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11   # Seascapes as drivers of herbivore assemblages in coral reef ecosystems

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29   Running head: Seascapes as drivers of herbivory

30

31 **Abstract**

32   Herbivorous fish maintain a critical ecosystem function on coral reefs by grazing algae and

33   maintaining highly productive algal turf assemblages. Current paradigms implicate habitat

34   complexity, predation and primary productivity as major drivers of the distribution and abundance of

35   herbivorous fish, yet little is known about the relative contribution of these factors. Here, we compare

36   bottom-up and top-down drivers of notional herbivore assemblages across an environmental gradient

37   of wave exposure in the Palau archipelago. We surveyed herbivore assemblages at reef slopes (6 -

38   9m) across 18 sites, and quantified proxies of top-down control (predator biomass, habitat

39   complexity) and bottom-up drivers (net primary production, nutrients) at each site. Despite

40   substantial variability in herbivore biomass throughout the archipelago (6 to 65 g m^{-2}), general

41   additive models indicate that neither top-down nor bottom-up drivers significantly predicted biomass

42   or density of herbivores among sites. In contrast to expectations, herbivore biomass was highest at

43   sites with high predator biomass, low structural complexity and low benthic productivity. Rather, the

44   highest biomass of herbivores was associated with shallow, tidally emergent, productive reef flats

45   located adjacent to steep vertical walls ('drop-offs'). The emergent nature of this neighbouring habitat

46   precluded occupation by territorial fishes, and multiple species of herbivores were observed to make

47   foraging runs into this habitat once tidally inundated. We hypothesize that this habitat configuration

48   provides an important cross-habitat resource subsidy. Multivariate ordination and permutation of

49   herbivore communities revealed strong evidence for biogeographic partitioning throughout the

50   archipelago (western, south-western, inner eastern and outer eastern clusters), contributing to an

51   emerging picture that the habitat heterogeneity of seascapes can overwhelm the effects of

52   conventional top-down and bottom-up structuring of herbivory on coral reefs.

53   Key words: coral reefs, habitat heterogeneity, herbivory, productivity, seascapes, wave exposure

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Introduction

56 The role of top-down vs bottom-up processes in structuring assemblages has been a central debate in

57 ecology over the past century (Hairston et al. 1960, Matson and Hunter 1992, Menge 2000). Early

58 studies placed a strong emphasis on the importance of bottom-up regulation of assemblages, and

59 argued that predators are largely dependent on the seasonal flux of lower trophic levels (Elton 1927,

60 Lindeman 1942, Odum and Odum 1955). This viewpoint was challenged in the early 1960's by the

61 'green world hypothesis', which proposed that plant abundance was regulated through top-down

62 control of herbivores by predation (Hairston et al. 1960). Consequently, emphasis shifted towards

63 top-down control of ecosystem function and community structuring (Paine 1966, Estes and

64 Palmisano 1974). More recently, studies have moved away from the dichotomy of top-down vs

65 bottom-up paradigms (Hunter and Price 1992, Menge 1992), towards focusing on interactions among

66 bottom-up and top-down forcing in structuring assemblages (e.g. Menge 2000, Munch et al. 2005,

67 Hunt and McKinnell 2006). The extent to which relative ecological forces determine population

68 change and structure assemblages are largely context dependent (Menge 2000) and vary over

69 geographical scales (e.g. Gripenberg and Roslin 2007). While such studies are inherently challenging,

70 quantifying the relative strengths of top-down and bottom-up drivers is particularly difficult in marine

71 environments given the additional complexities of strong environmental drivers such as wave

72 exposure, light, and tidal flux (Bertness et al. 1999).

73 Herbivory is particularly complex in species-rich tropical marine ecosystems (Steneck et al. 2017).

74 Moreover, changes in herbivory can result in undesirable ecological outcomes as it does in many

75 ecosystems (Hughes et al. 2005, Estes et al. 2011, Verges et al. 2016). Like their temperate

76 counterparts, some coral reef systems appear to exhibit macroalgal regime shifts when herbivory is

77 depleted through processes like disease (Carpenter 1990) and fishing (Newman et al. 2006, Mumby et

78 al. 2013b). While high biomass of herbivores is correlated to low macroalgal cover at reef scales

79 (Williams and Polunin 2001, Fox and Bellwood 2007, Mumby et al. 2007, Wismer et al. 2009,

80 McClanahan et al. 2011), individual herbivore species have different roles in regulating and removing

81 macroalgae (Bellwood et al. 2006, Burkepile and Hay 2008). Despite the importance of herbivory for

82 resilience of coral reef ecosystems (Mumby and Harborne 2010, Graham et al. 2015), the relative

83 contributions of ecological and environmental drivers in structuring herbivorous fish assemblages on

84 Pacific reefs are little understood.

85 From a top-down perspective, predation exerts an important role in structuring the abundance and

86 distribution of coral reef fish (Hixon 2015). Smaller predators can have profound direct effects on
87 early post-settlement of herbivorous reef fish (Almany 2004, Heinlein et al. 2010, Feeney et al.
88 2012), creating "priority effects", where the species composition of resident reef fish regulate
89 community structure by inhibiting or enhancing recruitment of other reef fish species (Shulman et al.
90 1983, Almany 2004, Stallings 2008, Mumby et al. 2012). Predator-prey interactions can also have
91 indirect impacts on herbivore assemblages through behavioural modification, resulting in shifts in
92 foraging patterns and rates of algal consumption (Madin et al. 2011, Rizzari et al. 2014). Habitat
93 complexity plays an important role in mediating predation by providing increased availability of
94 refuges, resulting in enhanced recruitment and survival of prey fishes (Hixon and Beets 1993, Caley
95 and St John 1996). Consequently, herbivore biomass tends to increase with structural complexity
96 (Mumby and Wabnitz 2002, Verges et al. 2011, Bozec et al. 2013, Graham and Nash 2013).

97 From a bottom-up perspective, productivity plays an important role in regulating the structure of
98 coral reef food webs (Hatcher and Larkum 1983, Hatcher 1990). The high biomass of herbivorous
99 fish on undisturbed atolls are supported by highly productive algal turfs (Steneck 1988, Hatcher
100 1990). Ubiquitous in nature but diverse in composition, turf algae exhibit high mass-specific rates of
101 productivity (Steneck 1988), and have been described as "master producers in nutrient poor seas"
102 (Adey and Goertemiller 1987). Herbivore biomass is more strongly linked to rates of turf algal
103 productivity than to standing crop of turfs (Carpenter 1986, Russ 2003, Tootell and Steele 2016).
104 Benthic productivity is strongly influenced by local environmental factors such as light, nutrients,
105 substrate availability and water flow (Hatcher and Larkum 1983, Carpenter 1986, Steneck and
106 Dethier 1994) and varies across spatial scales and among habitats on coral reefs (Odum and Odum
107 1955, Klumpp and McKinnon 1992, Renken et al. 2010, Marshell and Mumby 2015). While several
108 studies have investigated bottom-up drivers of coral reef fish assemblages among habitats (e.g. reef
109 flat vs reef slope, Russ 2003) and exposure (e.g. windward vs leeward, Marshell and Mumby 2015),
110 the relationship between productivity and environmental drivers (primarily light and flow, Steneck
111 and Dethier 1994) across environmental gradients have not been studied widely. Moreover, insights
112 into the specific dietary targets of 'herbivores' are changing rapidly. For example, parrotfish of the
113 most speciose genus, *Scarus*, were thought to be primarily detritivorous (Choat et al. 2002, Wilson et
114 al. 2003), but there is now greater appreciation of the importance of cyanobacteria and endolithic
115 algae in their diet (Clements et al. 2017).

116 At larger spatial scales, habitat heterogeneity can play an important role in structuring herbivore
117 assemblages (Taylor 2014). In particular, fundamentally different reef geomorphologies (fringing

118   reefs, barrier reefs and atolls) appear to support different herbivore assemblages (Pinca et al. 2012,

119   Taylor et al. 2015), although the exact ecological mechanisms supporting these differences are

120   unclear. In theory, habitat heterogeneity driven by island geomorphology regulates the spatial

121   distribution and proximity of adjacent habitats (e.g. lagoons) that can act as resources (e.g. nursery

122   habitats), which in turn influences the diversity and abundance of herbivore assemblages (see

123   Harborne et al. 2016). While this phenomena has been explored at large geographic scales of

124   thousands of kilometres among Pacific islands (Pinca et al. 2012, Taylor et al. 2015), the extent to

125   which habitat heterogeneity and geomorphological zonation can influence herbivore assemblages at

126   smaller spatial scales (tens of kilometres) is unclear.

127   Here, we quantified seascape patterns of herbivore assemblages in a relatively lightly exploited

128   system in Palau (Micronesia, western Pacific). By quantifying top-down (predator biomass, structural

129   complexity) and bottom-up drivers (turf algal productivity, nutrients) across a gradient of wave

130   exposure and geomorphology types throughout the archipelago, we aimed to quantify the relative

131   contribution of these drivers in structuring herbivorous fish communities. Palau was chosen for two

132   reasons. First, it is one of few locations in the Pacific where predator biomass remains high, and shark

133   fisheries are banned entirely. Second, despite the existence of a herbivore fishery (Bejarano et al.

134   2013), herbivore densities are still regionally high (Mumby et al. 2013a), lightly fished, and benefit

135   from a series of no-take reserves throughout the Palau archipelago. We point out upfront that our

136   inclusion of species as notional herbivores follows Steneck et al. (2017) in that they have a functional

137   role in removing algal biomass on coral reefs, though many species derive their nutrition from

138   microorganisms that are either epilithic or endolithic (Clements et al. 2017).

139   **Methods**

140   *Site selection & geomorphological drivers*

141   Palau predominantly experiences north-eastern trade winds between December to March, and south-

142   west monsoonal winds between June to October (Appendix S1, Figure S1). All surveys and

143   experiments were conducted between the 3rd to the 16th of March 2012 (unless otherwise stated)

144   during a period of moderate north-eastern to eastern wind trade winds. Eighteen sites were selected

145   throughout the Palau archipelago (Micronesia) across a gradient of wave exposure (Figure 1) and

146   stratified to include both western (leeward, $n = 6$) and eastern locations (windward, $n = 12$). Surveys

147   and experimental manipulations were conducted at 6 – 9m depth on the reef slope at each site. Cross-

148   shelf profiles and depths of barrier reef sites and carbonate banks sites were quantified using a GPS

149   and a depth sounder at high tide. Benthic habitat maps of the Palau archipelago were obtained from

150   the National Oceanographic Institute (NOAA) National Centers for Coastal Ocean Science website

151   (https://coastalscience.noaa.gov/project/benthic-habitat-palau/).

152   Benthic cover was quantified at each site through $1m^2$ high-resolution photo-quadrats ($n = 25$ per

153   site, Canon G12 camera). Quadrats were surveyed at each site at the same time as herbivore surveys,

154   and were placed by using a randomly generated list of swimming directions (compass points) and a

155   list of numbers for distance, covering an area of approximately $450m^2$ of reef slope. Benthic cover

156   was estimated from photographs (scleractinian coral, soft coral / gorgonian / sponge, macroalgae,

157   and grazeable substrate [turf algae, crustose coralline algae and bare substrate combined]) using

158   CPCe (Kohler and Gill 2006). Additional line intercept transects (n = 3, 10 m length) laid parallel to

159   the reef slope were recorded by the same observer (RSS) to quantify turf algal cover and higher

160   resolution benthic cover (hard coral, soft coral / gorgonian / sponge, crustose coralline algae [CCA],

161   turf algae, macroalgae, *Lobophora* spp., non-crustose corallines, articulated corallines). Benthic

162   cover was recorded every centimetre, and turf algal height was measured at five points along the

163   transect to the nearest 0.5 mm using a vertical ruler. Turfs were defined as multi-species assemblages

164   of diminutive algae (primarily filamentous) with a typical canopy height of 1 - 10mm (Steneck

165   1988).

166   *Herbivore assemblage composition*

167   Herbivore assemblages were surveyed using 6 replicate 30 m by 4 m transects per site by the same

168   observer (PJM). Herbivores were identified to species but then categorised according to family level

169   and to functional groups (excavators, scrapers, grazers, browsers) following Green & Bellwood

170   (2009). While *Ctenochaetus striatus* is primarily a detritivore, it was included as a functional grazer

171   in the present study as it plays a key role in removing algal turfs (Marshell and Mumby 2012, 2015).

172   The identity, life phase (terminal, intermediate, and juvenile phases), and body length (total length to

173   the nearest cm) were recorded for each individual. The bumphead parrotfish (*Bolbometopon*

174   *muricatum*) were only observed at a single site, and due to their comparatively low densities and

175   large home ranges (~10km, Green et al. 2015), were excluded from further analysis. The lengths of

176   individual herbivores were converted to biomass based on allometric scaling relationships (Appendix

177   S1, Table S1). Significant differences between herbivore biomass and density between eastern and

178   western sites and between geomorphology types ("barrier-reefs" and "carbonate banks") were

179   determined using Kruskal-Wallis rank sum tests using the 'stats' package in R (R Development Core

181   *Environmental drivers*

182   Wave exposure, flow, light and temperature were quantified across all sites during the study period.

183   Wave exposure was determined using a fetch-based GIS approach at a 50 m spatial resolution (see

184   Roff et al. 2015 for further details). The study was conducted in early March 2012 during the months

185   where Palau experiences predominantly north-eastern trade winds prior to a switch to predominantly

186   south-west monsoonal winds between June to October (Appendix S1, Figure S1). To parameterise the

187   wave exposure model, in-situ hourly wind speed and direction were obtained for Koror Airport

188   between February and March 2012 from Weather Underground (www.wunderground.com/weather-

189   forecast/KA/Koror.html). The resultant values of wave exposure (j m^3) were log-normal transformed.

190   Flow at each site was quantified using using gypsum dissolution methods (see Marshell and Mumby

191   2015 for further details). All gypsum moulds were fixed approximately 30 cm above the reef

192   substrate for a 24-hour period. Upon recovery, moulds were dried and reweighed, and dissolution

193   rates were calculated from the difference between final and initial weights. Hobo™ pendant data

194   loggers were to record light intensity (lumens m^{-2}) and temperature at 5-minute intervals at each site.

195   Measurements of light intensity (lumens m^{-2}) were converted to PAR using published coefficients

196   (Long et al. 2012).

197   *Bottom-up drivers: productivity and nutrient loading*

198   Net primary productivity (NPP) of turf algae was quantified through a 10-day herbivore exclusion

199   experiment that quantified changes in turf growth (g mm^{-1} d^{-1}) and turf biomass (g m^{-2} d^{-1}). Terracotta

200   tiles (100 cm^2) were drilled to create micro-scale rugosity (100 holes, 1 mm width x 1 mm deep at

201   uniform spacing). Tiles were pre-conditioned for 60 days on racks in a uniform environment (facing

202   upwards) at one site (Site 4, Figure 1). To exclude the effects of large herbivores (>5 cm total length),

203   we constructed cages (30 x 30 x 40 cm) from PVC coated steel mesh (25 x 25 mm mesh size). Tiles

204   were mounted within cages facing upwards (Figure 2a). Hobo™ pendant data loggers were deployed

205   to measure light intensity and temperature inside and outside cages at each location. Water flow was

206   measured simultaneously inside and outside of cages by deploying gypsum moulds as described

207   previously.

208   Prior to the experiment, the tiles were collected and placed in aquaria with running seawater for 24

209   hours, and scrubbed gently to remove all turf algal biomass while maintaining holdfasts. At each site,

210   six cages, each containing a single tile, were attached to the substrate (n = 108 total). After 10 days,

211 turf height was measured in-situ (Figure 3b), and tiles were removed from the cage and sealed within

212 plastic bags to preserve turf biomass. Upon return to the lab, each tile was uniformly scraped to

213 remove all turf biomass, and the resultant turf condensed onto pre-weighed filters (~20 µm) using a

214 vacuum filter pump. Filters were washed in 10% hydrochloric acid to remove carbonate sediments,

215 rinsed, then dried in an oven at 65°C for 24 hours. The total biomass of the dried filters was then

216 subtracted from the initial filter weight to quantify NPP (g m^{-2} d^{-1}). General additive models (GAMs)

217 were used to determine the relative strengths of wave exposure, light and temperature in driving turf

218 productivity using the 'mgcv' package in R (Wood 2011).

219 As a subset of the Eastern sites were situated close to potential sources of nutrients from the sewage

220 outflow in Malakal harbour (Sites 1 to 6, Figure 1), we used stable isotope analysis δ^{15}N to detect

221 and map spatial patterns of nutrient inputs (Costanzo et al. 2001). Samples of macroalgae

222 (*Lobophora* spp., n = 5 per site) were sampled in 2014 across a gradient of sites in proximity to the

223 nutrient plume and at an adjacent remote 'control' site (see Appendix S1: Figure S2 for sampling

224 locations). *Lobophora* was chosen as: i) individual plants have a lower mass-specific productivity

225 compared to turf algae, and exhibit lower rates of turnover (Steneck and Dethier 1994), representing

226 greater time-averaging and exposure to potential nutrient sources, ii) *Lobophora* is a common algal

227 species among sampling sites, and iii) *Lobophora* has previously been used as an indicator species in

228 δ^{15}N studies of sewage pollution on coral reefs (Lapointe et al. 2011). Following collection, samples

229 were dried in a sample oven at 45°C and analysed for δ15N at the Stable Isotope Facility, University

230 of California in Davis (USA) using a PDZ Europa ANCAGSL elemental analyser interfaced with a

231 PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd, Cheshire, UK). A one-way ANOVA

232 was used to test for significant differences in δ^{15}N values, and a Dunnett's multiple comparisons test

233 was used to compare differences in δ^{15}N among sites (Appendix S1, Figure S1) using the 'stats' (R

234 Development Core Team 2017) and 'multcomp' (Hothorn et al. 2008) packages in R.

235 *Top-down drivers: structural complexity and predator biomass*

236 Structural complexity (defined as the physical three-dimensional structure) contributes to many

237 processes on coral reefs, and provides an important refuge from predation (Graham and Nash 2013).

238 Estimates of structural complexity at a reef scale were obtained by measuring the average maximum

239 vertical relief (i.e. the average distance in relief between the lowest and highest points of the reef

240 framework) among the 25 benthic quadrats (1m^2) following the approach of Harborne et al. (2012).

241 To quantify predator biomass, a subset of sites was re-surveyed in May 2016. Five consecutive timed

242 transects of 10 m width were visually surveyed for 5 minutes per site by the same observer (MP). A

243 GPS was towed behind the diver, and time was converted to total area per transect. The identity and

244 body length (total length to the nearest cm) were recorded for each individual. The lengths of

245 individuals were converted to biomass based on allometric scaling relationships (Appendix S1: Table

246 S2).

247 *Potential drivers of herbivore biomass*

248 General linear mixed models (GLMMs) and general additive mixed models (GAMMs) were used to

249 explore the effects of benthic community structure (coral cover, grazeable cover, measure),

250 environmental drivers (wave exposure, temperature, light, flow), top-down (predator biomass,

251 structural complexity) and bottom-up (NPP, net turf growth) drivers on the density and biomass of total

252 herbivores, family (Labridae, Acanthuridae, Siganidae) and functional groups (scrapers, grazers,

253 excavators, browsers), with side of the archipelago (eastern and western) added as a random factor.

254 Grazeable cover was defined as total substrate available for herbivore grazing, including CCA, turf

255 algae and macroalgae. Model analysis for was conducted in R using the 'stats' package for GLMs (R

256 Development Core Team 2017) and the 'mgcv' package for GAMMs (Wood 2011). Model selection in

257 GLMMs was conducted using the step function in the 'stats' package (R Development Core Team

258 2017). Diagnostic plots and tests for multicollinearity among predictors were conducted prior to

259 analysis using the 'pairs' and 'cor' functions in the 'graphics' and 'stats' packages in R (R

260 Development Core Team 2017).

261 *Biogeographic structuring of herbivore assemblages*

262 To explore spatial patterns in herbivore assemblage composition, an unconstrained PCoA (principle

263 coordinate analysis) ordination using a Bray-Curtis similarity matrix was conducted in the

264 perMANOVA + package for PRIMER v6 (Anderson et al. 2008). To determine spatial clustering and

265 similarity in herbivore assemblages, hierarchical cluster analysis (complete linkage) was used in

266 PRIMER v6 (Anderson et al. 2008). Distance-based linear modelling (DISTLM) was used to

267 determine the relative importance of explanatory variables on structuring herbivore assemblages.

268 Model selection was based on the Bayesian information criterion (BIC), and the BEST procedure was

269 used to identify the simplest models with the greatest explanatory power. Distance-based redundancy

270 (dbRDA) was used to perform a constrained ordination on the fitted values from the best fit model

271 (Anderson et al. 2008).

272 **Results**

273 *Benthic community structure*

274 Reef-scale benthic photo-quadrats in 2012 revealed variable but high levels of scleractinian coral

275 cover across all sites, ranging from 27% ± 2.9% (SE) to 82% ± 4.8 % (Figure 1). Macroalgal cover

276 was consistently low, ranging from 0 to 1.8% ± 0.2 %, while total grazeable cover (bare substrate,

277 turf algae and CCA cover combined) varied from 13.6% ± 4% to 71.4% ± 4.2% among sites (Figure

278 1). Detailed line intercept surveys at each site revealed varying levels of crustose coralline algae

279 ranging between 3.7% ± 1.2 % to 36.2% ± 1.8 %, turf algae cover ranging from 3.8% ± 1.6 % to

280 32.8% ± 5.6 %. Non-crustose coralline cover was consistently low, ranging between 0.7% ± 0.7 %

281 and 9.1% ± 1.3 %, while articulated coralline cover ranged from 0 to 16.2% ± 2.8 % (Appendix S1:

282 Table S1). In-situ observed turf heights were variable, ranging from 0.5% ± 0.1% to 2.7% ± 0.3%

283 mm among sites (Figure 1). Neither benthic cover nor turf heights differed significantly between

284 eastern and western sites (ANOVA, $p > 0.1$).

285 *Environmental drivers*

286 During the study period (3rd to the 16th of March 2012) Palau experienced strong north-easterly

287 winds, consistent with the dominant wind patterns experienced during the trade-winds (December to

288 March). Eastern exposed reefs experienced strong wave exposure during the study period, with

289 waves of 2 to 3 m height. Wave exposure maps overlapping the study period revealed a strong wave

290 exposure gradient on the eastern sites (sites 1 to 12) of 0.86 to 6.4 j m^{-3} (Appendix S1: Table S3),

291 while the leeward western sites experienced variable wave exposure. Measurements of flow

292 determined from gypsum moulds (percent dissolution) differed significantly among sites (ANOVA,

293 $F_{17} = 89.5$ $p < 0.001$), and exhibited a strong linear relationship to wave exposure (j m^{-3}, $R^2 = 0.74$, p

294 < 0.001). Temperature ranges across the study period were minimal (ranging between 27.7 to 30.1

295 °C, Appendix S1:Table S1), with no significant departures in temperature associated with typical

296 upwelling events in the archipelago (Wolanski et al. 2004). Maximum light levels (average daily

297 maximum PAR) over the study period ranged from 313 ± 45 to 574 ± 84 mol m^{-2}s^{-1}, and did not

298 vary significantly among sites (Appendix S1: Table S1).

299 *Herbivore biomass*

300 Surveys of herbivore assemblages revealed variable density and biomass among sites. Herbivore

301 density ranged fourfold from 0.1 ± 0.1 to 0.4 ± 0.1 individuals per m^{-2} (Figure 2 a,b), while herbivore

302 biomass varied nearly 10-fold, ranging from 5.6 ± 0.7 g m^{-2} to 66.4 ± 16.3 g m^{-2} (Figure 2 c,d).

303   Surgeonfish were the most abundant herbivore family across all sites, and rabbitfish were present at
304   all sites, albeit at low densities (Figure 2 a). From a functional group perspective, browsers, scrapers
305   and grazers were present at all sites, yet excavators were not recorded at seven of the 12 of eastern
306   sites (Figure 2 c). Grazers were the numerically dominant herbivores across all sites, while browsers
307   were generally present in low density (Figure 2 b,d). Herbivore biomass was significantly higher at
308   western than eastern sites ($H_{14.39}$, $p < 0.001$). Significantly higher densities of excavators were
309   observed in the western reefs ($H_{11.12}$, $p < 0.05$, Appendix S1: Table S4), but differences were not
310   significant for the density and biomass of other functional groups (scrapers, grazers and browsers,
311   Appendix S1: Table S5).

312   *Bottom-up drivers: productivity and nutrification*

313   Two metrics of benthic primary productivity were derived from the tile caging experiment (Figure 3
314   a): NPP (g^{-1} m^{-2} day^{-1}) and turf growth (mm^{-1} day^{-1}). While mid-day light levels were reduced by an
315   average of 17% inside of cages when compared to ambient light, we observed no significant
316   differences in water motion between gypsum moulds inside and outside of cages (GLM, $p > 0.1$).
317   NPP ranged four-fold from 0.54 ± 0.1 to 2.2 ± 0.3 g^{-1} m^{-2} day^{-1} among sites, while net turf growth
318   ranged three-fold from 0.03 ± 0.02 to 0.09 ± 0.03 mm^{-1} day^{-1}. A clear pattern emerged during the
319   experiment in that sites with higher wave exposure exhibited greater rates of turf growth and biomass
320   (Figure 3 b). However, NPP and net turf growth exhibted different trends with increasing wave
321   exposure. NPP was non-linearly related to wave exposure (Figure 3c, GAM, $p < 0.05$, $R^2 = 0.23$,
322   deviance explained = 25.2%), in that at low wave exposures (<3 j m^{-3}), NPP was generally low (with
323   the exception of a single site, Figure 3c), while NPP was highest at intermediate wave exposures (4
324   to 5 j m^{-3}). At higher wave exposures (>5 j m^{-3}), NPP declined to intermediate levels (Fig 3 c).
325   Neither light nor temperature were significant predictors in the GAM model ($p > 0.1$). In contrast,
326   net turf growth was significantly linearly related to wave exposure ($p < 0.05$, $R^2 = 0.3$, deviance
327   explained = 31.2%), in that turf growth was lowest at low wave exposure, and highest at high wave
328   exposures (Figure 3 d). Neither light nor temperature interacted with wave exposure to drive net turf
329   growth ($p > 0.1$).

330   Spatial analysis of $\delta^{15}N$ values obtained from *Lobophora* samples revealed that while elevated levels
331   of nitrogen were detectable in immediate proximity to the sewage outflow plant in Malakal harbour
332   (< 2 km), elevated $\delta^{15}N$ values were not detectable at our study sites (>5km from the sewage
333   outflow, Appendix S1: Figure S3). Given the absence of elevated $\delta^{15}N$ in *Lobophora* samples at our

334   study sites, sewage-derived nutrient sources were not considered in further analysis in the present
335   study.

Top-down drivers: structural complexity and predator biomass

337   Structural complexity, as determined by maximum disparity in vertical relief, varied among sites,
338   ranging from 20.6 cm to 45.6 cm (Appendix S1: Table S1). Surveys of predator biomass revealed a
339   clear divide between eastern and western sites. Eastern sites had a relatively low biomass of
340   predators (1.9 ± 0.8 to 8.5 ± 1.5 g m^{-2}, Figure 4), which comprised smaller (<50cm total length)
341   Lutjanidae. In contrast, western sites had an order of magnitude higher biomass (40.8 ± 22.1 to 87.6
342   ± 63.4 g m^{-2}, Figure 4), including large schools of smaller Lutjanidae (<50cm total length,
343   predominantly *Lutjanus gibbus, L. kasmira and L. bohar*) that are capable of consuming juvenile reef
344   fish (Kulbicki et al. 2005), small to mid-size Carangidae (~50cm total length, predominantly *Caranx*
345   *melampygus*), and larger reef sharks (>100cm total length, predominantly *Carcharhinus*
346   *amblyrhynchos and Triaenodon obesus*).

Drivers of herbivore biomass

348   Total herbivore biomass did not conform to expectations, in that biomass was highest at western sites
349   which were characterised by low turf productivity (Figure 5a,b), low in-situ turf height (Figure 5c),
350   low structural complexity (Figure 5d), and high predator biomass (Figure 5e). Sites with low predator
351   biomass on the eastern coast had consistently low herbivore biomass (Figure 5e). No clear significant
352   relationship was observed between response variables (herbivore density and herbivore biomass at
353   family level or functional groups) and predictors associated with standard top-down or bottom-up
354   forcing (environmental, benthic structure, bottom-up drivers).

Biogeographic structuring of herbivore assemblages

356   Principle coordinate analysis (PCoA) ordination of herbivore densities revealed clear spatial
357   clustering of sites (Figure 6a). Eastern sites and western sites clustered at a 40% similarity level, and
358   four clear clusters were distinguished at the 50% similarity level (Appendix S1: Figure S4)
359   corresponding with geographic groups of inner eastern sites, outer eastern sites, western sites and
360   south-western sites (Figure 6b). Similarity percentage (SIMPER) analysis revealed that despite
361   significant differences in the density and biomass of herbivores among geographic regions (inner-
362   eastern, outer-eastern, western and south-western, Figure 3), the composition of herbivore
363   assemblages was relatively consistent in that the four most common herbivores (*Ctenochaetus*

364 *striatus*, *Chlorurus spilurus*, *Zebrasoma scopas* and *Acanthurus nigricans*) accounted for between

365 58.9 to 71.0 % of total density and between 44.2 to 58.9 % of the total biomass of herbivore

366 assemblages (Table 1).

367 At a seascape scale, the Palau archipelago corresponds to a spatial mosaic of different habitat types

368 (Figure 7). Inner eastern sites (sites 1 – 5) were situated on barrier reefs close to the main island, with

369 close proximity to lagoons and backreef habitats extensive seagrass and macroalgae (Figure 7). Outer

370 eastern sites (sites 6 – 12) were situated on exposed barrier reefs with a narrow back-reef habitat

371 dominated by turf and macroalgae, adjacent to a narrow lagoon with isolated patch-reefs (Figure 7).

372 Western sites (sites 13 – 15) correspond to sheltered barrier reef habitats adjacent to expansive back-

373 reef habitats dominated by macroalgae and turf algae, and an extensive western lagoon with a high

374 diversity and abundance of patch reef habitats (Figure 7). South-western sites (Sites 16 – 18) were

375 situated adjacent to "carbonate banks", characterised by a shallow, narrow tidally-emergent reef flat

376 adjacent to steep near-vertical walls (termed drop-offs). This geomorphological reef type is only

377 found in the south-western reefs of Palau adjacent to low islands (Figure 7) and differ from the barrier

378 reef sites (sites 1 – 15) in that reef flats are tidally emergent adjacent to the islands. The south-western

379 sites area situated close to an extensive mosaic of back-reef habitats dominated by large areas of

380 seagrass beds, macroalgae and turf algae.

381 Distance-based redundancy (dbRDA) indicates that the densities of the acanthurid *Zebrasoma scopas*

382 and the siganids *Siganus vulpus* and *Siganus stellatus* correlate strongly with inner eastern sites, and

383 the scarids *Chlorurus spilurus* and *Scarus schlegeli* and the siganids *Siganus spinus* and *Siganus*

384 *corallinus* correlate strongly with the eastern outer sites (Figure 6b). Consistent with the

385 unconstrained PCoA ordination, western and south-western sites differed in similarity from eastern

386 sites, and were strongly correlated with high densities of the scarids *Scarus prasiognathos*, *Scarus*

387 *rubrioviolaceus*, *Chlorurus microrhinos* and the acanthurids *Acanthurus lineatus* and *Acanthurus*

388 *nigricans* (Figure 6 c). The best-fit distance-based linear model (DISTLM) based upon benthic cover

389 from line intercept transects, benthic primary productivity and environmental data indicated wave

390 exposure, grazeable cover, structural complexity, in-situ turf height, net turf growth, and coral cover

391 as predictors, explaining a combined 49.8% of the variance (Table 2). None of the DISTLM

392 predictors were significant at the $\alpha = 0.05$ level, with the exception of in-situ turf height, which was

393 weakly correlated with inner eastern sites (Figure 6c), explaining 19.6% of the variance (Table 2).

394   Significant differences in herbivore density ($H_{21.13}$, $p < 0.001$) and biomass ($H_{29.61}$, $p < 0.001$) were

395   observed between barrier reefs and emergent carbonate banks. These differences were driven by a

396   significantly higher biomass of excavators ($H_{12.93}$, $p < 0.001$), scrapers ($H_{9.98}$, $p < 0.01$), and grazers

397   ($H_{10.93}$, $p < 0.001$) in emergent carbonate bank sites, as well as significantly higher biomass of

398   surgeonfish ($H_{12.1}$, $p < 0.01$) and parrotfish ($H_{25.62}$, $p < 0.01$). Biomass of browsers and rabbitfish did

399   not differ significantly between barrier reefs and emergent carbonate banks.

400   **Discussion**

401   Quantifying the relative strengths of top-down and bottom-up forcing is a key challenge in

402   understanding the community dynamics of terrestrial and marine ecosystems (Matson and Hunter

403   1992, Menge 2000). The effects of these drivers can be weak (Casey et al. 2016), strong (Paine

404   1980), or interactive (Rosemond et al. 1993), and often vary across spatial scales (Frank et al. 2007)

405   and environmental regimes (Hopcraft et al. 2010). Here, we aimed to compare the role of top-down

406   and bottom-up forces in structuring herbivorous fish communities across an environmental gradient.

407   Variability in herbivore assemblages was striking, with biomass ranging 10-fold across sites. Yet

408   neither of the standard drivers of fish biomass nor density conformed to expectations. Indeed, sites

409   with the highest herbivore biomass and densities were associated with conditions that are usually

410   expected to favour low herbivory: low structural complexity (few refugia from predators), low

411   benthic primary productivity (poor food supply), and high predator density (low survivorship).

412   Herbivore assemblages revealed clear spatial clustering of sites according to geographic regions

413   (inner-eastern, outer-eastern, western and south-western sites), corresponding with proximity to

414   different habitat types (back-reef habitats, islands, emergent banks, patch reefs and seagrass beds) at

415   seascape scales throughout the Palau archipelago.

416   In terms of bottom-up forcing, wave exposure can drive shallow benthic algal productivity by

417   reducing the benthic boundary layer and enhancing rates of nutrient and gas exchange between the

418   water and alga (Leigh et al. 1987, Renken et al. 2010, Roff et al. 2015). By experimentally excluding

419   herbivory, we quantified two metrics of turf productivity: NPP (g^{-1} m^{-2} day^{-1}) and net turf canopy

420   growth (mm^{-1} day^{-1}). The range of turf productivity values in the present study (0.54 ± 0.1 to $2.2 \pm$

421   0.3 g^{-1} m^{-2} day^{-1}) were within the range of previous studies of turf productivity recorded on Indo-

422   Pacific reefs (Hatcher 1981, Klumpp and Polunin 1990, Russ 2003, Marshell and Mumby 2015). At

423   high wave exposure sites, NPP values measured at our reef slope sites (6 - 9m depth) were equal to

424   values recorded from typically more productive shallow reef crest environments (Russ 2003). Growth

of caged canopies was linearly related to wave exposure across the environmental gradient, in that turf heights were 4-fold higher in sites with high wave exposures than low exposure. In contrast, NPP exhibited a non-linear response with peak biomass at intermediate exposure. We attribute this non-linear response to the effects of wave shear on turf communities, where part of the algal canopy is dislodged under high wave shear (Fig. 2b), yielding a potentially-misleading estimate of productivity. Studies of temperate mid-littoral turf communities support this hypothesis in that fine and delicate turf algae decrease in abundance with inc`reasing wave heights (Whorff et al. 1995). Alternatively, a trade-off may exist between mechanical robustness and photosynthesis, whereby photosynthetic production peaks at semi-exposed sites and declines at higher exposures, as observed in temperate kelp (Jackelman and Bolton 1990). Previous studies have implied the importance of bottom-up drivers in driving herbivore assemblages, with rates of turf algal productivity strongly predicting herbivore biomass (Carpenter 1986, Russ 2003, Tootell and Steele 2016). However, we found no clear link between total herbivore biomass and either NPP (g^{-1} m^{-2} day^{-1}) or net turf growth (mm^{-1} day^{-1}). Emerging evidence from feeding observations and trophic anatomy indicates that parrotfishes are not primary consumers of algae, and instead target cyanobacteria and microorganisms within reef substrates and early stage algae (Clements et al. 2017). Similarly, while *C. striatus* is functionally classed as a grazer/detritivore (Marshell and Mumby 2012, Brandl and Bellwood 2016) as it is capable of removing large quantities of algal turfs (Marshall, Mumby unpublished observational and experimental data from Palau), it derives nutrition from combing detritus trapped in algal turfs rather than acting as a primary consumer of turf algae (Choat and Bellwood 1985). Thus, turf algal productivity may be decoupled from nutritional value for several of the major herbivore groups, which would in part explain the lack of clear relationships among bottom-up drivers and herbivore biomass observed in the present study.

From a top-down perspective, coral reef fishes are typically subjected to intense predation, especially by mid-trophic-level piscivores targeting recruiting fish (Almany 2004, Heinlein et al. 2010, Feeney et al. 2012), and high levels of predator biomass can result in smaller sizes and reduced longevity in adult herbivores (Ruttenberg et al. 2011). Predator densities exhibited a strong east-west divide, with western sites supporting an average 17-fold higher biomass. The underlying drivers for the east vs west divide in predator biomass is unclear, but the profound difference has been consistent over the past 15 years of surveys throughout the archipelago and exhibits no seasonal trends (PJM, YG, pers. obs.). Predators were dominated by transient predators, including snappers (Lutjanidae), jacks (Carangidae) and cornetfish (Fistularidae), that have previously been documented to prey on new

457   recruits (Hixon and Carr 1997, Sancho et al. 1997). In particular, the high biomass of sharks
458   (particularly *Carcharhinus amblyrhynchos*) appears to be related to habitat preference for high tidal
459   flow promontories on the west of the archipelago (Vianna et al. 2013), while the higher densities of
460   Serranidae and Lutjanidae may be related to proximity to spawning aggregations on the west of the
461   archipelago (Colin 2012). From a behavioural perspective, that such a high biomass of herbivores
462   coexists with high predator biomass is perhaps surprising given that the foraging of surgeonfish and
463   rabbitfishes is reportedly affected by the presence of predators (Rizzari et al. 2014), and that field
464   observations suggest that surgeonfish (including *Acanthurus lineatus*, a species common in high
465   predator biomass sites) actively flee territories when large predatory carangids are present (Robertson
466   et al. 1979).

467   In principle, fish may cope with higher predator densities if structural refugia are available (Hixon
468   and Carr 1997, Nash et al. 2013, Rogers et al. 2014). Yet the complexity of reefs associated with high
469   herbivore densities was unremarkable and lower than several other sites. Thus, not only were
470   herbivores in close proximity to many potential predators but their opportunities to shelter were
471   limited. Two mechanisms might explain the apparent weakness of top-down forcing. First, even
472   solitary fishes were observed to form transient schools during predator ambush events that typically
473   started with large carangids, closely followed by large labrids (e.g., *Cheilinus undulatus*) and reef
474   sharks (PJM, pers. obs). Thus, schooling offers a means of reducing predation risk as it does in
475   pelagic environments. Moreover, the low structural complexity of such reefs may aid the detection of
476   ambush events (sensu Rilov et al. 2007). A second mechanism is that some of the larger herbivorous
477   species could attain a size escape from predators as has been described for Caribbean parrotfishes
478   (Mumby et al. 2006).

479   In the absence of clear top-down and bottom-up drivers, other ecological and environmental drivers
480   may influence herbivore biomass. Coral cover and total grazeable cover have previously been
481   correlated with herbivore biomass (Williams and Polunin 2001, Mumby et al. 2013a), although
482   neither appears to have a measurable effect in the present study. Similarly, measured in-situ turf
483   heights and turf cover at each site were a poor predictor of herbivore biomass. The highest in-situ turf
484   heights were recorded at high exposure and low herbivore biomass sites on the east of the
485   archipelago, which highlights the importance of herbivory in regulating turf canopy heights at
486   exposed higher productivity sites (Mumby et al. 2013a). While we recorded high wave exposure in
487   the eastern sites during the study period from the north-eastern trade winds (December to March), the
488   Palau archipelago experiences a seasonal transition to predominantly south-west monsoonal winds

between June to October (Appendix S1: Figure S1). Yet, multi-year monitoring of herbivore
assemblages on the eastern sites (Appendix S1: Figure S5) indicates that herbivore assemblages are
temporally stable and do not experience corresponding seasonal switches. Further, herbivore biomass
was not significantly related to wave exposure, despite higher turf productivity at higher exposures on
the eastern sites. Finally, higher herbivore biomass at the south-western sites is unlikely to reflect
ephemeral spawning aggregations, as studies on the eastern reefs of the archipelago (site #1 in our
study) indicate that two of the most common species in our surveys (*C. striatus* and *C. spilurus*)
migrate no more than 100 to 200 m from territories to spawn (Hamner et al. 2007).

We hypothesize that the carbonate bank geomorphology that characterises sites in the south-west of
the archipelago may constitute a cross-habitat food subsidy that drives elevated herbivore biomass. At
low tides, reef flat environments adjacent to reef slopes at carbonate bank sites are emergent, which
prevents the establishment of territories by the grazing surgeonfish *C. striatus*, *A. nigricans*, and *A.
lineatus* that are typically dominant in reef flat environments (Robertson et al. 1979). Previous studies
of *A. lineatus* indicate that during low spring tides, individuals that had established inter-tidal
territories on the reef flat are forced into reef slope environments (Craig 1996). Our observations
confirmed that reef fish were not maintaining territories when the emergent (to semi-emergent) bank
became inundated. From an ecological perspective, emergent reef flats have three characteristics that
make them a highly desirable foraging ground for fishes on the reef slope. First, being a shallow reef
flat habitat, it has moderate to high levels of primary productivity (Hatcher 1990), and potentially
represents a source of high organic detritus that is likely to be favoured by herbivores (Purcell and
Bellwood 2001). Second, given the tidal range and emergent nature of the habitat, its resources are
not defended by resident territorial fishes that can interfere with foraging by non-territorial
individuals (Robertson et al. 1979). Third, it lies in close proximity (within tens of metres) to the
main reef slope, which permits foraging excursions when the tide is sufficiently high. We observed
such excursions to the outer reef flat for multiple species including surgeonfish (*A. triostegus*, *A.
olivaceus*, *C. striatus*, *A. nigricans*, *A. nigrofuscus*, *N. literatus*) and parrotfish (*C. spilurus*, *S.
globiceps*, and *S. psittacus*). The trophic importance of subsidies across habitat boundaries can be
substantial (Marczak et al. 2007), and further studies are needed to quantify the extent of inter-tidal
reef flat subsidies.

At a seascape scale, our analysis indicates that the Palau archipelago represents a spatial mosaic of
diverse habitat types, including forereefs, reef flats, patch reefs, and backreef habitats dominated by
turf algae, macroalgae and seagrass beds (Figure 7). At the assemblage level, herbivores exhibited

521 clear geographic partitioning: four clusters were evident at the 50% similarity level that correspond to
522 geographic groups separated by tens of kilometres: inner-eastern, outer-eastern, western and south-
523 western sites. While all sites were located in barrier reef environments at 6 - 9m depth, significant
524 differences exist in habitat heterogeneity at the seascape scale and reef geomorphology (Maragos and
525 Cook 1995, Donaldson 2002). Inner-eastern sites were located on fringing barrier reefs adjacent to
526 high islands, with extensive seagrass beds in the backreef; outer-eastern sites were located on a short
527 section of barrier reef with narrow lagoonal and backreef environments, western sites were located on
528 an extensive barrier reefs adjacent to extensive lagoonal habitats with diverse patch reefs, south-west
529 sites are located on carbonate banks characterised by narrow emergent reef flats adjacent to low
530 islands and extensive seagrass habitats in neighbouring backreef habitats (Figure 7). Such strong
531 geographic structuring of herbivore assemblages suggests geomorphology and habitat heterogeneity
532 at a seascape scale (i.e. diversity and size of adjacent habitats) as a key driver of herbivore
533 assemblage composition, as has previously been implicated for fish assemblages (Pinca et al. 2012,
534 Taylor et al. 2015, Heenan et al. 2016). Indeed, habitat heterogeneity has previously been implicated
535 as a strong driver of fish diversity in the Palau archipelago, with higher species richness recorded in
536 the western and south-western sites than eastern sites due to the extensive reef development and
537 proximity to the expansive lagoon (Donaldson 2002).

538 Theoretically, geomorphology and habitat heterogeneity can exert an indirect influence on fish
539 assemblages in at least two ways. First, the spatial distribution of reefs can influence physical
540 oceanographic patterns, in turn generating eddies that enhance retention of pre-settlement fish
541 (Burgess et al. 2007). In Palau, hydrodynamic modelling indicates that larval retention is spatially
542 patchy at an archipelago scale, with high levels of larval retention in the lagoon and western reefs
543 (Golbuu et al. 2012). Secondly, adjacent habitats in coral reef seascapes (e.g. seagrass, mangroves,
544 backreef habitat, fringing nearshore reefs and lagoons) can act as nursery habitats in Indo-Pacific
545 ecosystems (Bellwood and Choat 1989, Aswani and Hamilton 2004, Unsworth et al. 2007, DeMartini
546 et al. 2013), contributing to fish density and diversity on adjacent coral reefs (Dorenbosch et al.
547 2005a). Studies of lagoonal habitats in Moorea indicate that juvenile parrotfish recruit to fringing and
548 backreef nursery habitats, and migrate to reef-slopes habitats after reaching a length of ∼10 cm
549 (Adam et al. 2011). Similarly, juvenile parrotfish (*B. muricatum*, *C. spilurus*, *Hipposcarus longiceps,*
550 *S. ghobban* & *S. schlegeli*) have been recorded in branching *Acropora* habitat in lagoonal fringing
551 reefs (Hamilton et al. 2017) and seagrass beds adjacent to coral reef habitats (Dorenbosch et al.
552 2005b, Unsworth et al. 2007), while juvenile acanthurids have been reported from seagrass beds

553 (Dorenbosch et al. 2005a), nearshore fringing reef (Lecchini and Galzin 2005) and lagoonal habitats
554 (Mellin et al. 2007). While some juvenile rabbitfish species appear to exert strong levels of site
555 attachment (Bellwood et al. 2016), other reef-species (e.g. *S. spinus and S. stellatus*) are found in
556 adjacent seagrass habitats (Gell and Whittington 2002, Shibuno et al. 2008). Thus, the configuration
557 of the seascape and proximity of nursery habitat to forereef sites can influence the biomass of
558 herbivorous fish either directly through habitat use (e.g. Aswani and Hamilton 2004), or because their
559 predators or competitors benefit from such nurseries (Harborne et al. 2016).

560 At an assemblage level, potential insight into geographical clustering and can be drawn from species
561 ecology in terms of resource use, and habitat preference. For example, inner-east sites had higher
562 densities of the siganids *Siganus vulpinus* and *Siganus stellatus*, and the acanthurid *Zebrasoma*
563 *scopas*. In general, siganids are able to exploit crevices microhabitats more efficiently than
564 acanthurids, and feed within structurally complex and less accessible areas of reef (Fox and Bellwood
565 2013). With a small body size and elongated rostrum compared to other acanthurids, *Z. scopas* is
566 adapted to feeding in crevices (Robertson et al. 1979). The higher densities of these three species
567 seems likely to be related to their ability to exploit unique microhabitat niches within the expanses of
568 branching *Acropora* spp. at the inner east sites. While herbivores are commonly broadly separated
569 into functional groups, remarkable diversity in feeding preference exists within groups and families
570 (e.g. Choat et al. 2002). Thus, the relatively high density of specialists such as *S. spinus* at outer
571 eastern sites may reflect differences in food availability among sites, as *S. spinus* exhibits strong
572 preferences for habitats with specific algal types including red and green algae (Bryan 1975, Hoey et
573 al. 2013), although the precise nutritional targets are unclear. Environmental filtering may also
574 influence the behaviour and distribution of herbivores on coral reefs (Bejarano et al. 2017). Higher
575 densities of *A. lineatus* on the western sites are consistent with previous studies indicating preference
576 for sites not directly exposed to prevailing winds (Choat and Bellwood 1985).

577 While site and environmental differences appear to explain some of the variance in assemblage
578 composition, geographic variance may be unrelated to resources within sites. As highlighted
579 previously, the proximity of sites in the south-western reefs to emergent tidal reef flat subsidies may
580 play a resource structuring effect on herbivore assemblages. At archipelago scales, the distribution of
581 the parrotfish *Scarus schlegeli* is strongly associated with outer eastern sites, and largely absent from
582 the western sites. Yet, the diet of *S. schlegeli* overlaps with that of *C. spilurus* and *C. microrhinos*
583 (Choat et al. 2002) that are abundant on the western sites, indicating that resource availability is likely
584 not to be a limiting factor in their distribution. Across Micronesia, *Sc. schlegeli* exhibits a preference

585   for island types with fringing reefs and limited back-reef or lagoon (Taylor et al. 2015), which is

586   consistent with our finding that *S. schlegeli* are predominant in the outer east sites with poorly

587   developed back reefs and narrow lagoons (Figure 7). Similarly, *S. rubroviolaceus* is frequently

588   observed across Micronesia at sites with steep vertical walls (Taylor et al. 2015), which is consistent

589   with higher densities on the western sites close to vertical drop-offs and a paucity on eastern sites in

590   our study. In the absence of clear top-down, bottom-up or environmental drivers, the high biomass of

591   large excavating and scraping parrotfish (*C. microrhinos*, *C. ocellatus* and *S. prasiognathos*) in the

592   south-western sites may reflect proximity to the abundant and diverse mosaic of seagrass and patch

593   reef nursery habitats (Unsworth et al. 2007, Adam et al. 2011) in the south-west of the archipelago

594   (Figure 7). Indeed, surveys of patch reefs in the western lagoon indicate the presence of juvenile *C.*

595   *ocellatus* and *Sc. prasiognathos* (GR & PJM unpublished data).

596   Our results highlight an emerging picture of the role of habitat heterogeneity and reef geomorphology

597   in structuring reef fish assemblages (Pinca et al. 2012, Taylor et al. 2015). Here, we show that these

598   effects appear to dwarf the importance of habitat complexity, primary productivity and predator

599   density – at least at an archipelago scale. We provide a mechanistic hypothesis to account for some of

600   these geomorphological effects (food subsidy) but this warrants further testing. The structuring role

601   of geomorphology has been studied in many terrestrial systems and can influence the species richness

602   of plant assemblages at landscape scales (Nichols et al. 1998, Rose and Malanson 2012). In terrestrial

603   ecosystems, habitat heterogeneity has also been shown to be a strong predictor of species richness of

604   forest birds (Boecklen 1986), and plays a key role in structuring avian communities in grassland

605   habitats (Wiens 1974).

606   As key functional groups of herbivorous fish play important roles in the prevention and possible

607   reversal of phase shifts (Green and Bellwood 2009), our finding that herbivore communities are

608   influenced by habitat heterogeneity has potential implications for ecosystem functioning. For

609   example, key species of Siganidae that exhibit a strong preference for feeding on the phaeophyte

610   *Sargassum* macroalgae (Mantyka and Bellwood 2007b, a, Cvitanovic and Bellwood 2009) were

611   strongly associated with eastern barrier reefs. Similarly, excavating parrotfish (namely *Chlorurus*

612   *microrhinos*) that play an important role in coral reef resilience by actively eroding reef substrates

613   and opening up substrates for coral recruitment (Green and Bellwood 2009, Davis et al. 2017) were

614   preferentially associated with western barrier reef sites and emergent carbonate banks and were

615   depauperate from the eastern reefs. Thus, geographic partitioning of herbivore communities driven by

616   habitat associations at archipelago scales may intrinsically affect the resilience of reefs following

617 disturbance. From a management perspective, the variability in herbivore communities throughout the

618 Palau archipelago appears to be indirect and unpredictable, unlike predictable responses to

619 environmental gradients such as wave exposure (e.g. Roff et al. 2015, Bejarano et al. 2017). While

620 the paradigm of mangrove and seagrass nursery habitat for parrotfish has been primarily described

621 from Caribbean reefs, evidence suggests that adjacent lagoonal, seagrass and nearshore habitats act as

622 nurseries for a range of common Indo-Pacific herbivores (Aswani and Hamilton 2004, Dorenbosch et

623 al. 2005a, Unsworth et al. 2007, Adam et al. 2011). Further studies focusing on the dependence

624 herbivores on specific nursery habitats and subsequent movement across habitats will be likely be

625 critical to understanding patterns of herbivory at seascape scales.

626 **References**

627 Adam, T. C., R. J. Schmitt, S. J. Holbrook, A. J. Brooks, P. J. Edmunds, R. C. Carpenter, and G.

628   Bernadi. 2011. Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a

629   large-scale perturbation. PLoS ONE **6**:e23717.

630 Adey, W. H., and T. Goertemiller. 1987. Coral reef algal turfs - master producers in nutrient poor seas.

631   Phycologia **26**:374-386.

632 Almany, G. R. 2004. Priority effects in coral reef fish communities of the Great Barrier Reef. Ecology

633   **85**:2872-2880.

634 Anderson, M. A., R. N. Gorley, and R. K. Clarke. 2008. PRIMER: guide to software and statistical

635   methods. Plymouth Marine Laboratory Plymouth.

636 Aswani, S., and R. J. Hamilton. 2004. Integrating indigenous ecological knowledge and customary sea

637   tenure with marine and social science for conservation of bumphead parrotfish (*Bolbometopon*

638   *muricatum*) in the Roviana Lagoon, Solomon Islands. Environmental Conservation **31**:69-83.

639 Battista, T. A., B. M. Costa, and S. M. Anderson. 2007. Shallow-Water Benthic Habitats of the

640   Republic of Palau (DVD). NOAA Technical Memorandum NOS NCCOS 59, Biogeography

641   Branch. Silver Spring, MD.

642 Bejarano, S., Y. Golbuu, T. Sapolu, and P. J. Mumby. 2013. Ecological risk and the exploitation of

643   herbivorous reef fish across Micronesia. Marine Ecology Progress Series **482**:197-+.

644 Bejarano, S., J. B. Jouffray, I. Chollett, R. Allen, G. Roff, A. Marshell, R. Steneck, S. C. A. Ferse, and

645   P. J. Mumby. 2017. The shape of success in a turbulent world: wave exposure filtering of coral

646   reef herbivory. Functional Ecology **31**:1312-1324.

647   Bellwood, D. R., and J. H. Choat. 1989. A description of the juvenile phase colour patterns of 24
648   parrotish species (family Scaridae) from the Great Barrier Reef, Australia. Records of the
649   Australian Museum **41**:1-41.

650   Bellwood, D. R., C. H. R. Goatley, J. A. Khan, and S. B. Tebbett. 2016. Site fidelity and homing in
651   juvenile rabbitfishes (Siganidae). Coral Reefs **35**.

652   Bellwood, D. R., T. P. Hughes, and A. S. Hoey. 2006. Sleeping functional group drives coral-reef
653   recovery. Current Biology **16**:2434-2439.

654   Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the
655   relative contribution of positive and negative interactions in rocky intertidal communities.
656   Ecology **80**:2711-2726.

657   Boecklen, W. J. 1986. Effects of Habitat Heterogeneity on the Species Area Relationships of Forest
658   Birds. Journal of Biogeography **13**:59-68.

659   Bozec, Y. M., L. Yakob, S. Bejarano, and P. J. Mumby. 2013. Reciprocal facilitation and non-linearity
660   maintain habitat engineering on coral reefs. Oikos **122**:428-440.

661   Brandl, S. J., and D. R. Bellwood. 2016. Microtopographic refuges shape consumer-producer dynamics
662   by mediating consumer functional diversity. Oecologia **182**:203-217.

663   Bryan, P. G. 1975. Food-Habits, Functional Digestive Morphology, and Assimilation Efficiency of
664   Rabbitfish Siganus-Spinus (Pisces, Siganidae) on Guam. Pacific Science **29**:269-277.

665   Burgess, S. C., M. J. Kingsford, and K. P. Black. 2007. Influence of tidal eddies and wind on the
666   distribution of presettlement fishes around One Tree Island, Great Barrier Reef. Marine
667   Ecology-Progress Series **341**:233-242.

668   Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect
669   community structure and function on a coral reef. Proceedings of the National Academy of
670   Sciences of the United States of America **105**:16201-16206.

671   Caley, M. J., and J. St John. 1996. Refuge availability structures assemblages of tropical reef fishes.
672   Journal of Animal Ecology **65**:414-428.

673   Carpenter, R. C. 1986. Partitioning herbivory and its effects on coral reef algal communities.
674   Ecological Monographs **56**:345-364.

675   Carpenter, R. C. 1990. Mass mortality of *Diadema antillarum* 1. Long-term effects on sea urchin
676   population dynamics and coral reef algal communities. Marine Biology **104**:67-77.

677   Casey, J. M., A. H. Baird, S. J. Brandl, M. O. Hoogenboom, J. R. Rizzari, A. J. Frisch, C. E. Mirbach,
678   and S. R. Connolly. 2016. A test of trophic cascade theory: fish and benthic assemblages across
679   a predator density gradient on coral reefs. Oikos.

680 Choat, J. H., and D. R. Bellwood. 1985. Interactions Amongst Herbivorous Fishes on a Coral-Reef -
681   Influence of Spatial Variation. Marine Biology **89**:221-234.

682 Choat, J. H., K. D. Clements, and W. D. Robbins. 2002. The trophic status of herbivorous fishes on
683   coral reefs - I: Dietary analyses. Marine Biology **140**:613-623.

684 Clements, K. D., D. P. German, J. Piche, A. Tribollet, and J. H. Choat. 2017. Integrating ecological
685   roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes
686   as microphages. Biological Journal of the Linnean Society **120**:729-751.

687 Colin, P. L. 2012. Timing and location of aggregation and spawning in reef fishes. Pages 117-158 Reef
688   fish spawning aggregations: biology, research and management. Springer.

689 Costanzo, S. D., M. J. O'Donohue, W. C. Dennison, N. R. Loneragan, and M. Thomas. 2001. A new
690   approach for detecting and mapping sewage impacts. Marine Pollution Bulletin **42**:149-156.

691 Craig, P. 1996. Intertidal territoriality and time-budget of the surgeonfish, Acanthurus lineatus, in
692   American Samoa. Environmental Biology of Fishes **46**:27-36.

693 Cvitanovic, C., and D. R. Bellwood. 2009. Local variation in herbivore feeding activity on an inshore
694   reef of the Great Barrier Reef. Coral Reefs **28**:127-133.

695 Davis, K., P. M. Carlson, C. G. Lowe, R. R. Warner, and J. E. Caselle. 2017. Parrotfish movement
696   patterns vary with spatiotemporal scale. Marine Ecology Progress Series **577**:149-164.

697 DeMartini, E., P. Jokiel, J. Beets, Y. Stender, C. Storlazzi, D. Minton, and E. Conklin. 2013.
698   Terrigenous sediment impact on coral recruitment and growth affects the use of coral habitat by
699   recruit parrotfishes (F. Scaridae). Journal of Coastal Conservation **17**:417-429.

700 Donaldson, T. J. 2002. High islands versus low islands: A comparison of fish faunal composition of the
701   Palau Islands. Environmental Biology of Fishes **65**:241-248.

702 Dorenbosch, M., M. G. G. Grol, M. J. A. Christianen, I. Nagelkerken, and G. van der Velde. 2005a.
703   Indo-Pacific seagrass beds and mangroves contribute to fish density coral and diversity on
704   adjacent reefs. Marine Ecology-Progress Series **302**:63-76.

705 Dorenbosch, M., M. G. G. Grol, I. Nagelkerken, and G. van der Velde. 2005b. Distribution of coral
706   reef fishes along a coral reef-seagrass gradient: edge effects and habitat segregation. Marine
707   Ecology-Progress Series **299**:277-288.

708 Elton, C. S. 1927. Animal ecology. The MacMillan Company, New York.

709 Estes, J. A., and J. F. Palmisano. 1974. Sea Otters - Their Role in Structuring Nearshore Communities.
710   Science **185**:1058-1060.

711 Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E.
712   Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E.

713   K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E.
714   Sinclair, M. E. Soule, R. Virtanen, and D. A. Wardle. 2011. Trophic Downgrading of Planet
715   Earth. Science **333**:301-306.

716 Feeney, W. E., O. M. Lonnstedt, Y. Bosiger, J. Martin, G. P. Jones, R. J. Rowe, and M. I. McCormick.
717   2012. High rate of prey consumption in a small predatory fish on coral reefs. Coral Reefs
718   **31**:909-918.

719 Fox, R. J., and D. R. Bellwood. 2007. Quantifying herbivory across a coral reef depth gradient. Marine
720   Ecology-Progress Series **339**:49-59.

721 Fox, R. J., and D. R. Bellwood. 2013. Niche partitioning of feeding microhabitats produces a unique
722   function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. Coral Reefs
723   **32**:13-23.

724 Frank, K. T., B. Petrie, and N. L. Shackell. 2007. The ups and downs of trophic control in continental
725   shelf ecosystems. Trends in Ecology & Evolution **22**:236-242.

726 Gell, F., and M. W. Whittington. 2002. Diversity of fishes in seagrass beds in the Quirimba
727   Archipelago, northern Mozambique. Marine and Freshwater Research **53**.

728 Golbuu, Y., E. Wolanski, J. W. Idechong, S. Victor, A. L. Isechal, N. W. Oldiais, D. Idip, R. H.
729   Richmond, and R. van Woesik. 2012. Predicting Coral Recruitment in Palau's Complex Reef
730   Archipelago. PLoS ONE **7**.

731 Graham, N. A. J., S. Jennings, M. A. MacNeil, D. Mouillot, and S. K. Wilson. 2015. Predicting
732   climate-driven regime shifts versus rebound potential in coral reefs. Nature **518**:94-+.

733 Graham, N. A. J., and K. L. Nash. 2013. The importance of structural complexity in coral reef
734   ecosystems. Coral Reefs **32**:315-326.

735 Green, A. L., and D. R. Bellwood. 2009. Monitoring functional groups of herbivorous reef fishes as
736   indicators of coral reef resilience. IUCN, Gland, Switzerland.

737 Green, A. L., A. P. Maypa, G. R. Almany, K. L. Rhodes, R. Weeks, R. A. Abesamis, M. G. Gleason, P.
738   J. Mumby, and A. T. White. 2015. Larval dispersal and movement patterns of coral reef fishes,
739   and implications for marine reserve network design. Biological Reviews **90**:1215-1247.

740 Gripenberg, S., and T. Roslin. 2007. Up or down in space? Uniting the bottom-up versus top-down
741   paradigm and spatial ecology. Oikos **116**:181-188.

742 Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community Structure, Population Control, and
743   Competition. American Naturalist **94**:421-425.

744 Hamilton, R. J., G. R. Almany, C. J. Brown, J. Pita, N. A. Peterson, and H. Choat. 2017. Logging
745   degrades nursery habitat for an iconic coral reef fish. Biological Conservation **210**:273-280.

746   Hamner, W. M., P. L. Colin, and P. P. Hamner. 2007. Export-import dynamics of zooplankton on a
747   coral reef in Palau. Marine Ecology-Progress Series **334**:83-92.

748   Harborne, A. R., P. J. Mumby, and R. Ferrari. 2012. The effectiveness of different meso-scale rugosity
749   metrics for predicting intra-habitat variation in coral-reef fish assemblages. Environmental
750   Biology of Fishes **94**:431-442.

751   Harborne, A. R., I. Nagelkerken, N. H. Wolff, Y. M. Bozec, M. Dorenbosch, M. G. G. Grol, and P. J.
752   Mumby. 2016. Direct and indirect effects of nursery habitats on coral-reef fish assemblages,
753   grazing pressure and benthic dynamics. Oikos **125**:957-967.

754   Hatcher, B. 1981. The interaction between grazing organisms and the epilithic algal community of a
755   coral reef: a quantitative assessment. Pages 515-524 *in* Proceedings of the Fourth International
756   Coral Reef Symposium. University of the Philippines, Quezon City, Manila, Philippines.

757   Hatcher, B. G. 1990. Coral reef primary productivity - a hierarchy of pattern and process. Trends in
758   Ecology & Evolution **5**:149-155.

759   Hatcher, B. G., and A. W. D. Larkum. 1983. An experimental analysis of factors controlling the
760   standing crop of epilithic algal community on a coral reef. Journal of Experimental Marine
761   Biology and Ecology **69**:61-84.

762   Heenan, A., A. Hoey, G. J. Williams, and I. D. Williams. 2016. Natural bounds on herbivorous coral
763   reef fishes. Proceedings of the Royal Society B-Biological Sciences **283**:20161716.

764   Heinlein, J. M., A. C. Stier, and M. A. Steele. 2010. Predators reduce abundance and species richness
765   of coral reef fish recruits via non-selective predation. Coral Reefs **29**:527-532.

766   Hixon, M. A. 2015. Predation: piscivory and the ecology of coral reef fishes. Pages 41-52 *in* C. Mora,
767   editor. Ecology of fishes on coral reefs. Cambridge University Press.

768   Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral reef fish
769   assemblages. Ecological Monographs **63**:77-101.

770   Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population
771   regulation in marine fish. Science **277**:946-949.

772   Hoey, A. S., S. J. Brandl, and D. R. Bellwood. 2013. Diet and cross-shelf distribution of rabbitfishes (f.
773   Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. Coral Reefs
774   **32**:973-984.

775   Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating
776   regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution
777   **25**:119-128.

778 Hothorn, T., F. Bretz, and P. Westfall. 2008. Simultaneous inference in general parametric models.
779   Biometrical Journal **50**:346-363.

780 Hughes, T. P., D. R. Bellwood, C. Folke, R. S. Steneck, and J. Wilson. 2005. New paradigms for
781   supporting the resilience of marine ecosystems. Trends in Ecology & Evolution **20**:380-386.

782 Hunt, G. L., and S. McKinnell. 2006. Interplay between top-down, bottom-up, and wasp-waist control
783   in marine ecosystems. Progress in Oceanography **68**:115-124.

784 Hunter, M. D., and P. W. Price. 1992. Playing Chutes and Ladders - Heterogeneity and the Relative
785   Roles of Bottom-up and Top-down Forces in Natural Communities. Ecology **73**:724-732.

786 Jackelman, J. J., and J. J. Bolton. 1990. Form Variation and Productivity of an Intertidal Foliose
787   Gigartina Species (Rhodophyta) in Relation to Wave Exposure. Hydrobiologia **204**:57-64.

788 Klumpp, D. W., and A. D. McKinnon. 1992. Community structure, biomass and productivity of
789   epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales.
790   Marine Ecology-Progress Series **86**:77-89.

791 Klumpp, D. W., and N. V. C. Polunin. 1990. Algal production, grazers, and habitat partitioning on a
792   coral reef: positive correlation between grazing rate and food availability. Pages 372-388 *in*
793   Trophic relationship in the marine environment. Proceedings of the 24th European Marine
794   Biology Symposium. Aberdeen University Press, Aberdeen, UK.

795 Kohler, K. E., and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic
796   program for the determination of coral and substrate coverage using random point count
797   methodology. Computers & Geosciences **32**:1259-1269.

798 Kulbicki, M., Y. M. Bozec, P. Labrosse, Y. Letourneur, G. Mou-Tham, and L. Wantiez. 2005. Diet
799   composition of carnivorous fishes from coral reef lagoons of New Caledonia. Aquatic Living
800   Resources **18**:231-250.

801 Lapointe, B. E., K. Thacker, C. Hanson, and L. Getten. 2011. Sewage pollution in Negril, Jamaica:
802   effects on nutrition and ecology of coral reef macroalgae. Chinese Journal of Oceanology and
803   Limnology **29**:775-789.

804 Lecchini, D., and R. Galzin. 2005. Spatial repartition and ontogenetic shifts in habitat use by coral reef
805   fishes (Moorea, French Polynesia). Marine Biology **147**:47-58.

806 Leigh, E. G., R. T. Paine, J. F. Quinn, and T. H. Suchanek. 1987. Wave Energy and Intertidal
807   Productivity. Proceedings of the National Academy of Sciences of the United States of America
808   **84**:1314-1318.

809 Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology **23**:399-418.

810   Long, M. H., J. E. Rheuban, P. Berg, and J. C. Zieman. 2012. A comparison and correction of light
811   intensity loggers to photosynthetically active radiation sensors. Limnology and Oceanography-
812   Methods **10**:416-424.

813   Madin, E. M. P., J. S. Madin, and D. J. Booth. 2011. Landscape of fear visible from space. Scientific
814   Reports **1**.

815   Mantyka, C. S., and D. R. Bellwood. 2007a. Direct evaluation of macroalgal removal by herbivorous
816   coral reef fishes. Coral Reefs **26**:435-442.

817   Mantyka, C. S., and D. R. Bellwood. 2007b. Macroalgal grazing selectivity among herbivorous coral
818   reef fishes. Marine Ecology-Progress Series **352**:177-185.

819   Maragos, J. E., and C. W. Cook. 1995. The 1991-1992 rapid ecological assessment of Palau's coral
820   reefs. Coral Reefs **14**:237-252.

821   Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: Trophic level, habitat,
822   and productivity shape the food web effects of resource subsidies. Ecology **88**:140-148.

823   Marshell, A., and P. J. Mumby. 2012. Revisiting the functional roles of the surgeonfish Acanthurus
824   nigrofuscus and Ctenochaetus striatus. Coral Reefs **31**:1093-1101.

825   Marshell, A., and P. J. Mumby. 2015. The role of surgeonfish (Acanthuridae) in maintaining algal turf
826   biomass on coral reefs. Journal of Experimental Marine Biology and Ecology **473**:152-160.

827   Matson, P. A., and M. D. Hunter. 1992. The Relative Contributions of Top-down and Bottom-up
828   Forces in Population and Community Ecology. Ecology **73**:723-723.

829   McClanahan, T. R., N. A. J. Graham, M. A. MacNeil, N. A. Muthiga, J. E. Cinner, J. H. Bruggemann,
830   and S. K. Wilson. 2011. Critical thresholds and tangible targets for ecosystem-based
831   management of coral reef fisheries. Proceedings of the National Academy of Sciences of the
832   United States of America **108**:17230-17233.

833   Mellin, C., M. Kulbicki, and D. Ponton. 2007. Seasonal and ontogenetic patterns of habitat use in coral
834   reef fish juveniles. Estuarine Coastal and Shelf Science **75**:481-491.

835   Menge, B. A. 1992. Community Regulation - under What Conditions Are Bottom-up Factors Important
836   on Rocky Shores. Ecology **73**:755-765.

837   Menge, B. A. 2000. Top-down and bottom-up community regulation in marine rocky intertidal
838   habitats. Journal of Experimental Marine Biology and Ecology **250**:257-289.

839   Mumby, P. J., S. Bejarano, Y. Golbuu, R. S. Steneck, S. N. Arnold, R. van Woesik, and A. M.
840   Friedlander. 2013a. Empirical relationships among resilience indicators on Micronesian coral
841   reefs. Coral Reefs **32**:213-226.

Mumby, P. J., C. P. Dahlgren, A. R. Harborne, C. V. Kappel, F. Micheli, D. R. Brumbaugh, K. E. Holmes, J. M. Mendes, K. Broad, J. N. Sanchirico, K. Buch, S. Box, R. W. Stoffle, and A. B. Gill. 2006. Fishing, trophic cascades, and the process of grazing on coral reefs. Science **311**:98-101.

Mumby, P. J., and A. R. Harborne. 2010. Marine Reserves Enhance the Recovery of Corals on Caribbean Reefs. PLoS ONE **5**:-.

Mumby, P. J., A. R. Harborne, J. Williams, C. V. Kappel, D. R. Brumbaugh, F. Micheli, K. E. Holmes, C. P. Dahlgren, C. B. Paris, and P. G. Blackwell. 2007. Trophic cascade facilitates coral recruitment in a marine reserve. Proceedings of the National Academy of Sciences of the United States of America **104**:8362-8367.

Mumby, P. J., R. S. Steneck, A. J. Edwards, R. Ferrari, R. Coleman, A. R. Harborne, and J. P. Gibson. 2012. Fishing down a Caribbean food web relaxes trophic cascades. Marine Ecology Progress Series **445**:13-24.

Mumby, P. J., R. S. Steneck, and A. Hastings. 2013b. Evidence for and against the existence of alternate attractors on coral reefs. Oikos **122**:481-491.

Mumby, P. J., and C. C. C. Wabnitz. 2002. Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. Environmental Biology of Fishes **63**:265-279.

Munch, S. B., M. L. Snover, G. M. Watters, and M. Mangel. 2005. A unified treatment of top-down and bottom-up control of reproduction in populations. Ecology Letters **8**:691-695.

Nash, K. L., N. A. J. Graham, S. K. Wilson, and D. R. Bellwood. 2013. Cross-scale Habitat Structure Drives Fish Body Size Distributions on Coral Reefs. Ecosystems **16**:478-490.

Newman, M. J. H., G. A. Paredes, E. Sala, and J. B. C. Jackson. 2006. Structure of Caribbean coral reef communities across a large gradient of fish biomass. Ecology Letters **9**:1216-1227.

Nichols, W. F., K. T. Killingbeck, and P. V. August. 1998. The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. Conservation Biology **12**:371-379.

Odum, H. T., and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecological Monographs **25**:291-320.

Paine, R. T. 1966. Food Web Complexity and Species Diversity. American Naturalist **100**:65-+.

Paine, R. T. 1980. Food Webs - Linkage, Interaction Strength and Community Infrastructure - the 3rd Tansley Lecture. Journal of Animal Ecology **49**:667-685.

Pinca, S., M. Kronen, F. Magron, B. McArdle, L. Vigliola, M. Kulbicki, and S. Andrefouet. 2012. Relative importance of habitat and fishing in influencing reef fish communities across seventeen Pacific Island Countries and Territories. Fish and Fisheries **13**:361-379.

875   Purcell, S. W., and D. R. Bellwood. 2001. Spatial patterns of epilithic algal and detrital resources on a
876   windward coral reef. Coral Reefs **20**:117-125.

877   R Development Core Team. 2017. R: A language and environment for statistical computing. R
878   Foundation for Statistical Computing, Vienna, Austria.

879   Renken, H., P. J. Mumby, I. Matsikis, and H. J. Edwards. 2010. Effects of physical environmental
880   conditions on the patch dynamics of Dictyota pulchella and Lobophora variegata on Caribbean
881   coral reefs. Marine Ecology Progress Series **403**:63-74.

882   Rilov, G., W. F. Figueira, S. J. Lyman, and L. B. Crowder. 2007. Complex habitats may not always
883   benefit prey: linking visual field with reef fish behavior and distribution. Marine Ecology-
884   Progress Series **329**:225-238.

885   Rizzari, J. R., A. J. Frisch, A. S. Hoey, and M. I. McCormick. 2014. Not worth the risk: apex predators
886   suppress herbivory on coral reefs. Oikos **123**:829-836.

887   Robertson, D. R., N. V. C. Polunin, and K. Leighton. 1979. The behavioral ecology of three Indian
888   Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon* and *Zebrasoma scopas*): their
889   feeding strategies, and social and mating systems. Environmental Biology of Fishes **4**:125-170.

890   Roff, G., I. Chollett, C. Doropoulos, Y. Golbuu, N. H. Steneck, A. L. Isechal, R. van Woesik, and P. J.
891   Mumby. 2015. Exposure-driven macroalgal phase shift following catastrophic disturbance on
892   coral reefs. Coral Reefs **34**:715-725.

893   Rogers, A., J. L. Blanchard, and P. J. Mumby. 2014. Vulnerability of Coral Reef Fisheries to a Loss of
894   Structural Complexity. Current Biology **24**:1000-1005.

895   Rose, J. P., and G. P. Malanson. 2012. Microtopographic heterogeneity constrains alpine plant
896   diversity, Glacier National Park, MT. Plant Ecology **213**:955-965.

897   Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and Bottom-up Control of
898   Stream Periphyton - Effects of Nutrients and Herbivores. Ecology **74**:1264-1280.

899   Russ, G. R. 2003. Grazer biomass correlates more strongly with production than with biomass of algal
900   turfs on a coral reef. Coral Reefs **22**:63-67.

901   Ruttenberg, B. I., S. L. Hamilton, S. M. Walsh, M. K. Donovan, A. Friedlander, E. DeMartini, E. Sala,
902   and S. A. Sandin. 2011. Predator-Induced Demographic Shifts in Coral Reef Fish Assemblages.
903   PLoS ONE **6**.

904   Sancho, G., D. Ma, and P. S. Lobel. 1997. Behavioral observations of an upcurrent reef colonization
905   event by larval surgeonfish Ctenochaetus strigosus (Acanthuridae). Marine Ecology-Progress
906   Series **153**:311-315.

907   Shibuno, T., Y. Nakamura, M. Horinouchi, and M. Sano. 2008. Habitat use patterns of fishes across the
908   mangrove-seagrass-coral reef seascape at Ishigaki Island, southern Japan. Ichthyological
909   Research **55**:218-237.

910   Shulman, M. J., J. C. Ogden, J. P. Ebersole, W. N. Mcfarland, S. L. Miller, and N. G. Wolf. 1983.
911   Priority Effects in the Recruitment of Juvenile Coral-Reef Fishes. Ecology **64**:1508-1513.

912   Stallings, C. D. 2008. Indirect effects of an exploited predator on recruitment of coral-reef fishes.
913   Ecology **89**:2090-2095.

914   Steneck, R. S. 1988. Herbivory on coral reefs: a synthesis. Pages 37-49 *in* Proceedings of the 6th
915   international Coral Reef Symposium, Townsville, Australia.

916   Steneck, R. S., D. R. Bellwood, and M. E. Hay. 2017. Herbivory in the marine realm. Current Biology
917   **27**:R484-R489.

918   Steneck, R. S., and M. N. Dethier. 1994. A Functional-Group Approach to the Structure of Algal-
919   Dominated Communities. Oikos **69**:476-498.

920   Taylor, B. M. 2014. Drivers of protogynous sex change differ across spatial scales. Proceedings of the
921   Royal Society B-Biological Sciences **281**.

922   Taylor, B. M., S. J. Lindfield, and J. H. Choat. 2015. Hierarchical and scale-dependent effects of
923   fishing pressure and environment on the structure and size distribution of parrotfish
924   communities. Ecography **38**:520-530.

925   Tootell, J. S., and M. A. Steele. 2016. Distribution, behavior, and condition of herbivorous fishes on
926   coral reefs track algal resources. Oecologia **181**:13-24.

927   Unsworth, R. K. F., J. D. Taylor, A. Powell, J. J. Bell, and D. J. Smith. 2007. The contribution of scarid
928   herbivory to seagrass ecosystem dynamics in the Indo-Pacific. Estuarine Coastal and Shelf
929   Science **74**:53-62.

930   Verges, A., C. Doropoulos, H. Malcolm, M. Skye, M. Garcia-Piza, E. M. Marzinelli, A. H. Campbell,
931   E. Ballesteros, A. Hoey, A. Vila-Concejo, Y. M. Bozec, and P. D. Steinberg. 2016. Long-term
932   empirical evidence of ocean warming leading to tropicalization of fish communities, increased
933   herbivory, and loss of kelp. Proceedings of the National Academy of Sciences **113**:13791-
934   13796.

935   Verges, A., M. A. Vanderklift, C. Doropoulos, and G. A. Hyndes. 2011. Spatial Patterns in Herbivory
936   on a Coral Reef Are Influenced by Structural Complexity but Not by Algal Traits. PLoS ONE
937   **6**.

938 Vianna, G. M. S., M. G. Meekan, J. J. Meeuwig, and C. W. Speed. 2013. Environmental Influences on
939   Patterns of Vertical Movement and Site Fidelity of Grey Reef Sharks (Carcharhinus
940   amblyrhynchos) at Aggregation Sites. PLoS ONE **8**.

941 Whorff, J. S., L. L. Whorff, and M. H. Sweet. 1995. Spatial Variation in an Algal Turf Community
942   with Respect to Substratum Slope and Wave Height. Journal of the Marine Biological
943   Association of the United Kingdom **75**:429-444.

944 Wiens, J. A. 1974. Habitat Heterogeneity and Avian Community Structure in North-American
945   Grasslands. American Midland Naturalist **91**:195-213.

946 Williams, I. D., and N. V. C. Polunin. 2001. Large-scale associations between macroalgal cover and
947   grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs **19**:358-366.

948 Wilson, S. K., D. R. Bellwood, J. H. Choat, and M. J. Furnas. 2003. Detritus in the epilithic algal
949   matrix and its use by coral reef fishes. Pages 279-309 Oceanography and Marine Biology, Vol
950   41.

951 Wismer, S., A. S. Hoey, and D. R. Bellwood. 2009. Cross-shelf benthic community structure on the
952   Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Marine
953   Ecology-Progress Series **376**:45-54.

954 Wolanski, E., P. Colin, J. Naithani, E. Deleersnijder, and Y. Golbuu. 2004. Large amplitude, leaky,
955   island-generated, internal waves around Palau, Micronesia. Estuarine Coastal and Shelf Science
956   **60**:705-716.

957 Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of
958   semiparametric generalized linear models. Journal of the Royal Statistical Society Series B-
959   Statistical Methodology **73**:3-36.

960 **Data Availability**

961 Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.0145sn6

962 **Table 1** Summary of SIMPER results for density and biomass of herbivore assemblages across the biogeographic groups (contributions

963 less than 90% are not displayed). Density and biomass are presented as mean ± standard error for each biogeographic grouping.

964

Characteristic	Inner East	Outer East	West	Southwest
Density (no./m^2)	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1	0.2 ± 0.1
Average similarity (%)	67.9	69.0	65.4	69.6
Species (contribution, %)	*Ctenochaetus striatus* (22.7)	*Ctenochaetus striatus* (28.9)	*Ctenochaetus striatus* (28.8)	*Ctenochaetus striatus* (29.2)
	Chlorurus spilurus (19.8)	*Chlorurus spilurus* (17.0)	*Acanthurus nigricans* (21.8)	*Acanthurus nigricans* (15.1)
	Zebrasoma scopas (18.5)	*Zebrasoma scopas* (8.6)	*Zebrasoma scopas* (10.6)	*Zebrasoma scopas* (8.1)
	Siganus vulpinus (7.8)	*Naso lituratus* (8.3)	*Chlorurus spilurus* (9.8)	*Chlorurus spilurus* (7.5)
	Scarus niger (6.8)	*Acanthurus nigricans* (7.1)	*Scarus niger* (9.3)	*Scarus prasiognathos* (7.1)
	Scarus dimidiatus (4.5)	*Scarus niger* (5.7)	*Naso lituratus* (9.1)	*Cetoscarus ocellatus* (6.3)
	Naso lituratus (3.6)	*Scarus schegeli* (5.3)	*Cetoscarus ocellatus* (5.4)	*Acanthurus pyroferus* (5.6)
	Siganus stellatus (3.1)	*Scarus spinus* (4.9)		*Scarus niger* (3.9)
	Acanthurus pyroferus (2.5)	*Scarus corallinus* (3.6)		*Siganus puellus* (3.4)
	Siganus doliatus (1.6)	*Siganus puellus* (2.3)		*Scarus dimidiatus* (3.4)
				Naso lituratus (3.1)
Biomass (g/m^2)	10.7 ± 2.2	17.6 ± 1.6	13.9 ± 1.2	52.9 ± 5.9
Average similarity (%)	64.1	63	56.1	59.6
Species (contribution, %)	*Ctenochaetus striatus* (23.3)	*Ctenochaetus striatus* (28.0)	*Ctenochaetus striatus* (24.7)	*Ctenochaetus striatus* (22.8)
	Chlorurus spilurus (20.0)	*Chlorurus spilurus* (17.2)	*Acanthurus nigricans* (19.4)	*Cetoscarus ocellatus* (14.25)
	Zebrasoma scopas (13.6)	*Naso lituratus* (12.1)	*Naso lituratus* (12.8)	*Scarus prasiognathos* (13.3)
	Scarus niger (7.9)	*Scarus niger* (7.2)	*Scarus niger* (12.4)	*Acanthurus nigricans* (10.8)
	Siganus vulpinus (6.8)	*Scarus schegeli* (6.5)	*Cetoscarus ocellatus* (8.7)	*Chlorurus spilurus* (6.4)
	Scarus dimidiatus (5.5)	*Zebrasoma scopas* (5.9)	*Chlorurus spilurus* (8.1)	*Chlorurus microrhinos* (5.6)
	Naso lituratus (4.9)	*Acanthurus nigricans* (5.4)	*Zebrasoma scopas* (6.7)	*Scarus rubroviolaceus* (5.5)
	Siganus stellatus (2.6)	*Scarus spinus* (4.7)		*Zebrasoma scopas* (4.2)

	Siganus doliatus (1.5)	*Scarus corallinus* (2.3)		*Scarus dimidiatus* (4.1)
		Siganus puellus (2.2)		*Naso lituratus* (4.1)

965

966

Table 2 Summary of results from distance based linear modelling (DistLM) of key drivers of herbivore assemblage composition. SS = sum of squares, Prop = proportion of variance explained, Cum = cumulative proportion of variance explained, Adj R^2 = proportion of variance explained adjusted by the number of independent variables, df = degrees of freedom.

Variable	Adj R2	SS	Pseudo-F	P	Prop	Cum	df
Marginal tests							
Exposure		1276.9	1.557	0.115	0.09		
Grazeable cover		1493.6	1.852	0.077	0.10		
Structural complexity		1471.7	1.822	0.072	0.10		
In-situ turf height		2822.6	3.902	0.005	0.20		
Net turf growth		1032.9	1.237	0.292	0.07		
Coral cover		1413.3	1.742	0.076	0.10		
Sequential tests							
+ Exposure	0.03	1276.9	1.557	0.121	0.09	0.09	16
+ Grazeable cover	0.06	1203.2	1.515	0.136	0.08	0.17	15
+ Structural complexity	0.12	1473.6	1.975	0.076	0.10	0.27	14

+ In-situ turf height	0.29	2614.8	4.342	0.002	0.18	0.46	13
+ Net turf growth	0.23	38.329	0.059	1	0.00	0.46	12
+ Coral cover	0.22	565.78	0.861	0.575		0.50	11

970

Figures

972 **Figure 1** Study sites on the western and eastern sides of the Palau archipelago (inset), and wave
973 exposure, benthic cover (pie charts) and in-situ turf height measurements (bar plots).

974 **Figure 2** Site level variability in herbivore density according to a) family groups, b) functional
975 groups, and herbivore biomass according to c) family groups, and d) functional groups.

976 **Figure 3** a) representative photograph of the experimental tile setup within herbivore exclusion cage
977 3 days following deployment, b) representative photographs of low and high exposure tiles 10 days
978 following deployment, non-linear response of exposure driven net primary production (NPP, g^{-1} m^{-2}
979 day^{-1}) with wave exposure, d) non-linear response of exposure driven net turf canopy growth (mm^{-1}
980 day^{-1}) with wave exposure.
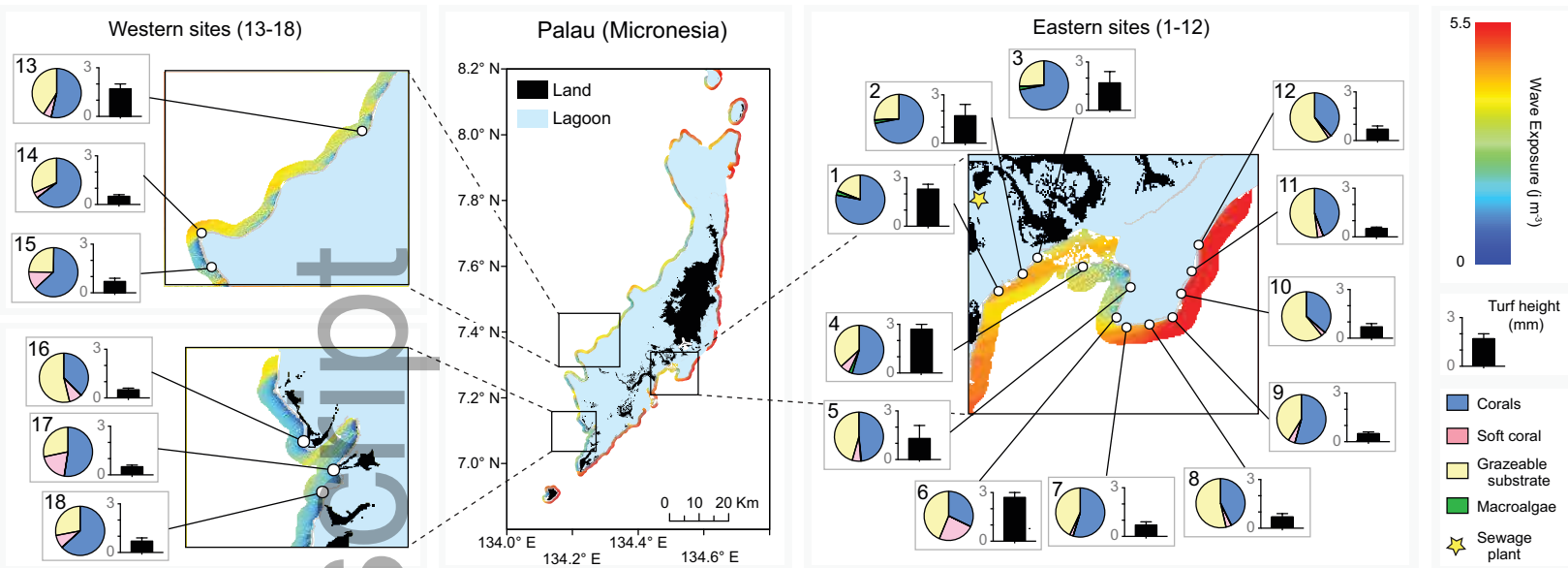
981 **Figure 4** Biomass of predatory fish (g m^{-2}) according to a) size class (< 50 cm, 50 - 100 cm, >100
982 cm) and b) family group (Carcharinidae, Lutjanidae, Carangidae, Lethrinidae, Fistularidae, and
983 'other').

984 **Figure 5** Relationship between herbivore biomass and a) Net turf growth, b) Net primary production,
985 c) in-situ measured turf height, d) wave exposure, e) structural complexity, and f) predator biomass (±
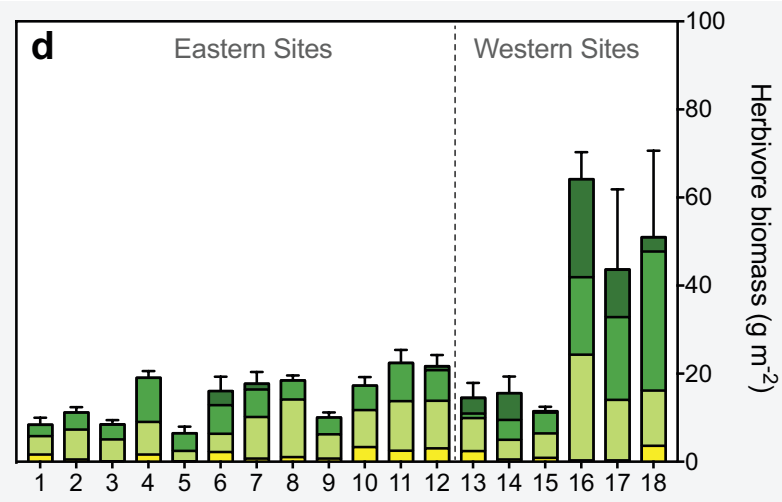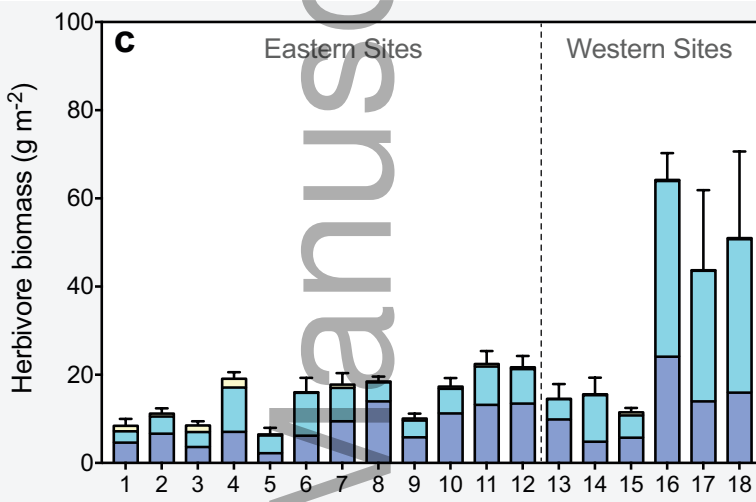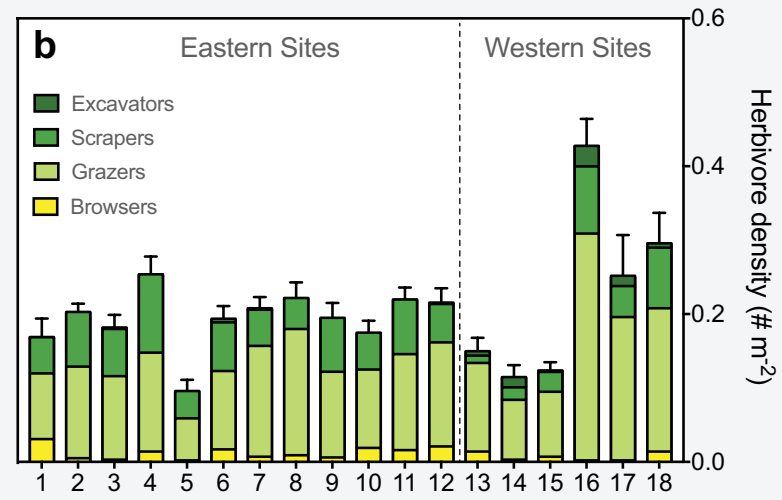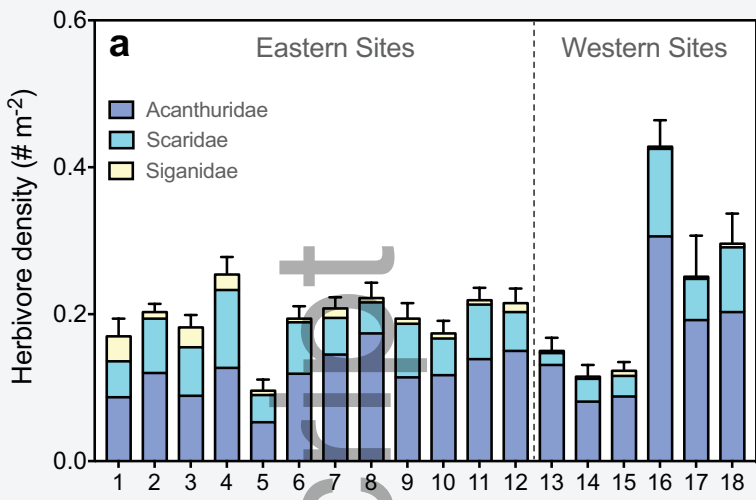986 SE, circles = east sites, square = west sites).

987 **Figure 6** a) Principal Coordinates Ordination (PCoA) of sites and biogeographic split (50% similarity
988 level), b) geographic location of sites according to PCoA clustering, c) distance-based redundancy
989 analyses (dbRDA) ordination of herbivore species and environmental drivers.

990 **Figure 7** Seascape patterns and habitat heterogeneity among sites in the Palau archipelago (Battista et
991 al. 2007), and representative cross shelf profiles of the two different geomorphology types (barrier
992 reefs and emergent carbonate banks flats).

Western sites (13-18)

Palau (Micronesia)

Eastern sites (1-12)

ecm_1336_f1.eps

Wave Exposure (j m⁻³)

Turf height (mm)

Corals
Soft coral
Grazeable substrate
Macroalgae
Sewage plant

ecm_1336_f2.eps

a

b

c

Net primary production (g per m² per day)

Wave exposure (j m⁻³)

d

Caged turf growth (mm per day)

Wave exposure (j m⁻³)

a

Mesopredator biomass (g per m^{-2})

Eastern sites | Western sites

- >100 cm
- 50-100 cm
- <50 cm

Sites: 1, 5, 7, 11, 13, 15, 16, 17, 18

b

Mesopredator biomass (g per m^{-2})

Eastern sites | Western sites

- Carcharhinidae
- Lutjanidae
- Carangidae
- Lethrinidae
- Fistularidae
- Other

Sites

ecm_1336_f4.eps

ecm_1336_f5.eps

a

West

South west

East inner

East outer

PCO2 (16.6% of total variation)

PCO1 (33.2% of total variation)

b

West

South west

East inner

East outer

0   10   20 Km

c

dbRDA2 (51.5% of fitted, 12.5% of total variation)

Scarus prasiognathos

Acanthurus lineatus
Scarus rubroviolaceus
Chlororus microrhinus
Acanthurus nigricans

Ctenochaetus striatus

Coral cover

Rugosity

Measured turf height

Gross turf height

Exposure

Grazeable cover

Siganus stellatus
Zebrasoma scopas
Siganus vulpinus

Chlororus spilurus

Scarus schlegeli

Siganus corallinus
Siganus spinus

Palau archipelago_f7.pdf

Western sites

13

14

15

1km

Palau archipelago

- Shallow lagoon
- Emergent land
- Forereef habitat
- Patch reef
- Back-reef habitat
- Turf algae
- Macroalgae
- Seagrass

Inner eastern sites

1 2 3 4 5

1km

South western sites

16

17

18

1km

Outer eastern sites

12

11

10

6 7 8 9

1km

10km

Barrier reef (sites 1-15)

Highest astronomical tide
Lowest astronomical tide

Back reef
Reef flat
Reef slope

Cross shelf profile (distance in metres)

Emergent carbonate banks (sites 16-18)

Highest astronomical tide
Lowest astronomical tide

Island
Reef flat
Reef slope
Drop off

Cross shelf profile (distance in metres)