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1 To Submit to Advances in Marine Biology

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3 **The rise of octocoral forests on Caribbean reefs**

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21 **1.0. Abstract**

22 Coral reefs throughout the tropics have experienced large declines in abundance of
23 scleractinian corals over the last few decades, and some reefs are becoming functionally
24 dominated by animal taxa other than scleractinians. This phenomenon is striking on many
25 shallow reefs in the tropical western Atlantic, where arborescent octocorals now are numerically
26 and functionally dominant. Octocorals are one of several taxa that have been overlooked for
27 decades in analyses of coral reef community dynamics, and our understanding of why
28 octocorals are favored (whereas scleractinians are not) on some modern reefs, and how they
29 will affect the function of future reef communities, is not commensurate with the task of
30 scientifically responding to the coral reef crisis. We summarize the biological and ecological
31 features predisposing octocorals for success under contemporary conditions, and focus on
32 those features that could have generated resistance and resilience of octocoral populations to
33 environmental change on modern reefs. There is a rich set of opportunities for rapid
34 advancement in understanding the factors driving the success of octocorals on modern reefs,
35 but we underscore three lines of inquiry: (1) the functional implications of strongly mixotrophic,
36 polytrophic, and plastic nutrition, (2) the capacity to recruit at high densities and maintain rapid
37 initial rates of vertical growth, and (3) the emergent properties associated with dense animal
38 forests at high colony densities.

39

40 **2.0. Introduction**

41 Most tropical coral reefs have dramatically changed from those first experienced by Europeans
42 when they explored the tropics (Jackson 1997), and many reefs bear little resemblance to those
43 of the 1950s and 1960s (Goreau 1959; Loya 1972). These changes have been prominently
44 featured in empirical and theoretical analyses (Dudgeon et al. 2010; Hughes et al. 2018), and
45 have deeply penetrated into mainstream media. Yet the trends most frequently discussed --
46 declining abundances of stony coral and fishes (Jackson et al. 2001; Bellwood et al. 2004) -- are
47 narrow in taxonomic breadth given the high diversity of tropical reef communities (Connell 1978;
48 Huston 1985; Plaisance et al. 2011), and do not capture the full nature of the changes taking
49 place on tropical reefs.

50 Studies of the “usual suspects” on coral reefs capture the implications of changing community
51 structure as defined by the taxa that have been the focus of previous studies. Such studies have
52 limited ability to evaluate the functional and ecological implications of the state into which
53 modern reefs are transitioning. At one extreme, changes to coral reef communities have been
54 characterized as a descent to “slime” (Pandolfi et al. 2005). Yet at the other extreme there are
55 cases in which tropical reefs appear to be transitioning to domination by animal taxa other than
56 scleractinian corals (Norstrom et al. 2009).

57 A variety of taxa have replaced scleractinians on tropical reefs, including sponges,
58 corallimorpharians, tunicates, and octocorals (Norstrom et al. 2009). Sponges have been
59 suggested as a dominant member of future reef communities (Pawlik & McMurray 2020),
60 although evidence of this trend remains sparse (Wulff 2016). Octocorals, the focus of this
61 review, are functionally important on Caribbean and Indo-Pacific reefs (Cary 1914; Bayer 1961;
62 Goldberg 1973; Benayahu & Loya 1977; Reichelt et al. 1986), yet their biology has been
63 overlooked for decades. Unanswered questions regarding the transitions in community structure
64 taking place on reefs focus on the underlying mechanisms: do the species assemblages
65 represent stable communities, or placeholders on the road to slime? What are the implications
66 of these changes to reef ecosystem services? In the Caribbean, evidence that octocorals are
67 becoming more abundant and adopting greater functional roles than in the recent past (Ruzicka
68 et al. 2013; Lenz et al. 2015), suggests they may represent a “new normal” for these shallow
69 reefs (Lasker et al. 2020).

70 This review focuses on the biology and ecology of octocorals on present-day coral reefs in the
71 tropical western Atlantic. Rather than presenting a comprehensive review of this topic (which

72 has been covered [Kupfner Johnson and Hallock 2020]), we interpret the task through the prism
73 of the ecological changes underway on reefs in the tropical western Atlantic to favor octocorals
74 (Ruzicka et al. 2013; Lenz et al. 2015; Tsounis & Edmunds 2017). We address the features of
75 octocorals that promote their ecological success in habitats where they are exposed to the
76 same conditions driving large declines in abundance of scleractinians (Hughes 1994; Jackson et
77 al. 2014), and we explore how octocorals alter their habitat. We focus on the tropical western
78 Atlantic because the demise of scleractinian-dominated reefs in this region is well advanced
79 (Jackson et al. 2014, Bruno & Selig 2007; Roff & Mumby 2012). The ecological future of coral
80 reefs remains uncertain, but it is reasonable to hypothesize that present-day reefs in the tropical
81 western Atlantic provide a glimpse of the broader future of “coral” reefs in the Anthropocene
82 (Hughes et al. 2017).

83 Much of the scientific history of modern coral reefs has addressed declines in population sizes
84 of fishes and large vertebrates that began in the 1500s (Jackson 1997). Large-scale reductions
85 in the abundance of scleractinians are more recent, and virtually were absent from the literature
86 before Indo-Pacific reefs were devastated by crown of thorns sea stars in the 1960s (Weber &
87 Woodhead 1970). The last 50 y has seen widespread mortality of scleractinians through natural
88 and anthropogenic disturbances (e.g., Jackson et al. 2014; Birkeland 2015), but these losses
89 have been modest compared to the mortalities resulting from thermal bleaching driven by global
90 warming, effects that will be amplified by ocean acidification (Hoegh-Guldberg et al. 2007).
91 These events have transitioned many reefs into a phase functionally dominated by taxa other
92 than scleractinians, usually macroalgae (Roff & Mumby 2012), and some examples may
93 represent alternative stable states (Dudgeon et al. 2010; Schmitt et al. 2019).

94 The functional attributes of reefs depleted of scleractinians are different from those of reefs
95 dominated by this taxon. As ecosystem engineers (Jones et al. 1994), reduced abundances of
96 scleractinians deprive coral reefs of their capacity to produce a massive, wave resistant platform
97 (Stoddart 1969), within which habitats are created for other taxa (Alvarez-Filip et al. 2009). The
98 loss of scleractinians suggests the reef framework will succumb to net dissolution through ocean
99 acidification (Eyre et al. 2018), thereby threatening the goods and services delivered by
100 scleractinian corals (Birkeland 2015). Yet the critical question is not whether coral reefs will
101 disappear, but in what form will they persist? Against this backdrop, we evaluate the factors
102 favoring increased abundances of octocorals in the tropical western Atlantic (Figs. 1, 2). Neglect
103 of the taxa (e.g., octocorals) that now are dominating coral reefs deprives ecologists of the
104 capacity to understand the attributes of present-day reef communities. This also means that

105 there is a limited understanding of the potential for a return to a scleractinian-dominated state
106 should the environmental conditions favoring scleractinian mortality reverse.

107 The context for this review is created by evidence that octocorals have become more abundant
108 in the tropical western Atlantic (Fig. 3). Ruzicka et al. (2013) were the first to describe changes
109 in the community structure of Caribbean reefs in favor of octocorals versus scleractinians.

110 Although ecological analyses of octocorals have remained scarce, a data compilation for 1968-
111 2013 supports the hypothesis that octocorals have increased in abundance (Lenz et al. 2015;
112 Tsounis & Edmunds 2017). Analyses of reefs in St. John from 2014-present also support this
113 hypothesis, as well as the notion that octocoral domination is the “new normal” for shallow
114 Caribbean reefs (Lasker et al. 2020). Updating Lenz et al. (2015) with results published since
115 2013, including our analyses from St. John reveals that the trends reported in Lenz et al. (2015)
116 have continued. The data suggest that the region-wide abundance of octocorals has risen 84%
117 since 1968-90 (versus 2015-2019), and now represents a mean density of 9.2 ± 2.2 colonies m^{-2}
118 (Fig. 3, averaged over 2015-2019, $n = 48$).

119 **3.0. Historical context**

120 Octocorals have been ecologically meaningful members of reef communities in the tropical
121 western Atlantic for as long as researchers have described reefs. In 1915, Lewis R. Cary wrote,
122 “*On many reef areas in the Florida-Antillean region the areas occupied by stony corals and*
123 *calcareous algae are relatively small while flexible alcyonaria or the family Gorgonaceae make*
124 *up the most characteristic feature of the fauna*” (Cary 1915). While that characterization lacks
125 the quantitative data of modern ecology, it is clear that flexible, arborescent octocorals, which
126 are commonly referred to as gorgonians (Gorgonaceae is no longer a recognized taxon), have
127 long been recognized as important on reefs throughout the tropical western Atlantic.

128 Tracing the origins of the Caribbean octocoral fauna is difficult. There is not much of a fossil
129 record of octocorals because their largely proteinaceous skeletons reduce the likelihood of
130 preservation, and their sclerites are only visible as microfossils, and being composed of high Mg
131 calcite, they are unlikely to be preserved. In some cases, evidence of Octocorals in the fossil
132 records is indirect, such as the presence of *Cyphoma* sp., a specialist octocoral grazer, in fossil
133 Pleistocene reef deposits (Fig. 4), indicating octocorals have been members of Caribbean reef
134 communities for at least 120,000 years. Direct evidence includes gorgoniid and plexaurid
135 sclerites which have been found in the Lower Oligocene (27 to 34 million years ago) of
136 Mississippi (Giammonna & Stanton 1980). Some species have secondary calcification in their

137 central axis, and gorgoniid holdfasts and branch fragments have been found preserved in
138 deposits from Texas, dating from the Middle Eocene (47 to 41 million years ago) (Kocurko &
139 Kocurko 1992). Both reports of fossilized octocorals come from the Gulf of Mexico in
140 depositional environments reflecting “hard ground” habitats that are subject to bouts of clastic
141 deposition.

142 The lack of a robust fossil record relegates much of the evolutionary history of the Caribbean
143 octocoral fauna to conjecture. It is likely that it has paralleled that of the scleractinians, with one
144 noteworthy difference, the diversification of plexaurids. At the start of the Tertiary, the ancestral
145 Caribbean fauna probably was part of the circumtropical Tethys Sea fauna, and was steadily
146 isolated from the Eurasian fauna as the Atlantic grew and westward currents weakened (von der
147 Heydt & Dijkstra 2006). Connectivity with reefs in the Indo-Pacific, to the west, would already
148 have been low due to both the distances and the generally westward flowing circumtropical
149 surface currents (von der Heydt & Dijkstra 2006), much as the Eastern Pacific is currently
150 isolated. Over that span of time, the scleractinians were subject to several episodes of faunal
151 turnover (Budd 2000). If changes affecting the octocorals were similar to those affecting the
152 scleractinians, those events would have marked the start of the development of the endemic
153 octocoral fauna of the tropical western Atlantic. Two plexaurid genera, *Plexaura* and *Eunicea*
154 are endemic to the Caribbean/western Atlantic and the *Eunicea* underwent extensive
155 diversification generating the 16 currently recognized species (Cordeiro et al. 2020). A relatively
156 recent diversification in these genera is suggested by the low levels of sequence divergence
157 among species in those genera compared to patterns in the gorgoniids, which have broader
158 geographic distributions. The ecological and evolutionary consequences of diversification are
159 complex and undoubtedly case specific (c.f., Tanentzap et al. 2020). This diversification may
160 have laid the foundations of increased abundance of octocorals on modern reefs, but it is also
161 possible that the specialization implied by diversification will put octocorals at greater risk of
162 extinction as the environment continues to change.

163 **4.0. Octocorals - the right taxon at the right moment**

164 The increasing abundance of octocorals (Lenz et al. 2015; Tsounis & Edmunds 2017; Fig. 3)
165 has been driven by multiple factors, but the change can be characterized as resilience driven by
166 recruitment following disturbance events in concert with resistance driven by the survival of
167 adults. This is summarized in Fig. 5, which illustrates how mortality of scleractinian corals has
168 made substratum available which has subsequently been occupied by octocorals. The relevant
169 question becomes, why, unlike the scleractinians, are octocorals surviving on present-day reefs,

170 both in the context of adult survival and ecological resilience following major disturbances? Our
171 knowledge of the basic biology of octocorals has lagged behind that of scleractinians, and we
172 have too often assumed that our knowledge of scleractinians carries over to the octocorals.
173 Octocoral biology is not identical to that of scleractinians, but only a few studies have focused
174 on the ways in which they differ. Studies of octocorals also have been limited because the
175 species are difficult to delineate, and taxonomic identification at species level is difficult,
176 particularly underwater. Acknowledging these limits, we focus our review on those aspects of
177 octocoral autecology that may predispose them for high survival on tropical western Atlantic
178 reefs in the Anthropocene.

179 *Trophic status*

180 Almost all octocorals on the Western Atlantic reefs host symbiodinacean dinoflagellate algae,
181 which suggests that, as for the scleractinians, photosynthate from their symbionts plays a large
182 role in their diet. As light declines with depth, azooxanthellate species (lacking algal symbionts),
183 become common, and when the entire tropical western Atlantic is considered, there are as
184 many azooxanthellate as zooxanthellate species (Schubert et al. 2016). If the number of
185 species can be interpreted as a measure of ecological success, then a heterotrophic feeding
186 strategy has been as successful as the mixotrophic feeding of shallow water octocorals.
187 However, in the shallow waters of Caribbean reefs, where the two modes of feeding could co-
188 occur, purely heterotrophic reef octocorals are almost entirely absent. Within families, such as
189 the Gorgoniidae, that are present in both shallow and deeper water, shallow water species are
190 more commonly zooxanthellate and the Caribbean reef gorgoniids are all zooxanthellate.

191 While a mixotrophic carbon budget dominates the octocoral reef fauna, the dominance of
192 heterotrophic octocorals in communities such as Mediterranean hard bottoms (Gili & Coma
193 1998) and the apparent resistance of octocorals to environmental degradation in the tropical
194 western Atlantic, has led to increasing scrutiny of the role of heterotrophy in the success of reef
195 octocorals. Heterotrophy among octocorals ranges from the ability to take up dissolved organic
196 matter, to the filtration of fine particulates ranging in size from bacteria to detritus, and finally, to
197 the active capture of zooplankton (Cocito et al. 2013). The hypothesized importance of
198 heterotrophy to the nutrition of tropical octocorals is attractive, but the evidence that
199 heterotrophy is the key to reef octocoral success is scant.

200 If the capacity for heterotrophy is one of the factors that has facilitated the recent success of
201 octocorals in the tropical western Atlantic, it appears unlikely to be due to the capture of

202 zooplankton such as invertebrate larvae, copepods, etc. Zooplankton feeding has been the
203 most commonly quantified mode of heterotrophy among octocorals, primarily because ingested
204 prey can be searched for in dissections of polyps (Lasker 1981). Surveys of Caribbean species
205 have found low numbers plankters within polyps (Lasker 1981, Ribes et al. 1998, Rossi et al.
206 2020), supporting the hypothesis of limited feeding on zooplankton. Levesque (1976) found that
207 *Leptogorgia virgulata* from North Carolina, which is not a typical member of the Caribbean reef
208 fauna, captured *Artemia* nauplii in an experimental setting. Lasker (1981) made similar
209 observations for some octocorals from reef communities, but also reports that three species of
210 Caribbean octocoral were incapable of capturing the highly motile zooplankton that were
211 attracted to lights at night. Capture and ingestion of artificial non-motile particulates has been
212 demonstrated for several Caribbean species (Lasker 1981, Lasker et al. 1983). The inability to
213 capture larger, faster zooplankton and the ability to capture non-motile particles, and plankters
214 that are poor swimmers, is probably related to the relatively simple cnidom present in octocorals
215 (Mariscal 1974; Fautin 2009). Differences in the cnidom between octocorals and other
216 anthozoans have not been quantified with respect to either the abundance of nematocysts or
217 their effectiveness in securing prey items.

218 Quantification of *in situ* zooplankton capture by tropical octocorals uniformly report low capture
219 rates. Lasker (1981) found one prey item in 100 polyps in *Briareum asbestinum* and
220 *Pseudoplexaura porosa* branches that were collected at night. Ribes et al. (1998) examined gut
221 content of *Pseudoplexaura porosa* and *Eunicea flexuosa* from samples collected over a 24 h
222 cycle and reported 0.03 to 0.1 prey polyp⁻¹, which they extrapolated to a feeding rate of 0.086 to
223 0.227 prey polyp⁻¹ day⁻¹. This rate corresponds to between 1 of 12 to 1 of 4 polyps capturing a
224 prey item each day. Ribes et al. (1998) estimated those capture rates accounted for < 1% of the
225 carbon required for a colony's basal metabolism. Rossi et al. (2020) report capture rates for
226 *Plexaurella nutans* and *Pterogorgia anceps* of 0.26 and 0.31 prey polyp⁻¹ day⁻¹ respectively, and
227 estimated heterotrophy could only account for 0.5 - 2.0% of colonies' metabolic needs.

228 The feeding rates observed among octocorals in the tropical western Atlantic are an interesting
229 contrast to those observed in two azooxanthellate species from the Mediterranean. Rossi et al.
230 (2004) report capture rates for *Leptogorgia sarmentosa* that can be extrapolated to 1.50 to 3.80
231 prey polyp⁻¹ day⁻¹ depending on the season. That feeding rate corresponds to 66% of a colony's
232 metabolic demand, based on estimates of carbon content of plankters, octocoral assimilation
233 efficiency, and octocoral respiration rates (Rossi et al. 2004, Ribes et al. 2003). Feeding rates
234 for the azooxanthellate Mediterranean octocoral *Paramuricea clavata* are 0.12 - 0.80 prey polyp⁻¹

235 1 day^{-1} (Coma et al. 1994). Although the capture rate is not as great as for *L. sarmentosa*,
236 zooplankton feeding by *P. clavata* accounts for ~ 50% of a colony's metabolic needs. As in the
237 Caribbean studies, the most commonly captured prey items were invertebrate larvae. Rossi et
238 al. (2004) suggest that preys are captured proportionate to their abundance in the water column.
239 This suggests the differences between octocorals from the Mediterranean and the tropical
240 western Atlantic may be more a function of the availability of plankton than inherent differences
241 in the species that have been studied. The one zooxanthellate species in the Mediterranean,
242 *Eunicella singularis*, has capture rates of 0.33 prey polyp $^{-1} \text{ day}^{-1}$ which was estimated to be 6-
243 30% of the colonies metabolic needs (Coma et al. 2015). That feeding rate is on the lower end
244 of the rates observed in the azooxanthellate species and the upper end of feeding rates
245 observed for Caribbean zooxanthellate gorgonians.

246 A relative inability to capture zooplankton does not preclude a large role for heterotrophy among
247 octocorals. Uptake of dissolved organic matter, and the successful capture/filtration of fine
248 particulate organic matter, nanoplankton, and phytoplankton may contribute to the species'
249 trophic strategies. Octocorals would seemingly be well adapted for the uptake of small
250 particulate matter. The presence of pinnules on the tentacles (Fig. 6) decreases the "sieve size"
251 of the tentacular crown and increases surface area both of which can be important components
252 of particulate capture abilities (Rubenstein & Koehl 1977). Uptake of phytoplankton has been
253 observed in experiments with octocorals other than Caribbean reef species. Roushdy and
254 Hansen (1961) reported uptake of phytoplankton in laboratory experiments with the temperate
255 alcyonacean *Alcyonium digitatum*. Fabricius et al. (1998) found that in the Red Sea the
256 azooxanthellate alcyonacean *Dendronephthya hemprichi* was able to capture 3-20 μm
257 phytoplankton at rates that provided carbon well beyond that required for basal metabolism
258 (zooplankton feeding contributed < 5% to the colony's metabolic needs). Tsounis et al (2006)
259 found that particulate organic matter was the main source of dietary carbon in *Corallium rubrum*.

260 Direct measures of nutritional modes for Caribbean octocorals are uncommon. Ribes et al.
261 (1998) measured predation on pico-, nano- and microplankton by *Eunicea flexuosa* within
262 incubation chambers that were placed *in situ* on the reef and were supplied with reef water.
263 Using flow cytometry to characterize changes in prey density they report uptake of
264 dinoflagellates, pennate diatoms and ciliates, among other particles. However, capture of those
265 organisms supplied half as much carbon as feeding on zooplankton, and in sum the two modes
266 of heterotrophy accounted for < 1% of the basal metabolic rate of *E. flexuosa*. Grazing on
267 plankters < 5 μm have not been detected. Although the role of heterotrophy in the nutrient

268 budget of *E. flexuosa* was small, Ribes et al. (1998) suggested that *E. flexuosa* alone was
269 capable of removing ~ 10% of the available diatoms, dinoflagellates, and ciliates in the water
270 column. That again suggests that heterotrophy may be limited by the availability of prey, which
271 would not be an unexpected result for what is functionally passive suspension feeding.

272 Given the difficulties of quantifying uptake rates of food items such as phytoplankton, ciliates
273 and bacteria, there has been increasing use of stable isotopes to identify the role of
274 heterotrophy in octocoral nutrition. Ward-Paige et al. (2005) suggest that *Plexaura homomalla*
275 and *Eunicea flexuosa* from sites with higher levels of eutrophication had $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values
276 indicative of greater reliance on heterotrophy. Rossi et al. (2018) present $\delta^{15}\text{N}$ of 4-8‰ and
277 $\delta^{13}\text{C}$ of -14 to -18‰ from 9 species from the Yucatan. Those values are consistent with a
278 dominantly autotrophic system but do not preclude heterotrophy. Baker et al. (2015, their
279 supplemental material) present $\delta^{13}\text{C}$ of host and symbiont from 11 species from coastal
280 Panamanian reefs. Seven of those species have mean tissue $\delta^{13}\text{C}$ values that are lower than
281 the mean symbiont $\delta^{13}\text{C}$ values, which is consistent with a signature of heterotrophy. However,
282 the differences between host and symbiont $\delta^{13}\text{C}$ are $< 1\text{‰}$. While indicative of multiple food
283 sources quantification of the relative roles of heterotrophy and autotrophy from stable isotope
284 data is difficult. The relationships between trophic status and stable isotope concentrations are
285 complex in symbiotic systems where compounds are recycled within the holobiont (Ferrier-
286 Pages & Leal 2019), and the isotopic signature of feeding on phytoplankton may be similar to
287 that of the photosynthate translocated from Symbiodiniaceae mutualists, which may further
288 complicate interpretation of results.

289 An interesting speculation is that the relative ineffectiveness of heterotrophic feeding among
290 Caribbean octocorals is related to the low productivity of tropical seawater. However, *D.*
291 *hemprichi*, which is azooxanthellate, effectively captured phytoplankton on a Red Sea coral reef
292 (Fabricius et al. 1998). An inverse association between heterotrophic capabilities and symbiosis
293 with Symbiodiniaceae is suggested from the more productive waters of the Mediterranean.
294 Zooplankton capture by *Eunicella singularis*, the one zooxanthellate species in the fauna,
295 accounts for less of its metabolic demands than the two azooxanthellate species that have been
296 studied. In a study of scleractinians, Grottoli et al. (2006) reported increased feeding among
297 bleached colonies of *Montipora capitata* compared to unbleached colonies. Among the
298 octocorals it would be interesting to determine the extent to which differences in behavior, or

299 perhaps the cnidom, can explain different feeding capabilities and to determine the extent to
300 which those characteristics exhibit plasticity.

301 Direct measures of the contribution of autotrophy to metabolic needs of Caribbean octocorals
302 are more available than measures of heterotrophy. Rossi et al. (2018) measured P:R ratios that
303 were > 1.0 for all 10 species investigated and Rossi et al. (2020) found seasonal differences in
304 both metabolic rate and gross photosynthetic rates, but P:R ratios ≥ 1 throughout the year.

305 Baker et al. (2015) report P:R ratios ranging from of 0.7 - 1.6. Both studies acknowledge some
306 likely heterotrophic inputs to the carbon budget of these organisms, but based on P:R quotients
307 determined in oxygen units much of their daily nutrition could have been met through the carbon
308 fixed and translocated from their algal symbionts.

309 A hypothesized relationship between the ecological success of octocorals in the tropical western
310 Atlantic and heterotrophy remains to be experimentally tested. A complete evaluation will
311 require assessments of heterotrophy that go beyond measures of zooplankton capture to
312 consider the input of resources obtained from the capture of phytoplankton. Ribes et al. (1998),
313 for example, report that the capture of phytoplankton contributed < 1% of the carbon necessary
314 to meet the respiratory demand of *Eunicea flexuosa*. Studies are needed that evaluate carbon
315 (or energy) sources and sinks comprehensively, in compatible units, and under ecologically
316 relevant conditions that capture the complex flow regimes under which arborescent octocorals
317 function. Stable isotope analyses have promise in assessing trophic strategies of octocorals,
318 and have the benefit over other methods of being suitable for community-scale surveys and
319 integrating the effects of nutritional strategies over relevant time-scales of weeks-months.
320 However, the signature of consuming phytoplankton may be very similar to that of
321 photosynthate translocated from Symbiodiniaceae, and it will be necessary to develop tools
322 that can discriminate the carbon isotopic signatures of carbon translocated from
323 symbiodiniaceae versus the capture of phytoplankton.

324 *Growth form and growth rate*

325 The signature feature of all but two of the octocorals found on Caribbean coral reefs is their
326 arborescent colony form. All but *Erythropodium caribbeorum* and the encrusting form of
327 *Briareum asbestinum* (historically reported as *B. polyanthes*) exploit the water column from a
328 diminutive site of basal attachment (encrusting *B. asbestinum* also can take on an upright
329 aspect as it often grows on exposed axes of other octocoral species). A vertical morphological

330 strategy removes the colony from a variety of the vicissitudes of life on the substratum, elevating
331 colonies above processes such as scour by sediments, shading by macroalgae, and overgrowth
332 by other benthos.

333 Examination of the substratum on a coral reef quickly reveals that there is very little “open”
334 space on which organisms can recruit. Bare carbonate rock is very quickly colonized by an
335 array of algae and encrusting invertebrates. A variety of sessile invertebrates settle on crustose
336 coralline algae, but in general, potential competitors settle onto the substratum among but not
337 on already established benthos and then interact with their neighbors. The outcomes of those
338 interactions are determined by a variety of both direct and indirect processes (Chadwick &
339 Morrow 2011). Those potentially harmful interactions include the direct effects of overgrowth
340 and killing of the competitor’s tissue and indirect effects such as reducing access to resources
341 (i.e., shading or altering the boundary layer from which nutrients are extracted) or altering the
342 microenvironment (c.f., anoxic conditions under dense algal mats [Wangpraseurt et al. 2012]).

343 Although coral reefs are complex three-dimensional structures, overgrowth is primarily a two-
344 dimensional process, and elevating most of the gorgonian colony above the substratum
345 minimizes the interactions with competitors.. Many of the potential competitors of gorgonians
346 can grow over their holdfasts (e.g., Edmunds et al. 2019), but they tend not to grow up the
347 length of the primary branch and overgrowth of the base on its own will not necessarily weaken
348 a colony. Building a rigid structure on a flexible object also may be a limiting factor for some
349 competitors. Those structural constraints would seemingly be less important for potential
350 sponge competitors. Species such as *Desmapsamma anchorata* can be found on Caribbean
351 gorgonians, but probably settle on damaged areas on the colony where the axis is exposed
352 (McLean & Yoshioka 2008). Massive sponges such as *Xestospongia* spp. will “envelope”
353 gorgonians as they expand (McLean & Yoshioka 2007), but Caribbean sponges typically do not
354 spread along the substratum and up the base of most octocorals. Some Caribbean reef
355 sponges bore into the carbonate substratum, and the gorgonin core of gorgonians would not be
356 a suitable habitat for these species. Finally, peysonellid algal crusts (PAC, calcifying red
357 algae), notably those including *Ramicrusta* spp., recently have undergone rapid growth on some
358 Caribbean reefs (Eckrich & Engel 2013; Bramanti et al 2017). PAC is capable of overgrowing a
359 variety of benthic taxa, but it does not seem to grow up beyond the bases of octocorals
360 (Edmunds et al. 2019). The importance of vertical growth by octocorals may be accentuated on
361 present-day reefs, where the proliferation of turf and macroalgae over the past four decades
362 (Hughes 1994; Roff & Mumby 2012) has, at the least, altered the nature of boundary layer over

363 the substratum (c.f., Stocking et al. 2016; Wangpraseurt et al. 2012), thus placing strong
364 selective value on the ability to project above this layer. In some cases, however, vertical
365 branching growth could be counterproductive, such a in the case of the Lyngbya bloom in SE
366 Florida which were transported by water current and killed lots of gorgonians by entanglement
367 and subsequent suffocation (Paul et al. 2005). ,

368

369

370 An arborescent morphology is advantageous for colonies that are decimeters tall, but all
371 sexually produced colonies begin their benthic life as a single polyp. Per capita risk of mortality
372 decreases with increasing size among Caribbean octocorals (Lasker 1990, Gotelli 1991,
373 Yoshioka 1994) and octocorals in general (Garrabou & Harmelin 2002; Linares et al. 2007;
374 Santangelo et al. 2007; Bramanti et al. 2009). Data on survival of recently settled recruits are
375 limited. Lasker et al. (1998) settled *Plexaura kuna* larvae onto acrylic plates which were then
376 returned to the reef and survival tracked. Overall mortality was 0.03 day^{-1} , but survival was
377 substantially greater on the most protected area of the plate. Evans et al. (2013) found survival
378 of *B. asbestinum* on similar tiles to be 8% after 10 d on the reef. Following polyps that had
379 naturally recruited to ceramic tiles Wells et al. (submitted) observed mortality of 0.024 day^{-1} .
380 Extrapolating those data to an annual rate survival yields survival rates that range from
381 0.000018 to 0.048 . A number of researchers have characterized survival among small octocoral
382 colonies (Table 1). Those values are all higher than for survival of recently settled polyps, which
383 suggests that recruits that rapidly increase in size can lower their mortality rate, with rapid
384 growth to ~ 10 cm height further lowering the risk of mortality.

385 Growth rates of octocorals are markedly variable both within and between species, but all
386 illustrate the high degree to which octocorals exploit vertical growth to escape the risks of
387 mortality through increases in size. Species-specific growth rates among Caribbean gorgonians
388 range from 23.1 cm y^{-1} for *Antillogorgia acerosa* colonies from Colombia (Cadena & Sanchez
389 2010) to 0.8 cm y^{-1} among *Plexaurella dichotoma* colonies on the southwest coast of Puerto
390 Rico (Yoshioka & Yoshioka 1991). The range is even greater as most reported values are
391 averages. There also are location/habitat differences as suggested by the 5-fold difference in
392 observed growth rates of *A. acerosa* from Colombia and Puerto Rico. All of the studies that
393 have characterized growth also note many cases of negative growth (i.e., partial mortality)
394 presumably caused by some combination of predation, disease, and physical disturbance. For

395 instance, average growth of *Plexaura kuna* is 2 to 4 cm y⁻¹ lower than the potential growth
396 suggested by growth among colonies that had net positive growth (Table 2). The highest growth
397 rates are found among species with thin branches such as the *Antillogorgia* spp. Among those
398 species, recruits can escape the highest mortality section of the life table in one to two years
399 and reach 10 cm in 3 to 4 years. Given the variance associated with the averages and the
400 possibility of negative growth, many colonies will take longer to reach those milestones, while
401 some will do so in substantially less time. In contrast to the octocorals, scleractinians have lower
402 growth rates. Edmunds (2018) reported growth in colony diameter among small, < 4 cm
403 diameter scleractinians on St. John, Virgin Islands, ranging from -3.45 to 5.55 cm y⁻¹, but
404 average growth was 0.29 cm y⁻¹. Edmunds (2018) noted that the data for scleractinians did not
405 support an expectation of rapid growth that could provide a refuge in size. Growth at the colony
406 edge does not elevate colonies above the substratum, and most scleractinians expand their
407 base well before substantial vertical growth occurs.

408 *Reproductive Biology*

409 Reproductive strategies among Caribbean octocorals are not dramatically different from those
410 observed in Caribbean scleractinians (as described in Szmant 1986; Carlon 1999). The one
411 difference is the occurrence of surface brooding, in which eggs are released but remain on the
412 branch surface until they develop (Benayahu & Loya 1983). With respect to fertilization and then
413 subsequent dispersal, the strategy is akin to internal brooding. The four combinations of
414 sexuality and mode of spawning are almost equally common among the scleractinians (Baird et
415 al. 2011), but all of the Caribbean reef gorgonians are gonochoric (Kahng et al. 2011) and the
416 majority are broadcast spawners. The mode of reproduction appears to correlate with
417 biogeographic patterns in the Western Atlantic. Species richness is relatively uniform throughout
418 the Caribbean with differences between areas reflecting combinations of the habitats studied
419 and the intensity of surveys. However, on the reefs of Bermuda, the most isolated of Western
420 Atlantic reef complexes, brooding and surface brooding octocorals make up a smaller proportion
421 of the fauna than in the Caribbean and Florida (Table 3, Test of independence, $G = 4.09$, $p =$
422 0.04).

423 Egg size might also affect the recruitment of octocorals and scleractinians. Large egg size
424 implies greater parental provisioning which can then affect some combination of longevity in the
425 water column (i.e., greater dispersal), size at metamorphosis and recruit survival (Vance 1973,
426 Hartmann et al. 2013, but see Bernardo 1996). Our knowledge of gamete traits for octocorals is

427 incomplete, but Caribbean octocorals for which there are data (6 species, Kahng et al. 2011)
428 have mean oocyte diameters of 722 μm , and produce 2.6 mature oocytes polyp⁻¹. In contrast,
429 the eggs of Caribbean scleractinians have a mean diameter of 317 μm and produce on average
430 130 oocytes polyp⁻¹ (data from Szmant 1986). Genetic analysis of *A. elisabethae*, a surface
431 brooder, suggests modal dispersal distances of 100 m to 1 km in The Bahamas (Lasker & Porto
432 Hannes 2015). In biophysical model simulations of the dispersal of *A. americana*, which is a
433 broadcast spawner, Coelho (2018) reports a median dispersal distance of 39 km with more
434 settlement within 1 km than any other distance. If these congeners are representative of the
435 Western Atlantic reef fauna, octocorals generally have modest dispersal distances even in the
436 widely distributed *A. americana*.

437 We have relatively limited knowledge on how reproduction and dispersal of octocorals translates
438 into settlement, but there are data on octocoral recruitment at several Caribbean sites.

439 Recruitment, the first appearance of an individual in a population (Caley et al. 1996), is
440 operationally defined in manners that often are unique to individual studies. Recruitment in
441 annual surveys of octocorals has been quantified as the appearance of small colonies whose
442 height suggests they are a year or less old. Height from ≤ 3 cm (Lasker 1990) to ≤ 6 cm
443 (Yoshioka 1997) have been used. As discussed above, the height of a 1 year old recruit can
444 vary considerably both within and especially among species. Thus, any height-based definition
445 of a recruit will err by excluding fast growing recruits and by including colonies that are over a
446 year old. As importantly, because recruits that have died do not leave a skeleton behind,
447 recruitment based on annual or even monthly surveys will miss the settlement of individuals that
448 subsequently died.

449 We compiled published, octocoral recruitment data to address two questions: (1) is there
450 evidence of changing rates of octocoral recruitment, and (2) are there differences in rates of
451 recruitment between octocorals and scleractinians? The former addresses the issue of whether
452 changing conditions on reefs have altered any of the processes controlling successful
453 recruitment, and the latter provides insight into whether the current differences in the
454 demographics of octocorals and scleractinians might occur in the early life history stages that
455 control recruitment. Our data compilation yielded 18 studies that together provided 198 records
456 of the density of octocoral recruits. Most data were for individuals 3–6 cm tall, which probably

457 are about one year in age, although a handful of records of polyps settling on tiles were
458 obtained. Most records were for octocorals pooled among taxa, but substantial records also
459 were obtained for *Antillogorgia* spp. (n = 63, mostly *A. elisabethae*, *A. acerosa*, *A. americana*
460 and *A. rigida*), plexaurids (n = 40, mostly *P. kuna*), and *Pseudoplexaura* spp. (n = 11). To
461 provide a comparative context to these data, we included 13 years of scleractinian recruitment
462 to settlement tiles deployed at ~ 5-m depth in St. John, and a decade of density data for juvenile
463 scleractinians on natural reef surfaces (Edmunds 2018, and unpublished data). Densities of
464 octocoral recruits in these annual surveys ranged from 0 to 84 colonies m⁻², and the highest
465 recorded density was from 1985 on the south shore of Puerto Rico (Yoshioka 1996). These data
466 substantially underestimate settlement. Surveys that were conducted 1-2 months after spawning
467 over 4 y found recruitment at sites in the Bahamas for *Antillogorgia* spp. that ranged from 3 to
468 231 recruits m⁻² (Lasker & Porto Hannes, submitted). Annual versus monthly surveys for
469 *Plexaura kuna* recruits in the San Blas Islands, Panama, generated recruitment rates of 0.37
470 individuals m⁻² (annual) and 1.0 individuals m⁻² (monthly). Finally, surveys of tiles deployed on
471 the south shore of St John, Virgin Islands, that were conducted at 3 day intervals found
472 recruitment over a 19 d period of 443 individuals m⁻² (Wells et al. submitted). Although they are
473 an incomplete characterization of the processes controlling recruitment, the data address the
474 presence of temporal patterns. Overall, octocoral recruitment was unrelated to time from 1962
475 to 2019 (r = -0.06, df = 196, P = 0.40).

476 From 1962–2019, octocoral recruitment has remained lower than the median recruitment of
477 scleractinians in St. John from 2007–2019 (126 corals m⁻²) (Figs. 7, 8). The scleractinian
478 recruitment data probably include many individuals that settled and did not survive until
479 detection at the annual sampling. The few data on octocorals that provide more effective
480 summaries of settlement than the annual surveys, suggest that the disparity between octocoral
481 and scleractinian recruitment may not be as great as suggested in Figs. 7 and 8. The octocoral
482 annual recruitment data are comparable to numbers of living ≤ 4-cm diameter scleractinian
483 data. These data suggest that scleractinians have greater, or perhaps similar recruitment as the
484 octocorals, and thus the failure of scleractinian populations to recover may be more related to
485 their post-settlement survival than to settlement.

486 *Bleaching*

487 Over the last four decades bleaching has been responsible for widespread scleractinian
488 mortality (Hoegh-Guldberg et al. 2007; Hughes et al. 2017; Oliver et al. 2018), but the effects on
489 octocorals may be less severe. Bleaching, the paling of tissue as chlorophyll and algal cells are
490 lost from the holobiont (Lesser 2011) is elicited by a variety of environmental conditions (Gates
491 1990; Glynn 1993; vanOppen & Lough 2018), the best known of which is elevated seawater
492 temperature (Brown 1997; Lough & vanOppen 2018). Although bleached octocorals were
493 present in some of the first reports of Caribbean bleaching (Lasker et al. 1984), the notion has
494 persisted that octocorals are more resistant than scleractinians to warm water bleaching (Prada
495 et al. 2010; Goulet et al. 2017). However, an explicit test of this hypothesis has yet to be
496 conducted. It is unclear whether octocorals are less susceptible than scleractinians, or whether
497 bleaching has been more conspicuous on scleractinian-dominated reefs and thus more
498 commonly reported.

499 Lasker et al. (1984) reported limited bleaching of octocorals during the 1983 Caribbean
500 bleaching event, but Hannes (2009) and Prada et al. (2010) report more extensive bleaching of
501 octocorals in the 2005 bleaching events in the Florida Keys and southwest coast of Puerto Rico.
502 In those studies, *Plexaurella*, *Pterogorgia*, *Muricea* and *Briareum* were the most common
503 species to bleach. Mortality has been observed among *Plexaurella* (MA Coffroth, pers comm)
504 and significant mortality has been reported for *Muricea* (Prada et al. 2010). Reliance on
505 autotrophy does not appear to explain sensitivity to bleaching. For instance, two *Plexaurella*
506 spp. and *Briareum asbestinum* are among the small number of taxa that bleach and they have
507 the lowest P:R ratios reported in the Rossi et al. (2018) study.

508 The relative success of octocorals and the variance among octocoral species during
509 scleractinian coral bleaching events may be associated with the Symbiodiniaceae species that
510 they host. *B. asbestinum*, which harbors a *Brevolium* sp. as an adult (B178 in the nomenclature
511 of Lewis & Coffroth 2004), is one of the few octocorals that visibly bleaches (Lasker et al. 1984;
512 Goulet & Coffroth 2004). Poland (2010) observed a loss of B178 from *B. asbestinum* under
513 heat-induced stress bleaching, and Lewis & Coffroth (2004) reported a loss of B178 from *B.*
514 *asbestinum* under dark-induced stress bleaching. Poland and Coffroth (2019) suggested that
515 colonies with this symbiont type are more susceptible to bleaching in a perturbed environment.
516 Hosting thermal tolerant symbionts, which may be the more general case among octocorals,
517 may be a key aspect of their continued success on Caribbean reefs.

518 *Disease*

519 Octocorals are affected by a diversity of diseases (Kim 2016; Weil et al. 2016), many similar in
520 etiology to the numerous diseases affecting scleractinians (Weil & Rogers 2011). Like most
521 aspects of octocoral biology, diseases of this taxon have been less well studied than in
522 scleractinians, although *Aspergillus* and its effects on *Gorgonia* is an exception (Smith et al.
523 1996; Geiser et al. 1998). While population sizes of *G. ventalina* throughout the Caribbean were
524 depressed by this disease, there were signs of acquired resistance which ultimately attenuated
525 further population decline due to Aspergillosis (Bruno et al. 2011). The analysis of this disease
526 illustrates the potential threats to octocorals of emerging diseases (Weil & Rogers 2011; Weil et
527 al. 2016). However, while numerous diseases of octocorals in the tropical western Atlantic have
528 been documented, with the exception of Aspergillosis, they have not had the impacts on
529 populations and communities that diseases such as white band disease (Aronson & Precht
530 2001) and most recently stony coral tissue loss disease (Muller et al. 2020) have had on
531 scleractinians. Octocorals have robust immune systems (van de Water et al. 2018) and it is
532 tempting to think they may be less susceptible to epizootics than scleractinians. However,
533 octocorals have undergone catastrophic losses due to disease in the Mediterranean (Coma et
534 al. 2004, 2006; Linares et al. 2005). Furthermore, disease incidence in octocorals as for
535 scleractinians appears to increase with temperature (van der Water et al. 2018). In a world with
536 increasing likelihood of disease outbreaks (Maynard et al. 2015) there is no certainty that
537 octocorals will not also be subject to more significant disease outbreaks.

538

539 *Ocean acidification*

540 Coral reef biology has been transformed by an appreciation of the threats posed to calcareous
541 taxa by ocean acidification (OA) (Chan & Connolly 2012; Kroeker et al. 2013), which is driven by
542 rising atmospheric CO₂ and its effects on seawater chemistry. The effects of these trends on
543 scleractinian corals have been extensively studied to reveal inhibitory effects on net calcification
544 (Chan & Connolly 2012; Kroeker et al. 2013; Comeau et al. 2014). However, the effects of OA,
545 particularly the consequences of exposure to low pH and elevated pCO₂, have diverse
546 implications for scleractinians, including gamete mobility, fertilization success (Albright 2011),
547 recruitment (Albright et al. 2010; Doropoulos et al. 2012), and abundance (Kroeker et al. 2013).
548 Since octocorals do not produce a massive calcareous skeleton, it is reasonable to hypothesize
549 that they will be less affected by OA than scleractinians. However, while octocorals are “soft”

550 they contain calcified sclerites that have important functional implications for skeletal strength
551 and flexibility (Bayer 1961). Moreover, there are signs that the capacity to deposit these
552 structures is impaired under OA (Gomez et al. 2015; Bramanti et al. 2013), although octocoral
553 tissue appears to reduce or prevent dissolution of sclerites under low pH (7.3 and 7.8) (Gabay
554 et al. 2014).

555 The trend for increasing abundance of octocorals in the tropical western Atlantic could reflect
556 the appearance of communities composed of new combinations of taxa reflecting prevailing
557 physical and chemical conditions, but comparison of present-day octocoral communities in St.
558 John (Tsounis & Edmunds 2017) with older studies from Jamaica (Kinzie 1973; Wahle 1980)
559 and Puerto Rico (Yoshioka & Yoshioka 1987, 1991, and others) reveal broad similarities
560 between historic and extant communities. Current evidence therefore favors a “habitat
561 expansion” of historic octocoral communities rather than the development of a “novel
562 community” per se.

563 **5.0 Resilience and resistance of modern octocoral communities.**

564 In Section 4 we highlighted aspects of the biology of octocorals that have served them well in
565 mediating recent increases in abundance. In this section we address features of their ecology
566 that may be critical to determining whether they will persist or are simply a placeholder
567 community in an ecological succession driven by the continuing anthropogenic alteration of
568 tropical reef environments.

569 *Disturbance, Resilience and the Octocoral Forest*

570 To the extent that octocorals have increased in abundance on Caribbean reefs (Ruzicka et al.
571 2013; Lenz et al. 2015; Lasker et al. 2020), it is reasonable to now examine their resilience. The
572 lack of analyses of octocoral communities with high taxonomic resolution and decadal resolution
573 impedes the capacity to test for community resilience, but in those cases where appropriate
574 information is available, the results suggest octocorals, unlike scleractinians, have exhibited
575 resilience. St. John octocorals communities, which were analyzed with genus resolution, quickly
576 recovered from hurricanes and bleaching from 1987-2013 (Tsounis & Edmunds 2017) (Fig. 9).
577 Where species resolution has been applied, results from 2014-2019 reveal resilience in the face
578 of the unprecedented Category 5 hurricanes in 2017 (Lasker et al. 2020).

579 The origins of that resilience are largely the traits that have enabled their survival under steady
580 state conditions. First, as described above, the morphological strategy and rapid linear growth of

581 arborescent octocorals provides a means by which recruits can rapidly grow to adult size and
582 avoid mortality in the benthos where they can be smothered by macroalgae. Second, and in
583 contrast to scleractinians, octocoral recruitment enables recovery from events such as
584 hurricanes (Lasker et al. 2020). Third, while octocorals are not immune to bleaching and
585 disease, they have been less affected by these disturbances than scleractinians. Fourth, historic
586 and recent surveys of octocoral communities reveal high species diversity. Recent research is
587 beginning to reveal the extent to which octocoral species differ from one another with respect to
588 their nutritional strategies, structure, and symbiont performance (Rossi et al. 2018, 2020). It is
589 interesting to speculate that the co-occurrence of morphologically similar species result in a high
590 degree of functional redundancy (Rosenfeld 2002), which could contribute to high community
591 resilience.

592 Finally, we need to consider the degree to which octocoral communities and octocoral forests
593 (*sensu* Rossi et al 2017) modify their environment, and thus their interactions with the physical
594 environment and with each other. It is this last component that we focus on in this section. A
595 terrestrial forest biome classically is defined as a complex ecosystem consisting mainly of trees,
596 which are the ecosystem engineers of the community (*sensu* Jones et al. 1994). The central
597 characteristic of a forest is the emergent property of the three-dimensional structure, which
598 supports biodiversity and provides shelter and food for numerous species of plants and animals
599 (Sasaki & Putz 2009). Physically, a forest can be divided into several zones, among them the
600 distal canopy composed of leaves and branches, and the understory community that operates in
601 physical conditions that differ from those prevailing outside the forest. On tropical reefs,
602 scleractinians, octocorals, and hydrocorals, are the “trees,” the ecosystem engineers of the
603 community (Rossi et al. 2017) (Figs. 10, 11). Like terrestrial forests, octocoral forests generate
604 three- dimensional frameworks with high structural complexity. While lacking basal roots and the
605 capacity for basal-distal internal transport, dense populations of arborescent octocorals share
606 many functional similarities with terrestrial forests. Viewing octocoral communities in this
607 manner identifies theoretical and empirical approaches that may be important in understanding
608 the processes responsible for structuring and maintaining octocoral forests.

609 **6.0. Canopies formed by dense stands of octocorals**

610 Structure-forming marine organisms can take on the role of ecosystem engineers (Jones et al.
611 1997). They modify, create, and maintain habitat and their presence can define entire
612 ecosystems, including, for example kelp forests, mangroves and coral reefs (Bruno & Bertness

613 2001). Arborescent octocorals that form dense canopies modify the physical and chemical
614 environmental conditions and can also be considered ecosystem engineers.

615 *Effects on seawater currents*

616 Habitat modifications by erect canopies include, for example, alterations of the mean turbulent
617 flow of seawater, affecting sedimentation and propagule retention (Reidenbach et al. 2007;
618 Folkard 2019). When the density of octocorals is high enough to obstruct flow, colonies produce
619 wakes that affect the flow of seawater itself, with strong spatial variations of the flow (i.e.,
620 turbulence) over a region known as the roughness sublayer (RSL) (Guizien & Ghisalberti 2016).
621 In a spatially homogeneous canopy, two sections can be distinguished within the RSL: a lower
622 part (i.e., within the canopy) and an upper part, which extends ~ 2–3 times the height of the
623 canopy above the seafloor (Macdonald 2000).

624 Changes in flow over and through an octocoral canopy should also affect the physico-chemical
625 environment beneath the canopy and conditions within the canopy are likely to differ from those
626 outside of the canopy (Umanzor et al. 2018), thereby creating a unique in-canopy microclimate.
627 Inside a dense octocoral canopy, the modification of the flow is associated with changes in the
628 sedimentation regime. Both deposition and resuspension are expected to be affected by higher
629 turbulence in the upper RSL, and the lower flow velocity beneath the canopy (Reidenbach et al.
630 2007). In fact, in the portion of the water column above the canopy affected by downward vector
631 of flow (upper RSL; Fig. 12), dissolved nutrients and particulate material should be transported
632 into the canopy, thus increasing deposition. This mass transfer could also increase capture
633 rates by octocoral polyps. The slow passage of water in the lower RSL (beneath canopy; Fig
634 12), can lead to an accumulation of the products released by understory species (e.g. DOC) and
635 to a depletion of the nutrients consumed by those species (e.g. oxygen). Hauri et al. (2010)
636 showed that the reduction in oxygen and the increase in DOC concentration below dense
637 canopies of macroalgae, negatively affected the understory corals.

638 The effect of the canopy on the water flow within octocoral forests on St. John has been
639 examined by measuring the current speed across the bottom boundary layer at different
640 octocoral densities and over a vertical profile from the seafloor to 3 m above the seafloor.
641 Measures with an Acoustic Doppler Current Profiler (ADCP) provide high spatial resolution to
642 distinguish current profiles at 3 cm intervals. The octocoral canopy affected the RSL at densities
643 > 7 colonies m^{-2} , suggesting a threshold in colony density above which the canopy has a

644 hydrodynamic effect, which is expressed as a decay in the exponential flow velocity in the lower
645 portion of the RSL (i.e. within the canopy) (Fig. 12). In the upper portion of the RSL, enhanced
646 turbulence extends above the canopy to 130% of the total height of the canopy, thus creating a
647 downward vector of flow (in the Z axis) (L. Bramanti unpublished data). The turbulence structure
648 within the canopy affects resuspension and sedimentation (Cerpovicz & Lasker submitted), and
649 the increased turbulence over the RSL may modify the supply of waterborne resources (e.g.,
650 zooplankton and nutrients) to the octocoral colonies beneath the canopy as well as the
651 understory community. This effect would affect resource competition between community
652 members with an advantage for the species in the higher portion of the canopy which would
653 experience higher supply of waterborne resources generating a trophic shadow (*sensu* Porter
654 1976) over the understory community which would experience a reduced flux. The potential
655 importance of resource competition is suggested by the work of Kim & Lasker (1997) who
656 showed that *Plexaura homomalla* branches in the center of a linear array of branches had lower
657 growth rates than the exterior branches.

658 *Shading*

659 The shading of light by closely-spaced octocoral colonies may also influence autotrophy among
660 neighboring colonies as well as members of the understory community. Reduction of photon flux
661 density (PFD) beneath octocoral colonies, which is inversely proportional to the distance from
662 the colony holdfast, has been observed on the shallow (< 9 m depth) reefs of St. John (Nelson
663 2017). PFD inside and outside gorgonian canopies at a density of 8 colonies m⁻² was on
664 average ~ 40% lower than outside the canopy.

665 Moreover, wave-driven movement of gorgonian colonies can generate sunflecks on the seafloor
666 that affect understory organisms (Iluz et al. 2012). In situ measurements found that in-canopy
667 PFD regimes were more variable than outside the canopy when averaged over 6 to 10 seconds
668 intervals, suggesting the presence of sun flecks (J. Girard, unpublished data). However, on the
669 shallow reef of St. John, the community structure of the understory algae and invertebrates was
670 not associated with the presence of the octocoral canopy, or the perturbed light regime it
671 created (J. Girard, unpublished data).

672 *Self-thinning*

673 Competition would seem to be an inevitable consequence of the presence of a canopy in which
674 colonies can restrict the access of adjacent colonies to light and nutrients (Kim & Lasker 1997),

675 or directly interfere with each other (Gambrel & Lasker 2016). Sessile organisms cannot escape
676 those effects, and growth will be affected by the density of potential competitors. In plant
677 communities this is manifested as the self-thinning “rule” Tadaki & Shidei 1959, Yoda et al.
678 1963). Self-thinning refers to a reduction in the number of surviving individuals in a cohort as
679 those individuals increase in size, presumably due to competition for limiting resources, such as
680 food or space (Fréchette & Lefaivre 1990). As a result, there is an inverse relationship between
681 the average size of individuals (i.e., biomass) and population density (Westoby 1981; White et
682 al. 2007). In recent years, support for the self-thinning rule has come from several coral
683 populations. Linares et al. (2008) found that self-thinning applies to the Mediterranean
684 gorgonian *Paramuricea clavata*, but not to *Eunicella singularis*. The applicability of self-thinning
685 to the precious Mediterranean red coral, *Corallium rubrum*, was rejected by Garrabou et al.
686 (2017) based on a study conducted at ≤ 30 -m depth and focusing on colonies ≤ 9 -cm tall.

687 However, when this species was studied over a wider depth range (i.e., ≤ 155 m) and included
688 colonies as big as 35-cm tall, self-thinning emerged as a potential mechanism driving
689 differences between the shallow and deep water populations (Cau et al. 2016), as predicted by
690 modeling (Bramanti et al. 2009).

691 In tropical octocoral communities, evidence of self-thinning has rarely been sought (Nelson
692 2017). Edmunds and Lasker (2019) tested for self-thinning in octocoral communities in shallow
693 water off St. John, U.S. Virgin Islands (Fig. 13). They found weak evidence for such
694 relationships but only at two of six sites. At one site, the density of octocorals was high in 2014,
695 and declined over four years with a weak trend of increasing height (as required for self-
696 thinning). At a second site, densities initially categorized as intermediate, changed over time,
697 but they increased while sizes declined (which is inconsistent with self-thinning). Densities and
698 heights of all octocorals did not change at the other four sites (Fig. 13).

699 Finding self-thinning is consistent with the presence of common competitive interactions. Not
700 finding such effects in communities composed of multiple species with a range of ages does not
701 demonstrate an absence of competition. The self-thinning concept was developed and tested in
702 monocultures of even-aged trees (Westoby 1984; Weller 1987). Future research should
703 combine measures of density and size at the population level (i.e., by species) in order to focus
704 on evaluating the extent to which self-thinning might affect octocoral community dynamics, and
705 the conditions under which its effects might be most strongly expressed. Understanding if the

706 self-thinning rule scales up from populations to multispecific communities would improve
707 capacities both to evaluate the stability of communities formed by arborescent octocorals, and
708 to predict the effects of future disturbances (Linares et al. 2008).

709 *Density-dependent recruitment.*

710 Among the biological processes affected by density dependent mechanisms, recruitment is one
711 of the most studied (Hixon et al. 2002). Classically, a decline in per-capita recruitment with rising
712 population density can regulate population density at a finite size (Caley et al. 1996). In the US
713 Virgin Islands, for example, a diverse octocoral community (Tsounis et al. 2018) produces a
714 dense animal forest consisting of an upper canopy and a shaded understory community (Figs.
715 1,14). Within the understory, octocoral recruitment is positively associated with the density of
716 adults (pooled among taxa or for all plexaurids), suggesting that recruitment for this group is
717 density dependent (Privitera-Johnson et al. 2015) (Fig. 13). Density associated recruitment was
718 not characteristic of all octocoral species, and while it was well developed for *Gorgonia*
719 *ventalina*, it was absent for *Antillologorgia* spp.

720 **7.0. Goods and services delivered by octocorals**

721 Ecosystems and their constituent species often provide benefits to human life, and these
722 benefits are characterized as goods and ecosystem services (Daily 2003). Goods include
723 seafood, biomass fuels (Mooney et al. 2009), and many pharmaceuticals (Rodríguez 1995),
724 while services can range from carbon sinks (Wild et al. 2011), erosion protection (Sheppard et
725 al. 2005), to attractions for recreation and tourism (Graham & Nash 2013).

726 The principal ecosystem service that Caribbean octocoral canopies provide is habitat structure..
727 Physical structure provided by corals generally increases biodiversity of associated organisms,
728 such as invertebrates and fish (Reaka-Kudla 1997). Similarly, octocoral canopies increase
729 surface cover that acts as living space, and partition space to provide refuge from predators
730 (Tsounis et al. 2020), and by creating a three-dimensional structure the canopy should reduce
731 the visual detection of benthic organisms by fish predators hunting in demersal waters (e.g.,
732 Dahlgren & Eggleston 2000; Anderson 2001; Walter & Haynes 2006; Pollux et al. 2007).
733 Caribbean fishes therefore seek octocoral canopies for visual cover that can hide individual fish
734 and confuse their visual predators (Tsounis et al. 2020). Little is known at present about
735 associations of the invertebrate fauna with Caribbean octocorals, but preliminary data indicate
736 that invertebrate communities at the south shore of St. John, US Virgin Islands, are composed

737 of 66 genera and 82 species, with communities (based on organism abundance) consisting of
738 38.5% Scleractinia, 41.0% Porifera, 5.4% Annelida, 2.1% Echinodermata, 1.7% Mollusca, 2.3%
739 Chordata, 0.4% Arthropoda, and 8.5% non-scleractinian Cnidarians (J. Girard pers. comm.).
740 This associated invertebrate fauna increases the diversity and productivity of octocoral habitat,
741 and likely provides the base for a food chain that has cascading effects into commercial
742 fisheries of carnivorous fish species.

743 Octocoral habitat is being increasingly used as commercial fishing grounds in the Caribbean,
744 such as in the US Virgin Islands (), as a result of degrading structural complexity of reefs (Wolff
745 et al., 1999; Alvarez-Filip et al., 2009). While no data confirm increases of fish biomass under
746 octocoral canopies, the concentration of constant fish presence into a specific location due to
747 attraction (Tsounis et al. 2020) is arguably an ecosystem service of octocoral communities. It
748 reduces fishing effort and makes fisheries more profitable.

749 Octocoral communities may influence reef succession and aid the development of stony coral
750 reefs (and associated ecosystem services). Increased feeding rates of demersal fishes
751 (including herbivores) within octocoral canopies (Tsounis et al. 2020) may mediate a top-down
752 control by herbivores on macroalgae (Mumby 2006; Hughes et al. 2007; Adam et al. 2015). If
753 octocorals act as a pioneer species (sensu Connell & Slatyer 1977), they may play a key role in
754 regime shifts between coral- and macroalgal- dominated states.

755 There are no estimates that quantify the productivity and carbon budgets of octocoral forests in
756 the tropical western Atlantic, but octocorals contribute to the carbonate budget on reefs. Cary
757 (1915) estimated that octocorals in an area of high density (15.9 octocorals m⁻²) produced up to
758 13.6 kg m⁻² of limestone per year of calcium carbonate in the form of spicules supplied to the
759 sediment. His estimate was based on an observed average mortality of 17.2% of the octocoral
760 fauna (a conservative estimate of dead skeletons present on the reef), in a 5-year study from
761 1910-1915) (Cary 1915). The proportion of those sclerites that become incorporated into the
762 sediments and ultimately lithified is unknown.

763 Octocorals are also a source of bioactive metabolites. These compounds have promising
764 pharmaceutical activity, and octocorals have long been systematically screened for biomedical
765 and cosmetic value (Gerhart & Coll 1993; Rodríguez 1995). Direct harvesting of octocorals for
766 extraction of commercially important compounds occurs with *Antillogorgia* (*Pseudopterogorgia*)
767 *elisabethae* on the shallow reefs of the Little Bahama Bank (Goffredo & Lasker 2008). A.

768 *elisabethae* contains pseudopterosins (Look et al. 1986), that are used by the cosmetic industry
769 for their anti-inflammatory and analgesic properties (Castanaro & Lasker 2003). The fishery for
770 *A. elisabethae* is regulated by the Bahamas Department of Marine Resources, and has an
771 estimated annual value of \$ 3–4 million (Bruckner 2002), meeting an estimated demand of 30–
772 45 tons of *A. elisabethae* per year (Puyana et al. 2004). Finally, octocorals can also be goods
773 themselves, as some species are globally harvested (legally and illegally) for use of their
774 skeleton as raw material in jewelry, or for use of entire small colonies in the aquarium curio
775 trade (Tsounis et al. 2010).

776 **8. The future**

777 *Research priorities.* The future of coral reefs in the 21st century will be different from the past,
778 particularly in the tropical western Atlantic. Our premise has been that octocorals are well suited
779 for the conditions of future reefs, but that conclusion is primarily built on observational data, and
780 research that experimentally explores those conclusions is essential. Furthermore, if octocorals
781 are well adapted to current conditions, it is critical that we determine the extent to which that
782 capacity will continue to promote their success as environmental conditions further change. The
783 degree to which octocorals modify environmental conditions and, in turn, affect the stability and
784 resilience of the ecosystem, requires further study. Finally, understanding how octocoral
785 populations interact with each other and other reef taxa is critical in evaluating how reef
786 communities might change over time. Below we highlight critical needs for future research on
787 octocorals in the context of understanding their roles on future reefs on which they will likely
788 dominate.

789 *1. Discerning and identifying species.* Correctly delineating species and identifying colonies is
790 critical to understanding the dynamics, physiology, and ecology of octocoral communities. On
791 reefs in the tropical western Atlantic, numerous species of octocorals share similar gross
792 morphology and can only be distinguished through analyses of sclerites sampled through
793 voucher specimens and analyzed in the laboratory (Bayer 1961). Those characterizations are
794 further complicated by genetic data (c.f. Prada & Helberg 2013), which suggest many species
795 designations require revision. The inability to quickly and reliably identify octocorals underwater
796 during ecological surveys remains a significant impediment to progress in understanding the
797 biology of this taxon, and the implications of upward trends in their abundance and spatial
798 extent on present day reefs (Kupfner Johnson & Hallock 2020).

799 2. *Bleaching*. Much of the current success of octocorals on western Atlantic reefs may be due
800 to their relative resistance to thermal stress and bleaching. Experimental studies are needed to
801 identify the mechanistic basis of that resistance, to identify the role of the host and
802 Symbiodiniaceae symbionts, and to characterize the variation that occurs between species and
803 habitats.

804 3. *Recruitment*. The colonization of substratum released through mortality of scleractinians may
805 also be a critical component of the modern success of octocorals. Despite little is known about
806 the processes controlling octocoral recruitment, we have some indications of possible
807 mechanisms:

808 1) Octocoral recruitment declined following Hurricanes Irma and Maria on St. John, and then
809 recovered in density after one year (Lasker et al. 2020). However we do not know if the
810 recruitment decline was a consequence of the reduced fecundity caused by damage to adult
811 colonies or if it was due to adverse environmental conditions in the months following the
812 hurricanes.

813 2) There is some evidence for positive associations between adult abundances and recruitment,
814 but we need to determine if that reflects habitats that are especially suitable for both adults and
815 settlers or if the octocoral forest modulate flow in a manner that provides a positive feedback on
816 recruitment.

817 Most importantly, whatever they are the process regulating octocoral recruitment, we need to
818 ascertain how it will be affected by future changes in the environment.

819 4. *Mixotrophy*. Complete trophic analyses of multiple octocoral species are needed. The extent
820 to which varying levels of heterotrophy and autotrophy explain the success of the octocorals and
821 their diversity is unknown. Relevant data are beginning to emerge for octocorals (Rossi et al.
822 2018, 2020), but much more is needed, particularly under ecologically relevant conditions that
823 capture the complex hydrodynamic regimes under which branching octocorals operate.

824 5. *Octocoral demography*. The upward trend in abundance of octocorals on reefs in the tropical
825 western Atlantic reflects successful recruitment and growth over shrinkage and mortality. Since
826 little is known about the biology of octocorals in this region, their demographics are even less
827 understood. Demographic models exist for only a handful of species (e.g., Gotelli 1991; Lasker
828 1991; Yoshioka 1994; Goffredo & Lasker 2008; Bruno et al. 2011; Bramanti et al. 2009; 2014;
829 Santangelo et al 2007; Linares & Doak 2010). Demographic models can identify life history

830 characters that are key factors in controlling population abundance and generate hypotheses
831 regarding the processes controlling population growth. More detailed spatial knowledge on
832 octocoral distribution and demography will be key to identifying threats to octocoral communities
833 as well as the services they provide.

834 *6. Holistic analyses of coral reef communities.* For decades, coral reef biology has advanced
835 through analyses focused on scleractinians or only a handful of benthic groups (e.g.,
836 scleractinians, macroalgae, and crustose coralline algae), and in the majority of cases only one
837 variable at the time (e.g. acidification or temperature or disease outbreaks) have been analyzed
838 to describe the changes taking place. As scleractinians have become rare, these “traditional”
839 functional groups have less influence on the ecological processes affecting benthic
840 communities, and now the future of “coral” reefs arguably is best described by focusing on non-
841 scleractinian taxa, including octocorals. Analyses of percentage planar cover of the benthos
842 have, to date, served the research community well in understanding how reefs have changed,
843 and in what form they currently exist. Reefs dominated by different taxa are less tractable to
844 these approaches, particularly as taxonomic resolution will be challenged by the profusion of
845 morphologically similar, but genetically diverse, taxa including sponges and octocorals. Where
846 these taxa are tall and erect, their planar cover provides a poor proxy for biomass or ecological
847 impact, and in these cases, quantification will need to move beyond this simple metric. Finally,
848 holistic analyses taking into account interactions of octocorals with other taxa will be key to
849 evaluate ecosystem services.

850 **Summary**

851 Although octocorals have been recognized as important on coral reefs throughout the tropical
852 western Atlantic for over a century (Cary 1914), and were prominently featured in some of the
853 earliest modern ecological studies of these reefs (Kinzie 1973), they have remained
854 understudied for over 50 years. Most studies described deteriorating communities by the
855 abundances of scleractinians and reef fishes and the modern notion of the “coral reef crisis” was
856 born (Hughes 1994; Gardner et al. 2003; Bellwood et al. 2004). In the new millenium, it has
857 become clear that the dynamics of octocorals differs from that of scleractinians. They have
858 increased in abundance and expandedg the spatial extent of occupied reef surfaces (Ruzicka et
859 al. 2013; Lenz et al. 2015; Sanchez et al. 2019).

860 With fewer scleractinians to study and community dynamics influenced more strongly by other
861 taxa, biologists increasingly study octocorals. (Kupfner Johnson & Hallock, 2020). This review

862 focused on the ecology of octocorals and on the characteristics that could have favored their
863 increasing abundance. The reviewed trends point to the ecological significance of a tree-like
864 morphology and the exploitation of the seawater volume above the benthos as reasons for the
865 success of octocorals on modern reefs. The region-wide population decline of branching
866 *Acropora* spp. (Aronson & Precht 2001) left the functional niche of the water column
867 underexploited by sessile taxa. The capacity for rapid linear growth allows octocorals to quickly
868 evade competition with benthic macroalgae, and transition through the risky small size classes
869 to reduce post-settlement mortality. By growing in dense clusters and forming dense forests
870 (Rossi et al. 2017), octocorals benefit from canopy formation, promoting particle capture, larval
871 retention, and beneficially exploiting hydrodynamic regimes (Guizien & Ghisalberti 2017).

872 While there is compelling evidence that octocorals are gaining greater ecological significance on
873 the coral reefs of the tropical western Atlantic, it remains unknown whether they are ecological
874 “placeholders” on the “slippery slope to slime” (Pandolfi et al. 2005), or a “new normal” that will
875 define the structure and function of “coral” reefs for centuries (or longer). The notion that
876 Caribbean reef communities might be dominated for at least a few decades by octocorals,
877 highlights the ecological opportunities remaining. This provides an alternative to focusing solely
878 on the extinction of scleractinians and the loss of coral reef ecosystems (Hoegh-Guldberg et al.
879 2007; Carpenter et al. 2008). While octocorals can deliver many goods and services similar to
880 those of scleractinians, their inability to deliver a calcified, sturdy and wave resistant reef
881 framework filled with countless habitats for other taxa, means that “octocoral forests” cannot be
882 considered replacements for what is being lost with living coral reefs. Nevertheless, they likely
883 will characterize a large part of what we have, rather than what we might want, so this is the
884 time to continue and expand studies of their biology and ecology.

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- 1437

1438 **Tables**

1439 Table 1. Annual survival of octocoral colonies

Species	Locations	Size Class (cm)	Survival	Source
<i>Leptogorgia virgulata</i>	Gulf of Mexico	0.5 - 4.0	0.780	Gotelli 1991
		4.5 - 8.0	0.880	
		8.5 - 12.0	0.964	
<i>Plexaura kuna</i>	Caribbean - Panama	< 10	0.49	Lasker 1990
		10-19.9	0.82	
<i>Paramuricea clavata</i>	Mediterranean - Spain, two sites	0.3- 3.0	0.667 - 0.769	Linares et al. 2007
		3.0 -10.0	0.636 - 0.768	
		11 - 20	0.770 - 0.962	
<i>Antillogorgia</i> spp.	Caribbean - Puerto Rico	< 6	0.768	Yoshioka 1991
		6 - 10	0.893	
		11- 15	0.939	

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1441

1442 Table 2. Growth rates of Caribbean gorgonians.

Species	Location(s)	Colony Size	Growth (cm/y)	Reference
<i>Antillogorgia acerosa</i>	Colombia, Puerto Rico		23.05, 2.12, 4.48, 5.17	Cardena and Sanchez, 2010; Yoshioka & Yoshioka, 1991; Borgstein et al., 2020
<i>Antillogorgia americana</i>	Puerto Rico (3 sites)		3.44, 4.48, 5.08	Yoshioka & Yoshioka, 1991; Borgstein et al., 2020
		<10 cm	3.73	
<i>Antillogorgia elisabethae</i>	The Bahamas	10 - 19.9 cm	4.54	Lasker et al 2003
		20 - 29.9 cm	3.87	
<i>Briareum asbestinum</i>	Panama, Puerto Rico		5.93, 3.01	Brazeau & Lasker 1992, Borgstein et al., 2019
<i>Eunicea calyculata</i>	Puerto Rico		1.98	Borgstein et al., 2020
<i>Eunicea flexuosa</i>	Puerto Rico		2.15, 1.77, 2.98	Yoshioka & Yoshioka, 1991; Borgstein et al., 2020
<i>Eunicea laciniata</i>	Puerto Rico		3.01	Borgstein et al., 2020
<i>Eunicea laxispica</i>	Puerto Rico		2.21, 3.49	Yoshioka & Yoshioka, 1991; Borgstein et al., 2020
<i>Eunicea succinea</i>	Puerto Rico		1.36	Borgstein et al., 2020
<i>Eunicea tourneforti</i>	Puerto Rico		2.06, 2.76	Yoshioka & Yoshioka, 1991; Borgstein et al., 2020
<i>Gorgonia ventalina</i>	Puerto Rico		3.74	Borgstein et al., 2020
<i>Muricea elongata</i>	Puerto Rico		3.71	Borgstein et al., 2020
<i>Muriceopsis flavida</i>	Puerto Rico		1.85, 4.52	Yoshioka & Yoshioka, 1991; Borgstein et al., 2020
<i>P. wagnaari</i>	Puerto Rico		2.57, 2.13	Yoshioka & Yoshioka, 1991
<i>Plexaura homomalla</i>	Puerto Rico		1.99, 3.71	Yoshioka & Yoshioka, 1991; Borgstein et al., 2020
<i>Plexaura kukenthali</i>	Puerto Rico		1.18	Yoshioka & Yoshioka, 1991
		<10	3.9	
<i>Plexaura kuna</i>	Panama	10-19.9	3.49	Lasker 1990
		>20 cm	3.77	
<i>Plexaurella dichotoma</i>	Puerto Rico		0.8	Yoshioka & Yoshioka, 1991
<i>Plexaurella</i> spp.	Puerto Rico		2.63	Borgstein et al., 2020
<i>Pseudoplexaura porosa</i>	Puerto Rico		1.98, 2.22	Yoshioka & Yoshioka, 1992
<i>Pseudoplexaura</i> spp.	Puerto Rico		3.58	Borgstein et al., 2020

1443 Growth rates from Borgstein et al. (2020) were taken from their Figure 1 and are median values.

1444 All other rates are averages. Calculations excluded cases of negative growth.

1445 Unless indicated growth rates are for colonies >10 cm height

1446

1447 Table 3. Number of octocoral species found in Bermuda compared to the Caribbean and
1448 Florida, with respect to reproductive mode. Totals are limited by the number of species for which
1449 reproductive mode and sexuality are known.

Reproductive mode	Caribbean	Bermuda
Brooder & External Brooder	11	2
Spawner	12	11

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1452 **Legends**

1453 Fig. 1. A typical octocoral forest at ~ 8-m depth at Booby Rock, St. John (US Virgin Islands), in
1454 2013. Such forests are dominated by a high density of octocorals, with some reaching >
1455 1 m height. These communities are not “new” per se (cf. Kinzie 1973), but in the last few
1456 decades they have increased in spatial extent. The canopy created by octocoral forests
1457 forms an understory habitat that contributes to the emergent functional properties of the
1458 forest.

1459 Fig. 2. Schematic illustrating the community structure of present-day reefs in the tropical
1460 western Atlantic in which scleractinians, macroalgae, and octocorals compete for
1461 dominance. Sponges can also occupy substantial portions of benthic space, but time
1462 series data for this taxon are sparse, and in St. John, they do not appear to have played
1463 a dominant role in occupying space for over 26 years. Environmental conditions and
1464 biotic processes over the last few decades have favored rising abundances of
1465 arborescent octocorals relative to the other benthic space holders.

1466 Fig. 3. Octocoral density from 1968 to 2019 in the tropical western Atlantic, as compiled from
1467 published and unpublished sources (updated from Lenz et al. [2015]). Red shows data
1468 from St. John, black shows all other data.

1469 Fig. 4. *Cyphoma* sp. found in reef deposits of a Pleistocene Reef, San Salvador, The Bahamas.
1470 The reef has been dated to 120,000 to 132,000 BP (Chen et al. 1991).

1471 Fig. 5. Schematic illustrating hypotheses by which octocorals attain enhanced resilience
1472 following disturbance, and promoting an octocoral-dominated community (A-D in a
1473 chronology). A) A coral reef before a major disturbance with a few large colonies of
1474 scleractinians and octocorals, as well as their recruits. Differences in recruit positioning
1475 reflect dissimilar settlement niches, and octocorals are constrained by their inability to
1476 settle on living scleractinians. B) Immediately after a disturbance that has killed many
1477 scleractinians and some octocorals. C) Octocorals and scleractinians recruit. The altered
1478 abundance and distribution of octocorals relative to scleractinians reflects differences in
1479 larval supply, and the increase in substrata matching octocoral settlement niches. D)
1480 With time, mature octocorals dominate the benthos. Canopy effects on recruitment
1481 enhance self-seeding, which differentially benefits octocorals due to their greater
1482 abundance and high reproductive output. Macroalgae, which are not shown, are

1483 common in B, C, and D and have less effect on octocorals due to the octocorals' escape
1484 in size (height).

1485 Fig. 6. Expanded polyps of *Antillogorgia elisabethae* illustrating how the tentacles and pinnules
1486 create a complex surface for capturing particles. (Photo, H.R. Lasker).

1487 Fig. 7. Density of recruits of octocorals (colonies 3–6 cm tall) and scleractinians (recruits on tiles
1488 at 5-m depth in St. John, mean \pm SE) from 1962 to 2019. Over this period, octocoral
1489 recruitment statistically has not changed.

1490 Fig. 8. Box plots displaying a comparison of density of octocoral recruits (colonies 3–6 cm tall)
1491 and recruits (corals on settlement tiles) and small colonies (\leq 4-cm diameter) of
1492 scleractinians. Scleractinian data come from St. John, and refer to the use of settlement
1493 tiles at \sim 5-m depth, or surveys of natural reef surfaces (at 5–9-m depth).

1494 Fig. 8. Abundance (mean \pm SE) of octocorals and cover of stony corals on two reefs in St. John,
1495 US Virgin Islands (after Tsounis & Edmunds 2017). Population sizes shown from 1987 to
1496 2013 and the plots contrast resilience for octocorals (high resilience, blue) versus stony
1497 corals (low resilience, red).

1498 Fig. 10. Long-lived organisms with three-dimensional structures that function as ecosystem
1499 engineers. (A) Trees, and (B) arborescent octocorals on the reefs of St. John.

1500 Fig. 11. Branching morphology. A: *Muriceopsis* sp. B: *Pinus* sp.

1501 Fig. 12. Schematic showing the development of the roughness sublayer (RSL) as a function of
1502 the canopy formed by octocorals.

1503 Fig. 13. Relationships between size (height) and density (holdfasts in each quadrat) over time
1504 (2014–2017) for arborescent octocorals (pooled among taxa) at six sites on shallow
1505 reefs in St. John (after Edmunds & Lasker 2019) (mean \pm SE). Height and density
1506 changed over time at White Point, and density changed at East Tektite; variation in
1507 height and density was not significant at any other site. These data were used as a test
1508 of self-thinning, with only weak evidence in support of the hypothesis at East Tektite.

1509 Fig. 14. Schematic displaying the interaction of an octocoral forest with moving seawater and
1510 the capacity to entrain, trap, and retain propagules that can support density dependent
1511 recruitment (credit M. Lenz).

1512 Fig. 15. Evidence of density associated recruitment (colonies \leq 4-cm tall) of arborescent
1513 octocorals on the shallow reefs of St. John in 2013 (10 sites) and 2014 (8 sites) (after
1514 Privitera-Johnson et al. 2015).

1515

1516 Fig. 1

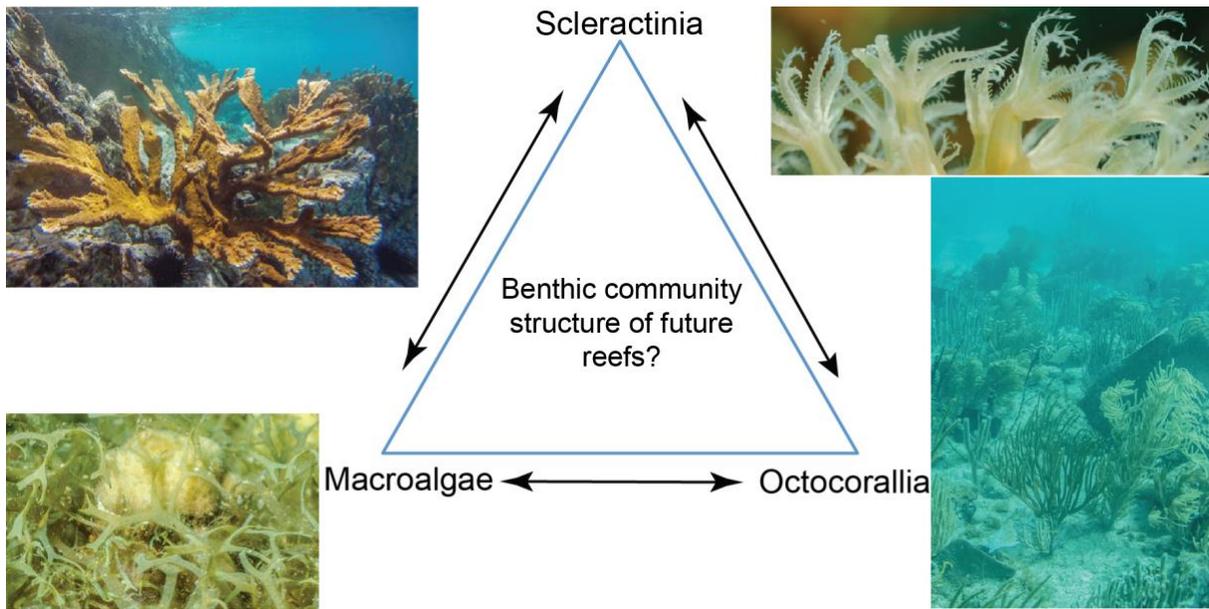


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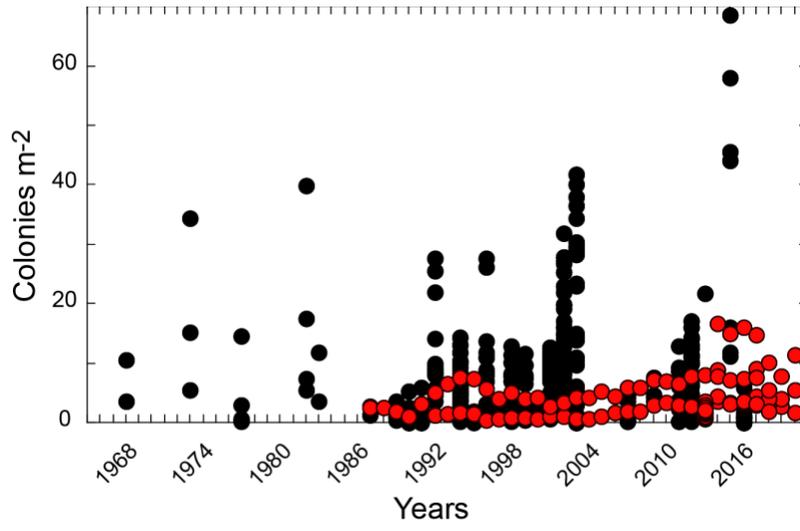
1520 Fig. 2



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1523 Fig. 3



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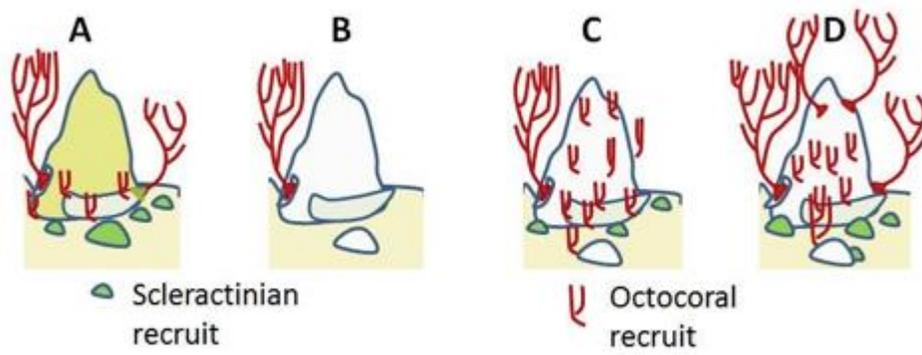
1527 Fig. 4



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1530 Fig. 5



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1534 Fig. 6

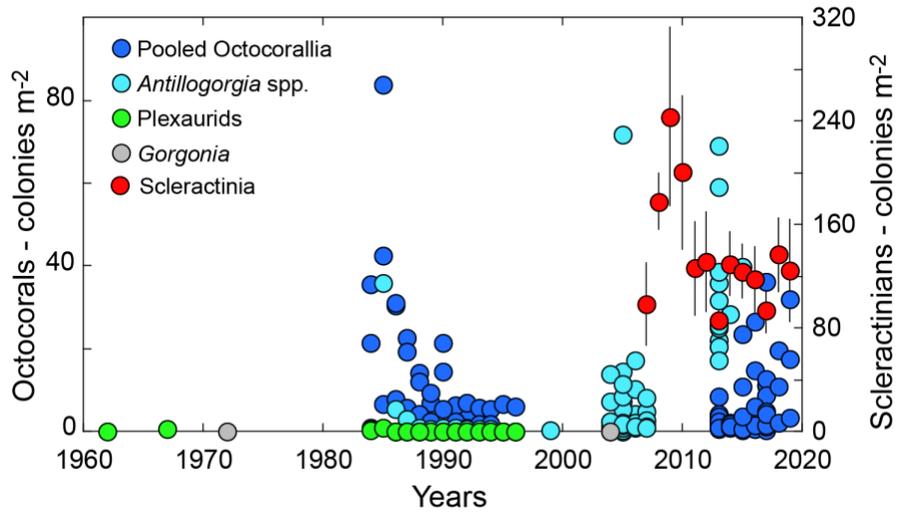


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1538 Fig. 7

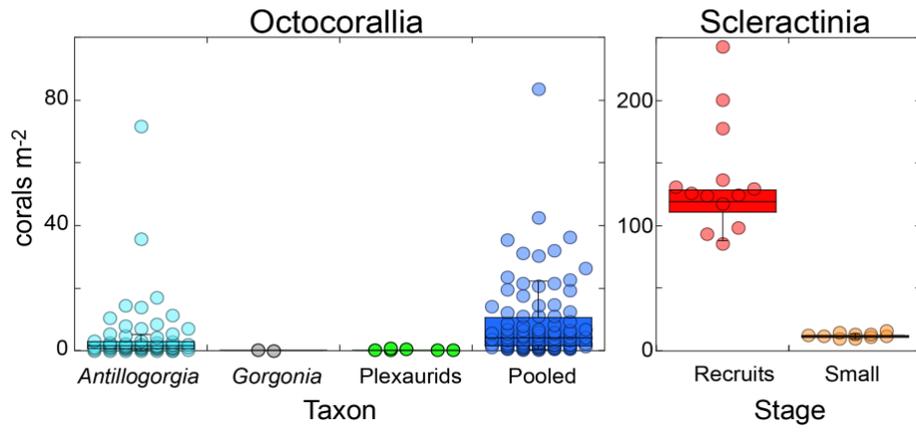


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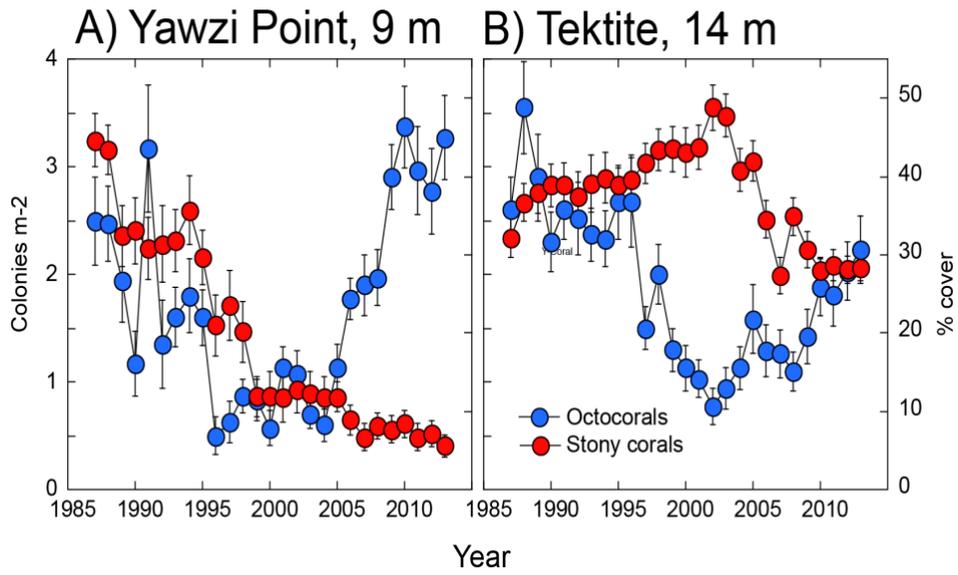
1542 Fig. 8



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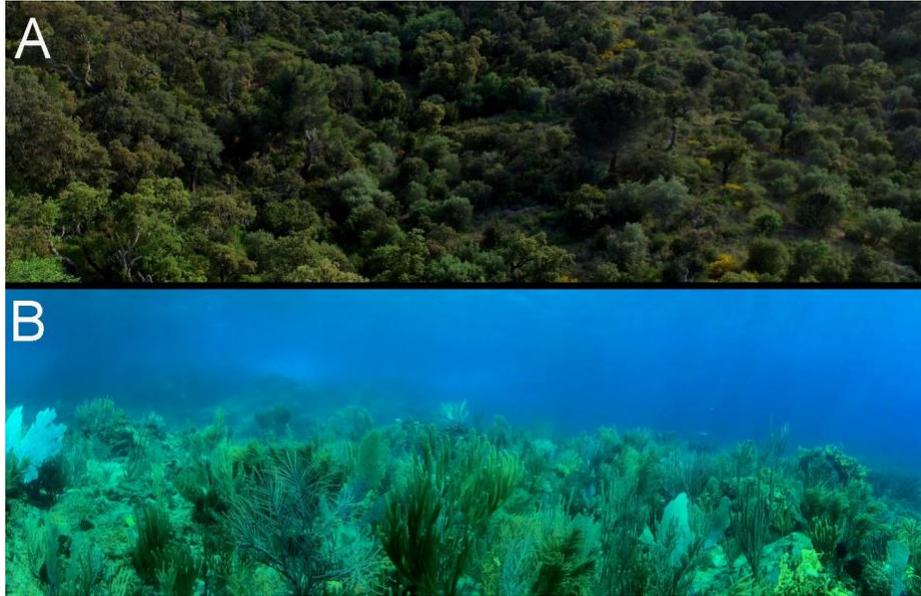
1545 Fig. 9



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1548 Fig. 10

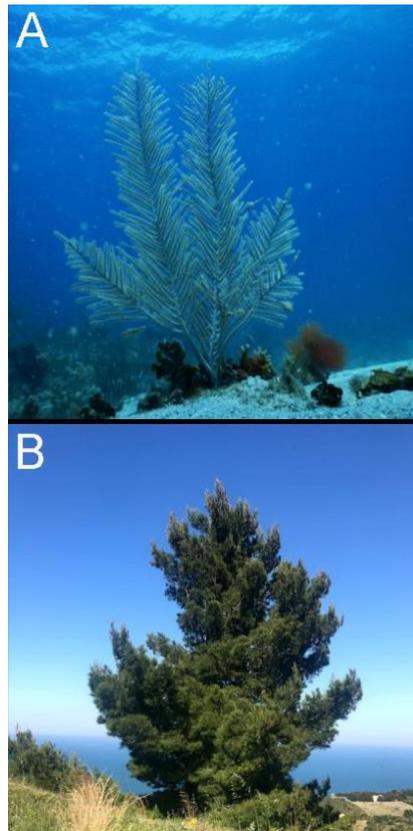


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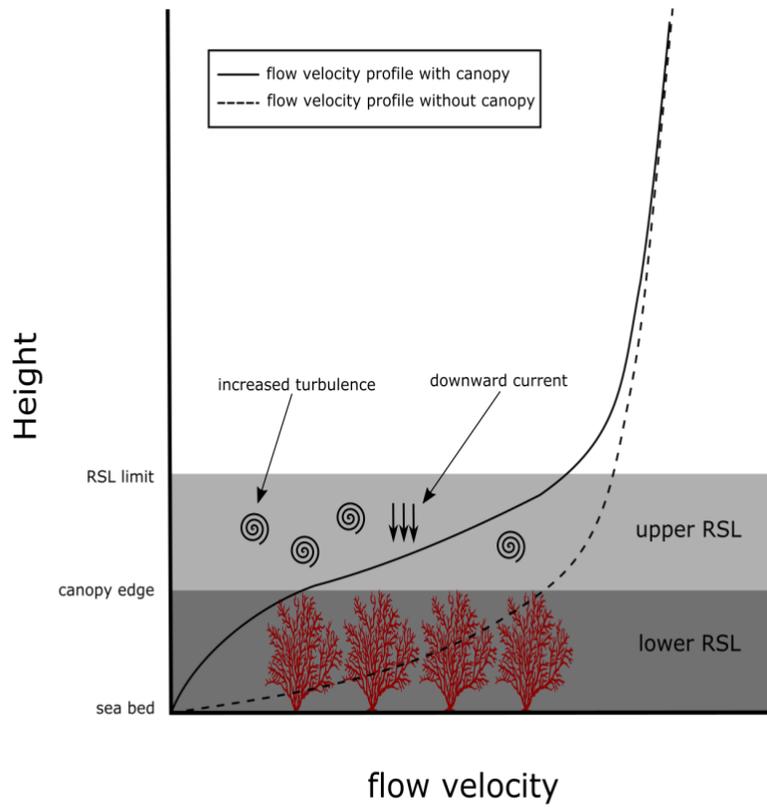
1552 Fig. 11



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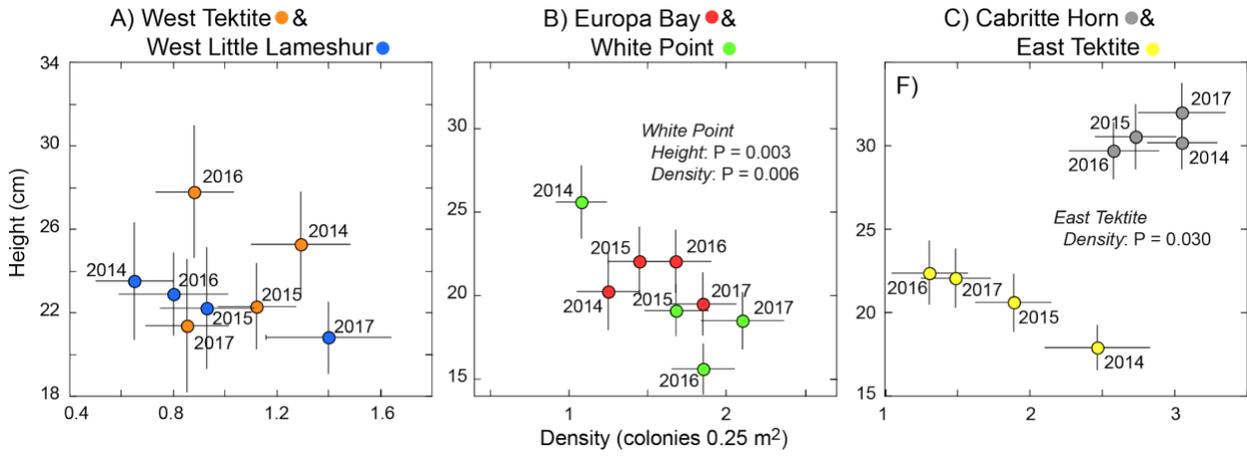
1555 Fig. 12



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1558 Fig. 13

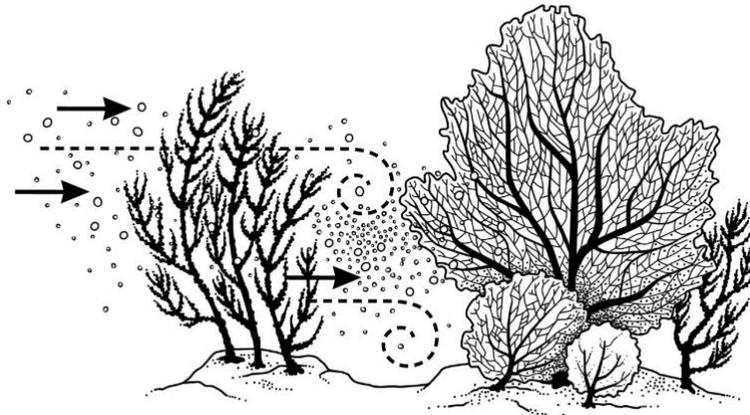


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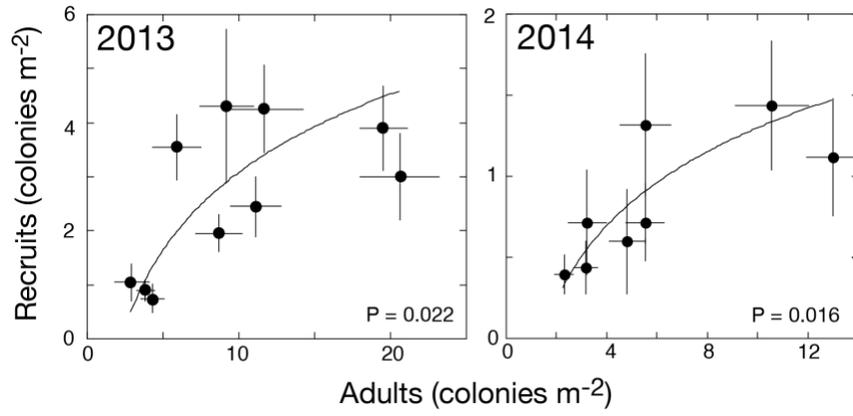
1562 Fig. 14



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1565 Fig. 15



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