

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](#)

Author contributions: SJB, CRF, RJC, PF designed the study and collected data. SRS devised methods to analyze epiphyte loading and edited early versions of the manuscript. SJB wrote the manuscript with feedback from all authors.

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 planci* (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 planci* 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 m² 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 m² 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 m². 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 ≥ 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

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 $100 \times$ 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; 25×25×30cm³ L×W×H) constructed
185 from hardware cloth with 1 cm openings. Light restriction by caging material was <10%
186 with no measurable 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 ($\Delta\text{AIC}=0$) and highest AICc weight or,
201 if AICs were similar ($\Delta\text{AIC}<3-4$), 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 $\cdot 0.0625 \text{ m}^{-2}$. Average density was
211 $19.8 \pm 1.9 \text{ SEM thalli} \cdot 0.0625 \text{ m}^{-2}$ 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 $11.4 \pm \text{SE } 1.9 \text{ cm}$, 10.3
217 $\pm \text{SE } 9.3 \text{ cm}$, and $11.3 \pm \text{SE } 2.7 \text{ cm}$ 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 $\cdot 0.0625 \text{ m}^{-2}$ 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 $\cdot 0.0625 \text{ m}^{-2}$ (max = 30% growth $\cdot 7 \text{ days}^{-1}$; 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 $\cdot 10 \text{ min}^{-1}$ was modelled as a linear increase

228 (Fig. 2 c; ESM S3). The relationship between bites $\cdot 10 \text{ min}^{-1}$ 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 photoinhibition (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

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
325 Manzello 2015).

326

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336

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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**

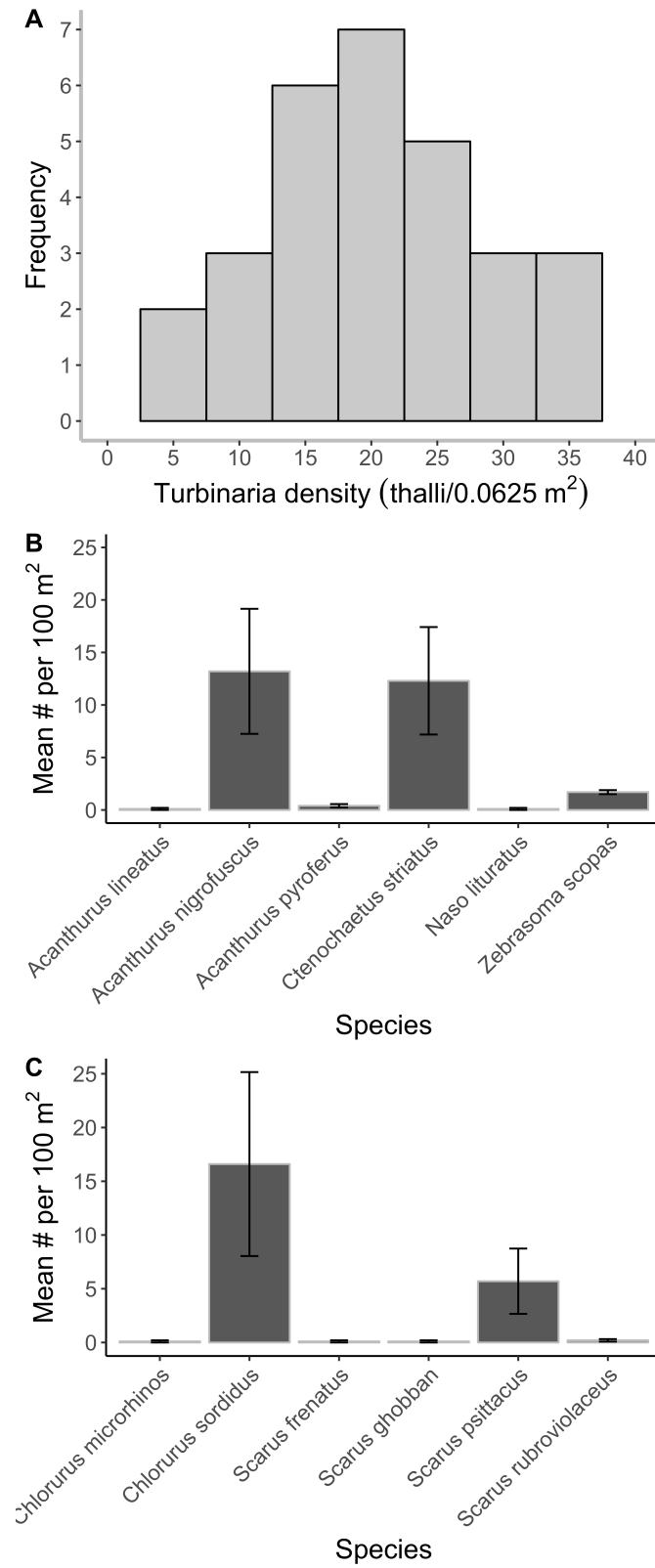
495 **Figure 1.** (A) Results of survey of density of *T. ornata* aggregations on a fringing reef in
496 Mo'orea, French Polynesia. Mean density per 100 m² (\pm SE) of (B) Acanthuridae and (C)
497 Labridae (tribe Scarinae) species documented by the MCR LTER in our study site in
498 August 2012.

499 **Figure 2.** Δ AICc 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.

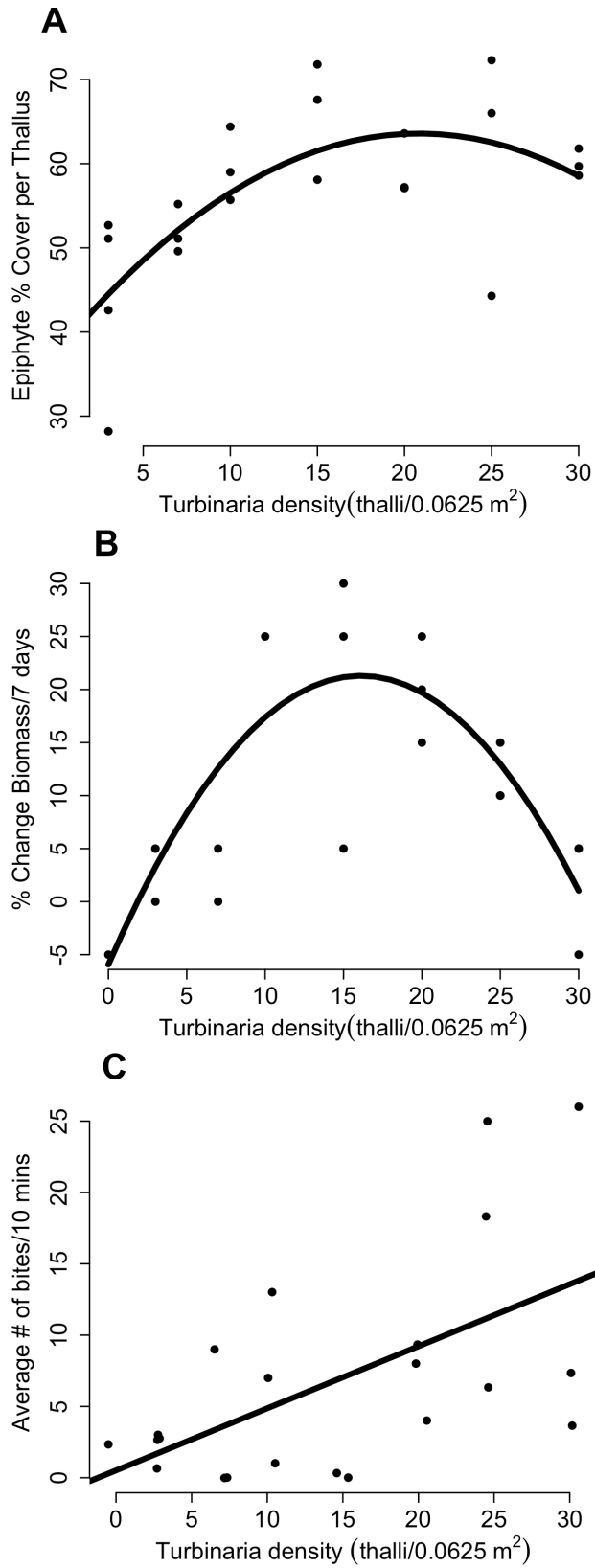
508

509 Figure 1



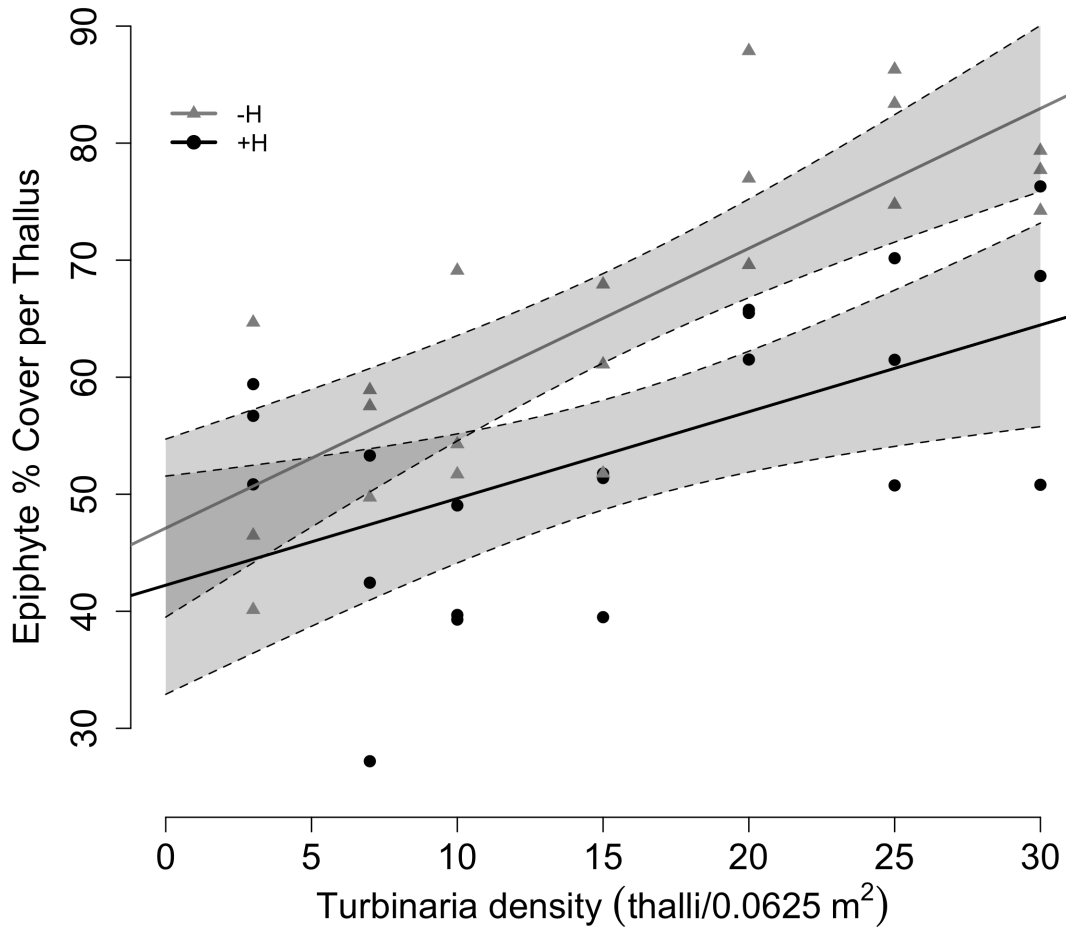
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511 Figure 2
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513

514 Figure 3



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