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The rise of octocoral forests on Caribbean reefs

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1.0. Abstract

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

2.0. Introduction

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

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

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

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

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

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

The context for this review is created by evidence that octocorals have become more abundant in the tropical western Atlantic (Fig. 3). Ruzicka et al. (2013) were the first to describe changes in the community structure of Caribbean reefs in favor of octocorals versus scleractinians. Although ecological analyses of octocorals have remained scarce, a data compilation for 1968-2013 supports the hypothesis that octocorals have increased in abundance (Lenz et al., 2015; Tsounis & Edmunds, 2017). Analyses of reefs in St. John from 2014-present also support this hypothesis, as well as the notion that octocoral domination is the “new normal” for shallow Caribbean reefs (Lasker et al., 2020). Updating Lenz et al. (2015) with results published since 2013, including our analyses from St. John reveals that the trends reported in Lenz et al. (2015) have continued Fig. 3). The data suggest that the region-wide abundance of octocorals has risen 84% since 1968-90 (versus 2015-2019), and now represents a mean density of 9.2 ± 2.2 colonies m^{-2} (averaged over 2015-2019, n = 48).

3.0. Historical context

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

Tracing the origins of the Caribbean octocoral fauna is difficult. There is not much of a fossil record of octocorals because their largely proteinaceous skeletons reduce the likelihood of preservation, and their sclerites are only visible as microfossils, and being composed of high Mg calcite, they are unlikely to be preserved. In some cases, evidence of Octocorals in the fossil records is indirect, such as the presence of *Cyphoma* sp., a specialist octocoral grazer, in fossil Pleistocene reef deposits (Fig. 4), indicating octocorals have been members of Caribbean reef communities for at least 120,000 years. Direct evidence includes gorgoniid and plexaurid sclerites, which have been found in the Lower Oligocene (27 to 34 million years ago) of Mississippi (Giammonna & Stanton, 1980). Some species have secondary calcification in their central axis, and gorgoniid holdfasts and branch fragments have been found preserved in deposits from Texas, dating from the Middle Eocene (47 to 41 million years ago) (Kocurko & Kocurko, 1992). Both reports of fossilized octocorals come from the Gulf of Mexico in depositional environments reflecting “hard ground” habitats that are subject to bouts of clastic deposition.

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

4.0. Octocorals - the right taxon at the right moment

The increasing abundance of octocorals (Lenz et al., 2015; Tsounis & Edmunds, 2017; Fig. 3) has been driven by multiple factors, but the change can be characterized as resilience driven by recruitment following disturbance events in concert with resistance driven by the survival of adults. This is summarized in Fig. 5, which illustrates how mortality of scleractinians has made substratum available for octocorals. The relevant question becomes, why, unlike the scleractinians, are octocorals surviving on present-day reefs, both in the context of adult survival and ecological resilience following major disturbances? Our knowledge of the basic biology of octocorals has lagged behind that of scleractinians, and we have too often assumed that our knowledge of scleractinians carries over to the octocorals. Octocoral biology is not identical to that of scleractinians, but only a few studies have focused on the ways in which they differ. Studies of octocorals also have been limited because the species are difficult to delineate, and taxonomic identification at species level is difficult. Acknowledging these limits, we focus our review on those aspects of octocoral autecology that may predispose them for high survival on tropical western Atlantic reefs in the Anthropocene.

Trophic status

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

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

If the capacity for heterotrophy is one of the factors facilitating the recent success of octocorals in the tropical western Atlantic, it appears unlikely to be due to the capture of zooplankton.

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

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

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

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

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

Direct measures of nutritional modes for Caribbean octocorals are uncommon. Ribes et al. (1998) measured predation on pico-, nano- and microplankton by *Eunicea flexuosa* within incubation chambers that were placed *in situ* on the reef and were supplied with reef water. Using flow cytometry to characterize changes in prey density they report uptake of dinoflagellates, pennate diatoms and ciliates, among other particles, which supplied half as much carbon as feeding on zooplankton. In sum the two modes of heterotrophy accounted for < 1% of the basal metabolic rate of *E. flexuosa*. Grazing on plankters < 5 µm has not been detected. Although the role of heterotrophy in the nutrient budget of *E. flexuosa* was small, Ribes et al. (1998) suggested that *E. flexuosa* alone was capable of removing ~ 10% of the available diatoms, dinoflagellates, and ciliates in the water column. That again suggests that heterotrophy may be limited by the availability of prey, which would not be an unexpected result for what is functionally passive suspension feeding.

Given the difficulties of quantifying uptake rates of food items such as phytoplankton, ciliates and bacteria, there has been increasing use of stable isotopes to identify the role of heterotrophy in octocoral nutrition. Ward-Paige et al. (2005) suggest that *Plexaura homomalla* and *Eunicea flexuosa* from sites with higher levels of eutrophication had δ^{15}N and δ^{13}C values indicative of greater reliance on heterotrophy. Rossi et al. (2018) present δ^{15}N of 4-8$^{0}/_{00}$ and δ^{13}C of -14 to -18$^{0}/_{00}$ from 9 species from the Yucatan. Those values are consistent with a dominantly autotrophic system but do not preclude heterotrophy. Baker et al. (2015, their supplemental material) present δ^{13}C of host and symbiont from 11 species from coastal Panamanian reefs. Seven of those species have mean tissue δ^{13}C values that are lower than the mean symbiont δ^{13}C values, which is consistent with a signature of heterotrophy. However, the differences between host and symbiont δ^{13}C are < 1$^{0}/_{00}$. While indicative of multiple food sources quantification of the relative roles of heterotrophy and autotrophy from stable isotope data is difficult. The relationships between trophic status and stable isotope concentrations are complex in symbiotic systems where compounds are recycled within the holobiont (Ferrier-Pages & Leal, 2019).

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

Direct measures of the contribution of autotrophy to metabolic needs of Caribbean octocorals are more available than measures of heterotrophy. Rossi et al. (2018) measured P:R ratios that were > 1.0 for all 10 species investigated, and while Rossi et al. (2020) found seasonal differences in both metabolic rate and gross photosynthetic rates, P:R ratios remained ≥ 1 throughout the year. Baker et al. (2015) report P:R ratios ranging from of 0.7 - 1.6. These studies acknowledge some likely heterotrophic inputs to the carbon budget of these organisms, but based on P:R ratios determined in oxygen units, much of the daily nutrition of the octocorals could have been met through the carbon fixed and translocated from algal symbionts.

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

Growth form and growth rate

The signature feature of all but two of the octocorals found on Caribbean coral reefs is their arborescent colony form. All but *Erythropodium caribbeaorum* and the encrusting form of *Briareum asbestinum* (historically reported as *B. polyanthes)* exploit the water column from a diminutive site of basal attachment (encrusting *B. asbestinum* also can take on an upright aspect as it often grows on exposed axes of other octocoral species). A vertical morphological strategy removes the colony from a variety of the vicissitudes of life on the substratum, elevating colonies above processes such as scour by sediments, shading by macroalgae, and overgrowth by other benthos.

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

Although coral reefs are complex 3-D structures, overgrowth is primarily a 2-D process, and elevating most of the gorgonian colony above the substratum minimizes the interactions with competitors. Many of the potential competitors of gorgonians can grow over their holdfasts (e.g., Edmunds et al., 2019), but they tend not to grow up the length of the primary branch, and overgrowth of the base on its own will not necessarily weaken a colony. Building a rigid structure on a flexible object also may be a limiting factor for some competitors. Those structural constraints would seemingly be less important for potential sponge competitors. Species such as *Desmapsamma anchorata* can be found on Caribbean gorgonians, but probably settle on damaged areas on the colony where the axis is exposed (McLean & Yoshioka, 2008). Massive sponges such as *Xestospongia* spp. will “envelope” gorgonians as they expand (McLean & Yoshioka, 2007), but Caribbean sponges typically do not spread along the substratum and up the base of octocorals. Some Caribbean reef sponges bore into the carbonate substratum, and the gorgonin core of gorgonians would not be a suitable habitat for these species. Finally, peyssonellid algal crusts (PAC, calcifying red algae), notably those including *Ramicrusta* spp., recently have undergone rapid growth on some Caribbean reefs (Eckrich & Engel 2013; Bramanti et al., 2017). PAC is capable of overgrowing a variety of benthic taxa, but it does not seem to grow up beyond the bases of octocorals (Edmunds et al., 2019). The importance of vertical growth by octocorals may be accentuated on present-day reefs, where the proliferation of turf and macroalgae over the past four decades (Hughes, 1994; Roff & Mumby, 2012) has, at the least, altered the nature of boundary layer over the substratum (c.f., Stocking et al., 2016; Wangpraseurt et al., 2012), thus placing strong selective value on the ability to project above this layer. In some cases, however, vertical branching growth could be counterproductive, such as in the case of the *Lyngbya* bloom in SE Florida, elements of which were transported by seawater current and killed gorgonians by entanglement and subsequent suffocation (Paul et al., 2005).

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

Growth rates of octocorals are markedly variable both within and between species, but all illustrate the high degree to which octocorals exploit vertical growth to escape the risks of mortality through increases in size. Species-specific growth rates among Caribbean gorgonians range from 23.1 cm y^{-1} for *Antillogorgia acerosa* colonies from Colombia (Cadena & Sanchez, 2010) to 0.8 cm y^{-1} among *Plexaurella dichotoma* colonies on the southwest coast of Puerto Rico (Yoshioka & Yoshioka, 1991). The range is even greater as most reported values are averages. There also are location/habitat differences as suggested by the 5-fold difference in observed growth rates of *A. acerosa* from Colombia and Puerto Rico. All of the studies that have characterized growth also note many cases of negative growth (i.e., partial mortality) presumably caused by some combination of predation, disease, and physical disturbance. For instance, average growth of *Plexaura kuna* is 2 to 4 cm y^{-1} lower than the potential growth suggested by growth among colonies that had net positive growth (Table 2). The highest growth rates are found among species with thin branches such as the *Antillogorgia* spp. (Borgstein et al., 2020). Among those species, recruits can escape the highest mortality section of the life table in one to two years and reach 10 cm in 3 to 4 years. Given the variance associated with the averages and the possibility of negative growth, many colonies will take longer to reach those milestones, while some will do so in substantially less time. In contrast to the octocorals, scleractinians have lower growth rates. Edmunds (2018) reported growth in colony diameter among small, < 4 cm diameter scleractinians on St. John, Virgin Islands, ranging from -3.45 to 5.55 cm y^{-1}, but average growth was 0.29 cm y^{-1}. Edmunds (2018) noted that the data for scleractinians did not support an expectation of rapid growth that could provide a refuge in size. Growth at the colony edge does not elevate colonies above the substratum, and most scleractinians expand their base before substantial vertical growth occurs.

Reproductive Biology

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

Egg size might also affect the recruitment of octocorals and scleractinians. Large egg size implies greater parental provisioning, which can then affect some combination of longevity in the water column (i.e., greater dispersal), size at metamorphosis and recruit survival (Vance, 1973; Hartmann et al., 2013; but see Bernardo, 1996). Our knowledge of gamete traits for octocorals is incomplete, but Caribbean octocorals for which there are data (6 species, Kahng et al., 2011) have mean oocyte diameters of 722 µm, and produce 2.6 mature oocytes $polyp^{-1}$. In contrast, the eggs of Caribbean scleractinians have a mean diameter of 317 µm and produce on average 130 oocytes $polyp^{-1}$ (data from Szmant, 1986). Genetic analysis of *A. elisabethae,* a surface brooder, suggests modal dispersal distances of 100 m to 1 km in The Bahamas (Lasker & Porto Hannes, 2015). In biophysical model simulations of the dispersal of *A. americana*, which is a broadcast spawner, Coelho (2018) reports a median dispersal distance of 39 km with more settlement within 1 km than any other distance. If these congeners are representative of the Western Atlantic reef fauna, octocorals generally have modest dispersal distances, even the widely distributed *A. americana*.

We have relatively limited knowledge on how reproduction and dispersal of octocorals translates into settlement, but there are data on octocoral recruitment at several Caribbean sites. Recruitment, the first appearance of an individual in a population (Caley et al., 1996), is operationally defined in manners that often are unique to individual studies. Recruitment in annual surveys of octocorals has been quantified as the appearance of small colonies whose height suggests they are a year or less old. Heights from ≤ 3 cm (Lasker, 1990) to ≤ 6 cm (Yoshioka, 1997) have been used. As discussed above, the height of a 1 year old recruit can vary considerably both within and especially among species. Thus, any height-based definition of a recruit will err by excluding fast growing recruits and by including colonies that are over a year old. As importantly, because recruits that have died do not leave a skeleton behind, recruitment based on annual or even monthly surveys will miss the settlement of individuals that subsequently died.

We compiled published, octocoral recruitment data to address two questions: (1) is there evidence of changing rates of octocoral recruitment, and (2) are there differences in rates of recruitment between octocorals and scleractinians? The former addresses the issue of whether changing conditions on reefs have altered any of the processes controlling successful recruitment, and the latter provides insight into whether the current differences in the demographics of octocorals and scleractinians might occur in the early life history stages that control recruitment. Our data compilation yielded 18 studies that together provided 198 records of the density of octocoral recruits. Most data were for individuals 3–6 cm tall, which probably are about one year in age, although a handful of records of polyps settling on tiles were obtained. Most records were for octocorals pooled among taxa, but substantial records also were obtained for *Antillogorgia* spp. (n = 63, mostly *A. elisabethae, A. acerosa, A. americana* and *A. rigida*), plexaurids (n = 40, mostly *P. kuna*), and *Pseudoplexaura* spp. (n = 11). To provide a comparative context to these data, we included 13 years of scleractinian recruitment to settlement tiles deployed at ~ 5-m depth in St. John, and a decade of density data for juvenile scleractinians on natural reef surfaces (Edmunds, 2018, and unpublished data). Densities of octocoral recruits in these annual surveys ranged from 0 to 84 colonies m^{-2}, and the highest recorded density was from 1985 on the south shore of Puerto Rico (Yoshioka, 1996). These data substantially underestimate settlement. Surveys that were conducted 1–2 months after spawning over 4 y found recruitment at sites in the Bahamas for *Antillogorgia* spp. that ranged from 3 to 231 recruits m^{-2} (Lasker & Porto Hannes, submitted). Annual versus monthly surveys for *Plexaura kuna* recruits in the San Blas Islands, Panama, generated recruitment rates of 0.37 individuals m^{-2} (annual) and 1.0 individuals m^{-2} (monthly). Finally, surveys of tiles deployed on the south shore of St John, Virgin Islands, that were conducted at 3 day intervals found recruitment over a 19 d period of 443 individuals m^{-2} (Wells et al. submitted). Although they are an incomplete characterization of the processes controlling recruitment, the data address the presence of temporal patterns. Overall, octocoral recruitment was unrelated to time from 1962 to 2019 (r = -0.06, df = 196, P = 0.40).

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

Bleaching

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

Lasker et al. (1984) reported limited bleaching of octocorals during the 1983 Caribbean bleaching event, but Hannes (2009) and Prada et al. (2010) report more extensive bleaching of octocorals in the 2005 bleaching events in the Florida Keys and southwest coast of Puerto Rico. In those studies, *Plexaurella, Pterogorgia, Muricea and Briareum* were the most common species to bleach. Mortality has been observed among *Plexaurella* (MA Coffroth, pers comm) and significant mortality has been reported for *Muricea* (Prada et al., 2010). Reliance on autotrophy does not appear to explain sensitivity to bleaching. For instance, two *Plexaurella* spp. and *Briareum asbestinum* are among the small number of taxa that bleach and they have the lowest P:R ratios reported in the Rossi et al. (2108) study.

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

Disease

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

Ocean acidification

Coral reef biology has been transformed by an appreciation of the threats posed to calcareous taxa by ocean acidification (OA) (Chan & Connolly, 2012; Kroeker et al., 2013), which is driven by rising atmospheric CO_2 and its effects on seawater chemistry. The effects of these trends on scleractinian corals have been extensively studied to reveal inhibitory effects on net calcification (Chan & Connelly, 2012; Kroeker et al., 2013; Comeau et al., 2014). The effects of OA, particularly the consequences of exposure to low pH and elevated pCO_2, have diverse implications for scleractinians, including gamete mobility, fertilization success (Albright, 2011), recruitment (Albright et al., 2010; Doropoulos et al., 2012), and abundance (Kroeker et al., 2013). Since octocorals do not produce a massive calcareous skeleton, it is reasonable to hypothesize that they will be less affected by OA than scleractinians. However, while octocorals are “soft” they contain calcified sclerites that have important functional implications for skeletal strength and flexibility (Bayer, 1961). There are signs that the capacity to deposit these structures is impaired under OA (Gomez et al., 2015; Bramanti et al., 2013), although octocoral tissue appears to reduce or prevent dissolution of sclerites under low pH (7.3 and 7.8) (Gabay et al., 2014).

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

5.0 Resilience and resistance of modern octocoral communities.

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

Disturbance, Resilience and the Octocoral Forest

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

The origins of that resilience are largely the traits that have enabled their survival under steady state conditions. First, as described above, the morphological strategy and rapid linear growth of arborescent octocorals provides a means by which recruits can rapidly grow to adult size and avoid mortality on the substratum where they can be smothered by macroalgae. Second, and in contrast to scleractinians, octocoral recruitment has enabled recovery from events such as hurricanes (Lasker et al., 2020). Third, while octocorals are not immune to bleaching and disease, they have been less affected by these disturbances than scleractinians. Fourth, historic and recent surveys of octocoral communities reveal high species diversity. Recent research is beginning to reveal the extent to which octocoral species differ from one another with respect to their nutritional strategies, structure, and symbiont performance (Rossi et al., 2018, 2020). It is interesting to speculate that the co-occurrence of morphologically similar species results in a high degree of functional redundancy (Rosenfeld, 2002), which could contribute to high community resilience.

Finally, we need to consider the degree to which octocoral communities and octocoral forests (sensu Rossi et al., 2017) modify their environment, and thus their interactions with the physical environment and with each other. It is this last component that we focus on in this section. A terrestrial forest biome classically is defined as a complex ecosystem consisting mainly of trees, which are the ecosystem engineers of the community (sensu Jones et al., 1994). The central characteristic of a forest is the emergent property of the three-dimensional structure, which supports biodiversity and provides shelter and food for numerous species of plants and animals (Sasaki & Putz, 2009). Physically, a forest can be divided into several zones, among them the distal canopy composed of leaves and branches, and the understory community that operates in physical conditions that differ from those prevailing outside the forest. On tropical reefs, scleractinians, octocorals, and hydrocorals, are the “trees,” the ecosystem engineers of the community (Rossi et al., 2017) (Figs. 10, 11). Like terrestrial forests, octocoral forests generate 3-D frameworks with high structural complexity. While lacking basal roots and the capacity for basal-distal internal transport, dense populations of arborescent octocorals share many functional similarities with terrestrial forests. Viewing octocoral communities in this manner identifies theoretical and empirical approaches that may be important in understanding the processes responsible for structuring and maintaining octocoral forests.

6.0. Canopies formed by dense stands of octocorals

Structure-forming marine organisms modify, create, and maintain habitat and their presence can define entire ecosystems, including, for example kelp forests, mangroves and coral reefs (Bruno & Bertness, 2001). Arborescent octocorals that form dense canopies modify the physical and chemical environmental conditions and can also be considered ecosystem engineers.

Effects on seawater currents

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

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

The effect of the canopy on the water flow within octocoral forests on St. John has been examined by measuring the current speed across the bottom boundary layer at different octocoral densities and over a vertical profile from the seafloor to 3 m above the seafloor. Measures with an Acoustic Doppler Current Profiler (ADCP) provide high spatial resolution to distinguish current profiles at 3 cm intervals. The octocoral canopy affected the RSL at densities > 7 colonies m^{-2}, suggesting a threshold in colony density above which the canopy has a hydrodynamic effect, which is expressed as a decay in the exponential flow velocity in the lower portion of the RSL (i.e. within the canopy) (Fig. 12). In the upper portion of the RSL, enhanced turbulence extends above the canopy to 130% of the total height of the canopy, thus creating a downward vector of flow (in the Z axis) (L. Bramanti unpublished data). The turbulence structure within the canopy affects resuspension and sedimentation (Cerpovicz & Lasker, submitted), and the increased turbulence over the RSL may modify the supply of waterborne resources (e.g., zooplankton and nutrients) to the octocoral colonies beneath the canopy as well as the understory community. This effect would affect resource competition between community members with an advantage for the species in the higher portion of the canopy which would experience higher supply of waterborne resources generating a trophic shadow (*sensu* Porter, 1976) over the understory community, which would experience a reduced particle flux. The potential importance of resource competition is suggested by Kim & Lasker (1997) who showed that *Plexaura homomalla* branches in the center of a linear array of branches had lower growth rates than the exterior branches.

Shading

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

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

Self-thinning

Competition would seem to be an inevitable consequence of the presence of a canopy in which colonies can restrict the access of adjacent colonies to light and nutrients (Kim & Lasker, 1997), or directly interfere with each other (Gambrel & Lasker, 2016). Sessile organisms cannot escape those effects, and growth will be affected by the density of potential competitors. In plant communities this is manifested as the self-thinning “rule” (Tadaki & Shidei,1959; Yoda et al., 1963). Self-thinning refers to a reduction in the number of surviving individuals in a cohort as those individuals increase in size, presumably due to competition for limiting resources, such as food or space (Fréchette & Lefaivre, 1990). As a result, there is an inverse relationship between the average size of individuals (i.e., biomass) and population density (Westoby, 1981; White et al., 2007). In recent years, support for the self-thinning rule has come from several coral populations. Linares et al. (2008) found that self-thinning applies to the Mediterranean gorgonian *Paramuricea clavata*, but not to *Eunicella singularis.* The applicability of self-thinning to the precious Mediterranean red coral, *Corallium rubrum*, was rejected by Garrabou et al.

(2017) based on a study conducted at ≤ 30-m depth and focusing on colonies ≤ 9-cm tall. However, when this species was studied over a wider depth range (i.e., ≤ 155 m) and included colonies as big as 35-cm tall, self-thinning emerged as a potential mechanism driving differences between the shallow- and deep- water populations (Cau et al., 2016), as predicted by modeling (Bramanti et al., 2009).

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

Finding self-thinning is consistent with the presence of common competitive interactions. Not finding such effects in communities composed of multiple species with a range of ages does not demonstrate an absence of competition. The self-thinning concept was developed and tested in monocultures of even-aged trees (Westoby, 1984; Weller, 1987). Future research should combine measures of density and size at the population level (i.e., by species) in order to focus on evaluating the extent to which self-thinning might affect octocoral community dynamics, and the conditions under which its effects might be most strongly expressed. Understanding if the self-thinning rule scales up from populations to multispecific communities would improve capacities both to evaluate the stability of communities formed by arborescent octocorals, and to predict the effects of future disturbances (Linares, et al. 2008).

Density-dependent recruitment.

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

7.0. Goods and services delivered by octocorals

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

The principal ecosystem service that Caribbean octocoral canopies provide is habitat structure. Physical structure provided by corals generally increases biodiversity of associated organisms, such as invertebrates and fish (Reaka-Kudla, 1997). Similarly, octocoral canopies increase surface cover that acts as living space, and partition space to provide refuge from predators (Tsounis et al., 2020), and by creating a 3-D structure, the canopy should reduce the visual detection of benthic organisms by fish predators hunting in demersal waters (e.g., Dahlgren & Eggleston, 2000; Anderson, 2001; Walter & Haynes, 2006; Pollux et al., 2007). Caribbean fishes associate with and dwell within octocoral canopies that are efficient at providing visual cover to individual fish that can confuse their visual predators (Tsounis et al., 2020). Little is known effects Caribbean of octocoral canopies on the invertebrate fauna, but preliminary data indicate that invertebrate communities at the south shore of St. John, US Virgin Islands, are composed of 66 genera and 82 species (J. Girard pers. comm.). Further research is required to quantify canopy-mediated increase of diversity and productivity, but it appears likely that the invertebrate fauna present provides a base for a food chain that has cascading effects into commercial fisheries of carnivorous fish species.

Octocoral habitat is being increasingly used as commercial fishing grounds in the Caribbean, such as in the US Virgin Islands (Wolff et al. 1999), as a result of degrading structural complexity of reefs (Wolff et al., 1999; Alvarez-Filip et al., 2009). While no data confirm increases of fish biomass under octocoral canopies, the concentration of fish in a specific location due to attraction (Tsounis et al., 2020) is arguably an ecosystem service of octocoral communities. Such effects, once detected, can reduce fishing effort and makes fisheries more profitable.

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

There are no estimates that quantify the productivity and carbon budgets of octocoral forests in the tropical western Atlantic, but octocorals are known to contribute to the carbonate budget of coral reefs. Cary (1915) estimated that octocorals occurring at high density (15.9 octocorals m^{-2}) produced up to 13.6 kg m^{-2} of calcium carbonate per year in the form of spicules supplied to the sediment. His estimate was based on an average mortality of 17.2% of the octocoral fauna (a conservative estimate of dead skeletons present on the reef), over 5 years from 1910 to 1915 (Cary, 1915). The proportion of those sclerites that become incorporated into the sediments and ultimately lithified is unknown.

Octocorals are also a source of bioactive metabolites. These compounds have promising pharmaceutical activity, and octocorals have long been systematically screened for secondary compounds with biomedical and cosmetic value (Gerhart & Coll, 1993; Rodríguez, 1995). Direct harvesting of octocorals for extraction of commercially important compounds occurs with *Antillogorgia* (*Pseudopterogorgia*) *elisabetha*e on the shallow reefs of the Little Bahama Bank (Goffredo & Lasker, 2008). *A. elisabethae* contains pseudopterosins (Look et al., 1986), that are used by the cosmetic industry for their anti-inflammatory and analgesic properties (Bruckner, 2002). The fishery for *A. elisabethae* is regulated by the Bahamas Department of Marine Resources, and when last reported had an estimated annual value of $ 3–4 million (Bruckner, 2002), meeting an estimated demand of 30–45 tons of *A. elisabethae* per year (Puyana et al., 2004). Finally, octocorals can also be goods themselves, as some species are globally harvested (legally and illegally) for use of their skeleton as raw material in jewelry, or for use of entire small colonies in the aquarium curio trade (Tsounis et al., 2010).

8. The future

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

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

2. *Bleaching.* Much of the current success of octocorals on western Atlantic reefs may be due to their relative resistance to thermal stress and bleaching. Extensive surveys during bleaching events and experimental studies are needed to identify the mechanistic basis of that resistance, to identify the role of the host and Symbiodiniacae symbionts, and to characterize the variation that occurs between species and habitats.

3. *Recruitment.* The colonization of substratum released through mortality of scleractinians may also be a critical component of the modern success of octocorals. Although little is known about the processes controlling octocoral recruitment, there are some indications for possible mechanisms:

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

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

Most importantly, whatever the process regulating octcocoral recruitment might be, we need to ascertain how they will be affected by future changes in the environment.

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

5. Octocoral demography. The upward trend in abundance of octocorals on reefs in the tropical western Atlantic reflects successful recruitment and growth over shrinkage and mortality. While little is known about the biology of octocorals in this region, their demographics are even less understood. Demographic models exist for only a handful of species (e.g., Gotelli, 1991; Lasker, 1991; Yoshioka, 1994; Goffredo & Lasker, 2008; Bruno et al., 2011; Bramanti et al., 2009; 2014; Santangelo et al., 2007; Linares & Doak, 2010). Demographic models can identify life history characteristics that are key factors in controlling population abundance and generate hypotheses regarding the processes controlling population growth. More detailed spatial knowledge on octocoral distribution and demography will be key to identifying threats to octocoral communities as well as the services they provide.

6. Holistic analyses of coral reef communities. For decades, coral reef biology has advanced through analyses focused on scleractinians or only a handful of benthic groups, and in the majority of cases the studies have focused on a single stressor (e.g., ocean acidification, temperature, disease etc.). As scleractinians have declined in abundance, “traditional” functional groups have less influence on the ecological processes affecting benthic communities, and now the future of “coral” reefs arguably is best described by focusing on a wide diversity of taxa. Reefs dominated by different taxa are less tractable to traditional approaches (e.g., benthic cover), particularly as taxonomic resolution will be challenged by the profusion of morphologically similar, but genetically diverse, taxa including sponges and octocorals. Where these taxa are tall and erect, their planar cover provides a poor proxy for biomass or ecological impact, and their quantification will need to move beyond this simple metric. Finally, holistic analyses that incorporate interactions of octocorals with other taxa will be key to evaluate ecosystem services.

Summary

Octocorals on reefs in the tropical western Atlantic have remained understudied for over 50 years. Most studies have described deteriorating reef communities by the abundances of scleractinians and reef fishes, leading to the modern notion of the “coral reef crisis” (Hughes, 1994; Gardner et al., 2003; Bellwood et al., 2004). The impact of those changes has been enormous, but those characterizations do not capture all of the dynamics of 21st century reefs. Octocorals have increased in abundance and expanded their occupancy of reef surfaces (Ruzicka et al., 2013; Lenz et al., 2015; Sanchez et al., 2019), and it has become clear that the dynamics of octocorals differs from that of scleractinians.

With fewer scleractinians to study and community dynamics influenced more strongly by other taxa, biologists increasingly study octocorals. (Kupfner Johnson & Hallock, 2020). This review focused on the ecology of octocorals and on the characteristics that could have favored their increasing abundance. The trends described above point to the ecological significance of a tree-like morphology and the exploitation of the seawater volume above the benthos as reasons for the success of octocorals on modern reefs. The region-wide population decline of branching *Acropora* spp. (Aronson & Precht, 2001) left the functional niche of the water column underexploited by sessile taxa. The capacity for rapid linear growth allows octocorals to quickly evade competition with benthic macroalgae, and transition through the risky small size classes to reduce post-settlement mortality. By growing in dense clusters and forming dense forests (Rossi et al., 2017), octocorals benefit from canopy formation, promoting particle capture, larval retention, and beneficially exploiting hydrodynamic regimes (Guizien & Ghisalberti, 2017).

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

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Tables

Table 1. Annual survival of octocoral colonies

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

Table 2. Growth rates of Caribbean gorgonians.

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

Growth rates from Borgstein et al. (2020) were taken from their Figure 1 and are median values.
All other rates are averages. Calculations excluded cases of negative growth.
Unless indicated grwoth rates are for colonies >10 cm height

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

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

Legends

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Fig. 1

Fig. 2

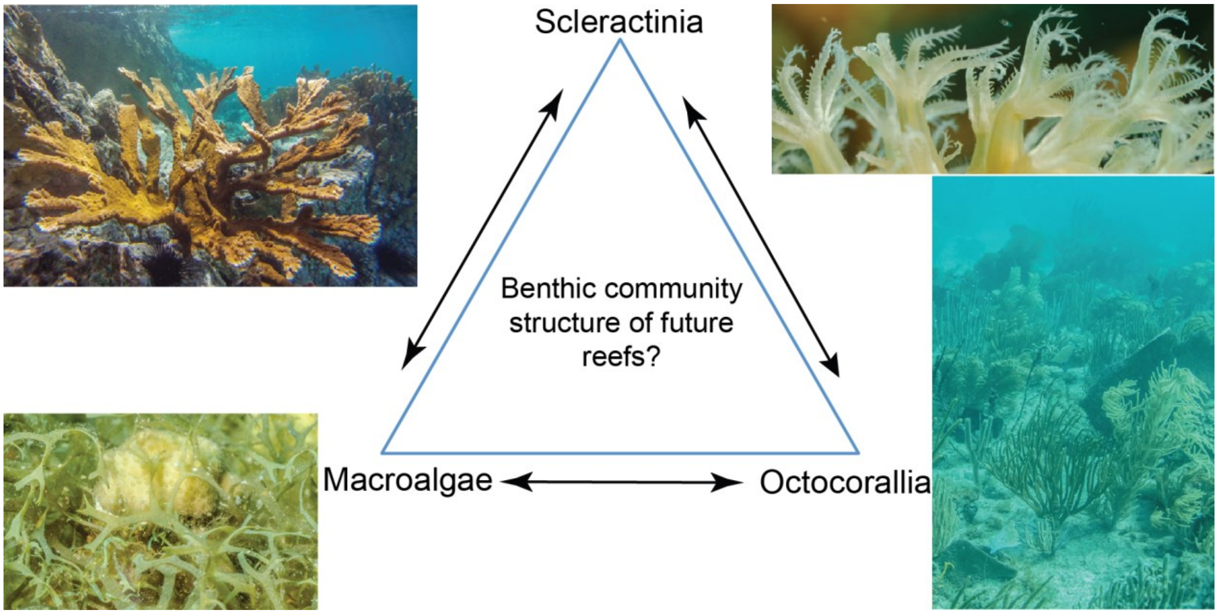

Scleractinia
Benthic community structure of future reefs?
Macroalgae
Octocorallia

Fig. 3

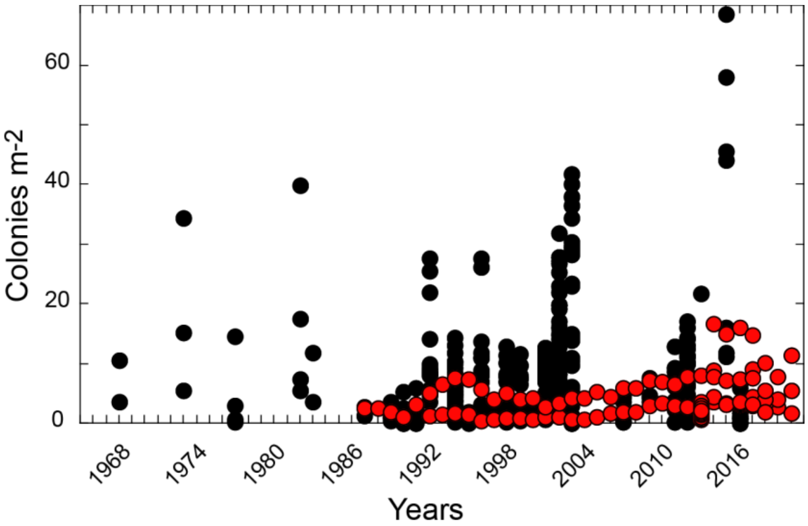

Colonies m-2
0
20
40
60
1968
1974
1980
1986
1992
1998
2004
2010
2016
Years

Fig. 4

Fig. 5

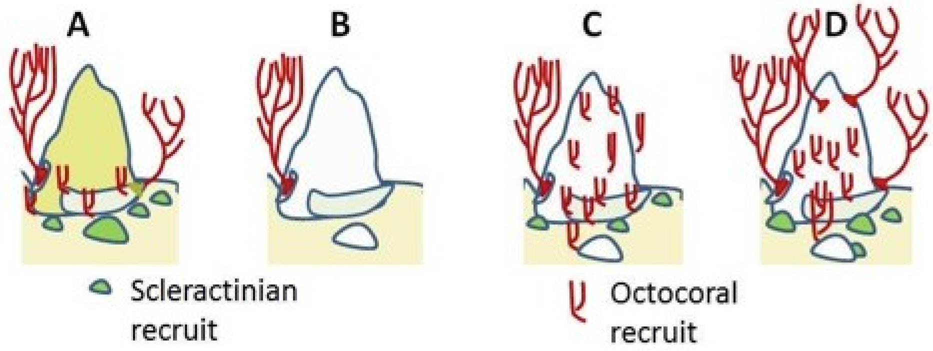


Fig. 6

Fig. 7

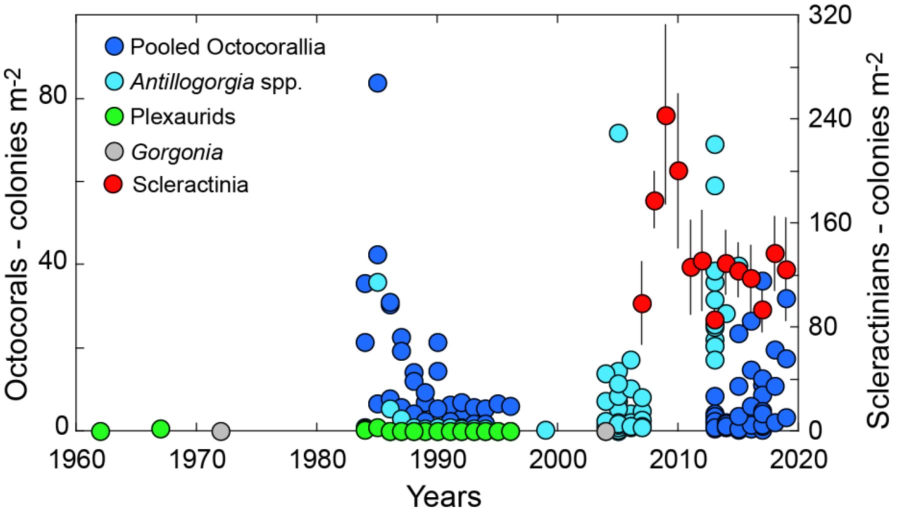

Pooled Octocorallia
Antillogorgia spp.
Plexaurids
Gorgonia
Scleractinia
Octocorals - colonies m-2
0
40
80
Scleractinians - colonies m-2
0
80
160
240
320
1960
1970
1980
1990
2000
2010
2020
Years

Fig. 8

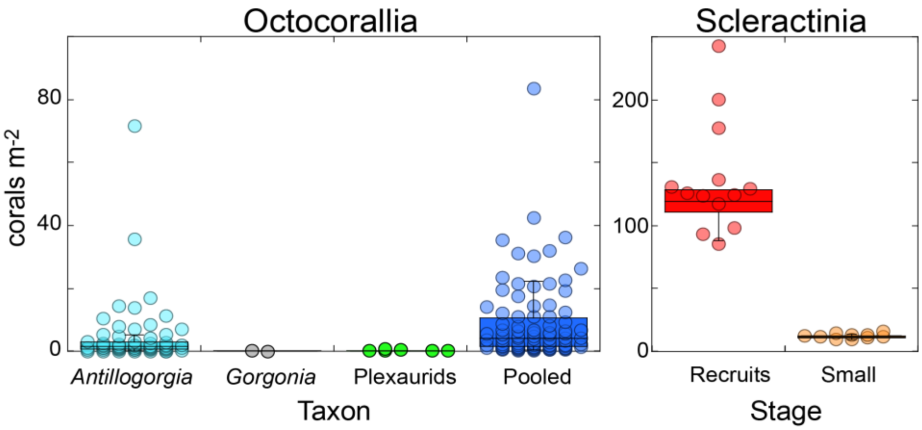

Octocorallia
Scleractinia
corals m-2
0
40
80
0
100
200
Antillogorgia
Gorgonia
Plexaurids
Pooled
Taxon
Recruits
Small
Stage

Fig. 9

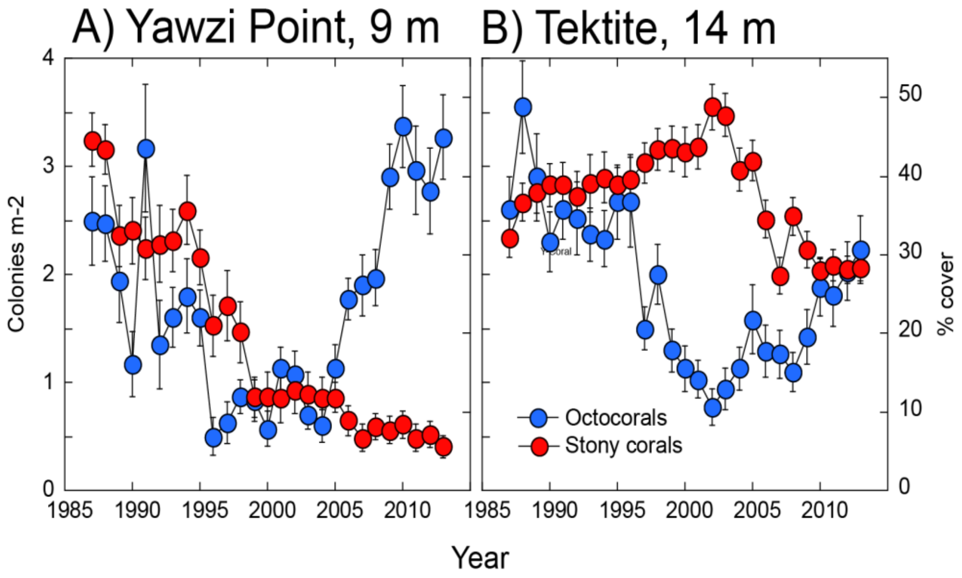

A) Yawzi Point, 9 m
B) Tektite, 14 m
Colonies m-2
% cover
Year
Octocorals
Stony corals
0
1
2
3
4
0
10
20
30
40
50
1985
1990
1995
2000
2005
2010

Fig. 10

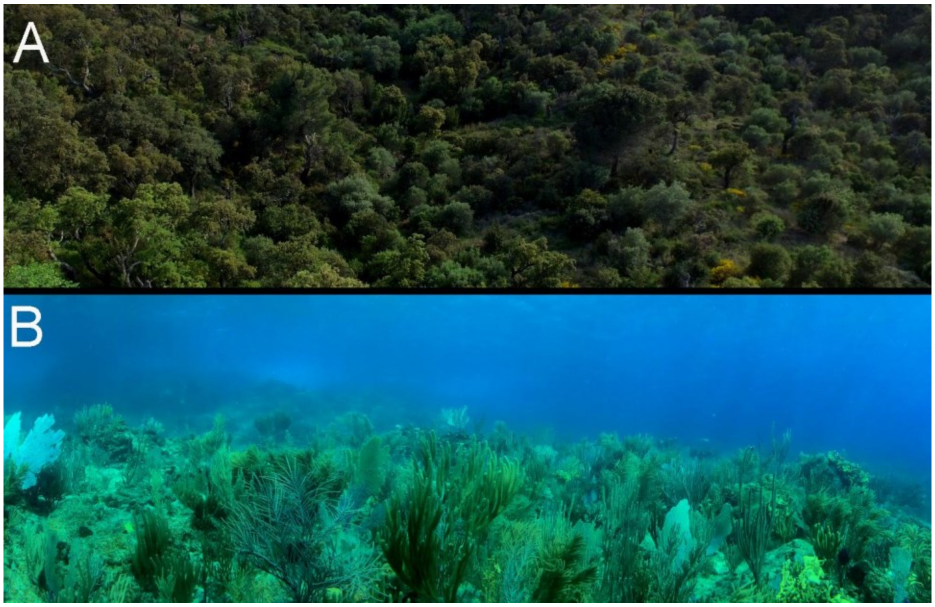
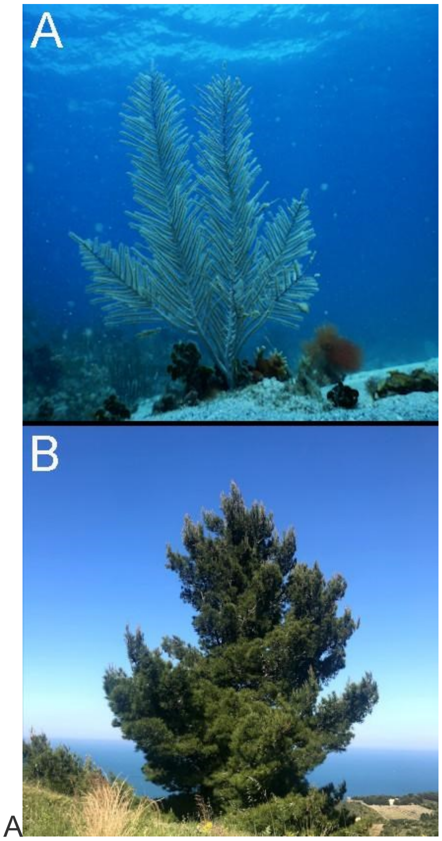


Fig. 11



A

Fig. 12

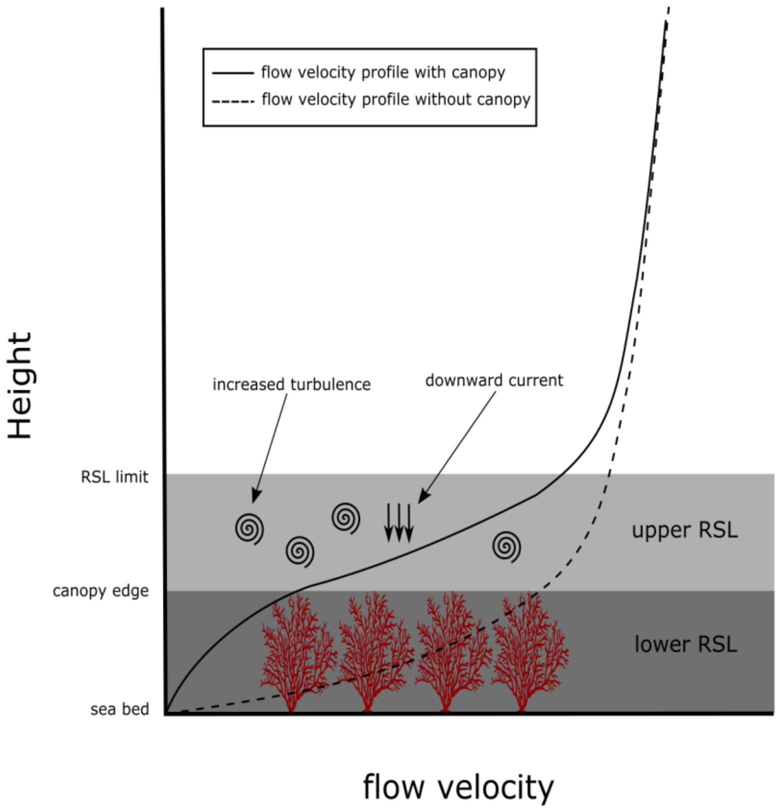

flow velocity profile with canopy
flow velocity profile without canopy
Height
increased turbulence
downward current
RSL limit
canopy edge
sea bed
upper RSL
lower RSL
flow velocity

Fig. 13

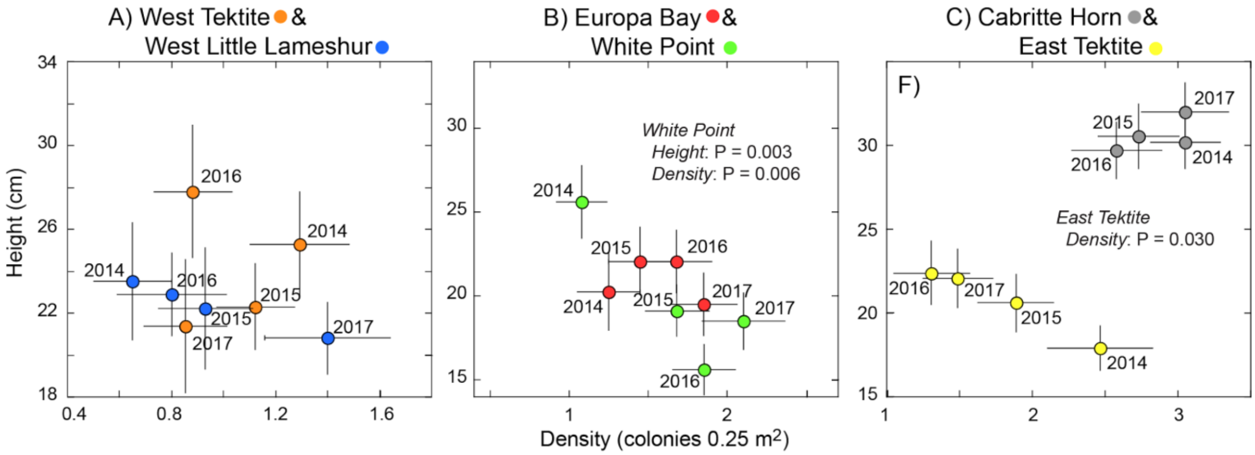

A) West Tektite ● &
West Little Lameshur ●
B) Europa Bay ● &
White Point ●
C) Cabritte Horn ● &
East Tektite ●
Height (cm)
34
30
26
22
18
0.4
0.8
1.2
1.6
2016
2014
2016
2015
2015
2017
2017
2014
White Point
Height: P = 0.003
Density: P = 0.006
30
25
20
15
1
2
2014
2015
2016
2014
2015
2017
2017
2016
Density (colonies 0.25 m2)
F)
2017
2015
2016
2014
East Tektite
Density: P = 0.030
30
25
20
15
1
2
3
2016
2017
2015
2014

Fig. 14

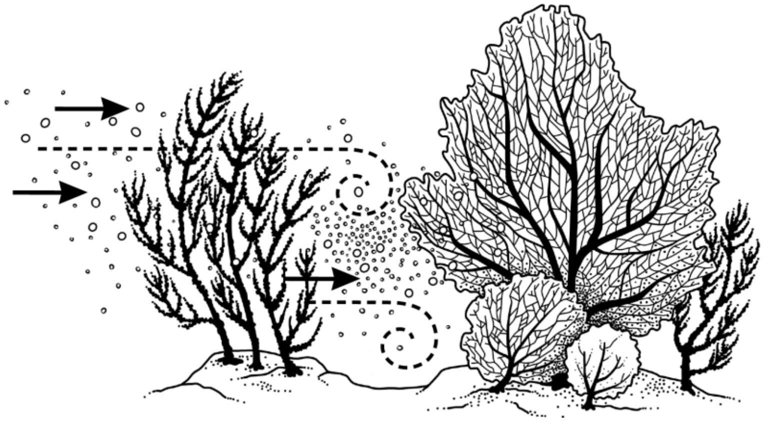
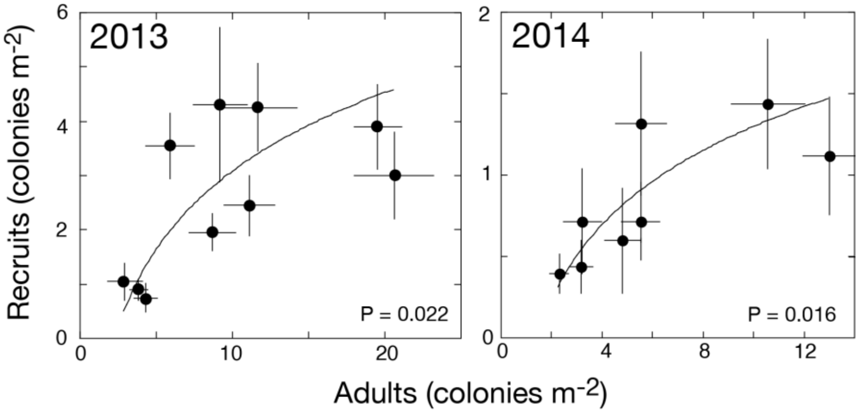


Fig. 15


2013
2014
Recruits (colonies m-2)
Adults (colonies m-2)
P = 0.022
P = 0.016
0
2
4
6
0
10
20
0
1
2
0
4
8
12