictors of 368 benthic community structure under low versus high local human impacts, we applied 369 model selection techniques using the *MuMIn* package (Barton, 2016). From an initial 370 model containing ten biophysical predictors (i.e. those included in the 'spatio-371 physical model' as well as biomass of herbivorous fish functional groups, and market 372 gravity - see Table 2), the dredge function was used to run all possible predictor 373 combinations and rank models from best to worst based on Akaike weight. The 374 function also returns a value between 0 and 1 for each predictor that reflects its 375 relative importance (RI), representing the total Akaike weight of all models containing 376 that predictor (i.e. higher values correspond to greater RI). Output models were 377 restricted to comprising a maximum of four predictors. One sample (Niue) was 378 removed from the model selection procedure due to a lack of data for market gravity 379 380 (i.e. n = 61). Model selection was run separately for sites with low and high levels of local human impact, and all models incorporated the *uGamm* wrapper function to 381 allow the inclusion of random effects consistent with 'spatio-physical' model 382 383 constructions. To assess incongruities between benthic communities exposed to different local human impact levels, we retained the 'best-fit' model structures (i.e. all 384 predictors included in models with Akaike weight >0.05) for each benthic response 385 variable, as well as the RI of individual predictors. 386

387

#### 388 2.3.4 Assumptions and sensitivity tests

All response variables were logit-transformed (appropriate for percentage data -389 Warton and Hui, 2011) using the *car* package, following adjustment using each 390 respective variable's minimum value >0. All model predictors were standardised (z-391 scores) to allow comparisons between predictors with largely varying effect sizes 392 and numeric values (Zuur et al., 2009). Model residuals were checked for the 393 394 violation of model assumptions using the *gam.check* function (see Supplementary Figure 5). As part of a sensitivity analysis, 'spatio-physical' models were additionally 395 run using  $\pm 5$  and  $\pm 10$  humans km<sup>-2</sup> reef as a threshold from which to categorise 396 'low' and 'high' impact sites, with consistent outcomes observed (see Supplementary 397 Table 3). Furthermore, we repeated the same for a range of thresholds based on 398 human density relative to outer reef area (as opposed to full reef area), again with 399 consistent outcomes observed (see Supplementary Table 4). 400

401 402

#### 403 **3 Results**

#### **3.1 Benthic assemblages under contrasting local human impacts**

Benthic communities subject to high local human impact were associated with lower live hard coral cover (-9.2% mean absolute coverage; *t*-test: p = 0.002; Figure 1A). However, the relative contribution of different coral morphologies within the live hard coral community did not differ significantly with local human impact level (Figure 1B). The only algal group that differed significantly depending on the local impact level was turf algae, which was higher under high local human impact (+10.7% mean absolute coverage; linear mixed effects model: p = 0.015; Figure 1C).



413

Benthic Type

**Figure 1** Boxplots detailing (**A**) benthic cover (%) of substrate types (from left to right; live hard coral, dead hard coral), (**B**) the relative proportion (%) of the three most dominant morphologies in the live hard coral community (branching, encrusting, massive), and (**C**) benthic cover (%) of different algal groups (CCA,

418 macroalgae, turf algae), at sites determined to have low or high local impacts.

Algorithm of the respective (p < 0.05) in cover of the respective

420 benthic variable between local impact levels according to two-sample *t*-tests, or for 421 turf algae according to linear mixed effect models incorporating *bias score* as a

- 422 random effect (see section 2.3.2).
- 423 424

#### 425 3.2 Predictive strength of 'spatio-physical' model

The pre-defined 'spatio-physical' model exhibited relatively high power in explaining benthic assemblage variance at sites with low local human impacts (mean Adj- $R^2 \pm$ SE; 0.35 ± 0.09; Figure 2), but model performance was severely compromised when local human impacts were high (0.10 ± 0.04; paired *t*-test: *p* = 0.01). When considering only the substrate types and dominant morphological groups (i.e. without the algal groups) the mean adjusted- $R^2$  for sites with low local human impacts increases to 0.44 ± 0.06 but stays unchanged at sites with high local human impacts.

When local human impacts were low, 'spatio-physical' predictors explained a high 433 proportion of the variance of live hard coral (Adj- $R^2 = 0.52$ ) and macroalgae (Adj- $R^2 =$ 434 0.59) cover, and the relative contribution of branching (Adj- $R^2 = 0.64$ ) and massive 435  $(Adj-R^2 = 0.50)$  coral morphologies. Conversely, these variables were consistently 436 poorly explained when local human impacts were high (Adj- $R^2 = 0.00, 0.26, 0.17,$ 437 0.10, respectively). No variance in turf algae was explained by this model for reefs at 438 either local human impact level. Significant differences in the power of the 'spatio-439 physical' model in explaining benthic assemblage variance between 'low' and 'high' 440 impact sites held constant when the threshold was moved  $\pm 5$  and 10 humans km<sup>-2</sup> 441 reef (i.e. paired *t*-test: p < 0.05; Supplementary Table 3). 442



CCA

Macroalgae

Turf algae

0.0

443



Figure 2 Explanatory power (Adj-R<sup>2</sup>) of the 'spatio-physical' model (including the
 predictors storm exposure, reef depth, latitude, and island relief) in predicting
 individual benthic responses (live hard coral, dead hard coral, the proportion of
 branching, encrusting, and massive morphologies, and cover of algal groups CCA,

0.4

Adj-R<sup>2</sup> value

0.6

449 macroalgae, and turf algae). Bars are absent where the Adj- $R^2$  value = 0.

0.2

450

#### 451 **3.3 Relative importance of predictors**

452 Best-fit' models tailored for each individual benthic variable comprised distinctly

different predictors depending on the level of local human impact (Figure 3A). Two of the predictors where discrepancies were most apparent were storm exposure and

grazer biomass, which were only selected for 'best-fit' models at sites with low and 455 high local human impacts, respectively. Similarly, reef depth was selected as part of 456 'best-fit' models for more response variables (live hard coral, branching 457 morphologies, and macroalgae) at sites with low local human impacts. Further 458 discrepancies under the two levels of local human impact were revealed by 459 comparing the mean RI of each predictor (Figure 3B,C), as the RI trends for 460 predictors almost reversed between low versus high local human impact sites. At 461 sites with low local human impacts, the individual predictors with the highest RI in 462 explaining benthic communities were storm exposure, scraper biomass, island relief, 463 followed by reef depth (Figure 3B). Contrastingly, apart from island relief which was 464 on average the most important predictor, storm exposure, scraper biomass, and reef 465 depth were among the least important predictors when local human impact was high 466 (Figure 3C). For benthic communities exposed to high local human impact, biomass 467 of grazers, detritivores, and browsers, as well as market gravity, ranked as the most 468 important predictors of benthic community structure. 469 470



471 472

Figure 3 (A) Outcome of model selection procedures: coloured boxes indicate that 473 the predictor was selected for 'best-fit' models (i.e. those with Akaike weight > 0.05) 474 at sites subject to low and/or high levels of local impacts. The overall mean relative 475 476 importance of each predictor (RI - based on total Akaike weight of all models including that predictor) in explaining the benthic response variables is shown 477 separately for sites subject to (B) low and (C) high local impacts. Note: though model 478 selection was limited to four predictors per model, all predictors included in models 479 with Akaike weight >0.05 are shown meaning there may be more than four predictors 480 shown within one impact level for a response variable. Model outputs for 'best-fit' 481 482 models are available in Supplementary Table 5. 483



#### 485

Number of storms passing within 50 km in previous 12 years

**Figure 4** Smoother plots of normalised residuals from generalised additive models with 95% confidence intervals (shaded areas) to exemplify discrepancies in response-predictor relationships between local impact levels, using storm exposure as an example. The plots represent the explanatory power of storm exposure in predicting (**A**) live hard coral cover, and the proportion of (**B**) branching, (**C**) encrusting, and (**D**) massive morphologies, separated for sites with low *versus* high

- 492 local impacts. Refer to Supplementary Figure 6 for all predictor-response plots from493 'best-fit' models.
- 494

495 Individual relationships of 'best-fit' predictors for each response variable further

- 496 emphasised discrepancies between benthic communities and environmental
- 497 predictors driven by local human impacts (for all plots see Supplementary Figure 6).
- 498 A clear example of this discrepancy can be seen in coral compositional changes with

increasing storm exposure. Whilst live hard coral cover remained unrelated to storm 499 exposure under both local human impact levels (Figure 4A), the morphological 500 composition was closely correlated with storm exposure at sites where local human 501 impacts were low (Figure 4B–D). Specifically, with increasing storm exposure, the 502 relative proportion of branching morphologies decreased significantly (Figure 4B), 503 whereas encrusting (Figure 4C) and massive (Figure 4D) morphologies increased. 504 505 No morphological changes with storm exposure were observed at sites with high local human impacts. Though these relationships appear primarily driven by few 506 points at the higher end of storm exposure, they remained consistent when all reefs 507 508 exposed to >10 storms were removed from the analysis - i.e. significant at 'low' impact sites (branching coral p = 0.02; encrusting coral p = 0.02; massive coral p = 0.02509 0.03), insignificant at 'high' impact sites (all morphological growth forms p > 0.05), 510 and no relationship for either impact for total live hard coral cover (p > 0.05). 511 512

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#### 514 **4 Discussion**

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Under increasing climate change-associated stressors and local anthropogenic 516 517 influence (Burke et al., 2011; Gattuso et al., 2015; IPCC, 2019), it is particularly important for researchers and planners to maximise the ability of models to predict 518 ecosystem futures to allow appropriate mitigation strategies to be implemented. This 519 study indicates that the role of local human impacts in changing coral reef ecological 520 communities and their responses to environmental drivers should be accounted for. 521 The results revealed that local human impacts influenced both benthic community 522 structure and relationships with biophysical predictors. Specifically, models based on 523 spatio-physical predictors (i.e. reef depth, latitude, storm exposure, and relief) 524 exhibited high power at explaining benthic assemblages under low local human 525 impacts but were strongly compromised where local human impacts were high. 526 527 Importantly, these outcomes remained similar when our threshold for human impacts, informed by previous work, was reduced or increased in the frame of a 528 sensitivity analysis. Increasing sewage input, agricultural run-off, and sedimentation 529 530 are potential changes associated with increasing human densities that reduce water quality and affect benthic communities (Fabricius, 2005; Fabricius et al., 2005; Ford 531 et al., 2017). Furthermore, as fishing removes biomass of functionally important fish 532 species, important top-down control of some benthic organisms is lost (Bellwood et 533 al., 2004). These localised human impacts may homogenise benthic communities by 534 driving ecological reorganisation that favours tolerant taxa (Darling et al., 2019). Our 535 results indicate that this homogenisation may be occurring at Pacific Island reefs that 536 are exposed to local human impacts, leading to novel systems that react 537 fundamentally differently and unpredictably to environmental predictors compared to 538 reefs less influenced by humans (Williams et al., 2015a). In turn, we expect that local 539 human impacts will influence responses of coral reefs to climate change-related 540 stressors, and that reefs close to human populations will require context-specific 541 management approaches to maximise their future sustainability and associated 542 543 critical ecosystem services (Moberg and Folke, 1999). 544 The results emphasise the variation in benthic assemblages that exists among

545 The results emphasise the variation in benthic assemblages that exists among 546 Pacific Island reefs exposed to different levels of local human impact. Benthic

547 communities were not restricted to distinct regimes dominated by either hard corals

or macroalgae, supporting previous studies from the Pacific (Bruno et al., 2009; 548 Albert et al., 2012; Jouffray et al., 2015, 2019; Smith et al., 2016). In fact, 549 macroalgae was the least common of all the algal groups, with turf algae and CCA 550 more prominent on these outer reefs. Reefs at sites with higher local human impacts 551 comprised significantly more turf algae and less live hard coral. Abundant and 552 diverse outer reef coral communities (e.g. Ellis et al., 2017) have likely retained 553 554 sensitive species, facilitating measurable differences (i.e. reductions in live hard coral cover) under higher local human impacts. Higher turf algae coverage at sites 555 with more local human impacts provides further evidence that turf algae may 556 557 become the dominant benthic group on degraded Pacific Island reefs (Jouffray et al., 2015; Smith et al., 2016; Tebbett and Bellwood, 2019). This may contrast with coral 558 reef systems in the Caribbean, where macroalgae naturally play a more dominant 559 560 role (Roff and Mumby, 2012). Furthermore, a signal of local human impact may have been detected if the data had distinguished macroalgae into fleshy/frondose and 561 calcified types (e.g. Smith et al., 2016; Cannon et al., 2019). A similar link between 562 human population size, hard coral cover, and turf algae has also recently been 563 564 reported from sites in the Indian Ocean (Brown et al., 2017).

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The 'spatio-physical' models were weak in explaining the variance of benthic 566 communities exposed to relatively more local human impacts. At these sites, model 567 selection identified mostly local biotic controls or ecological features such as fish 568 biomass and market gravity to be of highest relative importance. These results 569 suggest that reefs altered by chronic local human impacts become decoupled from 570 spatio-physical factors (Williams et al., 2015a) and become more related to factors 571 associated with human activities (e.g. market gravity) or local ecological features 572 573 (e.g. biomass of functional groups of fish). Interestingly, this outcome contrasts to recent findings by Robinson et al. (2018) who did not detect decoupling at inhabited 574 versus uninhabited reefs. Our different outcomes for decoupling could in part be 575 576 explained by Robinson et al. (2018) combining (i) hard corals and CCA, and (ii) fleshy macroalgae and turf algae, each of which we found to exhibit different 577 responses to local impacts (i.e. with higher local impacts hard coral cover reduced 578 whereas CCA remained unchanged, turf algae increased whereas macroalgae 579 remained unchanged). Model selection indicated that the specific spatio-physical 580 predictors whose influence were most disrupted by local human impacts were storm 581 exposure and reef depth. Storms can have mixed effects, benefitting reefs by 582 583 alleviating thermal stress during warmer summer months but also causing physical destruction, particularly to delicate branching coral morphologies, leading to a higher 584 proportion of more robust massive morphologies (Heron et al., 2005; Manzello et al., 585 586 2007). Accordingly, when local human impacts were low, coral communities comprised relatively less branching and more encrusting and massive morphologies 587 at sites subject to more frequent storms. However, relationships between storm 588 exposure and benthic assemblages were only observed at sites classified as having 589 low local human impacts. Returning to the concept that local human impacts drive 590 ecological reorganisation, we would expect reefs with less local human impacts to 591 592 harbour a great diversity of species and morphologies, thus allowing for greater levels of ecological reorganisation in response to a stormier environment (i.e. 593 favouring more robust morphologies). We anticipate that Pacific reefs would more 594 595 likely display this phenomenon than Caribbean reefs due to a significantly larger initial species pool, with greater response diversity and functional redundancy 596

affording a higher level of ecological insurance (Elmqvist et al., 2003; Bellwood et al., 597 2004; Nyström, 2006), and a loss of structurally-complex coral species throughout 598 most of the Caribbean over past decades (Alvarez-Filip et al., 2009). It would be 599 interesting to test whether storm exposure results in more conspicuous negative 600 impacts on coral cover (e.g. Gardner et al., 2005) in less diverse regions due to the 601 limited capacity for ecological reorganisation to a tolerant community, even in sites 602 603 with minimal local human impact. In terms of reef depth, benthic communities at sites with low local human impacts also exhibited a higher level of depth-structuring 604 (particularly in terms of coral cover and composition, consistent with Huston, 1985) 605 compared to those with high local human impacts. Island relief was also identified as 606 being a strong predictor of benthic community structure (despite being found to be a 607 weak predictor on central-western Pacific reefs - Robinson et al., 2018), and 608 interestingly this role was maintained regardless of local human impact level. 609 Importantly, when considering latitude - collinear with DHW/cumulative thermal 610 stress – as an individual predictor, our results neither contradict nor confirm previous 611 observations that local impacts exacerbate the sensitivity of coral communities to 612 613 thermal stress (Wiedenmann et al., 2013; Ellis et al., 2019), instead highlighting a large variance among sites. 614

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Thermal stress and the intensity of storms are projected to increase under future 616 climate change scenarios (IPCC, 2019), with profound implications for coral reefs 617 and adjacent ecosystems. Our findings suggest that while the effects of factors 618 associated with climate change (e.g. storm exposure) on Pacific reef benthic 619 assemblages may be reasonably well-predicted where local impacts are low, system 620 responses become less predictable as local human impacts increase. In both marine 621 622 and terrestrial systems, structural changes caused by local impacts have profoundly changed how ecosystems respond to natural stressors: for example, local stressors 623 have affected how parts of Australia's Great Barrier Reef have recovered from recent 624 climate change impacts (MacNeil et al., 2019; Mellin et al., 2019) and habitat 625 fragmentation and modification have exacerbated recent impacts of tropical and 626 temperate forest fires (Brando et al., 2014; Alencar et al., 2015; Taylor et al., 2016). 627 Because the effects of storms are strongly dependent not only on their intensity, but 628 also the extent of the fetch, their frequency, and intrinsic reef properties such as 629 topography (Lugo et al., 2000; Heron et al., 2005), this study incorporated all 630 recorded storms (category 1–5 on the Saffir-Simpson Hurricane Scale) passing 631 632 within 50 km of each site. We thus cannot deduce benthic community responses to increasing storm intensity, which is projected to occur (IPCC, 2019). 633

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Functional groups of herbivorous fishes also emerged to be of contrasting relative 635 importance depending on the level of local human impact, shifting from scrapers and 636 small excavators at less impacted reefs to grazers at more impacted reefs. Browsers 637 were of similar importance at reefs exposed to both local human impact levels, 638 perhaps linked to the fact that their food source (macroalgae) remained constant 639 regardless of local human impact level. Additional reasons for this could be that 640 browsers have remained more resilient to fishing pressure than other herbivores, or 641 that visual survey data does not accurately represent browser populations (for 642 example some browser species are known to be particularly wary of divers -643 644 Kulbicki, 1998). Fish that act on turf algae and/or on surfaces available for coral settlement seem to be more sensitive to local human impacts, likely in response to 645

benthic community shifts. Scrapers and small excavators clear substrate for 646 calcifiers, justifying their higher relative importance in models focused on less locally 647 impacted reefs where live hard coral cover was higher and conditions for settlement 648 and growth of juvenile corals were likely better (e.g. less nutrients, lower 649 sedimentation). Contrastingly, grazers crop and maintain algal turfs, explaining their 650 importance under higher local human impacts where turf algae were more dominant. 651 These results align with findings in the Hawaiian Archipelago, where biomass of 652 grazers and scrapers were the most important predictors of turf/macroalgal, and 653 calcified regimes, respectively (Jouffray et al., 2015; see also Robinson et al., 2018). 654 Though collinearity tests ruled out significant, potentially confounding relationships 655 between biomass of different functional groups with individual abiotic predictors, it is 656 important to acknowledge that fish communities themselves can be affected by 657 various physical predictors (Williams et al., 2015b; Samoilys et al., 2019), which 658 could in turn influence benthic structure. 659

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Other factors not included in these analyses are known to structure benthic 661 662 assemblages, including chlorophyll, SSTs, and wave exposure (Gove et al., 2013, 2015: Williams et al., 2013: Robinson et al., 2018: Darling et al., 2019), Remotely 663 sensed chlorophyll data captures offshore productivity, but we expected land-based 664 input to dominate many of these reefs which are close to land, while the survey 665 design (sometimes around the periphery of small islands/atolls) made wave 666 exposure challenging to quantify. Additionally, wave exposure, mean SSTs, and 667 climatological ranges can be relatively well-captured by latitude in the Pacific (Gove 668 et al., 2013). Also, although this study goes into more detail than many similar large-669 scale analyses by evaluating coral growth forms, it is still limited in its ability to 670 quantify ecological reorganisation, which would require higher resolution data (at 671 least family or genus). This limitation can be overcome by broad-scale surveys 672 refining the level at which hard coral communities are recorded, which will become 673 easier with improvements in automated software tools. These results do however 674 emphasise that even broad morphological groupings (i.e. branching, massive, 675 encrusting morphologies) provide pertinent information on ecological changes and 676 can improve model performance compared to when overall hard coral cover is 677 considered (Gove et al., 2015). 678

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Importantly, the threshold used in this study for determining low and high impact, 680 while informed by a previous study, was set a priori and thus does not allow defining 681 a 'carrying capacity' of human density – this would require a different survey design 682 and analytical approach, and should be pursued in future studies. We would 683 684 however suggest that although this metric is most applicable to areas where customary resource use is common practice, we anticipate that this threshold (25 685 humans km<sup>-2</sup> reef) is highly relevant across the Pacific region (i.e. given that it is a 686 median point in this dataset for which sites were selected due to being regionally 687 representative of fished areas). Furthermore, the study design was not originally 688 meant to address macroecological questions but was nonetheless the best available 689 690 to study the questions we were interested in (with incorporation of appropriate secondary data on local environmental context). Again, future studies should 691 address this by appropriate designs that allow for large-scale comparability and 692 693 collect both ecological and socio-economic local data. Our findings indicate that island relief is a factor that should be considered in designing regional sampling 694

programs with comparable sites. Finally, we should aim to obtain context-specific
information on factors associated with human population density (e.g. sewage
treatment presence, farming and associated fertiliser-usage) that strengthens our
ability to predict benthic communities under various levels of human population
density and improve its use as a proxy of local human impact.

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701 Our findings contribute to a better understanding of the role of local human impacts on diverse ecosystems such as tropical coral reefs. The results provide empirical 702 evidence that local human impacts drive conspicuous changes in benthic community 703 704 relationships with environmental predictors, with indications of ecological reorganisation. Even if decisive steps are taken to reduce fossil fuel emissions, most 705 reefs will suffer long-term degradation from the effects of climate change by 2050, 706 and >75% of reefs will experience annual severe bleaching (Frieler et al., 2013; van 707 Hooidonk et al., 2016). Our results show that local human impacts can lead to 708 increasingly unpredictable relationships between benthic communities and their 709 physical environment, and that overlooking their role could pave way to significant 710 711 errors in future projections, potentially compromising mitigation efforts.

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### 714 5 Conflict of Interest

The authors declare that the research was conducted in the absence of any
commercial or financial relationships that could be construed as a potential conflict of
interest.

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### 721 6 Author Contributions

AF developed the study idea with close support from JBJ, AN, BM and SF. AF led the statistical analyses together with input from JBJ, GW and SF. BM and FM provided expertise on the original data. All authors provided support throughout the interpretation of the results and development of the manuscript. All authors approve this final version.

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### 730 **7 Funding**

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The COFish and PROCFish-C Programmes were funded by the European Union.
AF, SB, and SF were funded by the (German) Federal Ministry of Education and
Research (BMBF) through the "Nachwuchsgruppen Globaler Wandel 4 + 1"
(REPICORE, grant number 01LN1303A).

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### 738 8 Acknowledgements

739

We would like to thank the Pacific Community survey team, in particular Samasoni
Sauni, Pierre Boblin, Ribanataake Awira, Laurent Vigliola, and Silvia Pinca, as well
as the fisheries officers across the PICTs who assisted with logistics and data

- collection. Data collection was made possible by the support of in-country Fisheries
   Divisions, as well as the chiefs and people of all local communities at the surveyed
   sites. The research reported in this paper contributes to the Programme on
   Ecosystem Change and Society (www.pecs-science.org).
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**Supplementary Figure 1** - Map of the 62 sites surveyed across 17 different Pacific Island countries and territories, coloured by local impact level.



**Supplementary Figure 2** - Number of sites by human density (humans km<sup>-2</sup> reef). Dashed line indicates threshold separating low impact from high impact sites.



**Supplementary Figure 3** - To account for possible spatial autocorrelation among sites, we included island cluster as a random effect within models (based on methodology of Williams et al. 2015\*). Island clusters were identified using (A) hierarchical clustering based on pairwise Euclidean distances between each of the 62 sites, by finding (B) an inflection point in the number of unique clusters and cluster distance which we identified to be at ~1300 km, resulting in ten unique island clusters.

\*Williams GJ, Gove JM, Eynaud Y, Zgliczynski BJ, Sandin SA. (2015) Local human impacts decouple natural biophysical relationships on Pacific coral reefs. *Ecography*, **38**, 751–761.



**Supplementary Figure 4** - Boxplots representing ranges of response variables recorded by the core survey diver team - the core survey team consisted of five divers, who recorded 94% of all transects. Additional surveyors were included in the remaining 6%. As surveyor bias is inherent to such datasets, we tested for surveyor effects on our response variables. These tests indicated that significantly higher turf algae coverage was reported by two of the core survey team (survey divers iii and v). It became apparent that even within one reef, there were discrepancies in the reported turf algae cover between these survey divers and survey divers i, ii, and iv. This was not an issue with other benthic groups nor morphological classifications of hard corals (i.e. massive, branching, and encrusting). To account for the differences in turf algae reporting, we scored the contribution of survey divers iii and v to total surveys at each reef on a continuous scale from 0 to 1 (i.e. 0 meaning survey divers iii and v were not present on any transects at the reef, and 1 meaning all transects at a reef were conducted by survey diver iii and/or v). This score (referred to as *bias\_score*) was included as a random effect in subsequent turf algae-focused models.

#### Live hard coral



#### Dead hard coral





8 .

-1.0

-1.5

Fitted Values

residuals

0.0

-1.0

-2.0

-2.0

Response





residuals

0.6

Histogram of residuals





#### Branching morphologies



#### Encrusting morphologies



#### Massive morphologies

-4 -3 -2 -1 0

Residuals



~

0 -

-0.6

-0.4

-0.2 0.0 0.2 0.4

Residuals

0.6

-1.6 -1.4 -1.2 -1.0

Fitted Values

4 -3

10

-1.8 -1.6 -1.4 -1.2 -1.0 -0.8 -0.6 -0.4

Fitted Values

#### Fleshy algae



Turf algae



**Supplementary Figure 5** - Residuals (\$gam.check) of 'spatio-physical' models (for each response variable (in order from top to bottom: live hard coral, dead hard coral, branching morphologies, encrusting morphologies, massive morphologies, CCA, macroalgae, turf algae). Left set of graphs = models based on low local impact sites (< 25 humans km<sup>-2</sup> reef); right set of graphs = models based on high local impact reefs (> 25 humans km<sup>-2</sup> reef):





(B)



**Supplementary Figure 6** – Individual relationships between selected predictors for each respective response variables as per 'best-fit' model outcomes. (A) Smoother plots of normalised residuals from generalised additive mixed effect models (*gamm4* package) with 95% confidence intervals (shaded areas). Plots are based on the \$gam output from these models. These graphs provide relationships between individual response variables and predictors that were selected for 'best-fit' models (those with Akaike weight > 0.05; see Figure 4; Supplementary Table 4) at outer reef sites with low and/or high local human impacts. Plots are provided in terms of reefs exposed to low (light grey/left panel) *versus* high (dark grey/right panel) local impact as determined using a threshold of 25 humans km<sup>-2</sup> reef. Large crosses (X) mean that the predictor was not selected for 'best-fit' models for reefs exposed to either impact level. (B) Boxplots conveying relationships between the predictor island relief and benthic response variables for which it was selected for 'best-fit' models (i.e. those with Akaike weight > 0.05; see Figure 4; Supplementary Table 4).

**Supplementary Table 1** - Table containing survey dates and timelines of disturbances (up to 12 years before surveys) with associated references provided.

\*Additional survey information: Criteria for site selection: (i) having active reef fisheries, (ii) being representative of the country, (iii) being relatively closed systems, (iv) being appropriate in size, (v) possessing diverse habitats\*, (vi) presenting no major logistical problems, (vii) having been previously investigated and (viii) presenting particular interest for the respective Fisheries Agency. For full details see Pinca et al. (2010). Originals surveys grouped reefs into four geomorphological structures, but this study focused only on outer (fore-) reefs (primarily due to replication). Though 63 individual outer reefs were surveyed, one reef had less than three replicate transects and thus was removed, leaving 62 replicate reefs.

Country	Sites & Survey Dates	History of Events	References
Cook Islands	Aitutaki, Feb-2007 Mangaia Oct-2007 Palmerston Feb-2007 Rarotonga Oct-2007	1997: Several cyclones (including Cyclone Martin – category 3) 2000: Mass bleaching event (up to 80% <i>Acropora</i> bleached in Rarotonga) 2002/2003: Major cyclone 2003/2004: Major cyclone 2004/2005: Several destructive cyclones (six)	Lovell 2001, Cumming et al. 2002, Salvat 2002, de Scally 2008, Pinca et al. 2009a
Fiji	Dromuna Apr-2003 Lakeba Jun-2003 Mali Jun-2003 Muiavuso Apr-2003	2000: Mass bleaching event (40–80% coral mortality) 2001: Minor bleaching 2002: Bleaching in shallow areas	Goreau et al. 2000, Cumming et al. 2002, Lovell et al. 2004, Friedman et al. 2010
French Polynesia	Fakarava Mar-2004 Maatea May-2006 Mataiea May/Jun-2003 Raivavae Mar-2004 Tikehau Oct-2003	<ul> <li>1994: Major bleaching but</li> <li>low mortality</li> <li>1997: Cyclone Martin hit</li> <li>(southern) French Polynesia.</li> <li>Patchy bleaching and</li> <li>mortality</li> <li>2002: Start of COTS</li> <li>outbreak (at Society</li> <li>Archipelago and Australes)</li> </ul>	Salvat 2002, Vieux et al. 2004, Adjeroud et al. 2005, Kronen et al. 2008a, Trapon et al. 2011

FSM	Piis-Panewu Apr-2006	2005: Concerning levels of	George et al.
	Riiken Apr-2006	COTs reported from rapid	2008, Kronen et
	Romanum Apr-2006	assessment	al. 2009a
	Yyin May-2006		
Kiribati	Abaiang Jun-2004	2003: Fish kill in atolls of	Awira et al. 2008,
	Abemama May-2004	Gilbert Islands	Donner et al.
	Kiritimati Sep-2004	2004: (post survey) first	2010
	Kuria May-2004	mass bleaching event	
		internationally reported	
Marshall	Ailuk Aug-2007	2001: Bleaching mortality	Beger et al. 2008
Islands	Arno Sep-2007	observed (particularly	Pinca et al. 2009b
	Laura Sep-2007	shallow Acropora)	
	Likiep Aug-2007	2003: Bleaching event, high	
		incidence of Acropora white	
		disease	
		2004: Elevated COTS	
		$(>1000 \text{ km}^{-2})$ found in	
		Majuro's SW lagoon, with	
		associated coral mortality	
		2006: Storm caused large	
		surf and storm surge	
		(become Typhoon Soulik) –	
		Acropora colonies damaged.	
		Also bleaching event with	
		up to 90% Acropora	
		bleaching (20–50%	
		mortality) in lagoons.	
Nauru	Nauru Oct-2005	2000: Phosphate reserves	Sulu et al. 2002
		are virtually exhausted (80%	Lovell et al. 2004.
		of the island's surface has	Sauni et al. 2007,
		been strip mined – mining	Chin et al. 2011
		started in 1908)	
		2002: High rainfall and	
		some bleaching	
		2003: Coral bleaching and	
		mass fish kills both linked to	
		elevated SSTs, strong	
		upwelling or drops in	
		dissolved oxygen levels.	
		2004: Large number of	

		seabirds found dead without	
		a known cause	
New	Luengoni Jun-2004	1998 and 2001: Extensive	Sulu et al. 2002,
Caledonia	Moindou May-2004	coral loss due to COTs,	Lovell et al. 2004,
	Ouasse Aug-2004	bleaching and disease	Kronen et al.
	Oundjo Feb-2004	2003: Cyclone (Erica) led to	2009b
	Thio Mar-2004	10–80% coral loss	
Niue	All Niue May-2005	2004: Major cyclone	Vieux et al. 2004,
		(Cyclone Heta – category 5)	Kronen et al.
		caused 20–90% reefs on the	2008b, Chin et al.
		western coast to be	2011
		flattened, hence live coral in	
		surveys sometimes <2%	
Palau	Airai Apr-2007	1998: Mass bleaching from	Friedman et al.
	Koror May-2007	El Niño reduced coral cover	2009a, Golbuu
	Ngarchelong Apr-2007	from 50–70% to 14–23%	2011
	Ngatpang Apr-2007	(exposed barrier reefs	
		suffered more than coastal	
		reefs). High mortality of soft	
		corals.	
		Area is not exposed to	
		cyclones and COTs	
		outbreaks remain local	
		events	
Papua	Andra Aug-2006	1996: Mass bleaching event	Lovell 2001,
New	Panapompom Nov-2006	(>50% corals at some sites)	Cumming et al.
Guinea	Sideia Oct-2006	1998: Mass bleaching from	2002, Foale 2006,
	Tsoilaunung Aug-2006	El Niño (75% Acropora	Friedman et al.
		affected at Kimbe Bay)	2009b
		1999: Bleaching event	
		2000/2001: Mass bleaching	
		event (>50% corals at some	
		sites)	
Samoa	Manono-uta Jun-2005	2004: Cyclone (Heta –	Sulu et al. 2002,
	Salelavalu Aug-2005	category 5) damaged 13% of	Lovell et al. 2004,
	Vailoa Jun-2005	coral reefs	Vunisea et al.
	Vaisala Aug-2005		2008, Chin et al.
			2011

Solomon	Chubikopi Dec-2006	2000: Mass bleaching	Lovell 2001,
Islands	Marau Jun-2006	2002: Major cyclone (Zoe –	Cumming et al.
	Nggela Jun-2006	category 5)	2002, Sulu et al.
	Rarumana Aug-2006		2002, Pinca et al.
			2009c
Tonga	Ha'afutu2 Sep-2008	1997: Cyclone (Hina –	Lovell 2001,
	Koulo Oct-2008	category 3)	Salvat 2002,
	Lofanga Oct-2008	1999: Cyclone (Cora –	Friedman et al.
	Manuka Sep-2008	category 3)	2009c
		2000: Cyclone (Mona –	
		category 3), mass bleaching	
		(up to 90% of Goniastrea	
		and <i>Platygyra</i> colonies	
		bleached)	
Tuvalu	Funafuti Nov-2004	1997: Major cyclones	Sulu et al. 2002,
	Niutao Apr-2005	(Oliwa and Keli)	Lovell et al. 2004,
	Nukufetau Oct/Nov-2004	2002: Mass bleaching (30–	Sauni et al. 2008
	Vaitipu Mar/Apr-2005	40% corals bleached)	
Vanuatu	Maskelynes Nov/Dec-	2001: Bleaching event	Sulu et al. 2002,
	2003	(documented in Moso but	Friedman et al.
	Moso Jul-2003	lack of monitoring data for	2008
	Paunangisu Jul-2003	other areas)	
	Uri-Uripiv Nov/Dec-		
	2003		
Wallis	All Futuna Nov-2005		Kronen et al.
and	Halalo Sep-2005		2008c
Futuna	Vailala Sep-2005		

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Functional group	Species	
Browsers	Calotomus carolinus	
Browsers	Calotomus spinidens	
Browsers	Kyphosus cinerascens	
Browsers	Kyphosus sp.	
Browsers	Kyphosus vaigiensis	
Browsers	Leptoscarus vaigiensis	
Browsers	Naso annulatus <sup>1</sup>	
Browsers	Naso brachycentron	
Browsers	Naso brevirostris <sup>1</sup>	
Browsers	Naso lituratus	
Browsers	Naso sp.	
Browsers	Naso tuberosus	
Browsers	Naso unicornis	
Browsers	Platax orbicularis	
Browsers	<i>Platax</i> sp.	
Browsers	Platax teira	
Browsers	Siganus canaliculatus	
Detritivores	Ctenochaetus binotatus	
Detritivores	Ctenochaetus cyanocheilus	
Detritivores	Ctenochaetus flavicauda	
Detritivores	Ctenochaetus hawaiiensis	
Detritivores	Ctenochaetus marginatus	
Detritivores	Ctenochaetus sp.	
Detritivores	Ctenochaetus striatus	
Detritivores	Ctenochaetus strigosus	
Detritivores	Ctenochaetus tominiensis	
Grazers	Acanthurus achilles	
Grazers	Acanthurus auranticavus	
Grazers	Acanthurus blochii	
Grazers	Acanthurus dussumieri	
Grazers	Acanthurus fowleri	
Grazers	Acanthurus guttatus	
Grazers	Acanthurus leucocheilus	
Grazers	Acanthurus leucopareius	
Grazers	Acanthurus lineatus	
Grazers	Acanthurus maculiceps	
Grazers	Acanthurus nigricans	
Grazers	Acanthurus nigricauda	
Grazers	Acanthurus nigrofuscus	
Grazers	Acanthurus nigroris	
Grazers	Acanthurus olivaceus	
Grazers	Acanthurus pyroferus	
Grazers	Acanthurus sp.	

**Supplementary Table 2** - Herbivorous fish recorded within surveys, classified into functional groups as specified in Heenan et al. (2016).

Functional group	Species
Grazers	Acanthurus triostegus
Grazers	Acanthurus xanthopterus
Grazers	Centropyge bicolor
Grazers	Centropyge bispinosa
Grazers	Centropyge flavissima
Grazers	Centropyge loricula
Grazers	Centropyge sp.
Grazers	Centropyge tibicen
Grazers	Centropyge vrolikii
Grazers	Siganus argenteus
Grazers	Siganus corallinus
Grazers	Siganus doliatus
Grazers	Siganus fuscescens
Grazers	Siganus guttatus
Grazers	Siganus lineatus
Grazers	Siganus niger
Grazers	Siganus puellus
Grazers	Siganus punctatissimus
Grazers	Siganus punctatus
Grazers	Siganus randalli
Grazers	Siganus sp.
Grazers	Siganus spinus
Grazers	Siganus stellatus
Grazers	Siganus uspi
Grazers	Siganus vermiculatus
Grazers	Siganus vulpinus
Grazers	Zebrasoma flavescens
Grazers	Zebrasoma rostratum
Grazers	Zebrasoma scopas
Grazers	Zebrasoma velifer
Scrapers / small excavators	Chlorurus bleekeri
Scrapers / small excavators	Chlorurus bowersi
Scrapers / small excavators	Chlorurus japanensis
Scrapers / small excavators	Chlorurus sordidus
Scrapers / small excavators	Chlorurus sp.
Scrapers / small excavators	Hipposcarus longiceps
Scrapers / small excavators	Scarus altipinnis
Scrapers / small excavators	Scarus chameleon
Scrapers / small excavators	Scarus dimidiatus
Scrapers / small excavators	Scarus festivus
Scrapers / small excavators	Scarus flavipectoralis
Scrapers / small excavators	Scarus forsteni
Scrapers / small excavators	Scarus frenatus
Scrapers / small excavators	Scarus ghobban
Scrapers / small excavators	Scarus globiceps
Scrapers / small excavators	Scarus hypselopterus

Functional group	Species
Scrapers / small excavators	Scarus longipinnis
Scrapers / small excavators	Scarus niger
Scrapers / small excavators	Scarus oviceps
Scrapers / small excavators	Scarus prasiognathos
Scrapers / small excavators	Scarus psittacus
Scrapers / small excavators	Scarus quoyi
Scrapers / small excavators	Scarus rivulatus
Scrapers / small excavators	Scarus schlegeli
Scrapers / small excavators	Scarus sp.
Scrapers / small excavators	Scarus spinus
Scrapers / small excavators	Scarus tricolor
Scrapers / small excavators	Scarus xanthopleura
Large excavators / bioeroders	Bolbometopon muricatum
Large excavators / bioeroders	Cetoscarus ocellatus <sup>2</sup>
Large excavators / bioeroders	Chlorurus frontalis <sup>2</sup>
Large excavators / bioeroders	Chlorurus microrhinos <sup>2</sup>
Large excavators / bioeroders	Scarus rubroviolaceus <sup>2</sup>

<sup>1</sup> classified as 'browser' until reaches 20 cm in length <sup>2</sup> classified as 'scraper/small excavator' when smaller than 35 cm in length, and 'large excavator/bioeroder' when larger than 35 cm in length

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**Supplementary Table 3** - As part of a sensitivity analysis, 'spatio-physical' models were additionally run using  $\pm 5$  and  $\pm 10$  humans km<sup>-2</sup> reef as a threshold from which to categorise 'low' and 'high' impact sites. Notably, site allocations were the same for 30 and 35 humans km<sup>-2</sup> reef (i.e. no sites had values between 30 and 35 humans km<sup>-2</sup> reef). Values in tables represent adjusted-R<sup>2</sup> values from GAMM models with structure as described in the manuscript. All outcomes were consistent with those found for the 25 humans km<sup>-2</sup> reef threshold, indicating the findings are robust.

	Threshold = 15 humans km <sup>-2</sup> reef		Threshold = 20 humans km <sup>-2</sup> reef	
	low (n=25)	high (n=37)	low (n=27)	high (n=35)
Live hard coral	0.69	0.00	0.49	0.00
Branching	0.66	0.09	0.63	0.07
Massive	0.41	0.00	0.55	0.02
Encrusting	0.09	0.00	0.04	0.00
Turf algae	0.00	0.00	0.00	0.00
Macroalgae	0.63	0.19	0.63	0.16
Dead hard coral	0.21	0.09	0.23	0.03
CCA	0.00	0.00	0.00	0.00
Average	0.34	0.05	0.32	0.04
t-test outcome	0.019		0.	015

	Threshold = 25 humans km <sup>-2</sup> reef		Threshold = 30/35 humans km <sup>-2</sup> reef	
	low (n=29)	high (n=33)	low (n=34)	high (n=28)
Live hard coral	0.52	0.00	0.50	0.00
Branching	0.64	0.17	0.64	0.01
Massive	0.50	0.10	0.47	0.00
Encrusting	0.19	0.00	0.08	0.06
Turf algae	0.00	0.00	0.00	0.00
Macroalgae	0.59	0.26	0.55	0.23
Dead hard coral	0.33	0.24	0.37	0.17
CCA	0.02	0.00	0.05	0.00
Average	0.35	0.10	0.33	0.06
t-test outcome	0.	010	0.	015

**Supplementary Table 4** - As an additional analysis, 'spatio-physical' models were run for human density as calculated per *outer reef area* only (i.e. human density per outer reef) using 60, 80 and 100 humans km<sup>-2</sup> outer reef as thresholds from which to categorise 'low' and 'high' impact sites (note: the thresholds are higher as the area of reef relative to humans is smaller when considering only outer reef). Values in tables represent adjusted-R<sup>2</sup> values from GAMM models with structure as described in the manuscript. All outcomes were consistent with those found for the 25 humans km<sup>-2</sup> reef threshold, indicating the findings are robust. While certain target fish species only occur on the outer reefs, some of the fishing and gleaning activity to meet protein demands would be focused on areas other than outer reefs. Furthermore, additional impacts by local human populations (in particular nutrient input) would be diluted in cases where large areas of backreef occur. Thus, even though there are trade-offs involved with either calculation of human density, we feel that human density per total reef area is the most appropriate proxy of local human impact, and thus present those values in the main manuscript.

	Threshold km <sup>-2</sup> or	= 60 humans uter reef	Threshold = 80 humans km <sup>-2</sup> outer reef					
	low (n=25)	high (n=37)	low (n=32)	high (n=30)				
Live hard coral	0.48	0.18	0.38	0.01				
Branching	0.33	0.12	0.33	0.20				
Massive	0.49	0.08	0.47	0.09				
Encrusting	0.00	0.00	0.00	0.00				
Turf algae	0.23	0.00	0.15	0.00				
Macroalgae	0.39	0.31	0.39	0.21				
Dead hard coral	0.28	0.00	0.20	0.02				
CCA	0.00	0.03	0.00	0.00				
Average	0.27	0.09	0.24	0.07				
t-test outcome	0.	012	0.011					

	Threshold = km <sup>-2</sup> or	= 100 humans uter reef						
	low (n=35)	high (n=27)						
Live hard coral	0.37	0.37						
Branching	0.35	0.35						
Massive	0.47	0.47						
Encrusting	0.00	0.00						
Turf algae	0.07	0.07						
Macroalgae	0.45	0.45						
Dead hard coral	0.20	0.20						
CCA	0.01	0.01						
Average	0.24	0.02						
t-test outcome	0.	0.009						

**Supplementary Table 5** - Best-fit model outcomes based on GAMM models (with island cluster as a random effect for all response variables, and surveyor bias as an additional random effect for turf algae). A '+' indicates that the predictor was selected by model selection procedures for the respective row's model. RI values in grey boxes under model selection output (boldface if predictor was selected by model selection procedures for models with Akaike weight >0.05). (A) outcomes for low local impact sites (< 25 humans km<sup>-2</sup> reef), (B) outcomes for high local impact sites (> 25 humans km<sup>-2</sup> reef).

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												adi-R2					
	relief	browsers	depth	detritivores	excavators	gravity	grazers	latitude	scrapers	storms	adj-R2	conditional	df	logLik	AICc	delta	weight
	-0.24		+								0.50	0.70	6.00	-13.18	42.20	0.00	0.27
											0.09	0.13	3.00	-18.29	43.50	1.36	0.14
			+	+					+		0.51	0.70	7.00	-12.19	43.70	1.54	0.13
LIVE CORAL			+								0.31	0.43	5.00	-15.83	44.30	2.10	0.10
		+									0.33	0.45	5.00	-15.93	44.50	2.29	0.09
	-0.19										0.21	0.29	4.00	-17.86	45.40	3.22	0.05
		+	+								0.48	0.67	7.00	-13.12	45.60	3.39	0.05
	0.42	0.18	0.66	0.01	0.01	0.01	0.01	0.01	0.20	0.01							
										+	0.55	0.59	5.00	-31.52	75.70	0.00	0.49
BRANCHING				+						+	0.64	0.68	7.00	-28.77	76.90	1.23	0.26
CORAL			+							+	0.60	0.63	7.00	-30.50	80.30	4.67	0.05
	0.06	0.02	0.06	0.30	0.05	0.01	0.02	0.04	0.02	1.00							
									+		0.48	0.51	5.00	-30.20	73.00	0.00	0.32
									+	+	0.60	0.64	7.00	-27.49	74.30	1.31	0.17
MASSIVE		+									0.37	0.40	5.00	-31.87	76.30	3.33	0.06
CORAL	-0.21								+		0.50	0.54	6.00	-30.33	76.50	3.46	0.06
	-0.43										0.34	0.37	4.00	-33.51	76.70	3.67	0.05
	0.22	0.13	0.03	0.06	0.01	0.05	0.05	0.03	0.73	0.27							
											0.10	0.12	3.00	-25.28	57.50	0.00	0.63
ENCRUSTING					+						0.20	0.24	5.00	-24.48	61.60	4.05	0.08
CORAL	0.09										0.12	0.14	4.00	-26.12	61.90	4.39	0.07
	0.10	0.01	0.02	0.05	0.11	0.01	0.04	0.02	0.02	0.05							
											0.18	0.18	4.00	-49.83	109.30	0.00	0.49
				+							0.25	0.26	6.00	-48.22	112.30	2.93	0.11
TURF ALGAE	-0.19										0.19	0.19	5.00	-49.95	112.50	3.19	0.10
					+						0.21	0.21	6.00	-48.66	113.10	3.81	0.07
	0.15	0.03	0.02	0.15	0.10	0.05	0.03	0.03	0.03	0.02							
	-0.83									+	0.50	0.51	6.00	-47.75	111.30	0.00	0.25
FLESHY	-0.96		+							+	0.64	0.65	8.00	-44.34	111.90	0.58	0.19
ALGAE	-1.00										0.31	0.32	4.00	-51.89	113.50	2.14	0.09
										+	0.36	0.37	5.00	-50.75	114.10	2.80	0.06
	0.72	0.13	0.25	0.03	0.07	0.02	0.02	0.13	0.07	0.79							
											0.00	0.00	3.00	-38.85	84.70	0.00	0.55
CCA	-0.25										0.06	0.07	4.00	-38.72	87.10	2.45	0.16
							+				0.03	0.03	5.00	-38.65	89.90	5.26	0.04
	0.22	0.03	0.05	0.02	0.02	0.02	0.06	0.04	0.04	0.03							
									+		0.39	0.48	5.00	-20.21	53.00	0.00	0.58
DEAD CORAL		+				1			+		0.52	0.64	7.00	-18.26	55.80	2.82	0.14
									+	+	0.51	0.63	7.00	-18.93	57.20	4.16	0.07
	0.06	0.16	0.02	0.01	0.01	0.01	0.01	0.01	0.89	0.13							

## (B)

												adj-R2					
	relief	browsers	depth	detritivores	excavators	gravity	grazers	latitude	scrapers	storms	adj-R2	conditional	df	logLik	AICc	delta	weight
LIVE CORAL											0.06	0.08	3.00	-23.00	52.90	0.00	0.44
	-0.25										0.15	0.20	4.00	-22.47	54.40	1.57	0.20
							+				0.21	0.28	5.00	-21.28	54.90	2.00	0.16
	0.25	0.03	0.04	0.02	0.01	0.05	0.23	0.04	0.01	0.01							
DRANCHING											0.03	0.04	3.00	-50.81	108.50	0.00	0.32
COPAL	-0.51										0.11	0.11	4.00	-49.80	109.10	0.60	0.23
CORAL				+							0.11	0.11	5.00	-49.71	111.70	3.25	0.06
	<u>0.41</u>	0.03	0.03	<u>0.13</u>	0.03	0.06	0.05	0.04	0.03	0.12							
											0.34	0.35	3.00	-47.54	101.90	0.00	0.34
									+		0.42	0.43	5.00	-46.27	104.80	2.91	0.08
MASSIVE	0.19										0.35	0.36	4.00	-47.71	104.90	2.96	0.08
CORAL							+				0.40	0.42	5.00	-46.42	105.10	3.20	0.07
			+								0.38	0.39	5.00	-46.42	105.10	3.21	0.07
				+							0.38	0.39	5.00	-46.46	105.20	3.29	0.07
	<u>0.16</u>	0.03	0.12	<u>0.12</u>	0.07	0.02	0.12	0.08	<u>0.14</u>	0.03							
											0.03	0.03	3.00	-40.01	86.90	0.00	0.25
ENIOPUIOTINIO						+					0.25	0.27	5.00	-37.35	87.00	0.13	0.24
ENCRUSTING				+							0.21	0.23	5.00	-38.19	88.70	1.81	0.10
CORAL		+				+					0.40	0.44	7.00	-35.19	89.00	2.17	0.09
	0.20										0.06	0.07	4.00	-40.20	89.90	3.01	0.06
	0.15	0.15	0.02	0.19	0.03	0.42	0.02	0.03	0.03	0.02							
											0.53	0.55	4.00	-44.78	99.00	0.00	0.62
TURF ALGAE	-0.04										0.53	0.55	5.00	-45.42	103.20	4.10	0.08
							+				0.58	0.60	6.00	-44.01	103.40	4.33	0.07
	0.11	0.02	0.06	0.04	0.03	0.02	0.10	0.03	0.02	0.02							
EL EQUIN											0.06	0.06	3.00	-54.46	115.80	0.00	0.33
FLESHY	-0.54										0.15	0.15	4.00	-53.49	116.50	0.69	0.23
ALGAE		+									0.11	0.11	5.00	-53.43	119.20	3.39	0.06
	0.36	0.10	0.03	0.07	0.03	0.04	0.04	0.07	0.06	0.07							
											0.05	0.06	3.00	-28.76	64.40	0.00	0.44
CCA		+									0.26	0.31	5.00	-26.36	65.00	0.65	0.32
	-0.07										0.06	0.07	4.00	-29.70	68.90	4.51	0.05
	0.08	0.38	0.02	0.02	0.02	0.05	0.01	0.02	0.02	0.02							
											0.00	0.00	3.00	-8.94	24.70	0.00	0.79
DEAD CORAL	0.00										0.00	0.00	4.00	-10.73	30.90	6.20	0.04
			1			1		+			0.10	0.28	5.00	-9.38	31.10	6.33	0.03
	0.04	0.03	0.02	0.01	0.02	0.01	0.03	0.04	0.02	0.01							