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2019

A rapidly expanding alga acts as a secondary foundational species providing novel ecosystem functions in the South Pacific

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1   **Title:** A rapidly expanding macroalga acts as a foundational species providing trophic
2   support and habitat in the South Pacific
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17 Manuscript Highlights:

18   1) We examined the functional role of a macroalga that is expanding on a coral reef
19   2) Primary producers were facilitated by increased density of the macroalga
20   3) Foraging by fish primary consumers increased due to increased algal resources

21 **Abstract**

22 Foundation species facilitate associated communities and provide key ecosystem

23 functions, making anthropogenically-driven phase shifts involving these species critically

24 important. One well documented such phase-shift has been from coral to algal

25 domination on tropical reefs. On South Pacific coral reefs, the macroalga *Turbinaria*

26 *ornata* has expanded its range and habitat but, unlike algae that often dominate after

27 phase-shifts, *T. ornata* is structurally complex and generally unpalatable to herbivores.

28 Therefore, it may serve a foundational role on coral reefs, such as providing habitat

29 structure to more palatable primary producers and corresponding trophic support to

30 fishes. We predicted increasing *T. ornata* density would facilitate growth of associated

31 algae, resulting in a positive trophic cascade to herbivorous fish. An experiment

32 manipulating *T. ornata* densities showed a unimodal relationship between *T. ornata* and

33 growth of understory algae, with optimal growth occurring at the most frequent natural

34 density. Epiphyte cover also increased with density until the same optimum, but remained

35 high with higher *T. ornata* densities. Foraging by herbivorous fishes increased linearly

36 with *T. ornata* density. An herbivore exclusion experiment confirmed *T. ornata*

37 facilitated epiphytes, but resource use of epiphytes by herbivores, though significant, was

38 not affected by *T. ornata* density. Therefore, *T. ornata* performs foundational roles

39 because it provides novel habitat to understory and epiphytic macroalgae and trophic

40 support to consumers, though likely this function is at the expense of the original

41 foundational corals.

42 Keywords: foundation species, phase-shift, macroalgae, coral reefs, herbivory, epiphytes,

43 foraging behavior

44   **Introduction**

45   Foundation species facilitate associated species and support ecosystem functions

46   through amelioration of harsh conditions, increased trophic support, and/or provision of

47   habitat (*sensu* Dayton 1972, Stachowicz 2001, Ellison and others 2005). Foundation

48   species often form habitat by providing physical structure for associated organisms to

49   grow on directly or in close proximity. For example, some epiphytes grow directly on

50   foundation species and are important for trophic support across systems (e.g. seagrasses,

51   Hughes and others 2004; freshwater macrophytes, Jaschinski and others 2011; oak trees,

52   Angelini and Silliman 2014). In addition, foundation species in many systems can

53   provide canopy that ameliorates harsh conditions (e.g. nutrient limitation,

54   photoinhibition, high wind or wave energy) for plants and macroalgae in the understory

55   (for example in terrestrial forests in Gentry and Dodson 1987, Ellison and others 2005;

56   kelp forests in Graham 2004). As the provision of structure, trophic support, and other

57   services by foundation species influences community composition and diversity, we need

58   a better understanding of the potential for species that may be favored by anthropogenic

59   induced phase-shifts to fill foundational roles.

60   Phase-shifts from one community state to another have been documented in

61   terrestrial, freshwater, and marine systems (Scheffer and others 2001; Folke and others

62   2004). This includes systems with structurally complex foundation species, such as

63   terrestrial forests and coral reefs. While the shifted species may occupy the same space,

64   they may not support the same functions as the original foundation species. For example,

65   fire suppression caused historically oak dominated forests to shift to shade tolerant trees

66   such as maples (Nowacki and Abrams 2008), and increasing human population density

67 and fire frequency turned shrubland into grassland (Talluto and Suding 2008). These

68 shifts in terrestrial foundation species due to anthropogenic influence resulted in drastic

69 changes to ecosystems, such as changing community structure and trophic support, as the

70 species that dominate after a phase-shift often do not support the same associated

71 organisms or ecosystem functions (e.g. coral reef examples in McCook 1999; temperate

72 forest examples in Ellison and others 2005). In marine systems, foundation species tend

73 to be structure-forming invertebrates (e.g. mussels, Suchanek 1992; corals, Hughes and

74 others 2010) or marine macrophytes (e.g. kelp, Graham 2004; seagrasses, Orth and others

75 2006; rocky shore macroalgae, Korpinen and others 2010) that are also experiencing

76 natural and human-driven phase-shifts (reviewed in deYoung and others 2008). For

77 example, coral reefs are well documented to experience phase-shifts to algal domination

78 due to nutrient enrichment and overfishing (reviewed by Hughes and others 2010). As it

79 is well documented that some ecosystems have been increasingly subjected to phase-

80 shifts (e.g. coral reefs; Hughes and others 2010, Dudgeon and others 2010) it is critical to

81 examine the potential for shifted species to perform foundational roles.

82   Corals are the dominant foundation species in tropical marine systems with hard

83 substrates, while in nutrient-rich temperate waters fleshy macroalgae often fill this role.

84 In previous experimental studies, phase-shifts on coral reefs involved fast growing,

85 palatable macroalgal species or multi-species turf algae (e.g. multiple species Lewis and

86 Wainwright 1985; *Cladophora* Smith and others 2005; turf and macroalgae in Smith and

87 others 2010; turf algae in Muthukrishnan and others 2016). Although coral reef

88 macroalgae tend to be smaller, more cryptic, and more ephemeral than temperate

89 macroalgae (reviewed by Fong and Paul 2011); there has been a recent increase in fleshy

90   macroalgae on disturbed coral reefs (*Turbinaria* in Payri 1984, Martinez and others 2007;

91   *Lobophora* in Jompa and McCook 2002; *Sargassum* in Hughes and others 2007). These

92   increases in fleshy macroalgae have been attributed to decreased herbivory for

93   *Sargassum* (Hughes and others 2007) or a combination of increased nutrient input and

94   decreased herbivory for *Turbinaria* (Bittick and others 2016) and *Lobophora* (Jompa and

95   McCook 2002). Whether these novel macroalgal communities that are complex, less

96   palatable, and persistent macroalgal serve foundational roles in tropical reef systems has

97   not been evaluated. Though it is widely acknowledged that algal-domination cannot

98   sustain net reef growth because loss of coral results in lower calcification (Gattuso and

99   others 1997), some coral reef macroalgae have been found to have positive impacts on

100   biomass of fish (turf algae, Tootell and Steele 2016), abundance and diversity of

101   invertebrates (Roff and others 2013), and macroalgal richness (Bittick and others 2010).

102   As fleshy macroalgae have increased on many coral reefs, it is important to determine

103   whether they function as foundation species and what ecosystem functions, if any, they

104   may provide.

105   Our overall objective was to evaluate if *Turbinaria ornata*, a marine macroalga

106   that is expanding its range and habitat use in the South Pacific (Payri 1984; Martinez and

107   others 2007), provides a foundational role following a phase-shift from coral dominance

108   after disturbance to tropical reefs. Negative impacts of *T. ornata* on coral have been

109   documented, including inhibiting coral recruits (Brandl and others 2013) and

110   outcompeting coral in high flow conditions (Brown and Carpenter 2014). In Mo'orea,

111   French Polynesia coral populations were recently decimated due to an outbreak of the

112   coralivorous seastar, *Acanthaster plancii* (Kayal and others 2012), and patches of *T.*

113 *ornata* increased in size and dominance on fringing and back reefs (Carpenter 2015;

114 Davis 2016). Further, *T. ornata* benefits from anthropogenic change as nutrient

115 enrichment cause a strengthening of physical anti-herbivory defenses and therefore

116 reduced herbivory (Bittick and others 2016). However, aggregations of *T. ornata* benefit

117 understory macroalgae (Bittick and others 2010) by providing a refuge from herbivores

118 thereby increasing species richness and it may protect invertebrates and juvenile fish

119 (*personal obs*). We predicted that *T. ornata* would perform roles typically associated with

120 structurally complex foundation species such as provision of habitat for primary

121 producers and trophic support to consumers. We ask: (1) Does *T. ornata* facilitate

122 epiphytic and understory macroalgae? and (2) Does this facilitation cascade up to

123 herbivorous fish through increased resources?

124 **Methods**

125 *Study site and survey* — The study site was a fringing patch reef at the mouth of

126 Opunohu Bay in Mo'orea, French Polynesia (17°28'59.81"S, 149°50'45.70"W). After the

127 2006-2010 *Acanthaster plancii* outbreak, and disturbance by 2010 hurricane Oli, coral

128 cover was lost across much of Mo'orea, and near zero at this site (Kayal and others

129 2012). *Turbinaria ornata* requires hard substrate to settle such as dead coral skeletons

130 and often grows in patches, or aggregations, of varying density (see ESM S1, Fig. S1). To

131 characterize the aggregations, we constructed a density-frequency distribution from

132 counts of thalli in 0.0625 m^2 areas (quadrats were 0.25m x 0.25m); we observed this area

133 of aggregations to be the most common on the nearshore reefs during our 2012-2014

134 study period. This is larger than the median patch size of 0.022 m^2 observed by Davis

135 (2016) in a 2012-2015 study. We randomly placed five 30 m transects, selected six

136   random points along each, and counted the number of thalli• 0.0625 m^{-2} in the nearest

137   aggregation (N=30). Surveys were conducted in May 2012.

138   To characterize species distribution and sizes of fish from dominant taxa, we

139   utilized survey data from the Moorea Coral Reef Long Term Ecological Research

140   program (MCR LTER). Four surveys were conducted in August 2012 at two sites on the

141   north shore near our study area. Fish were counted along a 50 m transect 5 meters wide

142   and identified to species with an estimate of size to the nearest cm. We calculated the

143   density of fish primary consumer species per 100 m^2. We also calculated average length

144   (+/- SE cm) for the three most abundant species.

145   *Density manipulation experiment—* To measure the effect of *T. ornata* density on

146   growth of epiphytic and understory algae and the consequences to herbivore foraging, we

147   thinned existing aggregations of *T. ornata* (randomly selected, but initially with $\geq$ 30

148   thalli • 0.0625 m^{-2}) to create plots of 8 densities: 0, 3, 7, 10, 15, 20, 25, and 30 thalli •

149   0.0625 m^{-2} (n=3). We avoided damselfish territories (family Pomacentridae), although a

150   territory subsequently encroached on a plot of 15 thalli • 0.0625 m^{-2} (reducing n to 2 for

151   this treatment). Treatments were maintained for 18 days in May 2012, during which we

152   conducted a growth bioassay within the experimental plots using a locally abundant

153   macroalga, *Padina boryana.* Two grams (standardized wet weight) of *P. boryana* were

154   placed in window screen cages and attached within the understory of each plot (see Fong

155   et al. 2006 for method). Algae were collected after 7 days (17-24 May, 2012), wet

156   weighed, and net growth was calculated as % change from initial wet weight.

157   At the end of the experiment, three *T. ornata* thalli (5-12 cm tall) were collected

158   randomly (except for plots where density=3 where all were collected) from each density

7

159 plot. Photos were taken of one side of each alga (see Electronic Supplementary Material

160 S1, Fig. S2) and percent cover of epiphytes quantified using the point intercept method in

161 ImageJ (U.S. National Institutes of Health). We first measured two-dimension area in

162 Image-J using the images. Due to varying image quality and *T. ornata* thalli size and

163 shape, we used the grid overlay feature scaled for each thalli. The spacing of the grid was

164 limited to whole pixel increments and scaled to produce a minimum of 30

165 random intersections. Grid overlays were between pixels, so the pixel to the top right was

166 evaluated. Percent epiphyte cover was calculated as 100* the ratio of intersections with

167 epiphytes present over the total intersections within the thalli area.

168   To determine the relationship between *T. ornata* density and herbivorous fish, we

169 observed and recorded foraging behavior within density plots. Each plot was observed by

170 the same individual on snorkel three times over the 18 days for 10 minutes (total 30

171 min/plot). The observer remained at least 5 meters away from the plot and recorded when

172 fish: 1) came within 0.25 meters of the plot and 2) took a bite from the canopy, stipe, or

173 understory of the algal aggregation. Only fish from dominant herbivorous taxa were

174 counted in our surveys. However, dominant species and sizes of herbivorous fish in this

175 site were identified in the LTER data (see above). Fish behavior observations of plots did

176 not begin until 72 hrs after plots were establish to allow for stabilization of epiphytes

177 after physical disturbance. All observations were conducted from 14-20 May, 2012 and a

178 paired t-test comparing frequency of bites by herbivorous fish from the first and last day

179 supports no significant changes in behavior over time (t=0.85, p=0.41).

180   *Epiphyte herbivory experiment*—To determine the influence of *T. ornata* density

181 and herbivory on epiphyte load, we conducted an *in situ* 2-factor experiment

182   manipulating *T. ornata* density (as above) and access to herbivores (+/- H). The

183   experiment was fully crossed with three replicates of each treatment (n = 48). Herbivore

184   access was limited by exclusion cages (5-sided; 25×25×30cm^3 L×W×H) constructed

185   from hardware cloth with 1 cm openings. Light restriction by caging material was <10%

186   with no measureable restriction to water flow in cages constructed of the same material

187   and used at the same site (Clausing and others 2014). Ten randomly-selected thalli were

188   collected from each plot and photos were taken for analysis of initial percent cover by

189   epiphytes. After 16 days (sensu Bittick and others 2010) during May-June 2014, cages

190   were removed and three thalli were collected from each plot, photographed, and analyzed

191   in ImageJ for final percent cover by epiphytes. Initial epiphyte cover was 61.6 +/- 5.6 %

192   SEM.

193   *Analysis*—All analyses were conducted in R (R Core Team 2015). For all

194   response variables, linear and/or non-linear least squares models were fit to the data and

195   compared by Akaike Information Criterion (AICc). We tested whether the relationships

196   between *T. ornata* density and both epiphytes and understory macroalgae were best

197   explained as either: (1) linear, (2) logistic (i.e. positive effects saturate at a certain

198   density), (3) exponential (i.e. positive effects increase fastest at lower densities with no

199   saturation) or (4) quadratic (i.e. positive effects decline after an optimal density)

200   equations. The model with the lowest AICc value (ΔAIC=0) and highest AICc weight or,

201   if AICs were similar (ΔAIC<3-4), the equation with the lowest number of parameters was

202   chosen by rule of parsimony (Burnham and others 2011) and presented for each data set.

203   Full model comparisons and fit are provided in ESM S3. Further, we expected foraging

204   behavior of herbivorous fish (as bites over a 10-minute observation period) would also

205   follow one of these patterns in response to availability of resources. The epiphyte

206   herbivory experiment was analyzed using analysis of covariance (ANCOVA) with caging

207   as the explanatory variable and density as a covariate.

208   **Results**

209   *Survey*— *Turbinaria ornata* density was normally distributed (Shapiro-Wilk W

210   Test, W=0.98, P<W=0.80) ranging from 0-40 thalli • 0.0625 m^{-2}. Average density was

211   19.8 ± 1.9 SEM thalli • 0.0625 m^{-2} and 83% of the aggregations were 30 thalli or less

212   (Figure 1 a). Approximately 80% of all fish observed approaching and foraging in the

213   density plots were acanthurids (see ESM S2 for distribution). From the MCR LTER 2012

214   annual survey data, the three most abundant species on the north shore fringing reef were:

215   *Chlorulus sordidus* (32%), *Acanthurus nigrofuscus* (26%) and *Ctenochaetus striatus*

216   (24%) (Fig. 1 b, c). The average lengths of these species were 11.4 +/- SE 1.9 cm, 10.3

217   +/- SE 9.3 cm, and 11.3 +/- SE 2.7 cm respectively.

218   *Density manipulation experiment*— There was an increase with density in

219   epiphyte cover on *T. ornata* thalli until an optimum of 15 thalli • 0.0625 m^{-2} area (Fig. 2

220   a). Treatments with 3 thalli had ~40% cover by epiphytes, which increased to ~65%

221   cover in the 15 thalli treatments and remained at this level at higher densities; thus, cover

222   saturated in a logistic fit (Fig. 2 a; ESM S3). Similarly, macroalgae used as a bioassay for

223   understory macroalgal growth increased in biomass with *T. ornata* density up to 15 thalli

224   • 0.0625 m^{-2} (max = 30% growth • 7 days^{-1}; Fig. 2 b). After this optimum, growth

225   declined precipitously to nearly zero in treatments with 30 thalli; this was best fit with a

226   quadratic equation (Fig. 1 b; ESM S3)

227   Foraging behavior measured as bites • 10 min^{-1} was modelled as a linear increase

228   (Fig. 2 c; ESM S3). The relationship between bites • 10 min^{-1} and *T. ornata* density was

229   positive, with no evidence of a decline. Of the 408 observed bites, 51% were taken from

230   the canopy, 8% along the algal stipe, and 40% in the understory at the margins of the

231   aggregation.

232   *Epiphyte herbivory experiment— T. ornata* density facilitated and herbivores

233   reduced abundance of epiphytes. Exclusion of herbivores and increasing *T. ornata*

234   density both resulted in higher epiphyte cover relative to low density with presence of

235   herbivores. As in the density manipulation experiment in 2012, the 2014 experiment

236   showed a positive effect of *T. ornata* density on epiphytes; however, this relationship was

237   linear instead of logistic (Fig. 3; ESM S3). We found a significant effect of caging

238   (F=16.92, P = 0.0002) on percent epiphyte coverage, which was further explained by the

239   covariate *T. ornata* density (F=36.43, P<0.0001). However, the accumulation of

240   epiphytes with density (slope) is not significantly different between herbivore treatments

241   (t-test, p=0.16). The ranges in percent cover by epiphytes in 2012 and 2014 were also

242   comparable across years (28.2–72.6 and 27.2–76.3, respectively).

243   **Discussion**

244   Our results demonstrated *Turbinaria ornata* performs the role of a foundation

245   species on fringing coral reefs in the South Pacific that have experienced phase-shifts to

246   macroalgae. We suggest this represents a facilitation cascade (e.g. Thomsen et al. 2010)

247   where *T. ornata* attaches to hard substrate formed by dead corals after a disturbance, and,

248   once established, performs the key foundational role of facilitating an associated

249   community. One line of evidence for its role as a foundation species is that, up to an

250   optimum, increasing density of *T. ornata* also increases the abundance of associated

251   primary producer groups such as epiphytes and understory macroalgae that are not

252   typically associated with coral dominated reefs (Fong and Paul 2011). Other ecosystem

253   functions that have been documented to increase with density of a macroalgal foundation

254   species include more efficient nutrient cycling (Human and others 2015) and reduced

255   photoinhibtion (Franklin and others 1996). In addition, the decline in growth of holdfast

256   macroalgae, but not epiphytes, in our experiment at high *T. ornata* densities may be

257   attributed to density-dependent increases in intensity of competition for light or nutrients.

258   This relationship has also been found in terrestrial forests where understory species can

259   survive in reduced light up to a critical threshold (Anderson and others 1969) and are

260   positively impacted by tree thinning (Canham and others 1990; Lieffers and others 1999),

261   but canopy-occupying species such as epiphytes benefit from larger trees and denser

262   canopies (Woods and others 2015). Similarly, epiphytes in the "canopy" of *T. ornata*

263   aggregations may not experience the same reduction in light or nutrients as understory

264   macroalgae. Whatever the mechanism involved, our study demonstrated that *T. ornata*

265   acts as a foundation species because, once it becomes abundant after a disturbance as it

266   facilitates an associated community of primary producers. How this ecosystem function

267   provided by *T. ornata* compares to those functions provides by the original, coral-

268   dominated foundation species is unknown, but certainly is a critical area for future

269   research as phase-shifts to macroalgal domination have occurred globally (reviewed in

270   Hughes and others 2010).

271   A second line of evidence that *T. ornata* is a foundation species is its facilitation

272   of reef consumers through enhanced food resources. Increased densities of *T. ornata*

273   aggregations caused a facilitation cascade in which more foraging by fish was supported

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274   as epiphyte load and macroalgal understory increased. This is consistent with examples in

275   terrestrial and aquatic systems in which trophic support and/or consumer abundance and

276   diversity is negatively impacted by the loss of a foundation species (Hughes and others

277   2004; Rohr and others 2011; Angelini and Silliman 2014); similarly, in our study reduced

278   density of *T. ornata* also reduced trophic support. In other systems, primary producers

279   such as macroalgae and understory plants increase trophic support and consumer species

280   diversity (e.g. kelp forests, Graham 2004; temperate forests, Gilliam 2007; marshes,

281   Angelini et al. 2015). While the majority of grazing occurred on epiphytes on the surface

282   of the thalli within aggregations, understory macroalgae at the aggregation's edges

283   provided additional resources to grazers. Taken together these findings suggest higher

284   density *T. ornata* aggregations provide more food to herbivorous fish than less dense

285   aggregations via increased supplies of epiphytes and understory macroalgae,

286   demonstrating its role as a foundation species through enhanced trophic support.

287   However, while our study compared trophic support across different densities of *T.*

288   *ornata,* we were unable to compare these to the ecosystem functions provided by corals

289   as they had been lost to predation. Thus, comparisons between the trophic support

290   provided by corals vs. *T. ornata* aggregations are needed to fully assess differences in

291   ecosystem functions supported by these alternative communities.

292   The effects of *T. ornata* were strongly density-dependent, a phenomenon that has

293   rarely been evaluated in studies examining foundational communities. Rather, most

294   studies assess impacts to associated species in the presence and absence of a focal

295   foundation species (e.g. Graham 2004, Angelini et al. 2015). However, there are

296   terrestrial studies that showed decreased tree canopy cover, which may be a proxy for

297 density, reduced richness and abundance of associated species (e.g. Caners et al. 2010,

298 Cach-Pérez et al. 2013), suggesting density effects may be important across systems.

299 Further, we found that density effects varied across associated functional groups, with

300 epiphytes responding linearly or logistically and understory macroalgae responding

301 unimodally to *T. ornata* density. One possible explanation for the macroalgal response is

302 nutrient or light limitation, which may have parallels in terrestrial systems. For example,

303 in forests, canopy cover can have a unimodal effect on understory plant growth and

304 diversity; in this case, nutrient input from the canopy has a positive effect while growth

305 and diversity are negatively affected by canopy closure, creating a hump-shaped response

306 to canopy cover (reviewed in Gilliam 2007). Thus, facilitation in the case of *T. ornata,* as

307 in terrestrial forests, is highly density-dependent, and the density of *T. ornata* that persists

308 after corals are removed by a disturbance can have a profound effect on reef community

309 structure.

310   In summary, our results demonstrated that *T. ornata* acts as a foundation species

311 where aggregations facilitate both primary producers and consumers on tropical reefs.

312 Further, we suggest this represents a facilitation cascade (Thomsen and others 2010)

313 where corals form the hard substrate to which *T. ornata* attaches, and *T. ornata* provides

314 habitat for epiphytes and increased trophic support for herbivorous fish. Much work is

315 still needed to understand the functional roles of foundation species in many systems,

316 especially when the foundation species dominates as the result of a phase-shift, as with

317 corals and some macroalgae. These phase-shifts are often the result of human impacts

318 that may cause "undesirable" changes to ecosystem functioning (see Ellison and others

319 2005 for terrestrial examples, coral reefs in Hughes and others 2010). However, in our

320   study, we found that a phase-shift to a different foundational species supports some

321   ecosystem functions, albeit likely very different than those supported by the original coral

322   community. However, even these functions may not be sustainable if *T. ornata*

323   domination persists at the expense of the original foundational coral community as

324   bioerosion will ultimately break down the reef structure (reviewed in Glynn and

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482   **Electronic Supplementary Material (ESM)**

483   **ESM S1** *Sample images of Turbinaria ornata.*

484   **Figure S1** *Examples of Turbinaria ornata aggregations on the reef.*

485   **Figure S2** *Example image of a Turbinaria ornata thallus with red and green algal*

486   *epiphytes growing on its blades.*

487   **ESM S1** *Fish abundances by Turbinaria ornata density at our site.*

488   **Figure S3** *Average abundances of fishes by family and T. ornata density.*

489   **ESM S3** *Least squares model fitting of the relationship between macroalgal*

490   *abundance and its epiphytes.*

491   **Table S1** *Comparison of linear, logistic, exponential, and quadratic least squares*

492   *models.*

493

494 **Figure Legends**

495 **Figure 1.** (A) Results of survey of density of *T. ornata* aggregations on a fringing reef in

496 Mo'orea, French Polynesia. Mean density per 100 m^2 (±SE) of (B) Acanthuridae and (C)

497 Labridae (tribe Scarinae) species documented by the MCR LTER in our study site in

498 August 2012.

499 **Figure 2.** ΔAICc selected models for: (A) relationship between *T. ornata* density and

500 percent epiphyte cover modelled as a logistic fit ($y = \frac{65.66x}{1.47+x}$, R^2=0.45, p<0.001) (B)

501 Growth of understory macroalgae in response to *T. ornata* canopy ($y = -7.01 +$

502 $3.28x - 0.10x^2$, R^2=0.62, p<0.001) (C) The number of bites by all fish had a positive

503 linear relationship with *T. ornata* density ($y = 1.49 + 0.42x$, R^2=0.30, and p<0.01).

504 **Figure 3**. Relationship between *T. ornata* density and percent epiphyte cover with

505 herbivores present (+H, grey, y = 42.228555 + 0.7414138*x, r^2=0.32, p<0.01) or absent

506 (-H, black, y = 47.105735 + 1.1951281*x, r^2=0.65, p<0.0001) and the respective 95%

507 confidence intervals between dotted lines.

508

509   Figure 1

A

Frequency (y-axis: 0 to 7)

Turbinaria density (thalli/0.0625 m^2) (x-axis: 0 to 40)

B

Mean # per 100 m^2 (y-axis: 0 to 25)

Species: Acanthurus lineatus, Acanthurus nigrofuscus, Acanthurus pyroferus, Ctenochaetus striatus, Naso lituratus, Zebrasoma scopas

C

Mean # per 100 m^2 (y-axis: 0 to 25)

Species: Chlorurus microrhinos, Chlorurus sordidus, Scarus frenatus, Scarus ghobban, Scarus psittacus, Scarus rubroviolaceus

510

511   Figure 2
512

514   Figure 3

515