Appendix 1: Coral 5-Year Status Review

2014-2020

Bibliography

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BACKGROUND AND SCOPE

There are seven species of Caribbean coral listed under the Endangered Species Act. Elkhorn coral (*Acropora palmata*) and staghorn coral (*Acropora cervicornis*) were listed as threated in 2006 (71 FR 26852). Pillar coral (*Dendrogyra cylindrus*), rough cactus coral (*Mycetopyllia ferox*), lobed star coral (*Orbicella annularis*), mountainous star coral (*Orbicella faveolata*), and boulder star coral (*Orbicella franksi*) were listed as threatened in 2014 (79 FR 53851). A status review of *A. palmata* and *A. cervicornis* was performed during the listing process for the five other coral species, and both Acropora species were re-affirmed as threatened in the 2014 listing rule (79 FR 53851).

This document summarizes information and literature published since 2014 to inform a review of the status of the seven threatened Caribbean coral species. Published literature was compiled using online databases, including BioOne Complete, EBSCO's Academic Search Ultimate, Google Scholar, JSTOR, PubMed (Medline), ProQuest Agricultural and Environmental Science Database, Science Direct, Scopus, and Web of Science Biological Abstracts, to identify relevant information for each of the ESA-listed species. Only English language materials were reviewed, and only literature relevant to the status and threats to the species is included in this review. Additionally, unpublished information was sought from the general public and the scientific community though email and notification in the Federal Register. The information gathered from all these sources is organized in this document by species, and subsequently organized under the categories below. If there was no information in a category, the category was omitted.

Biology and Life History Characteristics
These sections contain relevant information on topics including growth, calcification, survival rates, dispersal, larval settlement behavior and patterns, and feeding, as well as research on corals' complex associations with various species of algal endosymbionts.

Abundance, Population, and Demographic Features and Trends
These sections contain relevant information on population and abundance trends, demographic features such as size/age structures, colony sizes, and other demographic trends.

Genetic Assessment
These sections contain relevant information on genetics, genetic variation, and trends in genetic variation, including surveys of clonality and potential corridors for genetic drift.

Spatial Distribution
These sections contain relevant information on the respective species' spatial distribution and trends in spatial distribution.

Habitat and Ecosystem Conditions
These sections contain relevant information on the status of coral habitats, habitat suitability, and determination of sites as potential coral habitats.

Threat Assessment
These sections contain relevant information on current and potential threats to coral populations and coral health, which includes research on thermal and acidic stress, coral diseases, pollution, and predation.

Restoration and Conservation Methods
These sections contain relevant information on methods used for coral restoration purposes, including outplanting and constructing artificial reefs, as well as research that may inform how to optimize coral restoration efforts. This section pertains primarily to staghorn coral and elkhorn coral due to their common use in Caribbean reef restoration projects.

STAGHORN CORAL (ACROPORA CERVICORNIS)

Biology and Life History Characteristics

> Bedwell-Ivers, H. E., Koch, M. S., Peach, K. E., Joles, L., Dutra, E. & Manfrino, C. (2017). The role of *in hospite* zooxanthellae photophysiology and reef chemistry on elevated pCO2 effects in two branching Caribbean corals: Acropora cervicornis and Porites divaricata. *ICES J Mar Sci*, 74, 1103–1112.
> https://doi.org/10.1093/icesjms/fsw026

Previous studies suggest uniform reductions in coral calcification under ocean acidification (OA); however, greater tolerance has been observed under natural diel metabolic signals present on reefs. In addition, few studies have examined the role of *in hospite* zooxanthellae energetics on coral OA tolerance. In this study, we examined zooxanthellae photosynthesis and coral calcification responses using seawater with natural metabolic dissolved inorganic carbon (DIC) dynamics from a fringing back reef on Little Cayman Island, Caribbean. The experimental design included Acropora cervicornis and Porites divaricata microcolonies grown in continuously flowing seawater with (□1000 µatm) and without (□500 µatm) CO2 enrichment to year 2100 predicted levels. Calcification rates were measured weekly, while linear extension and zooxanthellae photosynthesis were determined at the termination of the 28 d experiment. Results showed A. cervicornis microcolonies maintained both photosynthesis and calcification under elevated CO2 partial pressure (pCO2) relative to controls. However, photosynthesis and calcification rates of P. divaricata microcolonies were reduced by □80 and 20%, respectively, under relatively high [DIC]:[H+] ratios and aragonite saturation states (Ωarag). Porites divaricata calcification response to elevated pCO2 was linked to photophysiological dysfunction of the algal symbiont, an indicator that this species was metabolically depressed under elevated pCO2. In contrast to calcification, linear extension rates were unaffected by pCO2 in both species. Future studies should investigate how elevated pCO2 may compromise zooxanthellae–coral interactions with an emphasis on DIC uptake pathways.

> Godoy-Vitorino, F., Ruiz-Diaz, C. P., Rivera-Seda, A., Ramírez-Lugo, J. S. & Toledo-Hernández, C. (2017). The microbial biosphere of the coral Acropora cervicornis in Northeastern Puerto Rico. *PeerJ*, 5, e3717.
> https://doi.org/10.7717/peerj.3717 (Godoy-Vitorino et al. 2017)

Background Coral reefs are the most biodiverse ecosystems in the marine realm, and they not only contribute a plethora of ecosystem services to other marine organisms, but they also are beneficial to humankind via, for instance, their role as nurseries for commercially important fish species. Corals are

considered holobionts (host + symbionts) since they are composed not only of coral polyps, but also algae, other microbial eukaryotes and prokaryotes. In recent years, Caribbean reef corals, including the once-common scleractinian coral Acropora cervicornis, have suffered unprecedented mortality due to climate change-related stressors. Unfortunately, our basic knowledge of the molecular ecophysiology of reef corals, particularly with respect to their complex bacterial microbiota, is currently too poor to project how climate change will affect this species. For instance, we do not know how light influences microbial communities of A. cervicornis, arguably the most endangered of all Caribbean coral species. To this end, we characterized the microbiota of A. cervicornis inhabiting water depths with different light regimes. Methods Six A. cervicornis fragments from different individuals were collected at two different depths (three at 1.5 m and three at 11 m) from a reef 3.2 km off the northeastern coast of Puerto Rico. We characterized the microbial communities by sequencing the 16S rRNA gene region V4 with the Illumina platform. Results A total of 173,137 good-quality sequences were binned into 803 OTUs with a 97% similarity. We uncovered eight bacterial phyla at both depths with a dominance of 725 Rickettsiales OTUs (Proteobacteria). A fewer number (38) of low dominance OTUs varied by depth and taxa enriched in shallow water corals included Proteobacteria (e.g. Rhodobacteraceae and Serratia) and Firmicutes (Streptococcus). Those enriched in deeper water corals featured different Proteobacterial taxa (Campylobacterales and Bradyrhizobium) and Firmicutes (Lactobacillus). Discussion Our results confirm that the microbiota of A. cervicornis inhabiting the northeastern region of Puerto Rico is dominated by a Rickettsiales-like bacterium and that there are significant changes in less dominant taxa at different water depths. These changes in less dominant taxa may potentially impact the coral's physiology, particularly with respect to its ability to respond to future increases in temperature and CO2.

Kuffner, I. B., Bartels, E., Stathakopoulos, A., Enochs, I. C., Kolodziej, G., Toth, L. T. & Manzello, D. P. (2017). Plasticity in skeletal characteristics of nursery-raised staghorn coral, Acropora cervicornis. *Coral Reefs* 36(3), 679–684. https://doi.org/10.1007/s00338-017-1560-2 (Kuffner et al. 2017)

Staghorn coral, Acropora cervicornis, is a threatened species and the primary focus of western Atlantic reef restoration efforts to date. We compared linear extension, calcification rate, and skeletal density of nursery-raised A. cervicornis branches reared for 6 months either on blocks attached to substratum or hanging from PVC trees in the water column. We demonstrate that branches grown on the substratum had significantly higher skeletal density, measured using computerized tomography, and lower linear extension rates compared to water-column fragments. Calcification rates determined with buoyant weighing were not statistically different between the two grow-out methods, but did vary among coral genotypes. Whereas skeletal density and extension rates were plastic traits that depended on grow-out method, calcification rate was conserved. Our results show that the two rearing methods generate the same amount of calcium carbonate skeleton but produce colonies with different skeletal characteristics and suggest that there is genetically based variability in coral calcification performance.

Lirman, D., Schopmeyer, S., Galvan, V., Drury, C., Baker, A. C. & Baums, I. B. (2014). Growth Dynamics of the Threatened Caribbean Staghorn Coral Acropora cervicornis: Influence of Host Genotype, Symbiont Identity, Colony Size, and Environmental Setting. *PLOS ONE*, 9(9),

e107253.
https://doi.org/10.1371/journal.pone.0107253 (Lirman et al. 2014)

Background The drastic decline in the abundance of Caribbean acroporid corals (Acropora cervicornis, A. palmata) has prompted the listing of this genus as threatened as well as the development of a regional propagation and restoration program. Using in situ underwater nurseries, we documented the influence of coral genotype and symbiont identity, colony size, and propagation method on the growth and branching patterns of staghorn corals in Florida and the Dominican Republic. Methodology/Principal Findings Individual tracking of> 1700 nursery-grown staghorn fragments and colonies from 37 distinct genotypes (identified using microsatellites) in Florida and the Dominican Republic revealed a significant positive relationship between size and growth, but a decreasing rate of productivity with increasing size. Pruning vigor (enhanced growth after fragmentation) was documented even in colonies that lost 95% of their coral tissue/skeleton, indicating that high productivity can be maintained within nurseries by sequentially fragmenting corals. A significant effect of coral genotype was documented for corals grown in a common-garden setting, with fast-growing genotypes growing up to an order of magnitude faster than slow-growing genotypes. Algal-symbiont identity established using qPCR techniques showed that clade A (likely Symbiodinium A3) was the dominant symbiont type for all coral genotypes, except for one coral genotype in the DR and two in Florida that were dominated by clade C, with A- and C-dominated genotypes having similar growth rates. Conclusion/Significance The threatened Caribbean staghorn coral is capable of extremely fast growth, with annual productivity rates exceeding 5 cm of new coral produced for every cm of existing coral. This species benefits from high fragment survivorship coupled by the pruning vigor experienced by the parent colonies after fragmentation. These life-history characteristics make A. cervicornis a successful candidate nursery species and provide optimism for the potential role that active propagation can play in the recovery of this keystone species.

Lohr, K. E., Khattri, R. B., Guingab-Cagmat, J., Camp, E. F., Merritt, M. E., Garrett, T. J. & Patterson, J. T. (2019). Metabolomic profiles differ among unique genotypes of a threatened Caribbean coral. *Scientific Reports*, 9(1), 6067.
https://doi.org/10.1038/s41598-019-42434-0 (Lohr et al. 2019)

Global threats to reefs require urgent efforts to resolve coral attributes that affect survival in a changing environment. Genetically different individuals of the same coral species are known to exhibit different responses to the same environmental conditions. New information on coral physiology, particularly as it relates to genotype, could aid in unraveling mechanisms that facilitate coral survival in the face of stressors. Metabolomic profiling detects a large subset of metabolites in an organism, and, when linked to metabolic pathways, can provide a snapshot of an organism's physiological state. Identifying metabolites associated with desirable, genotype-specific traits could improve coral selection for restoration and other interventions. A key step toward this goal is determining whether intraspecific variation in coral metabolite profiles can be detected for species of interest, however little information exists to illustrate such differences. To address this gap, we applied untargeted 1H-NMR and LC-MS metabolomic profiling to three genotypes of the threatened coral Acropora cervicornis. Both methods revealed distinct metabolite "fingerprints" for each genotype examined. A number of metabolites driving separation among genotypes were identified or putatively annotated. Pathway analysis suggested differences in protein synthesis among genotypes. For the first time, these data illustrate intraspecific variation in metabolomic

profiles for corals in a common garden. Our results contribute to the growing body of work on coral metabolomics and suggest future work could identify specific links between phenotype and metabolite profile in corals.

Mercado-Molina, A. E., Ruiz-Diaz, C. P. & Sabat, A. M. (2014). Survival, growth, and branch production of unattached fragments of the threatened hermatypic coral Acropora cervicornis. *Journal of Experimental Marine Biology and Ecology*, 457, 215–219. https://doi.org/10.1016/j.jembe.2014.04.017 (Mercado-Molina et al. 2014)

Fragmentation has been regarded as the most important reproductive strategy in the threatened reef building coral Acropora cervicornis. Before the Caribbean-wide collapse experienced by A. cervicornis, asexual reproduction may have served as an effective source of new colonies to sustain and/or enhance local population growth. However, baseline information on the demographic success of fragments in nature is limited, hampering our ability to estimate the real contribution of asexual fragmentation to current population growth. In this study, natural occurring fragments of A. cervicornis were monitored for 18months at two sites in Puerto Rico in order to quantify their survival, growth, and branching dynamics. Fragment survivorship did not exceed 26%, growth rates were relatively low with mean values ranging between 0.0242±0.0168 (SE) and 0.0906±0.0301 (SE) cmd−1, and fragments barely produced new branches. No significant differences were found when comparing these demographic traits for different size categories. The relative low rates of survival, growth and branch production of natural fragments suggest that asexual fragmentation may not currently be a significant source of recruits for populations of this threatened coral.

Miller, M. W., A. J. Bright, R. E. Pausch, and D. E. Williams. 2020. Larval longevity and competency patterns of Caribbean reef-building corals. PeerJ 8:e9705. https://peerj.com/articles/9705/ (Miller et al. 2020a)

The potential for long-distance larval dispersal depends on the longevity of planktonic, free-swimming larvae and their capacity to successfully recruit to reef habitat. We present multi-year laboratory observations of the persistence of planular larvae and settlement competency over time for cohorts derived from the same parental populations of the most important Caribbean reef building coral species, Orbicella faveolata and Acropora spp. Despite variability among years/cohorts, larvae of both species display capacity for extended longevity (up to 83 d) and competency (demonstrated at up to 48 d). Both species also displayed significantly reduced survivorship and lower realized settlement under elevated temperatures. Although the observed levels of settlement in 24 h competency assays was extremely variable, the timing of onset of competence were highly consistent among years/cohorts but distinct between species. Orbicella faveolata displayed onset of competence during day 3-5 or 4-7 (with or without exposure to positive settlement cue) after spawning; whereas, onset for Acropora spp. was day 7-8 or day 10-11 (with or without cue, respectively). This longer pre-competency period for Acropora spp. nonetheless corresponded to a greater persistence of A. palmata larvae to this age of competence (71-83% of initial cohort compared to 54-55% for O. faveolata). Such life history variation implies meaningful differences in likely dispersal potential between these imperiled reef-building species.

Miller, N., P. Maneval, C. Manfrino, T. K. Frazer, and J. L. Meyer. 2020. Spatial distribution of microbial communities among colonies and genotypes in nursery-reared Acropora cervicornis. PeerJ 8:e9635. https://pubmed.ncbi.nlm.nih.gov/32913671/ (Miller et al. 2020b)

Background. The architecturally important coral species Acropora cervicornis and A. palmata were historically common in the Caribbean, but have declined precipitously since the early 1980s. Substantial resources are currently being dedicated to coral gardening and the subsequent outplanting of asexually reproduced colonies of Acropora, activities that provide abundant biomass for both restoration efforts and for experimental studies to better understand the ecology of these critically endangered coral species. Methods. We characterized the bacterial and archaeal community composition of A. cervicornis corals in a Caribbean nursery to determine the heterogeneity of the microbiome within and among colonies. Samples were taken from three distinct locations (basal branch, intermediate branch, and branch tip) from colonies of three different coral genotypes. Results. Overall, microbial community composition was similar among colonies due to high relative abundances of the Rickettsiales genus MD3-55 (Candidatus Aquarickettsia) in nearly all samples. While microbial communities were not different among locations within the same colony, they were significantly different between coral genotypes. These findings suggest that sampling from any one location on a coral host is likely to provide a representative sample of the microbial community for the entire colony. Our results also suggest that subtle differences in microbiome composition may be influenced by the coral host, where different coral genotypes host slightly different microbiomes. Finally, this study provides baseline data for future studies seeking to understand the microbiome of nursery-reared A. cervicornis and its roles in coral health, adaptability, and resilience.

Paradis, B. T., Henry, R. P. & Chadwick, N. E. (2019). Compound effects of thermal stress and tissue abrasion on photosynthesis and respiration in the reef-building coral Acropora cervicornis (Lamarck, 1816). *Journal of Experimental Marine Biology and Ecology*, 521, 151222. https://doi.org/10.1016/j.jembe.2019.151222 (Paradis et al. 2019)

Reef-building corals are threatened by multiple stressors, including rising ocean temperatures due to anthropogenic climate change, and tissue abrasion inflicted by increasing frequencies of recreational diving on tropical reefs. Both can impair coral growth and survival, but interactive effects of temperature and abrasion remain unknown. We conducted laboratory experiments to investigate the metabolic physiology of endangered Caribbean staghorn corals Acropora cervicornis (Lamarck, 1816) in response to both types of stressors: (1) temperature variation (22, 25, 28, and 30 °C) and (2) tissue abrasion (15% of tissue removed vs. non-abraded controls). Using flow-through respirometry, we measured net photosynthesis and respiration in 26 coral fragments (6 genotypes) exposed to 8 treatment combinations (4 temperature × 2 abrasion treatments). In non-abraded corals, net photosynthesis peaked at 25 °C but respiration increased linearly with temperature. Higher temperatures caused a decline in the ratio of photosynthesis to respiration (P:R), wherein corals were unable to meet their metabolic energy needs (P:R < 1). In addition, there was a significant interaction effect between the two stressors, in which tissue abrasion impaired photosynthesis and augmented respiration, especially at higher temperatures. We conclude that under conditions of both diver damage and elevated temperature, A. cervicornis cannot meet its energetic demands. These results indicate impairment of coral resilience to temperature-induced bleaching in areas exposed to high levels of abrasion (i.e.: popular dive sites). This information provides a

scientific basis to support local reef management during climate change, and also reveals the metabolic processes that precede and underlie coral bleaching on tropical reefs.

> Ritson-Williams, R., Arnold, S. N. & Paul, V. J. (2020). The impact of macroalgae and cyanobacteria on larval survival and settlement of the scleractinian corals Acropora palmata, A. cervicornis and Pseudodiploria strigosa. *Mar Biol*, 167(3), 31. https://doi.org/10.1007/s00227-019-3639-5 (Ritson-Williams et al. 2020)

Coral reefs are threatened by multiple stressors that degrade these ecosystems and the ecosystem services they provide. Critical to the recovery of coral reefs after a disturbance is coral recruitment, but there is still little information about the types of benthic habitats that different species of coral larvae require for settlement. Settlement in the presence of different algae and cyanobacteria was tested for three coral species, Acropora palmata, Acropora cervicornis and Pseudodiploria strigosa. The experiments were conducted in larval chambers placed on the reef to ensure that coral larvae were exposed to natural light, seawater temperature and some water flow. Rates of settlement and metamorphosis were assessed by providing these coral larvae with a standard preferred settlement substratum (individuals of the crustose coralline algal species Hydrolithon boergesenii) with an attached treatment of a small piece of live algae or benthic cyanobacteria. The brown algae Dictyota pulchella and D. bartayresiana did not affect the survival or settlement of larvae of A. palmata in 2010, but D. pulchella did reduce larval survival in 2009. Of the cyanobacteria tested, Caldora penicillata decreased A. palmata survival and settlement. For A. cervicornis, neither Dictyota pulchella nor D. bartayresiana reduced survival or settlement in either 2009 or 2010. Algae and cyanobacteria had no effect on Pseudodiploria strigosa larval survival, but there was reduced settlement in the presence of the cyanobacterium Hormothamnion enteromorphoides. These larval experiments show that some macrophytes can reduce coral larval survival and settlement even in the presence of highly preferred substrata.

> Towle, E. K., Enochs, I. C. & Langdon, C. (2015). Threatened Caribbean Coral Is Able to Mitigate the Adverse Effects of Ocean Acidification on Calcification by Increasing Feeding Rate. *PLOS ONE*, 10(4), e0123394. https://doi.org/10.1371/journal.pone.0123394 (Towle et al. 2015)

Global climate change threatens coral growth and reef ecosystem health via ocean warming and ocean acidification (OA). Whereas the negative impacts of these stressors are increasingly well-documented, studies identifying pathways to resilience are still poorly understood. Heterotrophy has been shown to help corals experiencing decreases in growth due to either thermal or OA stress; however, the mechanism by which it mitigates these decreases remains unclear. This study tested the ability of coral heterotrophy to mitigate reductions in growth due to climate change stress in the critically endangered Caribbean coral Acropora cervicornis via changes in feeding rate and lipid content. Corals were either fed or unfed and exposed to elevated temperature (30°C), enriched pCO2 (800 ppm), or both (30°C/800 ppm) as compared to a control (26°C/390 ppm) for 8 weeks. Feeding rate and lipid content both increased in corals experiencing OA vs. present-day conditions, and were significantly correlated. Fed corals were able to maintain ambient growth rates at both elevated temperature and elevated CO2, while unfed corals experienced significant decreases in growth with respect to fed conspecifics. Our results show for the first

time that a threatened coral species can buffer OA-reduced calcification by increasing feeding rates and lipid content.

Abundance, Population, and Demographic Features and Trends

> Bruckner, A. W., Beck, B. & Renaud, P. (2014). The status of coral reefs and associated fishes and invertebrates of commercial importance in Pedro Bank, Jamaica. *Rev. Biol. Trop.*, 62, 11–24. https://doi.org/10.15517/rbt.v62i0.15898 (Bruckner et al. 2014)

The coral reefs located off the north coast of the Jamaican mainland are some of the best and most studied reefs in the world. Coral reefs of Pedro Bank, Jamaica were assessed in March, 2012 as part of the KSLOF Global Reef Expedition using a modified Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol. The main objectives were to: 1) characterize the distribution, structure and health of coral reefs; and 2) evaluate the population status of commercially important reef fishes and invertebrates. This work was conducted to assist in characterizing coral reef habitats within and outside a proposed fishery reserve, and identify other possible conservation zones. Within 20 reefs, live coral cover ranged from 4.9% to 19.2%. Coral communities were dominated by small corals (esp. Agaricia, Porites and Siderastrea) although many sites had high abundances of large colonies of Montastraea annularis and M. faveolata, and these were generally in good condition. A single area, within the proposed fishery reserve, had extensive Acropora cervicornis thickets, and several shallow locations had small, but recovering A. palmata stands. Macroalgal cover at all sites was relatively low, with only three sites having greater than 30% cover; crustose coralline algae (CCA) was high, with eight sites exceeding 20% cover. Fish biomass at all sites near the Cays was low, with a dominance of herbivores (parrotfish and surgeonfish) and a near absence of groupers, snappers and other commercially important species. While parrotfish were the most abundant fish, these were all extremely small (mean size= 12cm; <4% over 29cm), and they were dominated by red band parrotfish (Sparisoma aurofrenatum) followed by striped parrotfish (Scarus iseri). While coral communities remain in better condition than most coastal reefs in Jamaica, intense fishing pressure using fish traps (main target species: surgeonfish) and hookah/spear fishing (main target: parrotfish) is of grave concern to the future persistence of these reefs. The proposed fishery reserve encompasses some of the best coral reef habitat near the Cays, but this MPA should be expanded to encompass other habitats and MPAs should be considered for bank reefs at the northwestern end, as well as Banner Reef and Blowers Rock.

> Busch, J., Greer, L., Harbor, D., Wirth, K., Lescinsky, H., Curran, H. A. & de Beurs, K. (2016). Quantifying exceptionally large populations of Acropora spp. corals off Belize using sub-meter satellite imagery classification. *Bulletin of Marine Science*, 92, 265–283. https://doi.org/10.5343/bms.2015.1038 (Busch et al. 2016)

Caribbean coral reefs have experienced dramatic declines in live coral cover in recent decades. Primary branching framework Caribbean corals, Acropora cervicornis (Lamarck, 1816) and Acropora palmata (Lamarck, 1816), have suffered the greatest collapse. Coral Gardens, Belize, is one of few remaining, and perhaps the largest, refugia for abundant, healthy, but undocumented populations of both Acropora species in the Caribbean Sea. In the present study, GeoEye-1 multispectral satellite imagery of a 25 km2

reefal area near Ambergris Caye, Belize, was analyzed to identify live Acropora spp. cover. We used a supervised classification to predict occurrence of areas with live Acropora spp. and to separate them from other benthic cover types, such as sandy bottom, seagrass, and mixed massive coral species. We tested classification accuracy in the field, and new Acropora spp. patches were mapped using differential GPS. Of 11 predicted new areas of Acropora spp., eight were composed of healthy Acropora spp. An unsupervised classification of a red (Band 3):blue (Band 1) ratio calculation of the image successfully separated Acropora corals from other benthic cover, with an overall accuracy of 90%. Our study identified 7.58 ha of reef dominated by Acropora spp. at Coral Gardens, which is one of the largest populations in the Caribbean Sea. We suggest that Coral Gardens may be an important site for the study of modern Acropora spp. resilience. Our technique can be used as an efficient tool for genera-specific identification, monitoring, and conservation of populations of endangered Acropora spp.

Crabbe, M. J. C. (2014). Evidence of initial coral community recovery at Discovery Bay on Jamaica's North Coast. *Rev. Biol. Trop.*, 62, 137–140. https://doi.org/10.15517/rbt.v62i0.15908 (Crabbe 2014)

Current challenges to coral reef sustainability include overfishing, destructive fishing practices, bleaching, acidification, sea-level rise, starfish, algae, agricultural run-off, coastal and resort development, pollution, diseases, invasive species and hurricanes. We used SCUBA belt transects to record coral cover and digital image analysis in the Dairy Bull Reef off the north coast of Jamaica and found that it is a positive example of how reefs can recover after major environmental disturbance. Live coral cover increased from 13±5% in 2006 to 31±7% in 2008, while live Acropora cervicornis increased from 2±2% in 2006 to 22±7% in 2008. Coral cover levels were maintained until 2012.

Cramer, K. L., Jackson, J. B. C., Donovan, M. K., Greenstein, B. J., Korpanty, C. A., Cook, G. M. & Pandolfi, J. M. (2020). Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. *Science Advances*, 6(17), eaax9395. https://doi.org/10.1126/sciadv.aax9395 (Cramer et al. 2020)

The mass mortality of acroporid corals has transformed Caribbean reefs from coral- to macroalgal-dominated habitats since systematic monitoring began in the 1970s. Declines have been attributed to overfishing, pollution, sea urchin and coral disease, and climate change, but the mechanisms are unresolved due to the dearth of pre-1970s data. We used paleoecological, historical, and survey data to track Acropora presence and dominance throughout the Caribbean from the prehuman period to present. Declines in dominance from prehuman values first occurred in the 1950s for Acropora palmata and the 1960s for Acropora cervicornis, decades before outbreaks of acroporid disease or bleaching. We compared trends in Acropora dominance since 1950 to potential regional and local drivers. Human population negatively affected and consumption of fertilizer for agriculture positively affected A. palmata dominance, the latter likely due to lower human presence in agricultural areas. The earlier, local roots of Caribbean Acropora declines highlight the urgency of mitigating local human impacts.

D'Antonio, N. L., Gilliam, D. S. & Walker, B. K. (2016). Investigating the spatial distribution and effects of nearshore topography on Acropora cervicornis abundance in Southeast Florida.

PeerJ, 4, e2473.
https://doi.org/10.7717/peerj.2473 (D'Antonio et al. 2016)

Dense Acropora cervicornis aggregations, or patches, have been documented within nearshore habitats in Southeast Florida (SE FL) despite close proximity to numerous anthropogenic stressors and subjection to frequent natural disturbance events. Limited information has been published concerning the distribution and abundance of A. cervicornis outside of these known dense patches. The first goal of this study was to conduct a spatially extensive and inclusive survey (9.78 km2) to determine whether A. cervicornis distribution in the nearshore habitat of SE FL was spatially uniform or clustered. The second goal was to investigate potential relationships between broad-scale seafloor topography and A. cervicornis abundance using high resolution bathymetric data. Acropora cervicornis was distributed throughout the study area, and the Getis-Ord Gi* statistic and Anselin Local Moran's I spatial cluster analysis showed significant clustering along topographic features termed ridge crests. Significant clustering was further supported by the inverse distance weighted surface model. Ordinal logistic regression indicated 1) as distance from a ridge increases, odds of reduced A. cervicornis abundance increases; 2) as topographic elevation increases, odds of increased abundance increases; and 3) as mean depth increases, odds of increased abundance increases. This study provides detailed information on A. cervicornis distribution and abundance at a regional scale and supports modeling its distributions in similar habitats elsewhere throughout the western Atlantic and Caribbean. Acropora cervicornis is frequently observed and in areas an abundant species within the nearshore habitat along the SE FL portion of the Florida Reef Tract (FRT). This study provides a better understanding of local habitat associations thus facilitating appropriate management of the nearshore environment and species conservation. The portion of the FRT between Hillsboro and Port Everglades inlets should be considered for increased management and protection to reduce local stressors.

García-Urueña, R. & Garzón-Machado, M. A. (2020). Current status of Acropora palmata and Acropora cervicornis in the Colombian Caribbean: demography, coral cover and condition assessment. *Hydrobiologia*, 847(9), 2141–2153.
https://doi.org/10.1007/s10750-020-04238-6 (García-Urueña and Garzón-Machado 2020)

Acropora provides an example of reef degradation, as evidenced by population reductions in Caribbean reefs. However, data on the current status of Acropora populations in Colombia are lacking. In this study, reef habitats were surveyed for Acropora palmata and Acropora cervicornis throughout the Colombian Caribbean, and the size structure, coverage and colony conditions of their populations were evaluated. Acropora palmata size classes were negatively skewed, indicating low recruitment. This species exhibited a patch-type distribution around Tayrona, Isla Fuerte and Isla Arena; these localities exhibited the highest cover among the surveyed regions. The lowest coral cover was recorded for the Rosario Islands. Healthy colonies were dominant; however, disease and damselfish territories were common. The size class data of Acropora cervicornis indicated the persistence of small colonies; however, no recruits were observed. The distribution was dispersed, with important patches and the highest cover observed around the Urabá Gulf and Rosario Islands. Overall, the cover was lower than 10%. Few healthy colonies were observed, and macroalgae and sponges were common. Conservation and management efforts are required for both species; for Acropora palmata, efforts targeting the Rosario Islands are needed, whereas Acropora cervicornis is in critical condition throughout the Colombian Caribbean.

Goergen, E. A., Moulding, A. L., Walker, B. K. & Gilliam, D. S. (2019). Identifying Causes of Temporal Changes in Acropora cervicornis Populations and the Potential for Recovery. *Front. Mar. Sci.*, 6:36. https://doi.org/10.3389/fmars.2019.00036 (Goergen et al. 2019)

Corals, specifically the Atlantic staghorn coral, Acropora cervicornis, have become more vulnerable to disturbance events such as storms and disease and predation outbreaks. Since its population declines due to a wide spread disease event in the early 1980s, limited long-term monitoring studies describing the impact of current threats and potential recovery have been completed. The aim of this study was to document the impacts of environmental (tropical storms, increased wind) and biological (disease and predation) threats on A. cervicornis to further understand its dynamics and potential for recovery. Two high-density A. cervicornis patches (greater than 1 hectare each) were surveyed tri-annually (winter, summer, fall) from 2008-2016. Acropora cervicornis percent cover, canopy height, census of individuals (fragments, colonies and masses), and prevalence and occurrence of disease, predation, and bleaching were evaluated within permanent 3.5 m radial plots. Temporal variability was observed in mean percent live cover at both patches and resulted in an overall loss of tissue. Frequent disturbances such as tropical storms, hurricanes, and disease events caused increased, prolonged, and widespread mortality. Periods void of disturbance allowed for recovery and growth. Prevalence and occurrence of disease and predation were highly variable between monitoring events. They were also found to be significantly higher on masses (individuals ≥ 1.5 m) than on colonies and during summer surveys. These data indicate that substantial length of time between major disturbance events are necessary for recovery and growth of this species. The implication from these results is that given the current rates of growth, recruitment, and storm frequency, natural species recovery is unlikely unless larger scale issues are addressed such as climate change and ocean warming, which could reduce the intensity and frequency of disease and predation.

Goergen, E. A., K. Semon Lunz, and D. S. Gilliam. 2020. Spatial and temporal differences in Acropora cervicornis colony size and health. Pages 83-114 in B. M. Riegl, editor. Population Dynamics of the Reef Crisis, volume 87. Acadmic Press. https://www.elsevier.com/books/population-dynamics-of-the-reef-crisis/riegl/978-0-12-821529-6 (Goergen et al. 2020)

Little to no recovery in Acropora cervicornis populations has been documented since the 1970s and 1980s widespread disease events, and disease and predation appear to remain significant drivers of mortality. However, to date, demographic studies of A. cervicornis lack data temporally or spatially sufficient to quantify factors limiting recovery. Acropora cervicornis populations in three regions [Broward County (BWD), Middle Keys (MDK), and Dry Tortugas (DRTO)] of the Florida Reef Tract were surveyed up to three times per year from 2011 to 2015. Temporal and spatial differences were evaluated for colony size, live tissue volume, and prevalence and impact of disease and predation. Significantly larger colonies were reported in BWD, and at relatively deeper or more sheltered sites. At least 43% of colonies in each region were of reproductively capable size. Mean relative change in colony size between surveys (3–5 months) ranged from -20% to 19%. Disease and predation were consistently present in all regions, but levels varied significantly across space and time. Disease prevalence was the most variable condition (ranging from 0% to 28% per survey), increasing after periods of elevated temperatures and environmental

disturbances, and caused significantly more partial mortality than fireworm (Hermodice carunculata) or snail (Coralliophila spp.) predation. Recovery potential and long-term persistence of this species may be limited due to the persistent presence of disease and predation, and reproductive limitations. However, there is still potential at sites of greater depth and/or more protection hosted larger and healthier colonies creating potential refugia for this species.

González-Díaz, P., González-Sansón, G., Aguilar Betancourt, C., Álvarez Fernández, S. & Perera Pérez, O. (2018). Status of Cuban coral reefs. *Bulletin of Marine Science*, 94(2), 229–247. https://doi.org/10.5343/bms.2017.1035 (González-Díaz et al. 2018)

Cuban coral reefs have been called the "crown jewels of the Caribbean Sea," but there are few comparative data to validate this claim. Here, we provide an overview of Cuban coral reefs based on surveys carried out between 2010 and 2016 on seven of the main Cuban coral reef systems: Havana, Artemisa, Los Colorados, Punta Francés, Los Canarreos Archipelago, Península Ancón, and Jardines de la Reina. Ecological indicators were evaluated for each of these areas at the community level. Results suggest differences among benthic communities (corals, sponges, and gorgonians) that are most evident for reefs that develop near highly urbanized areas, such as Havana, than for those far from the coast and less accessible. Offshore reefs along the south-central coast at Jardines de la Reina and Península Ancón exhibited high coral density and diversity. Acropora cervicornis (Lamarck, 1816) and the Orbicella complex corals were uncommon, possibly indicating losses prior to our study due to coral diseases or competition with macroalgae. Siderastrea siderea (Ellis and Solander, 1786) was the most consistently-abundant species at all reef sites. The ecological condition at Jardines de la Reina and Península Ancón is comparatively healthy. Our study supports claims that some Cuban coral reef systems are probably among the best preserved in the Caribbean basin, but other highly impacted areas exhibit many of the degradation patterns that are common to the rest of the Caribbean region. Strong conservation strategies are required with regard to subsistence fisheries and pollution at highly-impacted reefs to stop further degradation, and reefs that appear healthy need protection to avoid degradation and maintain resilience.

Irwin, A., Greer, L., Humston, R., Devlin-Durante, M., Cabe, P., Lescinsky, H., Wirth, K., . . . Baums, I. B. (2017). Age and intraspecific diversity of resilient Acropora communities in Belize. *Coral Reefs*, 36(4)**,** 1111–1120. https://doi.org/10.1007/s00338-017-1602-9 (Irwin et al. 2017)

The corals Acropora palmata and A. cervicornis are important Caribbean reef-builders that have faced significant mortality in recent decades. While many studies have focused on the recent demise of these species, data from areas where Acropora spp. have continued to thrive are limited. Understanding the genetic diversity, recruitment, and temporal continuity of healthy populations of these threatened Acropora spp. and the hybrid they form (“Acropora prolifera”) may provide insights into the demographic processes governing them. We studied three reef sites with abundant A. cervicornis, A. palmata, and hybrid Acropora populations offshore of Ambergris Caye, Belize at Coral Gardens, Manatee Channel, and Rocky Point. Samples were collected from all three Acropora taxa. We used microsatellite markers to determine: (1) genotypic diversity; (2) dominant reproductive mode supporting local recruitment; (3) minimum and maximum genet age estimates for all three acroporids; and (4) the history of hybrid colonization at these sites. We found that Acropora populations were highly clonal with local recruitment

primarily occurring through asexual fragmentation. We also estimated the ages of 10 Acropora genets using recent methodology based on somatic mutation rates from genetic data. Results indicate minimum ages of 62–409 yr for A. cervicornis, 187–561 yr for A. palmata, and 156–281 yr for the Acropora hybrids at these sites. Our data indicate that existing A. cervicornis, A. palmata, and Acropora hybrid genets persisted during the 1980s Caribbean-wide Acropora spp. collapse, suggesting that these sites have been a refuge for Caribbean Acropora corals. Additionally, our data suggest that formation of extant hybrid Acropora genets pre-dates the widespread collapse of the parent taxa.

Mercado-Molina, A. E., Ruiz-Diaz, C. P., Pérez, M. E., Rodríguez-Barreras, R. & Sabat, A. M. (2015). Demography of the threatened coral Acropora cervicornis: implications for its management and conservation. *Coral Reefs*, 34(4), 1113–1124. https://doi.org/10.1007/s00338-015-1341-8 (Mercado-Molina et al. 2015a)

Populations of Acropora cervicornis have collapsed throughout the Caribbean. This situation has prompted the initiation of many restoration efforts; yet, there are insufficient demographic data and analyses to effectively guide these initiatives. In this study we assessed the spatiotemporal variability of A. cervicornis vital rates. We also developed a population matrix model to (1) evaluate the risk of population extinction, (2) estimate population growth rates (λ) considering different rates of colony fragmentation and fragment survival, (3) determine the demographic transition(s) that contribute the most to spatiotemporal differences in λs, and (4) analyze the effectiveness of outplanting coral fragments of different sizes. The model was parameterized by following the fate of 300 colonies from 2011 to 2013 at two localities in Puerto Rico. Demographic transitions varied spatiotemporally, with a significant interaction between location and time period on colony fate. Spatiotemporal variations in λ were also observed. During the first year, populations exhibited λs below equilibrium (0.918 and 0.948), followed by a dramatic decline at both sites (0.535 and 0.709) during the second year. The lower λs were caused by a decrease in the probability of stasis of large-sized colonies coupled with lack of sexual recruits and a meager contribution of asexual recruitment. Spatial variations in λs were largely due to differences in the probability of medium-sized colonies advancing to the largest size class. The viability analysis forecasts that the populations will reach quasi-extinction levels of 25 % of the initial population size in ≤16 yrs. Numerical simulations indicate that outplanting fragments ≥250 cm in total linear length (TLL) would result in a higher asymptotic population size than outplanting smaller fragments. We argue, however, that transplanting colonies ≤100 cm TLL will be a better management strategy because they can be produced faster and in higher numbers at coral nurseries.

Mercado-Molina, A. E., Ruiz-Diaz, C. P. & Sabat, A. M. (2018). Tissue loss rather than colony size determines the demographic fate of the branching coral Acropora cervicornis. *Marine Ecology Progress Series*, 597, 147–159. https://doi.org/10.3354/meps12578 (Mercado-Molina et al. 2018)

Partial mortality is a common process affecting coral colonies. Yet, the impact of tissue loss on the demography of the threatened reef-building coral Acropora cervicornis has been poorly investigated. This limits our understanding of how this species will fare under unfavorable environmental conditions. In this study, we examined the growth and survival of colonies with varying degrees of partial mortality, indicated by tissue loss, for 2 yr at 2 reefs in Puerto Rico. We found that irrespective of colony size, rates

of coral growth and survival declined significantly once the proportion of dead tissue exceeded 20% of the total colony size. Projections of state-matrix population models indicated that partial mortality could also have a negative impact at the population level. For instance, a 25% increase in the number of colonies with >20% tissue loss would reduce the time in which 75% of the population is lost by 3 to 4 yr. Our results provide a new perspective on the effect of partial mortality on the demography and population dynamics of A. cervicornis. First, 20% of tissue loss can be considered a threshold value in which colony fate and population growth are compromised. Second, colony size is not the most important determinant of a colony's demographic performance; instead, the surface area lost to partial mortality is a better predictor of colony growth and survivorship. Taking into consideration the relationship between partial mortality and the demographic fate of A. cervicornis can aid in the development of stronger conservation and restoration programs.

Mercado-Molina, A. E., A. M. Sabat, and E. A. Hernández-Delgado. 2020. Population dynamics of diseased corals: Effects of a Shut Down Reaction outbreak in Puerto Rican *Acropora cervicornis*. Pages 61-82 in B. M. Riegl, editor. Population Dynamics of the Reef Crisis. Academic Press. https://www.elsevier.com/books/population-dynamics-of-the-reef-crisis/riegl/978-0-12-821529-6 (Mercado-Molina et al. 2020)

Chronic coral reef degradation has been characterized by a significant decline in the population abundance and live tissue cover of scleractinian corals across the wider Caribbean. Acropora cervicornis is among the species whose populations have suffered an unprecedented collapse throughout the region. This species, which once dominated the shallow-water reef communities, is susceptible to a wide range of stressors, resulting in a general lack of recovery following disturbances. A. cervicornis is a critical contributor to the structure, function, and resilience of Caribbean coral reefs. Therefore, it is essential to identify the factors that influence their demographic and population performance. Diseases are one of the factors that are compromising the recovery of coral populations. In this chapter, we use size-based population matrix models to evaluate the population level effect of a Shut Down Reaction Disease (SDR) outbreak, one of the less-understood diseases affecting this coral. The model was parameterized by following the fate of 105 colonies for 2 years at Tamarindo reef in Culebra, Puerto Rico. SDR, which affected 78% of the population, led to a rapid decline in colony abundance. The estimated population growth rate (λ) for the diseased population was more than six times lower than would be expected for a population at equilibrium. It was found that colonies in the smaller size class ($\leq$100cm total linear length) were more likely to get infected and succumbing to the disease than larger colonies. Model simulations indicate that: (1) under the estimated λ, the population would reach extinction in 5 years; (2) an SDR outbreak as intense as the one observed in this study can lead to a notable decline in stochastic λs even when relatively rare (i.e. 10% probability of occurring); and (3) disease incidence as low as 5% can cause the population to lose its ecological functionality (e.g., reach a pseudo-extinction level of 10% of the initial population size) 33 years before disappearing. SDR and probably any other similarly virulent disease could thus be a major driver of local extinction events of A. cervicornis.

Miller, M. W., Lohr, K. E., Cameron, C. M., Williams, D. E. & Peters, E. C. (2014). Disease dynamics and potential mitigation among restored and wild staghorn coral, Acropora cervicornis.

PeerJ, 2, e541
https://doi.org/10.7717/peerj.541 (Miller et al. 2014)

The threatened status (both ecologically and legally) of Caribbean staghorn coral, Acropora cervicornis, has prompted rapidly expanding efforts in culture and restocking, although tissue loss diseases continue to affect populations. In this study, disease surveillance and histopathological characterization were used to compare disease dynamics and conditions in both restored and extant wild populations. Disease had devastating effects on both wild and restored populations, but dynamics were highly variable and appeared to be site-specific with no significant differences in disease prevalence between wild versus restored sites. A subset of 20 haphazardly selected colonies at each site observed over a four-month period revealed widely varying disease incidence, although not between restored and wild sites, and a case fatality rate of 8%. A tropical storm was the only discernable environmental trigger associated with a consistent spike in incidence across all sites. Lastly, two field mitigation techniques, (1) excision of apparently healthy branch tips from a diseased colony, and (2) placement of a band of epoxy fully enclosing the diseased margin, gave equivocal results with no significant benefit detected for either treatment compared to controls. Tissue condition of associated samples was fair to very poor; unsuccessful mitigation treatment samples had severe degeneration of mesenterial filament cnidoglandular bands. Polyp mucocytes in all samples were infected with suspect rickettsia-like organisms; however, no bacterial aggregates were found. No histological differences were found between disease lesions with gross signs fitting literature descriptions of white-band disease (WBD) and rapid tissue loss (RTL). Overall, our results do not support differing disease quality, quantity, dynamics, nor health management strategies between restored and wild colonies of A. cervicornis in the Florida Keys.

Weil, E., Hammerman, N. M., Becicka, R. L. & Cruz-Motta, J. J. (2020). Growth dynamics in Acropora cervicornis and A. prolifera in southwest Puerto Rico. *PeerJ*, 8, e8435. https://doi.org/10.7717/peerj.8435 (Weil et al. 2020)

Natural population recovery of Acropora palmata, A. cervicornis and their hybrid, Acropora prolifera, have fluctuated significantly after their Caribbean-wide, disease-induced mass mortality in the early 1980s. Even though significant recovery has been observed in a few localities, recurrent disease outbreaks, bleaching, storm damage, local environmental deterioration, algae smothering, predation, low sexual recruitment and low survivorship have affected the expected, quick recovery of these weedy species. In this study, the status of three recovering populations of A. cervicornis and two of A. prolifera were assessed over one year using coral growth and mortality metrics, and changes in their associated algae and fish/invertebrate communities in three localities in the La Parguera Natural Reserve (LPNR), southwest coast of Puerto Rico. Five branches were tagged in each of 29, medium size (1–2 m in diameter) A. cervicornis and 18 A. prolifera colonies in the Media Luna, Mario and San Cristobal reefs off LPNR. Branches were measured monthly, together with observations to evaluate associated disease(s), algae accumulation and predation. A. cervicornis grew faster [3.1 ± 0.44 cm/month (= 37.2 cm/y)] compared to A. prolifera [2.6 ± 0.41 cm/month (= 31.2 cm/y)], and growth was significantly higher during Winter-Spring compared to Summer-Fall for both taxa (3.5 ± 0.58 vs. 0.53 ± 0.15 cm/month in A. cervicornis, and 2.43 ± 0.71 vs. 0.27 ± 0.20 cm/month in A. prolifera, respectively). Algal accumulation was only observed in A. cervicornis, and was higher during Spring-Summer compared to Fall-Winter (6.1 ± 0.91 cm/month and 3.8 ± 0.29 cm/month, respectively, (PERMANOVA,

df = 2, MS = 10.2, p = 0.37)). Mortality associated with white band disease, algae smothering and fish/invertebrate predation was also higher in A. cervicornis and varied among colonies within sites, across sites and across season. The balance between tissue grow and mortality determines if colonies survive. This balance seems to be pushed to the high mortality side often by increasing frequency of high thermal anomalies, inducing bleaching and disease outbreaks and other factors, which have historically impacted the natural recovery of these taxa in the La Parguera Natural Reserve in Puerto Rico and possibly other areas in the region. Overall, results indicate variability in both growth and mortality rates in both taxa across localities and seasons, with A. cervicornis showing overall higher mortalities compared to A. prolifera.

Genetic Assessment

> Canty, S. W. J., G. Fox, J. K. Rowntree, and R. F. Preziosi. 2021. Genetic structure of a remnant Acropora cervicornis population. Sci Rep 11(1):3523. https://www.ncbi.nlm.nih.gov/pubmed/33568733 (Canty et al. 2021)

Amongst the global decline of coral reefs, hope spots such as Cordelia Bank in Honduras, have been identified. This site contains dense, remnant thickets of the endangered species Acropora cervicornis, which local managers and conservation organizations view as a potential source population for coral restoration projects. The aim of this study was to determine the genetic diversity of colonies across three banks within the protected area. We identified low genetic diversity (FST = 0.02) across the three banks, and genetic similarity of colonies ranged from 91.3 to 95.8% between the banks. Clonality rates were approximately 30% across the three banks, however, each genotype identified was unique to each bank. Despite the low genetic diversity, subtle genetic differences within and among banks were demonstrated, and these dense thickets were shown not to be comprised of a single or a few genotypes. The presence of multiple genotypes suggests A. cervicornis colonies from these banks could be used to maintain and enhance genetic diversity in restoration projects. Management of hope spots, such as Cordelia Bank, and the incorporation of genetic information into restoration projects to ensure genetic diversity within out-planted populations, will be critical in the ongoing challenge of conserving and preserving coral reefs.

> Drury, C., Dale, K. E., Panlilio, J. M., Miller, S. V., Lirman, D., Larson, E. A., . . . Oleksiak, M. F. (2016). Genomic variation among populations of threatened coral: Acropora cervicornis. *BMC Genomics*, 17(1), 1–14. https://doi.org/10.1186/s12864-016-2583-8 (Drury et al. 2016)

Acropora cervicornis, a threatened, keystone reef-building coral has undergone severe declines (>90 %) throughout the Caribbean. These declines could reduce genetic variation and thus hamper the species' ability to adapt. Active restoration strategies are a common conservation approach to mitigate species' declines and require genetic data on surviving populations to efficiently respond to declines while maintaining the genetic diversity needed to adapt to changing conditions. To evaluate active restoration strategies for the staghorn coral, the genetic diversity of A. cervicornis within and among populations was assessed in 77 individuals collected from 68 locations along the Florida Reef Tract (FRT) and in the Dominican Republic. Genotyping by Sequencing (GBS) identified 4,764 single nucleotide

polymorphisms (SNPs). Pairwise nucleotide differences (π) within a population are large (~37 %) and similar to π across all individuals. This high level of genetic diversity along the FRT is similar to the diversity within a small, isolated reef. Much of the genetic diversity (>90 %) exists within a population, yet GBS analysis shows significant variation along the FRT, including 300 SNPs with significant FST values and significant divergence relative to distance. There are also significant differences in SNP allele frequencies over small spatial scales, exemplified by the large FST values among corals collected within Miami-Dade county. Large standing diversity was found within each population even after recent declines in abundance, including significant, potentially adaptive divergence over short distances. The data here inform conservation and management actions by uncovering population structure and high levels of diversity maintained within coral collections among sites previously shown to have little genetic divergence. More broadly, this approach demonstrates the power of GBS to resolve differences among individuals and identify subtle genetic structure, informing conservation goals with evolutionary implications.

Drury, C., Schopmeyer, S., Goergen, E., Bartels, E., Nedimyer, K., Johnson, M., . . . Lirman, D. (2017). Genomic patterns in Acropora cervicornis show extensive population structure and variable genetic diversity. *Ecology and Evolution*, 7(16), 6188–6200. https://doi.org/10.1002/ece3.3184 (Drury et al. 2017b)

Threatened Caribbean coral communities can benefit from high-resolution genetic data used to inform management and conservation action. We use Genotyping by Sequencing (GBS) to investigate genetic patterns in the threatened coral, Acropora cervicornis, across the Florida Reef Tract (FRT) and the western Caribbean. Results show extensive population structure at regional scales and resolve previously unknown structure within the FRT. Different regions also exhibit up to threefold differences in genetic diversity (He), suggesting targeted management based on the goals and resources of each population is needed. Patterns of genetic diversity have a strong spatial component, and our results show Broward and the Lower Keys are among the most diverse populations in Florida. The genetic diversity of Caribbean staghorn coral is concentrated within populations and within individual reefs (AMOVA), highlighting the complex mosaic of population structure. This variance structure is similar over regional and local scales, which suggests that in situ nurseries are adequately capturing natural patterns of diversity, representing a resource that can replicate the average diversity of wild assemblages, serving to increase intraspecific diversity and potentially leading to improved biodiversity and ecosystem function. Results presented here can be translated into specific goals for the recovery of A. cervicornis, including active focus on low diversity areas, protection of high diversity and connectivity, and practical thresholds for responsible restoration.

Drury, C., Paris, C. B., Kourafalou, V. H. & Lirman, D. (2018). Dispersal capacity and genetic relatedness in Acropora cervicornis on the Florida Reef Tract. *Coral Reefs*, 37(2), 585–596. https://doi.org/10.1007/s00338-018-1683-0 (Drury et al. 2018)

Sexual reproduction in scleractinian corals is a critical component of species recovery, fostering population connectivity and enhancing genetic diveristy. The relative contribution of sexual reproduction to both connectivity and diversity in Acropora cervicornis may be variable due to this species' capacity to reproduce effectively by fragmentation. Using a biophysical model and genomic data in this threatened

species, we construct potential connectivity pathways on the Florida Reef Tract (FRT) and compare them to inferred migration rates derived from next-generation sequencing, using a link and node-based approach. Larval connectivity on the FRT can be divided into two zones: the northern region, where most transport is unidirectional to the north with the Florida Current, and the southern region that is more dynamic and exhibits complex spatial patterns. These biophysical linkages are poorly correlated with genetic connectivity patterns, which resolve many reciprocal connections and suggest a less sparse network. These results are difficult to reconcile with genetic data which indicate that individual reefs are diverse, suggesting important contributions of sexual reproduction and recruitment. Larval connectivity models highlight potential resources for recovery, such as areas with high larval export like the Lower Keys, or areas that are well connected to most other regions on the FRT, such as the Dry Tortugas.

Drury, C., Greer, J. B., Baums, I., Gintert, B. & Lirman, D. (2019). Clonal diversity impacts coral cover in Acropora cervicornis thickets: Potential relationships between density, growth, and polymorphisms. *Ecology and Evolution*, 9(8), 4518–4531. https://doi.org/10.1002/ece3.5035 (Drury et al. 2019)

As coral reefs decline, cryptic sources of resistance and resilience to stress may be increasingly important for the persistence of these communities. Among these sources, inter- and intraspecific diversity remain understudied on coral reefs but extensively impact a variety of traits in other ecosystems. We use a combination of field and sequencing data at two sites in Florida and two in the Dominican Republic to examine clonal diversity and genetic differentiation of high- and low-density aggregations of the threatened coral Acropora cervicornis in the Caribbean. We find that high-density aggregations called thickets are composed of up to 30 genotypes at a single site, but 47% of genotypes are also found as isolated, discrete colonies outside these aggregations. Genet–ramet ratios are comparable for thickets (0.636) and isolated colonies after rarefaction (0.569), suggesting the composition of each aggregation is not substantially different and highlighting interactions between colonies as a potential influence on structure. There are no differences in growth rate, but a significant positive correlation between genotypic diversity and coral cover, which may be due to the influence of interactions between colonies on survivorship or fragment retention during asexual reproduction. Many polymorphisms distinguish isolated colonies from thickets despite the shared genotypes found here, including putative nonsynonymous mutations that change amino acid sequence in 25 loci. These results highlight intraspecific diversity as a density-dependent factor that may impact traits important for the structure and function of coral reefs.

Hemond, E. M., Kaluziak, S. T. & Vollmer, S. V. (2014). The genetics of colony form and function in Caribbean Acropora corals. *BMC Genomics*, 15(1), 1–21. https://doi.org/10.1186/1471-2164-15-1133 (Hemond et al. 2014)

Colonial reef-building corals have evolved a broad spectrum of colony morphologies based on coordinated asexual reproduction of polyps on a secreted calcium carbonate skeleton. Though cnidarians have been shown to possess and use similar developmental genes to bilaterians during larval development and polyp formation, little is known about genetic regulation of colony morphology in hard corals. We used RNA-seq to evaluate transcriptomic differences between functionally distinct regions of the coral (apical branch tips and branch bases) in two species of Caribbean Acropora, the staghorn coral, A. cervicornis, and the elkhorn coral, A. palmata. Transcriptome-wide gene profiles differed significantly

between different parts of the coral colony as well as between species. Genes showing differential expression between branch tips and bases were involved in developmental signaling pathways, such as Wnt, Notch, and BMP, as well as pH regulation, ion transport, extracellular matrix production and other processes. Differences both within colonies and between species identify a relatively small number of genes that may contribute to the distinct "staghorn" versus "elkhorn" morphologies of these two sister species. The large number of differentially expressed genes supports a strong division of labor between coral branch tips and branch bases. Genes involved in growth of mature Acropora colonies include the classical signaling pathways associated with development of cnidarian larvae and polyps as well as morphological determination in higher metazoans.

> Japaud, A., Bouchon, C., Manceau, J.-L. & Fauvelot, C. (2015). High clonality in Acropora palmata and Acropora cervicornis populations of Guadeloupe, French Lesser Antilles. *Mar. Freshwater Res.*, 66(9), 847–851. https://doi.org/10.1071/MF14181 (Japaud et al. 2015)

Since the 1980s, population densities of Acroporidae have dramatically declined in the Caribbean Sea. Quantitative censuses of Acroporidae provide information on the number of colonies (i.e. ramets), but not on the number of genetically distinct individuals (i.e. genets). In this context, the aim of our study was to provide an overview of the genetic status of Acropora populations in Guadeloupe by examining the genotypic richness of Acropora palmata and Acropora cervicornis. Using 14 microsatellite loci, we found extremely low genotypic richness for both species from Caye-à-Dupont reef (i.e. 0.125 for A. palmata and nearly zero for A. cervicornis). Because genetic diversity contributes to the ability of organisms to evolve and adapt to new environmental conditions, our results are alarming in the context of ongoing global warming as long periods of clonal growth without sexual recruitment may lead to the extinction of these populations.

Spatial Distribution

> Hernández-Fernández, L., de Zayas, R. G., Olivera, Y. M., Amargós, F. P., López, C. B., Sotolongo, L. B. D., . . . Moret, F. S. (2019). Distribution and status of living colonies of Acropora spp. in the reef crests of a protected marine area of the Caribbean (Jardines de la Reina National Park, Cuba). *PeerJ*, 7, e6470. https://doi.org/10.7717/peerj.6470 (Hernandez-Fernandez et al. 2019)

The reef crests of the Jardines de la Reina National Park (JRNP) are largely formed by Acropora palmata, but colonies of A. cervicornis and the hybrid A. prolifera are also present. This study shows spatial distribution of colonies, thickets and live fragments of these species in the fore reefs. Snorkeling was used to perform the direct observations. The maximum diameter of 4,399 colonies of A. palmata was measured and the health of 3,546 colonies was evaluated. The same was done to 168 colonies of A. cervicornis and 104 colonies of A. prolifera. The influence of the location and marine currents on a number of living colonies of A. palmata was analyzed. For such purpose, reef crests were divided into segments of 500 m. The marine park was divided into two sectors: East and West. The Caballones Channel was used as the reference dividing line. The park was also divided into five reserve zones. We counted 7,276 live colonies

of Acropora spp. 1.4% was A. prolifera, 3.5% A. cervicornis and 95.1% A. palmata. There were 104 thickets of A. palmata, ranging from eight to 12 colonies, and 3,495 fragments; 0.6% was A. cervicornis and the rest A. palmata (99.4%). In the East sector, 263 colonies (3.8% of the total), six thickets (5.8%) and 32 fragments (1%) of A. palmate were recorded. In the same sector, there were 11 fragments (50%) of A.cervicornis and two (2%) colonies of A. prolifera. Health of A. palmata was evaluated as good and not so good in the study area. Health of A. cervicornis was critical and health of A. prolifera was good in all five reserve zones. There was a significant increase in the number of colonies from east to west ($X2 = 11.5$, $gl = 3.0$, $p = 0.009$). This corroborates the existence of important abundance differences between the eastern and the western region of the JRNP. A negative relationship was observed between the number of colonies and the distance from the channel ($X2 = 65.0$, $df = 3.0$, $p < 0.001$). The influence of the channel, for the live colonies of A. palmata is greater within the first 2,000 m. It then decreases until approximately 6,000 m, and no significant increase beyond. The orientation of the reef crests significantly influenced the abundance of the colonies ($X2 = 15.5$, $df = 2.9$, $p = 0.001$). The results presented here provide a baseline for future research on the status of the populations of Acropora spp., considering that there has been a certain recovery of the species A. palmata during the last 10–16 years. Given the current status of the populations of Acropora spp., conservation actions focusing A. cervicornis should be prioritized.

Habitat and Ecosystem Conditions

> de Bakker, D. M., van Duyl, F. C., Perry, C. T. & Meesters, E. H. (2019). Extreme spatial heterogeneity in carbonate accretion potential on a Caribbean fringing reef linked to local human disturbance gradients. *Global Change Biology*, 25(12), 4092–4104. https://doi.org/10.1111/gcb.14800 (de Bakker et al. 2019)

The capacity of coral reefs to maintain their structurally complex frameworks and to retain the potential for vertical accretion is vitally important to the persistence of their ecological functioning and the ecosystem services they sustain. However, datasets to support detailed along-coast assessments of framework production rates and accretion potential do not presently exist. Here, we estimate, based on gross bioaccretion and bioerosion measures, the carbonate budgets and resultant estimated accretion rates (EAR) of the shallow reef zone of leeward Bonaire – between 5 and 12 m depth – at unique fine spatial resolution along this coast (115 sites). Whilst the fringing reef of Bonaire is often reported to be in a better ecological condition than most sites throughout the wider Caribbean region, our data show that the carbonate budgets of the reefs and derived EAR varied considerably across this 58 km long fringing reef complex. Some areas, in particular the marine reserves, were indeed still dominated by structurally complex coral communities with high net carbonate production (>10 kg $CaCO_3$ m^{-2} $year^{-1}$), high live coral cover and complex structural topography. The majority of the studied sites, however, were defined by relatively low budget states (<2 kg $CaCO_3$ m^{-2} $year^{-1}$) or were in a state of net erosion. These data highlight the marked spatial heterogeneity that can occur in budget states, and thus in reef accretion potential, even between quite closely spaced areas of individual reef complexes. This heterogeneity is linked strongly to the degree of localized land-based impacts along the coast, and resultant differences in the abundance of reef framework building coral species. The major impact of this variability is that those sections of reef defined by low-accretion rates will have limited capacity to maintain their structural integrity and to keep pace with current projections of climate change induced sea-level rise (SLR), thus

posing a threat to reef functioning and biodiversity, potentially leading to trophic cascades. Since many Caribbean reefs are more severely degraded than those found around Bonaire, it is to be expected that the findings presented here are rather the rule than the exception, but the study also highlights the need for similar high spatial resolution (along-coast) assessments of budget states and accretion rates to meaningfully explore increasing coastal risk at the country level. The findings also more generally underline the significance of reducing local anthropogenic disturbance and restoring framework building coral assemblages. Appropriately focussed local preservation efforts may aid in averting future large-scale above reef water depth increases on Caribbean coral reefs and will limit the social and economic implications associated with the loss of reef goods and services.

Drury, C., Manzello, D. & Lirman, D. (2017). Genotype and local environment dynamically influence growth, disturbance response and survivorship in the threatened coral, Acropora cervicornis. *PLOS ONE*, 12, e0174000. https://doi.org/10.1371/journal.pone.0174000 (Drury et al. 2017a)

The relationship between the coral genotype and the environment is an important area of research in degraded coral reef ecosystems. We used a reciprocal outplanting experiment with 930 corals representing ten genotypes on each of eight reefs to investigate the influence of genotype and the environment on growth and survivorship in the threatened Caribbean staghorn coral, Acropora cervicornis. Coral genotype and site were strong drivers of coral growth and individual genotypes exhibited flexible, non-conserved reaction norms, complemented by ten-fold differences in growth between specific G-E combinations. Growth plasticity may diminish the influence of local adaptation, where foreign corals grew faster than native corals at their home sites. Novel combinations of environment and genotype also significantly affected disturbance response during and after the 2015 bleaching event, where these factors acted synergistically to drive variation in bleaching and recovery. Importantly, small differences in temperature stress elicit variable patterns of survivorship based on genotype and illustrate the importance of novel combinations of coral genetics and small differences between sites representing habitat refugia. In this context, acclimatization and flexibility is especially important given the long lifespan of corals coping with complex environmental change. The combined influence of site and genotype creates short-term differences in growth and survivorship, contributing to the standing genetic variation needed for adaptation to occur over longer timescales and the recovery of degraded reefs through natural mechanisms.

Hernández-Delgado, E. A., Acuña, A. M., Otaño-Cruz, A. & Suleiman-Ramos, S. E. (2014). Bomb-cratered coral reefs in Puerto Rico, the untold story about a novel habitat: from reef destruction to community-based ecological rehabilitation. *Rev. Biol. Trop.*, 62, 183–200. https://doi.org/10.15517/rbt.v62i0.15913 (Hernández-Delgado et al. 2014b)

Ecological impacts of military bombing activities in Puerto Rico have often been described as minimal, with recurrent allegations of confounding effects by hurricanes, coral diseases and local anthropogenic stressors. Reef craters, though isolated, are associated with major colony fragmentation and framework pulverization, with a net permanent loss of reef bio-construction. In contrast, adjacent non-bombarded reef sections have significantly higher benthic spatial relief and biodiversity. We compared benthic communities on 35-50 year-old bomb-cratered coral reefs at Culebra and Vieques Islands, with adjacent

non-impacted sites; 2) coral recruit density and fish community structure within and outside craters; and 3) early effects of a rehabilitation effort using low-tech Staghorn coral Acropora cervicornis farming. Reef craters ranged in size from approximately 50 to 400m2 and were largely dominated by heavily fragmented, flattened benthos, with coral cover usually below 2% and dominance by non-reef building taxa (i.e., filamentous algal turfs, macroalgae). Benthic spatial heterogeneity was lower within craters which also resulted in a lowered functional value as fish nursery ground. Fish species richness, abundance and biomass, and coral recruit density were lower within craters. Low-tech, community-based approaches to culture, harvest and transplant A. cervicornis into formerly bombarded grounds have proved successful in increasing percent coral cover, benthic spatial heterogeneity, and helping rehabilitate nursery ground functions.

van Woesik, R., Ripple, K. & Miller, S. L. (2018). Macroalgae reduces survival of nursery-reared Acropora corals in the Florida reef tract. *Restoration Ecology*, 26(3), 563–569. https://doi.org/10.1111/rec.12590 (van Woesik et al. 2018)

Recent declines in coral populations along the Florida reef tract have prompted the establishment of coral restoration programs which raise coral species, such as the threatened Acropora cervicornis, in nurseries ready for outplanting. Large numbers of nursery-reared coral colonies have been outplanted along the Florida reef tract in recent years, yet few studies have characterized benthic habitats that are considered optimal for colony survival. In 2016, we surveyed 23 A. cervicornis restoration sites, located at six different reefs in the upper Florida Keys. We examined the condition of the outplanted corals and quantified the benthic assemblages adjacent to the outplanted coral colonies. We found that where A. cervicornis survived for more than 1 year, the substrate significantly supported less brown macroalgae of the genus Dictyota than at sites where A. cervicornis had died. Coral survival was highest at sites with less than 15% Dictyota cover. These results suggest that the habitat conditions that supported Dictyota spp. were not conducive to A. cervicornis growth and survival. Restoration practitioners should avoid attaching nursery-raised corals to substrate with Dictyota spp. cover greater than 15%.

van Woesik, R., Roth, L. M., Brown, E. J., McCaffrey, K. R. & Roth, J. R. (2020). Niche space of corals along the Florida reef tract. *PLOS ONE*, 15, e0231104. https://doi.org/10.1371/journal.pone.0231104 (van Woesik et al. 2020b)

Over the last three decades corals have declined precipitously in the Florida Keys. Their population decline has prompted restoration effort. Yet, little effort has been invested in understanding the contemporary niche spaces of coral species, which could assist in prioritizing conservation habitats. We sought to predict the probability of occurrence of 23 coral species, including the critically endangered Acropora cervicornis, using observations at 985 sites from 2011–2015. We ran boosted regression trees to evaluate the relationship between the presence of these corals and eight potential environmental predictors: (i) bathymetry (m), (ii) mean of daily sea surface temperature (SST) (°C), (iii) variance of SST (°C), (iv) range of SST (°C), (v) chlorophyll-a concentration (mg m3), (vi) turbidity (m-1), (vii) wave energy (kJ m-2), and (viii) distance from coast (km). The Marquesas and the lower and upper Florida Keys were predicted to support the most suitable habitats for the 23 coral species examined. A. cervicornis had one of the smallest areas of suitable habitat, which was limited to the lower and upper Florida Keys, the Dry Tortugas, and nearshore Broward-Miami reefs. The best environmental predictors

of site occupancy of A. cervicornis were SST range (4–5°C) and turbidity (K490 between 0.15–0.25 m-1). Historically A. cervicornis was reported in clear oligotrophic waters, although the present results find the coral species surviving in nearshore turbid conditions. Nearshore, turbid reefs may shade corals during high-temperature events, and therefore nearshore reefs in south Florida may become important refuges for corals as the ocean temperatures continue to increase.

> Wirt, K. E., Hallock, P., Palandro, D. & Lunz, K. S. (2015). Potential Habitat of Acropora spp. on Reefs of Florida, Puerto Rico, and the US Virgin Islands. *Global Ecology and Conservation*, 3, 242–255. https://doi.org/10.1016/j.gecco.2014.12.001 (Wirt et al. 2015)

Elkhorn and staghorn corals (Acropora palmata, Acropora cervicornis) were listed in 2006 as threatened under the Endangered Species Act. The goal of this study was to create model potential-habitat maps for A. palmata and A. cervicornis, while identifying areas for possible re-establishment. These maps were created using a database of reported field observations in combination with existing benthic habitat maps. The mapped coral reef and hardbottom classifications throughout Florida, Puerto Rico, and the US Virgin Island reef tracts were used to generate potential-habitat polygons using buffers that incorporated 95% and 99% of reported observations of Acropora spp. Locations of 92% of A. palmata observations and 84% of A. cervicornis observations coincided with mapped coral reef or hard-bottom habitat throughout the study area. These results indicate that potential habitat for A. palmata is currently well defined throughout this region, but that potential habitat for A. cervicornis is more variable and has a wider range than that for A. palmata. This study provides a novel method of combining data sets at various geographic spatial scales and may be used to inform and refine the current National Oceanic and Atmospheric Administration critical habitat map.

Threat Assessment

Disease

> Certner, R. H. & Vollmer, S. V. (2015). Evidence for Autoinduction and Quorum Sensing in White Band Disease-Causing Microbes on Acropora cervicornis. *Scientific Reports*, 5(1), 11134. https://doi.org/10.1038/srep11134 (Certner and Vollmer 2015)

Coral reefs have entered a state of global decline party due to an increasing incidence of coral disease. However, the diversity and complexity of coral-associated bacterial communities has made identifying the mechanisms underlying disease transmission and progression extremely difficult. This study explores the effects of coral cell-free culture fluid (CFCF) and autoinducer (a quorum sensing signaling molecule) on coral-associated bacterial growth and on coral tissue loss respectively. All experiments were conducted using the endangered Caribbean coral Acropora cervicornis. Coral-associated microbes were grown on selective media infused with CFCF derived from healthy and white band disease-infected A. cervicornis. Exposure to diseased CFCF increased proliferation of Cytophaga-Flavobacterium spp. while exposure to healthy CFCF inhibited growth of this group. Exposure to either CFCF did not significantly affect Vibrio spp. growth. In order to test whether disease symptoms can be induced in healthy corals, A. cervicornis was exposed to bacterial assemblages supplemented with exogenous, purified autoinducer. Incubation

with autoinducer resulted in complete tissue loss in all corals tested in less than one week. These findings indicate that white band disease in A. cervicornis may be caused by opportunistic pathogenesis of resident microbes.

Certner, R. H. & Vollmer, S. V. (2018). Inhibiting bacterial quorum sensing arrests coral disease development and disease-associated microbes. *Environmental Microbiology*, 20(2), 645–657. https://doi.org/10.1111/1462-2920.13991 (Certner and Vollmer 2018)

Among the greatest threats to coral reefs are coral epizootics, which are increasing in frequency and severity across many reef ecosystems. In particular, white band disease (WBD) has devastated Caribbean acroporid populations since its initial outbreak in 1979. However, despite its widespread and damaging effects, the aetiology of WBD remains largely unresolved. Here, we examine the role of quorum sensing within bacterial communities associated with WBD-infected Acropora cervicornis. Microbial communities isolated from WBD-infected corals were exposed to quorum sensing inhibitor (QSI) – a N-acyl homoserine lactone autoinducer antagonist – and then dosed onto healthy test corals. WBD-associated bacteria supplemented with QSI lost the ability to establish disease, while healthy corals exposed to uninhibited WBD bacterial communities became infected within two days. Microbial 16S rRNA metagenomic sequencing analyses were then used to identify shifts in bacterial communities due to QSI exposure on WBD-associated bacterial communities. Our results demonstrated that Vibrionaceae and Flavobacteriaceae abundances were strongly inhibited by the addition of QSI to WBD-infected corals, whereas putative coral symbiont Endozoicomonas and Halomonadaceae abundances decrease dramatically in diseased corals.

Certner, R. H., Dwyer, A. M., Patterson, M. R. & Vollmer, S. V. (2017). Zooplankton as a potential vector for white band disease transmission in the endangered coral, Acropora cervicornis. *PeerJ*, 5, e3502. https://doi.org/10.7717/peerj.3502 (Certner et al. 2017)

Coral diseases are a leading factor contributing to the global decline of coral reefs, and yet mechanisms of disease transmission remain poorly understood. This study tested whether zooplankton can act as a vector for white band disease (WBD) in Acropora cervicornis. Natural zooplankton communities were collected from a coral reef in Bocas del Toro, Panama. Half of the zooplankton were treated with antibiotics for 24 h after which the antibiotic-treated and non-antibiotic-treated zooplankton were incubated with either seawater or tissue homogenates from corals exhibiting WBD-like symptoms. A total of 15 of the 30 asymptomatic A. cervicornis colonies exposed to zooplankton incubated in disease homogenate in tank-based experiments showed signs of WBD, regardless of prior antibiotic incubation. These results indicate that in our experimental conditions zooplankton were a vector for coral disease after exposure to disease-causing pathogens. Given the importance of heterotrophy on zooplankton to coral nutrition, this potential mode of disease transmission warrants further investigation.

Gignoux-Wolfsohn, S. A. & Vollmer, S. V. (2015). Identification of Candidate Coral Pathogens on White Band Disease-Infected Staghorn Coral. *PLOS ONE*, 10, e0134416. https://doi.org/10.1371/journal.pone.0134416 (Gignoux-Wolfsohn and Vollmer 2015)

Bacterial diseases affecting scleractinian corals pose an enormous threat to the health of coral reefs, yet we still have a limited understanding of the bacteria associated with coral diseases. White band disease is a bacterial disease that affects the two Caribbean acroporid corals, the staghorn coral Acropora cervicornis and the elkhorn coral A. palmate. Species of Vibrio and Rickettsia have both been identified as putative WBD pathogens. Here we used Illumina 16S rRNA gene sequencing to profile the bacterial communities associated with healthy and diseased A. cervicornis collected from four field sites during two different years. We also exposed corals in tanks to diseased and healthy (control) homogenates to reduce some of the natural variation of field-collected coral bacterial communities. Using a combination of multivariate analyses, we identified community-level changes between diseased and healthy corals in both the field-collected and tank-exposed datasets. We then identified changes in the abundances of individual operational taxonomic units (OTUs) between diseased and healthy corals. By comparing the diseased and healthy-associated bacteria in field-collected and tank-exposed corals, we were able to identify 16 healthy-associated OTUs and 106 consistently disease-associated OTUs, which are good candidates for putative WBD pathogens. A large percentage of these disease-associated OTUs belonged to the order Flavobacteriales. In addition, two of the putative pathogens identified here belong to orders previously suggested as WBD pathogens: Vibronales and Rickettsiales.

Gignoux-Wolfsohn, S. A., Aronson, F. M. & Vollmer, S. V. (2017). Complex interactions between potentially pathogenic, opportunistic, and resident bacteria emerge during infection on a reef-building coral. *FEMS Microbiol Ecol* 93(7). https://doi.org/10.1093/femsec/fix080 (Gignoux-Wolfsohn et al. 2017)

Increased bacterial diversity on diseased corals can obscure disease etiology and complicate our understanding of pathogenesis. To untangle microbes that may cause white band disease signs from microbes responding to disease, we inoculated healthy Acropora cervicornis corals with an infectious dose from visibly diseased corals. We sampled these dosed corals and healthy controls over time for sequencing of the bacterial 16S region. Endozoicomonas were associated with healthy fragments from 4/10 colonies, dominating microbiomes before dosing and decreasing over time only in corals that displayed disease signs, suggesting a role in disease resistance. We grouped disease-associated bacteria by when they increased in abundance (primary vs secondary) and whether they originated in the dose (colonizers) or the previously healthy corals (responders). We found that all primary responders increased in all dosed corals regardless of final disease state and are therefore unlikely to cause disease signs. In contrast, primary colonizers in the families Pasteurellaceae and Francisellaceae increased solely in dosed corals that ultimately displayed disease signs, and may be infectious foreign bacteria involved in the development of disease signs. Moving away from a static comparison of diseased and healthy bacterial communities, we provide a framework to identify key players in other coral diseases.

Gignoux-Wolfsohn, S. A., Precht, W. F., Peters, E. C., Gintert, B. E. & Kaufman, L. S. (2020). Ecology, histopathology, and microbial ecology of a white-band disease outbreak in the threatened staghorn coral Acropora cervicornis. *Diseases of Aquatic Organisms*, 137(3), 217–237. https://doi.org/10.3354/dao03441 (Gignoux-Wolfsohn et al. 2020)

This study is a multi-pronged description of a temperature-induced outbreak of white-band disease (WBD) that occurred in Acropora cervicornis off northern Miami Beach, Florida (USA), from July to October 2014. We describe the ecology of the disease and examine diseased corals using both histopathology and next-generation bacterial 16S gene sequencing, making it possible to better understand the effect this disease has on the coral holobiont, and to address some of the seeming contradictions among previous studies of WBD that employed either a purely histological or molecular approach. The outbreak began in July 2014, as sea surface temperatures reached 29°C, and peaked in mid-September, a month after the sea surface temperature maximum. The microscopic anatomy of apparently healthy portions of colonies displaying active disease signs appeared normal except for some tissue atrophy and dissociation of mesenterial filaments deep within the branch. Structural changes were more pronounced in visibly diseased fragments, with atrophy, necrosis, and lysing of surface and basal body wall and polyp structures at the tissue-loss margin. The only bacteria evident microscopically in both diseased and apparently healthy tissues with Giemsa staining was a Rickettsiales-like organism (RLO) occupying mucocytes. Sequencing also identified bacteria belonging to the order Rickettsiales in all fragments. When compared to apparently healthy fragments, diseased fragments had more diverse bacterial communities made up of many previously suggested potential primary pathogens and secondary (opportunistic) colonizers. Interactions between elevated seawater temperatures, the coral host, and pathogenic members of the diseased microbiome all contribute to the coral displaying signs of WBD.

Klinges, G., R. L. Maher, R. L. Vega Thurber, and E. M. Muller. 2020. Parasitic 'Candidatus Aquarickettsia rohweri' is a marker of disease susceptibility in Acropora cervicornis but is lost during thermal stress. Environ Microbiol 22(12):5341-5355. (Klinges et al. 2020)

Holobiont phenotype results from a combination of host and symbiont genotypes as well as from prevailing environmental conditions that alter the relationships among symbiotic members. Corals exemplify this concept, where shifts in the algal symbiont community can lead to some corals becoming more or less thermally tolerant. Despite linkage between coral bleaching and disease, the roles of symbiotic bacteria in holobiont resistance and susceptibility to disease remains less well understood. This study thus characterizes the microbiome of disease-resistant and -susceptible Acropora cervicornis coral genotypes (hereafter referred to simply as 'genotypes') before and after high temperature-mediated bleaching. We found that the intracellular bacterial parasite 'Ca. Aquarickettsia rohweri' was strikingly abundant in disease-susceptible genotypes. Disease-resistant genotypes, however, had notably more diverse and even communities, with correspondingly low abundances of 'Ca. Aquarickettsia'. Bleaching caused a dramatic reduction of 'Ca. Aquarickettsia' within disease-susceptible corals and led to an increase in bacterial community dispersion, as well as the proliferation of opportunists. Our data support the hypothesis that 'Ca. Aquarickettsia' species increase coral disease risk through two mechanisms: (i) the creation of host nutritional deficiencies leading to a compromised host-symbiont state and (ii) the opening of niche space for potential pathogens during thermal stress.

Libro, S. & Vollmer, S. V. (2016). Genetic Signature of Resistance to White Band Disease in the Caribbean Staghorn Coral Acropora cervicornis. *PLOS ONE*, 11(1), e0146636. https://doi.org/10.1371/journal.pone.0146636 (Libro and Vollmer 2016)

Coral reefs are declining worldwide due to multiple factors including rising sea surface temperature, ocean acidification, and disease outbreaks. Over the last 30 years, White Band Disease (WBD) alone has killed up to 95% of the Caribbean`s dominant shallow-water corals—the staghorn coral Acropora cervicornis and the elkhorn coral A. palmata. Both corals are now listed on the US Endangered Species Act, and while their recovery has been slow, recent transmission surveys indicate that more than 5% of staghorn corals are disease resistant. Here we compared transcriptome-wide gene expression between resistant and susceptible staghorn corals exposed to WBD using in situ transmission assays. We identified constitutive gene expression differences underlying disease resistance that are independent from the immune response associated with disease exposure. Genes involved in RNA interference-mediated gene silencing, including Argonaute were up-regulated in resistant corals, whereas heat shock proteins (HSPs) were down-regulated. Up-regulation of Argonaute proteins indicates that post-transcriptional gene silencing plays a key, but previously unsuspected role in coral immunity and disease resistance. Constitutive expression of HSPs has been linked to thermal resilience in other Acropora corals, suggesting that the down-regulation of HSPs in disease resistant staghorn corals may confer a dual benefit of thermal resilience.

Merselis, D. G., Lirman, D. & Rodriguez-Lanetty, M. (2018). Symbiotic immuno-suppression: is disease susceptibility the price of bleaching resistance? *PeerJ*, 6, e4494. https://doi.org/10.7717/peerj.4494 (Merselis et al. 2018)

Accelerating anthropogenic climate change threatens to destroy coral reefs worldwide through the processes of bleaching and disease. These major contributors to coral mortality are both closely linked with thermal stress intensified by anthropogenic climate change. Disease outbreaks typically follow bleaching events, but a direct positive linkage between bleaching and disease has been debated. By tracking 152 individual coral ramets through the 2014 mass bleaching in a South Florida coral restoration nursery, we revealed a highly significant negative correlation between bleaching and disease in the Caribbean staghorn coral, Acropora cervicornis. To explain these results, we propose a mechanism for transient immunological protection through coral bleaching: removal of Symbiodinium during bleaching may also temporarily eliminate suppressive symbiont modulation of host immunological function. We contextualize this hypothesis within an ecological perspective in order to generate testable predictions for future investigation.

Miller, M. W., Lohr, K. E., Cameron, C. M., Williams, D. E. & Peters, E. C. (2014). Disease dynamics and potential mitigation among restored and wild staghorn coral, Acropora cervicornis. *PeerJ*, 2, e541. https://doi.org/10.7717/peerj.541 (Miller et al. 2014)

The threatened status (both ecologically and legally) of Caribbean staghorn coral, Acropora cervicornis, has prompted rapidly expanding efforts in culture and restocking, although tissue loss diseases continue to affect populations. In this study, disease surveillance and histopathological characterization were used to compare disease dynamics and conditions in both restored and extant wild populations. Disease had devastating effects on both wild and restored populations, but dynamics were highly variable and appeared to be site-specific with no significant differences in disease prevalence between wild versus restored sites. A subset of 20 haphazardly selected colonies at each site observed over a four-month

period revealed widely varying disease incidence, although not between restored and wild sites, and a case fatality rate of 8%. A tropical storm was the only discernable environmental trigger associated with a consistent spike in incidence across all sites. Lastly, two field mitigation techniques, (1) excision of apparently healthy branch tips from a diseased colony, and (2) placement of a band of epoxy fully enclosing the diseased margin, gave equivocal results with no significant benefit detected for either treatment compared to controls. Tissue condition of associated samples was fair to very poor; unsuccessful mitigation treatment samples had severe degeneration of mesenterial filament cnidoglandular bands. Polyp mucocytes in all samples were infected with suspect rickettsia-like organisms; however, no bacterial aggregates were found. No histological differences were found between disease lesions with gross signs fitting literature descriptions of white-band disease (WBD) and rapid tissue loss (RTL). Overall, our results do not support differing disease quality, quantity, dynamics, nor health management strategies between restored and wild colonies of A. cervicornis in the Florida Keys.

Miller, M. W., Colburn, P. J., Pontes, E., Williams, D. E., Bright, A. J., Serrano, X. M. & Peters, E. C. (2019). Genotypic variation in disease susceptibility among cultured stocks of elkhorn and staghorn corals. *PeerJ*, 7, e6751. https://doi.org/10.7717/peerj.6751 (Miller et al. 2019)

Disease mortality has been a primary driver of population declines and the threatened status of the foundational Caribbean corals, Acropora palmata and A. cervicornis. There remain few tools to effectively manage coral disease. Substantial investment is flowing into in situ culture and population enhancement efforts, while disease takes a variable but sometimes high toll in restored populations. If genetic resistance to disease can be identified in these corals, it may be leveraged to improve resistance in restored populations and possibly lead to effective diagnostic tests and disease treatments. Using a standardized field protocol based on replicated direct-graft challenge assays, we quantified this important trait in cultured stocks from three field nurseries in the Florida Keys. Field tests of 12 genotypes of A. palmata and 31 genotypes of A. cervicornis revealed significant genotypic variation in disease susceptibility of both species measured both as risk of transmission (percent of exposed fragments that displayed tissue loss) and as the rate of tissue loss (cm2 d–1) in fragments with elicited lesions. These assay results provide a measure of relative disease resistance that can be incorporated, along with consideration of other important traits such as growth and reproductive success, into restoration strategies to yield more resilient populations.

Muller, E. M., Bartels, E. & Baums, I. B. (2018). Bleaching causes loss of disease resistance within the threatened coral species Acropora cervicornis. *eLife*, 7, e35066. https://doi.org/10.7554/eLife.35066 (Muller et al. 2018)

Determining the adaptive potential of foundation species, such as reef-building corals, is urgent as the oceans warm and coral populations decline. Theory predicts that corals may adapt to climate change via selection on standing genetic variation. Yet, corals face not only rising temperatures but also novel diseases. We studied the interaction between two major stressors affecting colonies of the threatened coral, Acropora cervicornis: white-band disease and high water temperature. We determined that 27% of A. cervicornis were disease resistant prior to a thermal anomaly. However, disease resistance was largely lost during a bleaching event because of more compromised coral hosts or increased pathogenic

dose/virulence. There was no tradeoff between disease resistance and temperature tolerance; disease susceptibility was independent of Symbiodinium strain. The present study shows that susceptibility to temperature stress creates an increased risk in disease-associated mortality, and only rare genets may maintain or gain infectious disease resistance under high temperature. We conclude that A. cervicornis populations in the lower Florida Keys harbor few existing genotypes that are resistant to both warming and disease.

> Randall, C. J. & van Woesik, R. (2015). Contemporary white-band disease in Caribbean corals driven by climate change. *Nature Climate Change*, 5(4), 375–379. https://doi.org/10.1038/nclimate2530 (Randall and van Woesik 2015)

Over the past 40 years, two of the dominant reef-building corals in the Caribbean, Acropora palmata and Acropora cervicornis, have experienced unprecedented declines. That loss has been largely attributed to a syndrome commonly referred to as white-band disease. Climate change-driven increases in sea surface temperature (SST) have been linked to several coral diseases, yet, despite decades of research, the attribution of white-band disease to climate change remains unknown. Here we hindcasted the potential relationship between recent ocean warming and outbreaks of white-band disease on acroporid corals. We quantified eight SST metrics, including rates of change in SST and contemporary thermal anomalies, and compared them with records of white-band disease on A. palmata and A. cervicornis from 473 sites across the Caribbean, surveyed from 1997 to 2004. The results of our models suggest that decades-long climate-driven changes in SST, increases in thermal minima, and the breach of thermal maxima have all played significant roles in the spread of white-band disease. We conclude that white-band disease has been strongly coupled with thermal stresses associated with climate change, which has contributed to the regional decline of these once-dominant reef-building corals.

> Rosales, S. M., Miller, M. W., Williams, D. E., Traylor-Knowles, N., Young, B. & Serrano, X. M. (2019). Microbiome differences in disease-resistant vs. susceptible Acropora corals subjected to disease challenge assays. *Scientific Reports*, 9(1), 18279. https://doi.org/10.1038/s41598-019-54855-y (Rosales et al. 2019)

In recent decades coral gardening has become increasingly popular to restore degraded reef ecosystems. However, the growth and survivorship of nursery-reared outplanted corals are highly variable. Scientists are trying to identify genotypes that show signs of disease resistance and leverage these genotypes in restoring more resilient populations. In a previous study, a field disease grafting assay was conducted on nursery-reared Acropora cervicornis and Acropora palmata to quantify relative disease susceptibility. In this study, we further evaluate this field assay by investigating putative disease-causing agents and the microbiome of corals with disease-resistant phenotypes. We conducted 16S rRNA gene high-throughput sequencing on A. cervicornis and A. palmata that were grafted (inoculated) with a diseased A. cervicornis fragment. We found that independent of health state, A. cervicornis and A. palmata had distinct alpha and beta diversity patterns from one another and distinct dominant bacteria. In addition, despite different microbiome patterns between both inoculated coral species, the genus Sphingomonadaceae was significantly found in both diseased coral species. Additionally, a core bacteria member from the order Myxococcales was found at relatively higher abundances in corals with lower rates of disease development following grafting. In all, we identified Sphingomonadaceae as a putative coral pathogen

and a bacterium from the order Myxococcales associated with corals that showed disease resistant phenotypes.

> Sweet, M. J., Croquer, A. & Bythell, J. C. (2014). Experimental antibiotic treatment identifies potential pathogens of white band disease in the endangered Caribbean coral Acropora cervicornis. *Proceedings of the Royal Society B: Biological Sciences*, 281, 1788. https://doi.org/10.1098/rspb.2014.0094 (Sweet et al. 2014)

Coral diseases have been increasingly reported over the past few decades and are a major contributor to coral decline worldwide. The Caribbean, in particular, has been noted as a hotspot for coral disease, and the aptly named white syndromes have caused the decline of the dominant reef building corals throughout their range. White band disease (WBD) has been implicated in the dramatic loss of Acropora cervicornis and Acropora palmata since the 1970s, resulting in both species being listed as critically endangered on the International Union for Conservation of Nature Red list. The causal agent of WBD remains unknown, although recent studies based on challenge experiments with filtrate from infected hosts concluded that the disease is probably caused by bacteria. Here, we report an experiment using four different antibiotic treatments, targeting different members of the disease-associated microbial community. Two antibiotics, ampicillin and paromomycin, arrested the disease completely, and by comparing with community shifts brought about by treatments that did not arrest the disease, we have identified the likely candidate causal agent or agents of WBD. Our interpretation of the experimental treatments is that one or a combination of up to three specific bacterial types, detected consistently in diseased corals but not detectable in healthy corals, are likely causal agents of WBD. In addition, a histophagous ciliate (Philaster lucinda) identical to that found consistently in association with white syndrome in Indo-Pacific acroporas was also consistently detected in all WBD samples and absent in healthy coral. Treatment with metronidazole reduced it to below detection limits, but did not arrest the disease. However, the microscopic disease signs changed, suggesting a secondary role in disease causation for this ciliate. In future studies to identify a causal agent of WBD via tests of Henle–Koch's postulates, it will be vital to experimentally control for populations of the other potential pathogens identified in this study.

> Verde, A., Bastidas, C. & Croquer, A. (2016). Tissue mortality by Caribbean ciliate infection and white band disease in three reef-building coral species. *PeerJ*, 4, e2196. https://doi.org/10.7717/peerj.2196 (Verde et al. 2016)

Caribbean ciliate infection (CCI) and white band disease (WBD) are diseases that affect a multitude of coral hosts and are associated with rapid rates of tissue losses, thus contributing to declining coral cover in Caribbean reefs. In this study we compared tissue mortality rates associated to CCI in three species of corals with different growth forms: Orbicella faveolata (massive-boulder), O. annularis (massive-columnar) and Acropora cervicornis (branching). We also compared mortality rates in colonies of A. cervicornis bearing WBD and CCI. The study was conducted at two locations in Los Roques Archipelago National Park between April 2012 and March 2013. In A. cervicornis, the rate of tissue loss was similar between WBD (0.8 ± 1 mm/day, mean ± SD) and CCI (0.7 ± 0.9 mm/day). However, mortality rate by CCI in A. cervicornis was faster than in the massive species O. faveolata (0.5 ± 0.6 mm/day) and O. annularis (0.3 ± 0.3 mm/day). Tissue regeneration was at least fifteen times slower than the mortality rates for both diseases regardless of coral species. This is the first study providing coral tissue mortality

and regeneration rates associated to CCI in colonies with massive morphologies, and it highlights the risks of further cover losses of the three most important reef-building species in the Caribbean.

Pollution, Acidification, and Thermal stress

> Bielmyer-Fraser, G. K., Patel, P., Capo, T. & Grosell, M. (2018). Physiological responses of corals to ocean acidification and copper exposure. *Marine Pollution Bulletin*, 133, 781–790. https://doi.org/10.1016/j.marpolbul.2018.06.048 (Bielmyer-Fraser et al. 2018)

Acidification and land-based sources of pollution have been linked to widespread declines of coral cover in coastal reef ecosystems. In this study, two coral species, Acropora cervicornis and Pocillopora damicornis were exposed to increased copper at two CO2 levels for 96 h. Copper accumulation and anti-oxidant enzyme activities were measured. Copper accumulation only increased in A. cervicornis zooxanthellae and corresponded with photosynthetic toxicity. Enzyme activities in both coral species were affected; however, A. cervicornis was more sensitive than P. damicornis, and zooxanthellae were more affected than animal fractions of holobionts. Generally, activities of all anti-oxidant enzymes increased, with copper exposure in corals; whereas, activities of glutathione reductase and to some degree glutathione peroxidase were observed due to increasing CO2 exposure alone. Exposure to copper in combination with higher CO2 resulted in a synergistic response in some cases. These results provide insight into mechanisms of copper and CO2 impacts in corals.

> Enochs, I. C., Manzello, D. P., Jones, P. J., Aguilar, C., Cohen, K., Valentino, L., . . . Lirman, D. (2018). The influence of diel carbonate chemistry fluctuations on the calcification rate of Acropora cervicornis under present day and future acidification conditions. *Journal of Experimental Marine Biology and Ecology*, 506, 135–143. https://doi.org/10.1016/j.jembe.2018.06.007 (Enochs et al. 2018)

Ocean acidification (OA) will result in lower calcification rates for numerous marine taxa, including many species of corals which create important reef habitat. Seawater carbonate chemistry fluctuates over cycles ranging from days to seasons, often driven by biological processes such as respiration and photosynthesis. The magnitude of diel fluctuations varies spatially and may become more pronounced in the future due to OA. Due to technical constraints, OA experiments that incorporate diel variability into treatments are few in number. As a result, the degree to which coral reef organisms are influenced by ambient daily carbonate chemistry variability is poorly understood. Here we describe an experiment conducted in a novel seawater system which can independently manipulate carbonate chemistry in 16 separate aquaria, in real time, allowing precise control of the mean and magnitude of pH oscillations while minimizing pseudoreplication. Five genotypes of the threatened Caribbean coral Acropora cervicornis were subjected to a total of five pH treatments, 7.80 ± 0.20, 7.80 ± 0.10, and 7.80 ± 0.00, as well as 8.05 ± 0.10 and 8.05 ± 0.00. Those corals exposed to variable contemporary conditions (8.05 ± 0.10) calcified faster than those in current and future static treatment levels, which did not significantly differ from each other. Variable contemporary pH also resulted in faster growth rates than highly variable future conditions (7.80 ± 0.20), but were not significantly different than future conditions with the same ±0.10 diel pH oscillation. These findings support the importance of incorporating diel

variability into OA experiments and suggest that more variable natural ecosystems may yield higher calcification rates for corals.

Kemp, D. W., Colella, M. A., Bartlett, L. A., Ruzicka, R. R., Porter, J. W. & Fitt, W. K. (2016). Life after cold death: reef coral and coral reef responses to the 2010 cold water anomaly in the Florida Keys. *Ecosphere*, 7(6), e01373. http://doi.org/10.1002/ecs2.1373 (Kemp et al. 2016)

Organismal and community-wide responses of reef-building corals are documented before and after a severe cold-water thermal anomaly that occurred in 2010 in the Florida Keys, USA. In January 2010 seawater temperatures dropped far below the normal minima (to <11°C), resulting in the largest documented coral mass mortality event ever recorded in the Florida Keys. Physiological measurements demonstrated species-specific thermal sensitivities to this environmental perturbation. Four common corals with narrow thermal tolerance, Acropora cervicornis, Orbicella annularis, O. faveolata, and Porites astreoides, sustained high mortality (>80%) on inshore reefs. In contrast, another common coral with a wide thermal tolerance, Siderastrea siderea, was not affected by this cold anomaly. We measured biomass, symbiotic algal densities (genus: Symbiodinium), chlorophyll a content, and maximum quantum efficiency of photosystem II for reef-building corals on a seasonal basis before and after the 2010 cold anomaly. Our data document a clear correspondence between physiological response, biomass levels, and survivorship among these five scleractinian coral species. These physiological findings are mirrored by in-shore benthic community monitoring data, which show the dramatic loss of the three cold-sensitive species and continued survival of the cold-tolerant species. Finally, we document recruitment and survival rates of newly settled reef-building corals on four inshore reefs, which experienced high coral mortality during the 2010 cold-kill. Interestingly, both a cold-tolerant species, S. siderea, and a cold-intolerant species, P. astreoides, were the most abundant species recruiting to these postdisturbance reefs.

Langdon, C., Albright, R., Baker, A. C. & Jones, P. (2018). Two threatened Caribbean coral species have contrasting responses to combined temperature and acidification stress. *Limnology and Oceanography*, 63(6), 2450–2464. https://doi.org/10.1002/lno.10952 (Langdon et al. 2018)

There is growing evidence that different coral species and algal symbionts (Symbiodinium spp.) can vary greatly in their response to rising temperatures and also ocean acidification. In a fully crossed factorial experimental design, two threatened Caribbean reef-building coral species, Acropora cervicornis hosting a mixture of Symbiodinium clades A and C and Orbicella faveolata hosting Symbiodinium D, were exposed to combinations of a normal (26°C) and elevated (32°C) temperature and normal (380 ppm) and elevated (800 ppm) CO2 for 62 d and then recovered at 26°C and 380 ppm or 32°C and 380 ppm for an additional 56 d. CO2 enrichment did not confer enhanced thermal tolerance as had been suggested in other studies. A. cervicornis was more sensitive to heat stress (maximum monthly mean + 1.5°C) experiencing 100% mortality after 25 d while all O. faveolata survived. Conversely, O. faveolata was more sensitive to high CO2 experiencing a 47% reduction in growth while A. cervicornis experienced no significant reduction. It is predicted that A. cervicornis is unlikely to survive past 2035. O. faveolata with D symbionts might survive to 2060 and later but its abundance will be impacted by CO2 effects on recruitment potential.

Parkinson, J. E., Bartels, E., Devlin-Durante, M., Lustic, C., Nedimyer, K., Schopmeyer, S., . . . Baums, I. B. (2018). Extensive transcriptional variation poses a challenge to thermal stress biomarker development for endangered corals. *Molecular Ecology*, 27(5), 1103–1119. https://doi.org/10.1111/mec.14517 (Parkinson et al. 2018)

As climate changes, sea surface temperature anomalies that negatively impact coral reef organisms continue to increase in frequency and intensity. Yet, despite widespread coral mortality, genetic diversity remains high even in those coral species listed as threatened. While this is good news in many ways, it presents a challenge for the development of biomarkers that can identify resilient or vulnerable genotypes. Taking advantage of three coral restoration nurseries in Florida that serve as long-term common garden experiments, we exposed over 30 genetically distinct Acropora cervicornis colonies to hot and cold temperature shocks seasonally and measured pooled gene expression responses using RNAseq. Targeting a subset of 20 genes, we designed a high-throughput qPCR array to quantify expression in all individuals separately under each treatment with the goal of identifying predictive and/or diagnostic thermal stress biomarkers. We observed extensive transcriptional variation in the population, suggesting abundant raw material is available for adaptation via natural selection. However, this high variation made it difficult to correlate gene expression changes with colony performance metrics such as growth, mortality and bleaching susceptibility. Nevertheless, we identified several promising diagnostic biomarkers for acute thermal stress that may improve coral restoration and climate change mitigation efforts in the future.

Rodriguez-Casariego, J. A., Ladd, M. C., Shantz, A. A., Lopes, C., Cheema, M. S., Kim, B., . . . Eirin-Lopez, J. M. (2018). Coral epigenetic responses to nutrient stress: Histone H2A.X phosphorylation dynamics and DNA methylation in the staghorn coral Acropora cervicornis. *Ecology and Evolution*, 8(23), 12193–12207. https://doi.org/10.1002/ece3.4678 (Rodriguez-Casariego et al. 2018)

Nutrient pollution and thermal stress constitute two of the main drivers of global change in the coastal oceans. While different studies have addressed the physiological effects and ecological consequences of these stressors in corals, the role of acquired modifications in the coral epigenome during acclimatory and adaptive responses remains unknown. The present work aims to address that gap by monitoring two types of epigenetic mechanisms, namely histone modifications and DNA methylation, during a 7-week-long experiment in which staghorn coral fragments (Acropora cervicornis) were exposed to nutrient stress (nitrogen, nitrogen + phosphorus) in the presence of thermal stress. The major conclusion of this experiment can be summarized by two main results: First, coral holobiont responses to the combined effects of nutrient enrichment and thermal stress involve the post-translational phosphorylation of the histone variant H2A.X (involved in responses to DNA damage), as well as nonsignificant modifications in DNA methylation trends. Second, the reduction in H2A.X phosphorylation (and the subsequent potential impairment of DNA repair mechanisms) observed after prolonged coral exposure to nitrogen enrichment and thermal stress is consistent with the symbiont-driven phosphorus limitation previously observed in corals subject to nitrogen enrichment. The alteration of this epigenetic mechanism could help to explain the synergistic effects of nutrient imbalance and thermal stress on coral fitness (i.e., increased bleaching and mortality) while supporting the positive effect of phosphorus addition to improving coral resilience to thermal stress. Overall, this work provides new insights into the role of epigenetic mechanisms during coral responses to global change, discussing future research directions and the

potential benefits for improving restoration, management and conservation of coral reef ecosystems worldwide.

> Rodríguez-Casariego, J. A., A. E. Mercado-Molina, D. Garcia-Souto, I. M. Ortiz-Rivera, C. Lopes, I. B. Baums, A. M. Sabat, and J. M. Eirin-Lopez. 2020. Genome-Wide DNA Methylation Analysis Reveals a Conserved Epigenetic Response to Seasonal Environmental Variation in the Staghorn Coral Acropora cervicornis. Frontiers in Marine Science 7:560424. doi: 10.3389/fmars.2020.560424 (Rodríguez-Casariego et al. 2020)

Epigenetic modifications such as DNA methylation have been shown to participate in plastic responses to environmental change in a wide range of organisms, including scleractinian corals. Unfortunately, the current understanding of the links between environmental signals, epigenetic modifications, and the subsequent consequences for acclimatory phenotypic changes remain obscure. Such a knowledge gap extends also to the dynamic nature of epigenetic changes, hampering our ability to ascertain the magnitude and extent of these responses under natural conditions. The present work aims to shed light on these subjects by examining temporal changes in genomewide patterns of DNA methylation in the staghorn coral Acropora cervicornis in the island of Culebra, PR. During a 17-month period, a total of 162 polymorphic loci were identified using Methylation-Sensitive Amplified Polymorphism (MSAP). Among them, 83 of these restriction fragments displayed changes in DNA methylation that were significantly correlated to seasonal variation as determined mostly by changes in sea water temperature. Remarkably, the observed time-dependent variation in DNA methylation patterns is consistent across coral genets, coral source sites and site specific conditions studied. Overall, these results are consistent with a conserved epigenetic response to seasonal environmental variation. These findings highlight the importance of including seasonal variability into experimental designs investigating the role of epigenetic mechanisms such as DNA methylation in responses to stress.

> Yetsko, K., M. Ross, A. Bellantuono, D. Merselis, M. Rodriquez-Lanetty, and M. R. Gilg. 2020. Genetic differences in thermal tolerance among colonies of threatened coral Acropora cervicornis: potential for adaptation to increasing temperature. Marine Ecology Progress Series 646:45-68. https://doi.org/10.3354/meps13407 (Yetsko et al. 2020)

Climate change is resulting in warmer temperatures that are negatively impacting corals. Understanding how much individuals within a population vary in their thermal tolerance and whether this variation is heritable is important in determining whether a species can adapt to climate change. To address this, Acropora cervicornis fragments from 20 genetically distinct colonies collected from the Coral Restoration Foundation Tavernier nursery (Florida, USA) were kept at either ambient (28 ± 1°C) or elevated (32 ± 1°C) temperatures, and mortality was monitored for 26 d. Both broad-sense (H2) and narrow-sense (h2) heritability of thermal tolerance were estimated to determine the amount of genetic variation underlying survival to elevated temperature. To understand the physiological basis of thermal tolerance, tissue from both treatments was taken 12 h after the start of the experiment to investigate gene expression at the mRNA and protein level between tolerant and susceptible colonies. Results revealed that this population has considerable total genetic variation in thermal tolerance (H 2 = 0.528), but low variance in relatedness among colonies prevented us from making any conclusions regarding h2. Despite high transcriptomic variability among and within colonies, 40 genes were consistently and significantly different between

tolerant and susceptible colonies, and could be potential biomarkers for thermal tolerance should they be verified in a larger sample. Overall, the results suggest that this population has substantial genetic variation for traits that directly impact thermal tolerance; however, their response to projected increases in temperature will depend on more precise estimates of the additive components of this variation (h2).

Predation

> Bright, A. J., Cameron, C. M. & Miller, M. W. (2015). Enhanced susceptibility to predation in corals of compromised condition. *PeerJ*, 3, e1239. https://doi.org/10.7717/peerj.1239 (Bright et al. 2015)

The marine gastropod, Coralliophila abbreviata, is an obligate corallivore that causes substantial mortality in Caribbean Acropora spp. Considering the imperiled status of Acropora cervicornis and A. palmata, a better understanding of ecological interactions resulting in tissue loss may enable more effective conservation strategies. We examined differences in susceptibility of A. cervicornis to C. abbreviata predation based on coral tissue condition. Coral tissue condition was a strong determinant of snail prey choice, with snails preferring A. cervicornis fragments that were diseased or mechanically damaged over healthy fragments. In addition, snails always chose fragments undergoing active predation by another snail, while showing no preference for a non-feeding snail when compared with an undisturbed prey fragment. These results indicate that the condition of A. cervicornis prey influenced foraging behavior of C. abbreviata, creating a potential feedback that may exacerbate damage from predation in coral populations compromised by other types of disturbance.

> Johnston, L. & Miller, M. W. (2014). Negative indirect effects of neighbors on imperiled scleractinian corals. *Coral Reefs*, 33(4), 1047–1056. https://doi.org/10.1007/s00338-014-1176-8 (Johnston and Miller 2014)

Predation pressure on an individual may be influenced by spatial associations with other organisms. In the case of rare and imperiled species, such indirect interactions may affect the persistence and recovery of local populations. This study examined the effects of coral neighborhood composition on the foraging behavior and impact of the corallivorous gastropod, Coralliophila abbreviata. We conducted a manipulative field experiment in which focal colonies of the threatened scleractinian coral Acropora cervicornis had no neighbors, conspecific neighbors, alternative prey (Orbicella faveolata) neighbors, or non-prey (Porites asteroides) neighbors. Individually tagged C. abbreviata were then seeded into the study area and allowed to colonize the experimental plots. Initial colonization was significantly affected by the species of neighboring corals and snail abundance after colonization was negatively correlated with focal colony growth. Snails exhibited a strong prey preference for A. cervicornis over O. faveolata and responded numerically to neighborhood quality (i.e., relative preference for neighboring corals). Thus, conspecific neighbors had the greatest predator-mediated negative effect on focal colony performance followed by O. faveolata neighbors. The results suggest that C. abbreviata mediate apparent competition between O. faveolata and A. cervicornis as both species contributed to the local abundance of their shared predator. Additionally, home range estimates for tagged C. abbreviata were calculated, compared among sexes, and found to be significantly greater for males than for females. Overall, this study sheds light on the foraging behavior of an important coral predator and highlights the potential importance of consumer-

mediated indirect interactions in the dynamics of severely reduced populations. The results also have direct implications for conservation and population enhancement efforts.

Schopmeyer, S. A. & Lirman, D. (2015). Occupation Dynamics and Impacts of Damselfish Territoriality on Recovering Populations of the Threatened Staghorn Coral, Acropora cervicornis. *PLOS ONE* 10(11), e0141302. https://doi.org/10.1371/journal.pone.0141302 (Schopmeyer and Lirman 2015)

Large-scale coral reef restoration is needed to help recover structure and function of degraded coral reef ecosystems and mitigate continued coral declines. In situ coral propagation and reef restoration efforts have scaled up significantly in past decades, particularly for the threatened Caribbean staghorn coral, Acropora cervicornis, but little is known about the role that native competitors and predators, such as farming damselfishes, have on the success of restoration. Steep declines in A. cervicornis abundance may have concentrated the negative impacts of damselfish algal farming on a much lower number of coral prey/colonies, thus creating a significant threat to the persistence and recovery of depleted coral populations. This is the first study to document the prevalence of resident damselfishes and negative effects of algal lawns on A. cervicornis along the Florida Reef Tract (FRT). Impacts of damselfish lawns on A. cervicornis colonies were more prevalent (21.6% of colonies) than those of other sources of mortality (i.e., disease (1.6%), algal/sponge overgrowth (5.6%), and corallivore predation (7.9%)), and damselfish activities caused the highest levels of tissue mortality (34.6%) among all coral stressors evaluated. The probability of damselfish occupation increased as coral colony size and complexity increased and coral growth rates were significantly lower in colonies with damselfish lawns (15.4 vs. 29.6 cm per year). Reduced growth and mortality of existing A. cervicornis populations may have a significant effect on population dynamics by potentially reducing important genetic diversity and the reproductive potential of depleted populations. On a positive note, however, the presence of resident damselfishes decreased predation by other corallivores, such as Coralliophila and Hermodice, and may offset some negative impacts caused by algal farming. While most negative impacts of damselfishes identified in this study affected large individual colonies and <50% of the A. cervicornis population along the FRT, the remaining wild staghorn population, along with the rapidly increasing restored populations, continue to fulfill important functional roles on coral reefs by providing essential habitat and refuge to other reef organisms. Although the effects of damselfish predation are, and will continue to be, pervasive, successful restoration efforts and strategic coral transplantation designs may help overcome damselfish damage by rapidly increasing A. cervicornis cover and abundance while also providing important information to educate future conservation and management decisions.

Shaver, E. C., Shantz, A. A., McMinds, R., Burkepile, D. E., Vega Thurber, R. L. & Silliman, B. R. (2017). Effects of predation and nutrient enrichment on the success and microbiome of a foundational coral. *Ecology*, 98(3), 830–839. https://doi.org/10.1002/ecy.1709 (Shaver et al. 2017)

By inflicting damage to prey tissues, consumer species may increase stress in prey hosts and reduce overall fitness (i.e., primary effects, such as growth or reproduction) or cause secondary effects by affecting prey interactions with other species such as microbes. However, little is known about how abiotic conditions affect the outcomes of these biotic interactions. In coral reef communities, both nutrient

enrichment and predation have been linked to reduced fitness and disease facilitation in corals, yet no study to date has tested their combined effects on corals or their associated microbial communities (i.e., microbiomes). Here, we assess the effects of grazing by a prevalent coral predator (the short coral snail, Coralliophila abbreviata) and nutrient enrichment on staghorn coral, Acropora cervicornis, and its microbiomes using a factorial experiment and high-throughput DNA sequencing. We found that predation, but not nutrients, significantly reduced coral growth and increased mortality, tissue loss, and turf algae colonization. Partial predation and nutrient enrichment both independently altered coral microbiomes such that one bacterial genus came to dominate the microbial community. Nutrient-enriched corals were associated with significant increases in Rickettsia-like organisms, which are currently one of several microbial groups being investigated as a disease agent in this coral species. However, we found no effects of nutrient enrichment on coral health, disease, or their predators. This research suggests that in the several months following coral transplantation (i.e., restoration) or disturbance (i.e., recovery), Caribbean acroporid corals appear to be highly susceptible to negative effects caused by predators, but not or not yet susceptible to nutrient enrichment despite changes to their microbial communities.

Restoration and Conservation Methods

> Calle-Triviño, J., Cortés-Useche, C., Sellares-Blasco, R. I. & Arias-González, J. E. (2018). Assisted fertilization of threatened Staghorn Coral to complement the restoration of nurseries in Southeastern Dominican Republic. *Regional Studies in Marine Science*, 18, 129–134. https://doi.org/10.1016/j.rsma.2018.02.002 (Calle-Triviño et al. 2018)

Acropora cervicornis and Acropora palmata have declined dramatically in the Caribbean since the early 80's, and are classified as Critically Endangered Species. To promote their recovery, restoration programs focusing on introducing fragmented specimens have been intensified. The current study was conducted in the south-eastern part of the Dominican Republic in September 2015 and August 2016. During these two periods, gametes from six mature colonies were collected from a five-year-old nursery with an area of 150 m2 at a depth of 12.5 m. 80% of the studied colonies spawned both years. Fertilization was assisted between 21:50 and 00:00 h, immediately after spawning. Fertilization and settlement rates were 90% and 50%, respectively. To our knowledge, this is the first scientific report on nursery propagated A. cervicornis spawning, assisted fertilization, larvae rearing and breeding.

> Calle-Triviño, J., Rivera-Madrid, R., León-Pech, M. G., Cortés-Useche, C., Sellares-Blasco, R. I., Aguilar-Espinosa, M. & Arias-González, J. E. (2020). Assessing and genotyping threatened staghorn coral Acropora cervicornis nurseries during restoration in southeast Dominican Republic. *PeerJ*, 8, e8863. https://doi.org/10.7717/peerj.8863 (Calle-Trivino et al. 2020)

Acropora cervicornis is a structurally and functionally important Caribbean coral species. Since the 1980s, it has suffered drastic population losses with no signs of recovery and has been classified as a critically endangered species. Its rapid growth rate makes it an excellent candidate for coral restoration programs. In 2011, the Fundación Dominicana de Estudios Marinos (Dominican Marine Studies Foundation, FUNDEMAR) began an A. cervicornis restoration program in Bayahibe, southeast Dominican Republic. In this study, we present the methodology and results of this program from its

conception through 2017, a preliminary analysis of the strong 2016 and 2017 cyclonic seasons in the greater Caribbean, and a genetic characterization of the "main nursery". The mean survival of the fragments over 12 months was 87.45 ± 4.85% and the mean productivity was 4.01 ± 1.88 cm year−1 for the eight nurseries. The mean survival of six outplanted sites over 12 months was 71.55 ± 10.4%, and the mean productivity was 3.03 ± 1.30 cm year−1. The most common cause of mortality during the first 12 months, in both nurseries and outplanted sites, was predation by the fireworm, Hermodice carunculata. We identified 32 multilocus genotypes from 145 total analyzed individuals. The results and techniques described here will aid in the development of current and future nursery and outplanted site restoration programs.

Cummings, K., Zuke, A., Stasio, B. D. & Krumholz, J. (2015). Coral Growth Assessment on an Established Artificial Reef in Antigua. *Ecological Rest.*, 33(1), 90–95. https://doi.org/10.3368/er.33.1.90 (Cummings et al. 2015)

Anthropogenic pressure on coral reef ecosystems has increased the need for effective restoration and rehabilitation as a management tool. However, quantifying the success of restoration projects can be difficult, and adequate monitoring data are scarce. This study compared growth rates over a six-year period of three Caribbean coral species, staghorn coral (Acropora cervicornis), elkhorn coral (Acropora palmata), and thick finger coral (Porites porites), transplanted on an artificial reef off Maiden Island, Antigua, to literature values for the same species growing on naturally formed reefs in the Caribbean region. The average growth rate of staghorn coral was considerably lower than growth rates reported in the literature, while elkhorn and finger corals showed growth rates similar to literature values. The observed inter- and intraspecific differences may be caused by species-specific growth requirements and/or restoration site conditions, factors that should be taken into account when planning future projects involving coral transplant or rescue. This study also determined the analytical precision of a 'low tech' monitoring method using a basic underwater digital camera and the software program ImageJ to measure growth rates of corals. Measurement error between volunteer analysts receiving only minimal training was shown to be very small, ranging from 0.37–1.40% depending on the coral species. This confirms the validity of this basic technique, particularly in cases where data are sparse and resources for monitoring are extremely limited.

Delgado, G. A. & Sharp, W. C. (2020). Capitalizing on an ecological process to aid coral reef ecosystem restoration: Can gastropod trophodynamics enhance coral survival? *Coral Reefs*, 39(2), 319–330. https://doi.org/10.1007/s00338-020-01893-y (Delgado and Sharp 2020)

Coral reefs in the Florida Keys have degraded in recent decades, prompting efforts to re-establish populations of staghorn coral, Acropora cervicornis, to restore structure and ecological function. However, predation on these corals by the corallivorous gastropod, Coralliophila galea, has been a substantial and chronic impediment to restoration efforts. Therefore, we conducted a series of manipulative laboratory experiments and a 2-week, in situ proof-of-concept trial to determine whether Thais deltoidea, a carnivorous gastropod that co-occurs with C. galea, can control C. galea corallivory and thus improve A. cervicornis survival. Our laboratory results showed that T. deltoidea preys upon C. galea, although it is not a preferred prey choice. Nevertheless, treatments with T. deltoidea had significantly

higher percentages of live coral tissue than when T. deltoidea was absent. This occurred not only because T. deltoidea consumed C. galea, but also because the presence of T. deltoidea elicited an escape response in C. galea, significantly reducing the amount of time C. galea spent feeding on A. cervicornis colonies. This trophic relationship was also seen in our in situ proof-of-concept trial. We observed significantly fewer C. galea on A. cervicornis when T. deltoidea was present which led to a higher, if not statistically significant, percentage of live tissue on our A. cervicornis outplants. Ecological processes need to be incorporated into coral reef ecosystem restoration to achieve positive outcomes. Integrating T. deltoidea into coral restoration efforts may improve success by mitigating C. galea corallivory through the non-consumptive, risk-adverse, escape response that T. deltoidea provokes, initiating a trophic cascade that improves the long-term survival of outplanted corals. Further research is needed to determine the long-term efficacy of this approach, but the addition of gastropod trophodynamics to coral reef ecosystem restoration may prove useful.

Flint, M. & Than, J. T. (2016). Potential spawn induction and suppression agents in Caribbean Acropora cervicornis corals of the Florida Keys. *PeerJ*, 4, e1982. https://doi.org/10.7717/peerj.1982 (Flint and Than 2016)

The enhanced ability to direct sexual reproduction may lead to improved restoration outcomes for Acropora cervicornis. Gravid fragments of A. cervicornis were maintained in a laboratory for two sequential trials in the seven days prior to natural spawning in the Florida Keys. Ten replicates of five chemicals known to affect spawning in various invertebrate taxa were tested. Hydrogen peroxide at 2 mM (70%) and L-5-hydroxytryptophan (5-HTP) at 5 (40%) and 20 µM (30%) induced spawning within 15.4 h, 38.8 h and 26.9 h of dosing at or above the rate of release of the control (30%) within 14.6 h. Serotonin acetate monohydrate at 1 µM (20%) and 10 µM (20%), naloxone hydrochloride dihydrate at 0.01 µM (10%) and potassium phosphate monobasic at 0.25 µM (0%) induced spawning at rates less than the control. Although the greatest number of fragments spawned using hydrogen peroxide, it was with 100% mortality. There was a significantly higher induction rate closer to natural spawn (Trial 2) compared with Trial 1 and no genotype effect. Mechanisms of action causing gamete release were not elucidated. In Caribbean staghorn corals, 5-HTP shows promise as a spawning induction agent if administered within 72 h of natural spawn and it will not result in excessive mortality. Phosphate chemicals may inhibit spawning. This is the first study of its kind on Caribbean acroporid corals and may offer an important conservation tool for biologists currently charged with restoring the imperiled Acropora reefs of the Florida Keys.

Forrester, G. E., Chan, M., Conetta, D., Dauksis, R., Nickles, K. & Siravo, A. (2019). Comparing the Efficiency of Nursery and Direct Transplanting Methods for Restoring Endangered Corals. *Ecological Restoration*, 37(2), 81–89. http://muse.jhu.edu/article/725208 (Forrester et al. 2019)

Restoration of plants, corals, and other sessile species often involves transplanting individuals to sites chosen for rehabilitation. Transplanted individuals are sometimes harvested directly from wild populations (direct transplanting), and sometimes propagated or cultured in a "nursery" before being transplanted (nursery outplanting). The ecological effectiveness and cost-efficiency of these methods have rarely been compared, so we performed an experiment to address this. Coral fragments, Acropora

cervicornis (n = 780), were collected and assigned to one of three treatments: 1) directly transplanted to a restoration site and placed loose on the reef; 2) directly transplanted and manually attached to the reef; 3) moved to a nursery site near the restoration site for three months before being transplanted and manually attached to the reef. Treatment 1 was inefficient simply because these corals survived poorly. After 15 months, the survival and growth of corals assigned to treatments 2 and 3 was similar. The nursery method (3) was more expensive and time-consuming than direct transplanting (2), so treatment 2 yielded twice as many surviving corals per hour of work invested and three times as many survivors per dollar of set-up costs as treatment 3. The net production of live coral tissue per hour or per dollar invested was also greatest for direct-attached transplants. Cost- and time-efficiency are important considerations for practitioners seeking to maximize the area of reef rehabilitated and, in this case study, were maximized by bypassing a nursery stage.

> Goergen, E. A. & Gilliam, D. S. (2018). Outplanting technique, host genotype, and site affect the initial success of outplanted Acropora cervicornis. *PeerJ*, 6, e4433. https://doi.org/10.7717/peerj.4433 (Goergen and Gilliam 2018)

Acropora cervicornis is the most widely used coral species for reef restoration in the greater Caribbean. However, outplanting methodologies (e.g., colony density, size, host genotype, and attachment technique) vary greatly, and to date have not been evaluated for optimality across multiple sites. Two experiments were completed during this study, the first evaluated the effects of attachment technique, colony size, and genotype by outplanting 405 A. cervicornis colonies, from ten genotypes, four size classes, and three attachment techniques (epoxy, nail and cable tie, or puck) across three sites. Colony survival, health condition, tissue productivity, and growth were assessed across one year for this experiment. The second experiment assessed the effect of colony density by outplanting colonies in plots of one, four, or 25 corals per 4 m2 across four separate sites. Plot survival and condition were evaluated across two years for this experiment in order to better capture the effect of increasing cover. Colonies attached with a nail and cable tie resulted in the highest survival regardless of colony size. Small corals had the lowest survival, but the greatest productivity. The majority of colony loss was attributed to missing colonies and was highest for pucks and small epoxied colonies. Disease and predation were observed at all sites, but did not affect all genotypes, however due to the overall low prevalence of either condition there were no significant differences found in any comparison. Low density plots had significantly higher survival and significantly lower prevalence of disease, predation, and missing colonies than high density plots. These results indicate that to increase initial outplant success, colonies of many genotypes should be outplanted to multiple sites using a nail and cable tie, in low densities, and with colonies over 15 cm total linear extension.

> Griffin, J. N., Schrack, E. C., Lewis, K., Baums, I. B., Soomdat, N. & Silliman, B. R. (2015). Density-dependent effects on initial growth of a branching coral under restoration. *Restoration Ecology*, 23(3), 197–200. https://doi.org/10.1111/rec.12173 (Griffin et al. 2015)

Coral reef restoration aims to help threatened coral ecosystems recover from recent severe declines. Here we address whether coral fragments should be out-planted individually or in larger aggregations. Theory suggests alternative possible outcomes: whereas out-plants within aggregations might suffer from

heightened negative interactions with neighbors (e.g. competition for space), they may alternatively benefit from positive interactions with neighbors (e.g. buffering wave disturbances). On a degraded reef in the Caribbean (St. Croix, USVI), using out-plants of the critically endangered staghorn coral Acropora cervicornis, we experimentally tested how aggregation density (1–20 out-planted coral fragments spaced at approximately 5 cm) influenced initial coral growth (over 3 months). Coral growth declined as a function of aggregation size, and out-plants within larger aggregations had fewer and shorter secondary branches on average, indicative of horizontal competition for space. Our results therefore suggest that wide spacing of individuals will maximize the initial growth of out-planted branching corals.

Henry, J. A., O'Neil, K. L. & Patterson, J. T. (2019). Native Herbivores Improve Sexual Propagation of Threatened Staghorn Coral Acropora cervicornis. *Front. Mar. Sci.*, 6:713. https://doi.org/10.3389/fmars.2019.00713 (Henry et al. 2019)

Staghorn coral Acropora cervicornis was once spatially dominant on Caribbean reefs but is now threatened throughout its range. In recent years, advancements in ex-situ sexual propagation of Caribbean corals have increased the viability of this management strategy. Thus, improving culture methods for sexually propagated corals is important to bolster the overall coral restoration portfolio and increase genetic diversity in restored populations. In both natural systems and culture scenarios, algae proliferation negatively impacts coral growth and survival. Growing coral with native herbivores may represent a strategy for increased efficiency. We tested A. cervicornis recruits raised in replicate aquaria with identical densities of juvenile Lithopoma americanum or juvenile Batillaria minima snails plus a no-snail control. Each of three replicates per treatment contained tiles with similar numbers of recently settled, visually healthy, A. cervicornis. Tiles were photographed every three weeks for five months and coral growth, survivability, turf algae cover, and crustose coralline algae (CCA) cover were quantified. Labor time for cleaning was carefully recorded for each treatment. Results indicated improved growth and survival when A. cervicornis recruits were raised with either snail species in comparison to a no-herbivore control. Further, including snails decreased labor and eliminated turf algae cover. Interestingly, L. americanum significantly reduced CCA cover relative to the other treatments. We report some of the highest survival rates observed to date for sexually propagated Atlantic corals. Ultimately, results suggest that rearing sexually propagated A. cervicornis with native herbivores could improve the ability to employ these corals in reef restoration.

Huntington, B. E., Miller, M. W., Pausch, R. & Richter, L. (2017). Facilitation in Caribbean coral reefs: high densities of staghorn coral foster greater coral condition and reef fish composition. *Oecologia*, 184(1), 247–257. https://doi.org/10.1007/s00442-017-3859-7 (Huntington et al. 2017)

Recovery of the threatened staghorn coral (Acropora cervicornis) is posited to play a key role in Caribbean reef resilience. At four Caribbean locations (including one restored and three extant populations), we quantified characteristics of contemporary staghorn coral across increasing conspecific densities, and investigated a hypothesis of facilitation between staghorn coral and reef fishes. High staghorn densities in the Dry Tortugas exhibited significantly less partial mortality, higher branch growth, and supported greater fish abundances compared to lower densities within the same population. In contrast, partial mortality, branch growth, and fish community composition did not vary with staghorn

density at the three other study locations where staghorn densities were lower overall. This suggests that density-dependent effects between the coral and fish community may only manifest at high staghorn densities. We then evaluated one facilitative mechanism for such density-dependence, whereby abundant fishes sheltering in dense staghorn aggregations deliver nutrients back to the coral, fueling faster coral growth, thereby creating more fish habitat. Indeed, dense staghorn aggregations within the Dry Tortugas exhibited significantly higher growth rates, tissue nitrogen, and zooxanthellae densities than sparse aggregations. Similarly, higher tissue nitrogen was induced in a macroalgae bioassay outplanted into the same dense and sparse aggregations, confirming greater bioavailability of nutrients at high staghorn densities. Our findings inform staghorn restoration efforts, suggesting that the most effective targets may be higher coral densities than previously thought. These coral-dense aggregations may reap the benefits of positive facilitation between the staghorn and fish community, favoring the growth and survivorship of this threatened species.

Ladd, M. C., Shantz, A. A., Nedimyer, K. & Burkepile, D. E. (2016). Density Dependence Drives Habitat Production and Survivorship of Acropora cervicornis Used for Restoration on a Caribbean Coral Reef. *Front. Mar. Sci.*, 3:261. https://doi.org/10.3389/fmars.2016.00261 (Ladd et al. 2016)

Abstract Coral restoration is gaining traction as a viable strategy to help restore degraded reefs. While the nascent field of coral restoration has rapidly progressed in the past decade, significant knowledge gaps remain regarding the drivers of restoration success that may impede our ability to effectively restore coral reef communities. Here, we conducted a field experiment to investigate the influence of coral density on the growth, habitat production, and survival of corals outplanted for restoration. We used nursery-raised colonies of Acropora cervicornis to experimentally establish populations of corals with either 3, 6, 12, or 24 corals within 4m2 plots, generating a gradient of coral densities ranging from 0.75 corals m-2 to 12 corals m-2. After 13 months we found that density had a significant effect on the growth, habitat production, and survivorship of restored corals. We found that coral survivorship increased as colony density decreased. Importantly, the signal of density dependent effects was context dependent. Our data suggest that positive density dependent effects influenced habitat production at densities of 3 corals m-2, but further increases in density resulted in negative density dependent effects with decreasing growth and survivorship of corals. These findings highlight the importance of density dependence for coral restoration planning and demonstrate the need to evaluate the influence of density for other coral species used for restoration. Further work focused on the mechanisms causing density dependence such as increased herbivory, rapid disease transmission, or altered predation rates are important next steps to advance our ability to effectively restore coral reefs.

Ladd, M. C., Shantz, A. A., Bartels, E. & Burkepile, D. E. (2017). Thermal stress reveals a genotype-specific tradeoff between growth and tissue loss in restored Acropora cervicornis. *Marine Ecology Progress Series*, 572, 129–139. https://doi.org/10.3354/meps12169 (Ladd et al. 2017)

Coral restoration is gaining attention as a viable strategy to restore degraded reefs, with large-scale restoration efforts underway worldwide. However, our understanding of the drivers of restoration success lags behind restoration activities, generating significant knowledge gaps that may impede our ability to

successfully restore coral reef communities. Here, we conducted a 21 mo field experiment to examine the influence of genotypic identity and diversity on coral growth, habitat production, and survivorship in restored corals. We used nursery-raised colonies of Acropora cervicornis, the predominant coral used for restoration in the Caribbean, to establish populations of either 1, 2, 4, or 6 distinct genotypes. Midway through our experiment, our study site experienced a 17 wk thermal stress event that allowed us to examine the influence of genotypic identity and diversity on the ability of restored corals to cope with thermal stress. After 21 mo we found no effect of genotypic diversity on restored corals, but that genotypes differed 3-fold in survivorship and 20 to 327% in habitat production. Initial growth rates showed a significant positive relationship with live tissue loss at the end of the experiment, suggesting a tradeoff between growth and the ability to recover from thermal stress. Our study suggests that genotypic identity is a critical factor to incorporate into coral restoration planning. Investigating the role of genotypic identity and diversity on the ability of restored corals to resist pervasive coral reef stressors, such as disease, predator outbreaks, and nutrient pollution, are critical steps in advancing coral restoration efforts.

Ladd, M. C., Burkepile, D. E. & Shantz, A. A. (2019). Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes. *Restoration Ecology*, 27(5), 1166–1176.
https://doi.org/10.1111/rec.12939 (Ladd et al. 2019)

The global decline of corals has created an urgent need for effective, science-based methods to augment coral populations and restore important ecosystem functions. To meet this challenge, the field of coral restoration has rapidly evolved over the past decade. However, despite widespread efforts to outplant corals and monitor survivorship, there is a shortage of information on the effects of coral restoration on reef communities or important ecosystem functions. To fill this knowledge gap, we examined the effects of restoration on three major criteria: diversity, community structure, and ecological processes. We conducted surveys of four restored sites in the Florida Keys ranging in restoration effort (500–2,300 corals outplanted) paired with surveys of nearby, unmanipulated control sites. Coral restoration successfully enhanced coral populations, increasing coral cover 4-fold, but manifested in limited differences in coral and fish communities. Some restored sites had higher abundance of herbivorous fish, rates of herbivory, or more juvenile-sized corals, but these effects were limited to individual reefs. Damselfish were consistently more abundant at restored compared to control sites. Despite augmenting target coral populations, 3 years of coral restoration has not facilitated many of the positive feedbacks that help reinforce coral success. In a time of increasingly frequent disturbances, it is urgent we hasten the speed at which reefs recover important ecological processes, such as herbivory and nutrient cycling, that make reefs more resistant and resilient if we are to achieve long-term restoration success.

Lohr, K. E. & Patterson, J. T. (2017). Intraspecific variation in phenotype among nursery-reared staghorn coral Acropora cervicornis (Lamarck, 1816). *Journal of Experimental Marine Biology and Ecology*, 486, 87–92.
https://doi.org/10.1016/j.jembe.2016.10.005 (Lohr and Patterson 2017)

Although genetic diversity is recognized as an important consideration for coral restoration, genotypes for use in restoration are not typically selected based on an evaluation of phenotype. Systematic

documentation of phenotypic variability within coral nurseries could inform restoration efforts. To quantify differences in phenotype, ten known genotypes of Acropora cervicornis in an established coral nursery in the Florida Keys were selected for study. Twelve 5-cm replicate colonies of each genotype were individually tagged for identification and suspended from four identical PVC tree structures within the nursery for grow-out. Total linear extension (TLE) and number of branches were measured at approximately 45-day intervals for a period of 13months. Buoyant weight was determined for each colony initially and after five and 13months in order to quantify calcification. Sub-lethal bleaching was observed among experimental colonies following a natural thermal stress event, and significant differences in bleaching prevalence were present among genotypes. At the conclusion of the study, significant differences in all growth parameters were detected among genotypes. Specific growth rate across genotypes decreased following bleaching. The ratio of buoyant weight to TLE varied among genotypes and decreased with increasing TLE, suggesting a potential tradeoff between extension and skeletal density in nursery-reared A. cervicornis. Phenotypic variation documented in this study has implications for nursery management and may be useful in selecting genotypes for A. cervicornis population enhancement.

Lohr, K. E., Bejarano, S., Lirman, D., Schopmeyer, S. & Manfrino, C. (2015). Optimizing the productivity of a coral nursery focused on staghorn coral Acropora cervicornis. *Endangered Species Research*, 27(3), 243–250. https://doi.org/10.3354/esr00667 (Lohr et al. 2015)

The rapid decline of the staghorn coral Acropora cervicornis throughout the Caribbean prompted the development of coral gardening as a management strategy to restore wild stocks. Given that coral gardening relies on propagating corals collected from wild donor colonies, it is imperative to optimize growth within a nursery to reduce dependence on wild collections. This study determined the maximum amount of coral that may be clipped from a colony during propagation without causing mortality or decreased growth. We applied 3 experimental treatments to 12 nursery-reared staghorn corals, in which 25, 50, or 75% of the colony's total biomass was removed and fragmented to create additional, smaller fragments. Four additional colonies served as unfragmented controls. Treatment had no effect on colony productivity, defined as the ratio of new tissue growth to initial colony size, over 87 d. Similarly, treatment had no effect on the rate at which colonies developed new branches. Results indicate that 75% of the biomass of staghorn colonies may be removed without affecting their growth. We anticipate that our observations will have practical applications for maximizing propagation of staghorn coral within nurseries throughout the wider Caribbean while minimizing the impact of this management measure on remnant wild populations.

Lohr, K. E., McNab, A. A. C., Manfrino, C. & Patterson, J. T. (2017). Assessment of wild and restored staghorn coral Acropora cervicornis across three reef zones in the Cayman Islands. *Regional Studies in Marine Science*, 9, 1–8. https://doi.org/10.1016/j.rsma.2016.11.003 (Lohr et al. 2017)

Interest in restoring staghorn coral Acropora cervicornis has grown following the widespread decline of this species in recent decades. To date, thousands of nursery-reared A. cervicornis have been outplanted to restore degraded reefs, but survivorship and growth among outplanted colonies can be spatially

variable. In particular, data on distribution of remnant wild populations and outplant performance in varying reef zones is lacking. To address this gap, we conducted a study to characterize existing wild populations and assess performance of nursery-reared, outplanted A. cervicornis among three reef zones of varying depth at Little Cayman Island: the shallow back reef (0–3 m), the intermediate spur-and-groove reef (8–15 m), and the deep reef terrace (>15 m). Wild populations of A. cervicornis were present in each reef zone, and colony height and prevalence of predation by Stegastes spp. were highest in the intermediate zone. For outplanted A. cervicornis, survivorship differed among sites and was lowest for outplants in the deep zone during the 85-day observation period. Post-outplant growth and branching was lowest among outplants in the shallow zone due to high rates of colony breakage. Following the conclusion of the study, a mortality event occurred in which 90% of outplants at the shallow plots died during a period of elevated sea temperature. The information provided in this study suggests that intermediate spur-and-groove reefs are optimal for outplanting activities in Little Cayman using existing restoration methods. These data could be useful for coral restoration practitioners and government agencies in the Caribbean, particularly the Cayman Islands, which is actively expanding its coral nursery program. New strategies must be developed to improve restoration outcomes in shallow and deep zones.

Lohr, K. E., Ripple, K. & Patterson, J. T. (2020). Differential disturbance effects and phenotypic plasticity among outplanted corals at patch and fore reef sites. *Journal for Nature Conservation*, 55, 125827.
https://doi.org/10.1016/j.jnc.2020.125827 (Lohr et al. 2020)

Practitioners have outplanted tens of thousands of nursery-reared coral colonies for restoration purposes, and interest in outplanting is increasing. However, restoration outcomes on natural reefs can be variable, and genotype- and site-specific differences have been reported. To systematically explore these differences, performance of restored corals was compared at two site types, and intraspecific variation in phenotype among six genotypes previously characterized in a nursery was simultaneously assessed. Nursery-reared Acropora cervicornis colonies were outplanted to geographically paired fore reef (n = 2) and patch reef (n = 2) sites. Colony growth and condition were monitored over one year. After the first monitoring visit, Hurricane Irma passed directly over outplant sites, providing an opportunity to examine disturbance effects across sites. In contrast to nursery results, growth did not vary among genotypes or sites either pre- or post-hurricane. Plasticity in pre-hurricane growth among sites was observed for one of the six genotypes examined. Stark differences in post-hurricane survival were observed between fore reef and patch reef sites: while 51.04 ± 9.38 % of outplanted colonies survived at patch reef sites, no colonies could be located at either fore reef site. Records from additional sites monitored by practitioners indicated higher outplant survival following hurricane disturbance at patch reef sites compared to fore reef sites. The lack of site or genotype effects on growth in A. cervicornis contrasts with a number of previous studies, however growth results were likely confounded by Hurricane Irma. Reduced structural complexity on Caribbean reefs may contribute to differential hurricane impacts between restored fore reefs and patch reefs. These results suggest that restoration practitioners should consider increasing effort on patch reef sites in restoration programs while also developing new strategies to foster resilience at fore reef sites.

Mercado-Molina, A. E., Ruiz-Diaz, C. P. & Sabat, A. M. (2015). Demographics and dynamics of two restored populations of the threatened reef-building coral Acropora cervicornis. *Journal for Nature Conservation*, 24, 17–23. https://doi.org/10.1016/j.jnc.2015.01.001 (Mercado-Molina et al. 2015b)

Acropora cervicornis is one of the principal reef-building organisms in the Caribbean; it is also considered one of the most threatened coral species. Due to its ecological importance and critical status it is the focus of many restoration and management initiatives. However, studies that quantitatively measure the efficacy or feasibility of these efforts are mostly lacking. In this study, nursery-reared fragments of A. cervicornis were transplanted to two reefs in Puerto Rico as part of a reef rehabilitation program, and their survival, growth, and branch production were measured for a year. We also evaluated the effect of this restoration on the dynamics and viability of the fragment populations by means of a simple model. Survival of outplanted fragments surpassed 60%. Colony growth rate varied between 0.20±0.18 and 0.29±0.21cmd−1 (mean±SD) whereas branch production ranged between 7.02±5.72 and 11.86±7.06 (mean±SD) branches per fragment per year. Survival did not vary considerably with respect to fragment size. In contrast, large fragments (≥25cm) grew faster and tended to produce more branches than smaller ones. Model simulations indicate that (1) in the absence of recruitment, and without any subsequent human intervention, restored populations will decrease below a quasi-extinction level of 25% of the initial population size after just 3 years and (2) transplanting at least 20 colony fragments per year (12% of initial population) is sufficient to keep the restored populations above the 25% threshold. We conclude that A. cervicornis may be a feasible species for restoration projects given sustained human intervention and that transplanting fragments of at least 25cm to reefs is an effective restoration protocol that requires minimum effort to maintain a viable restored population of this key reef-building coral.

Moulding, A.L, Griffin, S.P., Nemeth, M.I., and Ray, E.C. 2020. Caribbean *Acropora* Outplanting in U.S. Jurisdiction: 1993-2017. U.S. Dept. of Commerce, NOAA. NOAA Technical Memorandum NMFS-SER-10: 14 p. https://doi.org/10.25923/n4tx-1a30 (Moulding et al. 2020)

Mercado-Molina, A. E., Ruiz-Diaz, C. P. & Sabat, A. M. (2016). Branching dynamics of transplanted colonies of the threatened coral Acropora cervicornis: Morphogenesis, complexity, and modeling. *Journal of Experimental Marine Biology and Ecology*, 482, 134–141. https://doi.org/10.1016/j.jembe.2016.05.004 (Mercado-Molina et al. 2016)

Acropora cervicornis is a threatened Caribbean coral that depends on branch fragmentation to proliferate. Understanding the patterns of branch formation is, therefore, essential for the development of management and conservation initiatives. This study describes branch morphogenesis in 100 colony fragments that were transplanted to two reefs in Puerto Rico that differ in light intensity. Four morphometric variables were measured for one year: internode length, branch growth rate, the number of ramifying branches (mother branches; MB), and the number of branches produced (daughter branches; DB). Branching complexity was also evaluated using two indices: the Horton-Strahler bifurcation ratio (Rb) and the Carrillo-Mendoza branching index (CM-BI). A simple discrete model was constructed to estimate the number of harvestable branches over time. No spatial difference was observed when comparing the development of the primary branches, as the mean internode lengths, the mean extension rates, and the mean number of branches produced did not differ statistically between sites. Likewise,

internode lengths in secondary branches did not vary significantly between sites. In contrast, the mean branching and growth rates of secondary branches differed statistically between the two study locations. Significant spatial differences were also observed when comparing the total number of MB and the total number of DB but not for the ratio of DB to MB. The CM-BI was more appropriate than the Rb in describing the branching structure of A. cervicornis. The model provided a good fit to the observed branching dynamics; demonstrating its usefulness as a tool for predicting branch productivity of this species. The implications for restoration activities are discussed.

O'Donnell, K. E., Lohr, K. E., Bartels, E. & Patterson, J. T. (2017). Evaluation of staghorn coral (Acropora cervicornis, Lamarck 1816) production techniques in an ocean-based nursery with consideration of coral genotype. *Journal of Experimental Marine Biology and Ecology*, 487, 53–58.
https://doi.org/10.1016/j.jembe.2016.11.013 (O'Donnell et al. 2017)

Staghorn coral Acropora cervicornis is an important framework-building species that has declined severely throughout the Caribbean since the early 1980s. This species is now widely cultured in ocean-based nurseries to restore degraded populations. A variety of techniques have been adopted to grow A. cervicornis for restoration purposes, however the effect of each of these methods on nursery-reared corals is not well-understood. In particular, systematic evaluation of nursery-reared A. cervicornis between water column-suspended and benthic-attached culture methods is lacking. To better understand the effect of these techniques, a one-year A. cervicornis propagation experiment in the Florida Keys was conducted to compare growth, condition, and survivorship between common suspended (i.e. tree) and benthic-attached (i.e. block) grow-out methods. The effect of coral genotype on growth was also considered. Colonies were measured and monitored monthly from December 2014 until November 2015, when only three colonies had survived an extreme bleaching event. Colonies on trees grew up to three times faster than those on blocks and the location of colonies on trees did not affect growth. Genotype had a significant effect on colony growth, which was consistent across grow-out methods. Interestingly, colonies grown on blocks bleached sooner but survived longer than those on trees. These findings contribute to a growing understanding of A. cervicornis nursery culture, and could aid in the selection of culture methods and genotypes for coral nurseries throughout the wider Caribbean.

O'Donnell, K. E., Lohr, K. E., Bartels, E., Baums, I. B. & Patterson, J. T. (2018). Acropora cervicornis genet performance and symbiont identity throughout the restoration process. *Coral Reefs*, 37, 1109–1118.
https://doi.org/10.1007/s00338-018-01743-y (O'Donnell et al. 2018)

In the Caribbean, corals are commonly cultured in ocean-based nurseries and outplanted back to reefs for population enhancement. Intraspecific diversity in host and symbiont is an important consideration for nursery and resource managers. We built upon a previous study that quantified Acropora cervicornis growth phenotypes in a nursery by outplanting the same genets across two reef sites and tracking their performance for 1 yr. Further, we identified the Symbiodinium 'fitti' strains present in each of the A. cervicornis genets during the restoration process from the initial wild collection as early as 2008 to 24 months post-outplant in 2017. Survival to 1 yr post-outplant was consistent with regional averages and did not differ significantly among A. cervicornis genets or between outplant sites. Outplant site and host

genet had significant effects on coral growth. However, genet growth response did not depend on outplant site, providing no evidence for site-genet matching. Conversely, growth rates measured for each genet in the nursery were not predictive of performance following outplanting. Instead, A. cervicornis genets appear to exhibit differences in relative growth through the restoration process. Despite this variability, relative differences in growth among genets were consistent within a given timeframe, even across varying environments. Most colonies sampled were infected by one of five unique strains of S. 'fitti'. Host-symbiont specificity varied among coral genets, but four out of five genets exhibited spatial and/or temporal differences in symbiont strain composition throughout the restoration process. The ability for A. cervicornis to associate with more than one S. 'fitti' strain and the lack of correlation between nursery and outplant growth performance contribute to a growing understanding of the A. cervicornis population enhancement process.

Patterson, J. T., Flint, M., Than, J. & Watson, C. A. (2016). Evaluation of Substrate Properties for Settlement of Caribbean Staghorn Coral Acropora cervicornis Larvae in a Land-Based System. *North American Journal of Aquaculture*, 78, 337–345. https://doi.org/10.1080/15222055.2016.1185068 (Patterson et al. 2016)

Stony coral culture has recently been the focus of increasing interest and effort, with most production taking place by asexual reproduction through fragmentation. In corals grown for reef restoration, techniques for sexual propagation offer the potential to increase genetic diversity of species for which this is a concern. After decades of population decline, the Caribbean staghorn coral Acropora cervicornis was listed as threatened under the U.S. Endangered Species Act in 2006, along with its congener, elkhorn coral A. palmata. We used practical large-scale, land-based culture conditions with aquaria set up in a choice/no-choice design to test three substrate properties for their influence on settlement and metamorphosis in staghorn coral planula larvae. This transitional life stage is critical for sexual reproduction and currently represents a culture bottleneck. A total of 999 live primary polyps were produced across all experimental substrates. Planula larvae showed significant preference for substrates that were biologically conditioned, top oriented, and rugose. Conditioning was essentially prerequisite for settlement and metamorphosis, with orientation and texture also affecting larval settling. Although the ideal combination of substrate properties produced lower settling and metamorphosis rates than those observed in smaller-scale culture experiments with elkhorn coral, results are informative in the development of reliable aquaculture techniques for sexual propagation of Caribbean Acropora in land-based systems.

Ross, A. M. (2014). Genet and reef position effects in out-planting of nursery-grown Acropora cervicornis (Scleractinia:Acroporidae) in Montego Bay, Jamaica. *Rev. Biol. Trop.*, 62, 95–106. https://doi.org/10.15517/rbt.v62i0.15905 (Ross 2014)

The reef-building coral Acropora cervicornis was a dominant ecosystem element on the Caribbean reef until the 1980s, when it declined by some 97% due primarily to anthropogenic ecosystem changes and disease. This branching species expanded its colony footprint and achieved local dominance largely through fragmentation and regrowth, thus is suited to nursery culture towards restoration. In this experiment, fragments of Acropora cervicornis of four lineages or genets were followed and measured for growth and health over 12 months in 2006 and 2007 on buoyant drop-loop line nurseries at one shallow

and one deep fore-reef site in Montego Bay, Jamaica. Sixty-five of these corals were then out-planted to wild reef sites of similar depth and condition to their respective nurseries and monitored photographically for 11 months through 2007 and 2008. A period of rapid death was seen in the out-planted material at both sites over the first four months, followed by a period of relative stability or recuperation. Hermodice carunculata predation was the primary problem in the shallow fore-reef, and was combined with a banding syndrome at the deeper site. This syndrome was noted in the samples prior to planting, during a one week storage period on the seafloor. Continued slow decline occurred in the subsequent seven months in the shallow fore-reef site; however, regrowth was noted in the deeper site in the remaining material. Including these losses, final total live coral length was more than fourfold greater than the initial wild harvest: a net increase through multi-stage propagative restoration or coral gardening. Returns were noted particularly in the faster-growing genets of the nursery and larger planted corals tended to retain more material at eleven months, suggesting that propagative restoration programmes invest in stronger genets and larger corals. Adaptive management and maintenance gardening of the planted material and reef would likely have greatly improved outcomes.

Schopmeyer, S. A., Lirman, D., Bartels, E., Gilliam, D. S., Goergen, E. A., Griffin, S. P., . . . Walter, C. S. (2017). Regional restoration benchmarks for Acropora cervicornis. *Coral Reefs*, 36(4), 1047–1057. https://doi.org/10.1007/s00338-017-1596-3 (Schopmeyer et al. 2017)

Coral gardening plays an important role in the recovery of depleted populations of threatened Acropora cervicornis in the Caribbean. Over the past decade, high survival coupled with fast growth of in situ nursery corals have allowed practitioners to create healthy and genotypically diverse nursery stocks. Currently, thousands of corals are propagated and outplanted onto degraded reefs on a yearly basis, representing a substantial increase in the abundance, biomass, and overall footprint of A. cervicornis. Here, we combined an extensive dataset collected by restoration practitioners to document early (1–2 yr) restoration success metrics in Florida and Puerto Rico, USA. By reporting region-specific data on the impacts of fragment collection on donor colonies, survivorship and productivity of nursery corals, and survivorship and productivity of outplanted corals during normal conditions, we provide the basis for a stop-light indicator framework for new or existing restoration programs to evaluate their performance. We show that current restoration methods are very effective, that no excess damage is caused to donor colonies, and that once outplanted, corals behave just as wild colonies. We also provide science-based benchmarks that can be used by programs to evaluate successes and challenges of their efforts, and to make modifications where needed. We propose that up to 10% of the biomass can be collected from healthy, large A. cervicornis donor colonies for nursery propagation. We also propose the following benchmarks for the first year of activities for A. cervicornis restoration: (1) >75% live tissue cover on donor colonies; (2) >80% survivorship of nursery corals; and (3) >70% survivorship of outplanted corals. Finally, we report productivity means of 4.4 cm yr−1 for nursery corals and 4.8 cm yr−1 for outplants as a frame of reference for ranking performance within programs. Such benchmarks, and potential subsequent adaptive actions, are needed to fully assess the long-term success of coral restoration and species recovery programs.

Viehman, T.S., M. Nemeth, S.H. Groves, C.A. Buckel, S. Griffin, D. Field, T.D. Moore, J. Moore. 2020. Coral assessment and restoration in the U.S. Caribbean after 2017 hurricanes. NOAA National Ocean Service, National Centers for Coastal Ocean Science. NOAA Technical Memorandum 278. Silver Spring, MD. 64 pp. doi: 10.25923/7r0b-wc52. Data archive doi:10.25921/a1c4-bg06 for NCEI accession 0221189. (Viehman et al. 2020)

In September 2017, major Hurricanes Irma and Maria impacted Puerto Rico and the U.S. Virgin Islands (USVI) and caused considerable damage to shallow coral reefs. In February 2018, at the request of the Puerto Rico Department of Natural and Environmental Resources (PRDNER), the Federal Emergency Management Agency (FEMA) assigned the National Oceanic and Atmospheric Administration (NOAA) to conduct coral reef assessments and emergency coral stabilization activities in Puerto Rico as part of the Hurricane Maria response under the National Disaster Recovery Framework Natural and Cultural Resources Recovery Support Function. A total of 414,354 m2 of coral reef area, including over 87,000 corals, were assessed at 150 sites across Puerto Rico between February 27 and May 7, 2018. More than 8,700 corals were reattached at 35 reef sites in Puerto Rico. Prior to the FEMA effort, coral stabilization efforts were supported by NOAA and the National Fish and Wildlife Foundation (NFWF) in Puerto Rico and St. Thomas, USVI and reattached more than 7,500 corals at 28 additional sites. In total, coral stabilization efforts in PR and the USVI reattached 16,000 corals at 63 sites. Hurricane damage of destabilized, broken, and loose corals was observed at approximately 12% of shallow reefs assessed in Puerto Rico. Damage varied between geographic regions, sites, and species. The most severely impacted coral species include four listed as Threatened under the Endangered Species Act (ESA): Dendrogyra cylindrus (pillar coral), Acropora palmata (elkhorn coral), Orbicella annularis (lobed star coral), and Acropora cervicornis (staghorn coral). Considerable variability was observed between assessment sites in the extent of wave impacts to corals and reefs, likely due to reef exposure to the dominant wave energy and coral species, abundance, size, and morphology.

Woesik, R., R. B. Banister, E. Bartels, D. S. Gilliam, E. A. Goergen, C. Lustic, K. Maxwell, A. Moura, E. M. Muller, S. Schopmeyer, R. S. Winters, and D. Lirman. 2020. Differential survival of nursery-reared Acropora cervicornis outplants along the Florida reef tract. Restoration Ecology 29(1):1-10. https://doi.org/10.1111/rec.13302 (van Woesik et al. 2020a)

In recent decades, the Florida reef tract has lost over 95% of its coral cover. Although isolated coral assemblages persist, coral restoration programs are attempting to recover local coral populations. Listed as threatened under the Endangered Species Act, Acropora cervicornis is the most widely targeted coral species for restoration in Florida. Yet strategies are still maturing to enhance the survival of nursery-reared outplants of A. cervicornis colonies on natural reefs. This study examined the survival of 22,634 A. cervicornis colonies raised in nurseries along the Florida reef tract and outplanted to six reef habitats in seven geographical subregions between 2012 and 2018. A Cox proportional hazards regression was used within a Bayesian framework to examine the effects of seven variables: (1) coral-colony size at outplanting, (2) coral-colony attachment method, (3) genotypic diversity of outplanted A. cervicornis clusters, (4) reef habitat, (5) geographical subregion, (6) latitude, and (7) the year of monitoring. The best models included coral-colony size at outplanting, reef habitat, geographical subregion, and the year of monitoring. Survival was highest when colonies were larger than 15 cm (total linear extension), when outplanted to back-reef and fore-reef habitats, and when outplanted in Biscayne Bay and Broward–Miami

subregions, in the higher latitudes of the Florida reef tract. This study points to several variables that influence the survival of outplanted A. cervicornis colonies and highlights aneed to refine restoration strategies to help restore their population along the Florida reef tract.

> Ware, M., Garfield, E. N., Nedimyer, K., Levy, J., Kaufman, L., Precht, W., . . . Miller, S. L. (2020). Survivorship and growth in staghorn coral (Acropora cervicornis) outplanting projects in the Florida Keys National Marine Sanctuary. *PLOS ONE*, 15(5), e0231817. https://doi.org/10.1371/journal.pone.0231817 (Ware et al. 2020)

Significant population declines in Acropora cervicornis and A. palmata began in the 1970s and now exceed over 90%. The losses were caused by a combination of coral disease and bleaching, with possible contributions from other stressors, including pollution and predation. Reproduction in the wild by fragment regeneration and sexual recruitment is inadequate to offset population declines. Starting in 2007, the Coral Restoration Foundation™ evaluated the feasibility of outplanting A. cervicornis colonies to reefs in the Florida Keys to restore populations at sites where the species was previously abundant. Reported here are the results of 20 coral outplanting projects with each project defined as a cohort of colonies outplanted at the same time and location. Photogrammetric analysis and in situ monitoring (2007 to 2015) measured survivorship, growth, and condition of 2419 colonies. Survivorship was initially high but generally decreased after two years. Survivorship among projects based on colony counts ranged from 4% to 89% for seven cohorts monitored at least five years. Weibull survival models were used to estimate survivorship beyond the duration of the projects and ranged from approximately 0% to over 35% after five years and 0% to 10% after seven years. Growth rate averaged 10 cm/year during the first two years then plateaued in subsequent years. After four years, approximately one-third of surviving colonies were ≥ 50 cm in maximum diameter. Projects used three to sixteen different genotypes and significant differences did not occur in survivorship, condition, or growth. Restoration times for three reefs were calculated based on NOAA Recovery Plan (NRP) metrics (colony abundance and size) and the findings from projects reported here. Results support NRP conclusions that reducing stressors is required before significant population growth and recovery will occur. Until then, outplanting protects against local extinction and helps to maintain genetic diversity in the wild.

ELKHORN CORAL (ACROPORA PALMATA)

Biology and Life History Characteristics

> Antonio-Martínez, F., Henaut, Y., Vega-Zepeda, A., Cerón-Flores, A. I., Raigoza-Figueras, R., Cetz-Navarro, N. P. & Espinoza-Avalos, J. (2020). Leachate effects of pelagic Sargassum spp. on larval swimming behavior of the coral Acropora palmata. *Scientific Reports*, 10(1), 3910. https://doi.org/10.1038/s41598-020-60864-z (Antonio-Martinez et al. 2020)

An emerging disturbance for Caribbean reefs is the massive arrival of pelagic Sargassum, which deteriorates water quality due to the production of leachates. The highest arrivals of Sargassum took place when broadcasting corals spawned. We experimentally determined the effect of Sargassum leachates on

swimming behavior of Acropora palmata larvae through five treatments (control, stain (simulating 100% leachate color), and 25%, 50% and 100% Sargassum leachate concentrations) during 30 min (10 min of videos and 20 min of post-observations). In the videos, larvae with leachates reduced swimming speed, were positively geotactic, the percentage of individuals that swam in a spiral pattern increased, and most behavioral displacements occurred at lower frequencies than larvae without leachates. Moreover, symptomatic spiral behavior was higher in the presence of leachates, suggesting that this behavior may be an effect of pollution. During post-observations, most larvae with leachates were motionless. This is the first time that Sargassum leachates have been documented modifying larval swimming behavior, which may reduce larval dispersion and genetic diversity. We suggest that a future evaluation of the effects of leachates at lower concentrations and over longer periods of exposure is needed. The resilience of corals may be compromised if Sargassum arrivals become frequent events.

Baums, I. B., Devlin-Durante, M. K. & LaJeunesse, T. C. (2014). New insights into the dynamics between reef corals and their associated dinoflagellate endosymbionts from population genetic studies. *Molecular Ecology*, 23(17), 4203–4215. https://doi.org/10.1111/mec.12788 (Baums et al. 2014)

The mutualistic symbioses between reef-building corals and micro-algae form the basis of coral reef ecosystems, yet recent environmental changes threaten their survival. Diversity in host-symbiont pairings on the sub-species level could be an unrecognized source of functional variation in response to stress. The Caribbean elkhorn coral, Acropora palmata, associates predominantly with one symbiont species (Symbiodinium 'fitti'), facilitating investigations of individual-level (genotype) interactions. Individual genotypes of both host and symbiont were resolved across the entire species' range. Most colonies of a particular animal genotype were dominated by one symbiont genotype (or strain) that may persist in the host for decades or more. While Symbiodinium are primarily clonal, the occurrence of recombinant genotypes indicates sexual recombination is the source of this genetic variation, and some evidence suggests this happens within the host. When these data are examined at spatial scales spanning the entire distribution of A. palmata, gene flow among animal populations was an order of magnitude greater than among populations of the symbiont. This suggests that independent micro-evolutionary processes created dissimilar population genetic structures between host and symbiont. The lower effective dispersal exhibited by the dinoflagellate raises questions regarding the extent to which populations of host and symbiont can co-evolve during times of rapid and substantial climate change. However, these findings also support a growing body of evidence, suggesting that genotype-by-genotype interactions may provide significant physiological variation, influencing the adaptive potential of symbiotic reef corals to severe selection.

DeBose, J. L., Kiene, R. P. & Paul, V. J. (2015). Eggs and larvae of Acropora palmata and larvae of Porites astreoides contain high amounts of dimethylsulfoniopropionate. *Journal of Experimental Marine Biology and Ecology*, 473, 146–151. https://doi.org/10.1016/j.jembe.2015.08.015 (DeBose et al. 2015)

Coral holobionts, including their symbionts, are known to produce large amounts of dimethylsulfoniopropionate (DMSP), a compound which some corals use to mitigate oxidative stress; however, very little work has been done on the presence and use of DMSP in early life history stages of

coral, such as in eggs and larvae. This study shows that eggs and larvae, from Acropora palmata, and brooded larvae, from Porites astreoides, also contain high amounts of DMSP. Eggs and larvae of wild A. palmata were collected and contained extremely high levels of DMSP: 1.2µmol per larva and 359µmol per 100µL eggs. Larvae of P. astreoides were collected in flow-through laboratory tanks, from wild-collected parent colonies, over the course of the larval release cycle. In brooded larvae of P. astreoides, the amount of DMSP in larvae ranged from 11.6 to 1510nmol per larva; larval DMSP peaked by the second night of release and then decreased over the following release nights. These high levels in aposymbiotic eggs and larvae of A. palmata and the peaking trend in symbiotic larvae of P. astreoides are suggestive of parental provisioning. Given the large amounts of DMSP found in eggs and larvae, this study provides further evidence that even early life stages of the coral holobiont may benefit from the presence of DMSP.

Durante, M. K., Baums, I. B., Williams, D. E., Vohsen, S. & Kemp, D. W. (2019). What drives phenotypic divergence among coral clonemates of Acropora palmata? *Molecular Ecology*, 28(13), 3208–3224. https://doi.org/10.1111/mec.15140 (Durante et al. 2019)

Evolutionary rescue of populations depends on their ability to produce phenotypic variation that is heritable and adaptive. DNA mutations are the best understood mechanisms to create phenotypic variation, but other, less well-studied mechanisms exist. Marine benthic foundation species provide opportunities to study these mechanisms because many are dominated by isogenic stands produced through asexual reproduction. For example, Caribbean acroporid corals are long lived and reproduce asexually via breakage of branches. Fragmentation is often the dominant mode of local population maintenance. Thus, large genets with many ramets (colonies) are common. Here, we observed phenotypic variation in stress responses within genets following the coral bleaching events in 2014 and 2015 caused by high water temperatures. This was not due to genetic variation in their symbiotic dinoflagellates (Symbiodinium “fitti”) because each genet of this coral species typically harbours a single strain of S. “fitti”. Characterization of the microbiome via 16S tag sequencing correlated the abundance of only two microbiome members (Tepidiphilus, Endozoicomonas) with a bleaching response. Epigenetic changes were significantly correlated with the host's genetic background, the location of the sampled polyps within the colonies (e.g., branch vs. base of colony), and differences in the colonies’ condition during the bleaching event. We conclude that long-term microenvironmental differences led to changes in the way the ramets methylated their genomes, contributing to the differential bleaching response. However, most of the variation in differential bleaching response among clonemates of Acropora palmata remains unexplained. This research provides novel data and hypotheses to help understand intragenet variability in stress phenotypes of sessile marine species.

Miller, M. W. (2014). Post-settlement survivorship in two Caribbean broadcasting corals. *Coral Reefs*, 33(4), 1041–1046. https://doi.org/10.1007/s00338-014-1177-7 (Miller 2014)

The post-settlement phase of broadcast-spawned coral life histories is poorly known due to its almost complete undetectability and, hence, presumed low abundance in the field. We used lab-cultured settled polyps of two important Caribbean reef-building species with negligible larval recruitment to quantify

early post-settlement survivorship (6–9 weeks) over multiple years/cohorts and differing orientation on a reef in the Florida Keys. Orbicella faveolata showed significantly and consistently better survivorship in vertical rather than horizontal orientation, but no discernable growth overall. Meanwhile, Acropora palmata showed no significant difference in survivorship between orientations, but significantly greater growth in the horizontal orientation. Both species showed significant variation in mean survivorship between cohorts of different years; 0–47 % for O. faveolata and 12–49 % for A. palmata over the observed duration. These results demonstrate wide variation in success of cohorts and important differences in the larval recruitment capacities of these two important but imperiled reef-building species.

Miller, M. W., Williams, D. E. & Fisch, J. (2016). Genet-specific spawning patterns in Acropora palmata. *Coral Reefs*, 35(4), 1393–1398. https://doi.org/10.1007/s00338-016-1472-6 (Miller et al. 2016b)

The broadcast spawning elkhorn coral, Acropora palmata, requires outcrossing among different genets for effective fertilization. Hence, a low density of genets in parts of its range emphasizes the need for precise synchrony among neighboring genets as sperm concentration dilutes rapidly in open-ocean conditions. We documented the genet-specific nightly occurrence of spawning of A. palmata over 8 yr in a depauperate population in the Florida Keys to better understand this potential reproductive hurdle. The observed population failed to spawn within the predicted monthly window (nights 2–6 after the full moon in August) in three of the 8 yr of observation; negligible spawning was observed in a fourth year. Moreover, genet-specific patterns are evident in that (1) certain genets have significantly greater odds of spawning overall and (2) certain genets predictably spawn on the earlier and others on the later lunar nights within the predicted window. Given the already low genet density in this population, this pattern implies a substantial degree of wasted reproductive effort and supports the hypothesis that depensatory factors are impairing recovery in this species.

Miller, M. W., A. J. Bright, R. E. Pausch, and D. E. Williams. 2020. Larval longevity and competency patterns of Caribbean reef-building corals. PeerJ 8:e9705. https://peerj.com/articles/9705/ (Miller et al. 2020a)

The potential for long-distance larval dispersal depends on the longevity of planktonic, free-swimming larvae and their capacity to successfully recruit to reef habitat. We present multi-year laboratory observations of the persistence of planular larvae and settlement competency over time for cohorts derived from the same parental populations of the most important Caribbean reef building coral species, Orbicella faveolata and Acropora spp. Despite variability among years/cohorts, larvae of both species display capacity for extended longevity (up to 83 d) and competency (demonstrated at up to 48 d). Both species also displayed significantly reduced survivorship and lower realized settlement under elevated temperatures. Although the observed levels of settlement in 24 h competency assays was extremely variable, the timing of onset of competence were highly consistent among years/cohorts but distinct between species. Orbicella faveolata displayed onset of competence during day 3-5 or 4-7 (with or without exposure to positive settlement cue) after spawning; whereas, onset for Acropora spp. was day 7-8 or day 10-11 (with or without cue, respectively). This longer pre-competency period for Acropora spp. nonetheless corresponded to a greater persistence of A. palmata larvae to this age of competence (71-83%

of initial cohort compared to 54-55% for O. faveolata). Such life history variation implies meaningful differences in likely dispersal potential between these imperiled reef-building species.

Olsen, K., Sneed, J. M. & Paul, V. J. (2016). Differential larval settlement responses of Porites astreoides and Acropora palmata in the presence of the green alga Halimeda opuntia. *Coral Reefs*, 35(2), 521–525. https://doi.org/10.1007/s00338-015-1394-8 (Olsen et al. 2016)

Settlement is critical to maintaining coral cover on reefs, yet interspecific responses of coral planulae to common benthic macroalgae are not well characterized. Larval survival and settlement of two Caribbean reef-building corals, the broadcast-spawner Acropora palmata and the planulae-brooder Porites astreoides, were quantified following exposure to plastic algae controls and the green macroalga Halimeda opuntia. Survival and settlement rates were not significantly affected by the presence of H. opuntia in either species. However, ~10 % of P. astreoides larvae settled on the surface of the macroalga, whereas larvae of A. palmata did not. It is unlikely that corals that settle on macroalgae will survive post-settlement; therefore, H. opuntia may reduce the number of P. astreoides and other non-discriminatory larvae that survive to adulthood. Our results suggest that the presence of macroalgae on impacted reefs can have unexpected repercussions for coral recruitment and highlight discrepancies in settlement specificity between corals with distinct life history strategies.

Parkinson, J. E., Banaszak, A. T., Altman, N. S., LaJeunesse, T. C. & Baums, I. B. (2015). Intraspecific diversity among partners drives functional variation in coral symbioses. *Scientific Reports*, 5(1), 15667. https://doi.org/10.1038/srep15667 (Parkinson et al. 2015)

The capacity of coral-dinoflagellate mutualisms to adapt to a changing climate relies in part on standing variation in host and symbiont populations, but rarely have the interactions between symbiotic partners been considered at the level of individuals. Here, we tested the importance of inter-individual variation with respect to the physiology of coral holobionts. We identified six genetically distinct Acropora palmata coral colonies that all shared the same isoclonal Symbiodinium 'fitti' dinoflagellate strain. No other Symbiodinium could be detected in host tissues. We exposed fragments of each colony to extreme cold and found that the stress-induced change in symbiont photochemical efficiency varied up to 3.6-fold depending on host genetic background. The S. 'fitti' strain was least stressed when associating with hosts that significantly altered the expression of 184 genes under cold shock; it was most stressed in hosts that only adjusted 14 genes. Key expression differences among hosts were related to redox signaling and iron availability pathways. Fine-scale interactions among unique host colonies and symbiont strains provide an underappreciated source of raw material for natural selection in coral symbioses.

Piñón-González, V. M. & Banaszak, A. T. (2018). Effects of Partial Mortality on Growth, Reproduction and Total Lipid Content in the Elkhorn Coral Acropora palmata. *Front. Mar. Sci.*, 5, 396. https://doi.org/10.3389/fmars.2018.00396 (Piñón-González and Banaszak 2018)

Partial mortality (PM) is increasingly common in the Elkhorn coral Acropora palmata and, depending on the causative agent, is potentially lethal. The effects of PM on growth, reproduction and total lipid content in A. palmata were studied by sampling apparently healthy (AH) colonies in comparison with colonies showing signs of PM. Branch growth rates and lesion regeneration rates were estimated using monthly photographs over a four-month period prior to the summer spawning season. No differences were found in the growth rates of colonies with PM compared to AH colonies. The areas affected by PM did not regenerate during the period of the study. Colonization of the lesions by competing species and sediment cover were documented and did not show major changes. During the spawning season, percent fertilization, egg volume and embryonic development were evaluated for comparison between AH colonies and those with PM. Total lipids were also quantified in tissues from three branches per colony. Percentage fertilization was similar in both AH colonies and those with PM. Embryonic development was normal, regardless of proximity to the lesion borders. However, egg volume was significantly lower in PM colonies than in AH colonies. Lower lipid concentrations were found at the edges of the lesions and similar to those found at the growing edges of the branches. The lack of regeneration may be explained by the low lipid concentration, because the polyps adjacent to the lesion do not have an adequate energy budget as a result of the damage. This would also affect their ability to compete against organisms that colonize the site of the lesion, a distinct situation to the rapid regeneration rates characteristic of lesions due to physical injury of the colony. Therefore, we conclude that partial mortality in A. palmata affects the colony, inducing energetic stress due to both competition and decreased quality of the eggs.

Ricaurte, M., Schizas, N. V., Ciborowski, P. & Boukli, N. M. (2016). Proteomic analysis of bleached and unbleached Acropora palmata, a threatened coral species of the Caribbean. *Marine Pollution Bulletin*, 107(1), 224–232. https://doi.org/10.1016/j.marpolbul.2016.03.068 (Ricaurte et al. 2016)

There has been an increase in the scale and frequency of coral bleaching around the world due mainly to changes in sea temperature. This may occur at large scales, often resulting in significant decline in coral coverage. In order to understand the molecular and cellular basis of the ever-increasing incidence of coral bleaching, we have undertaken a comparative proteomic approach with the endangered Caribbean coral Acropora palmata. Using a proteomic tandem mass spectrometry approach, we identified 285 and 321 expressed protein signatures in bleached and unbleached A. palmata colonies, respectively, in southwestern Puerto Rico. Overall the expression level of 38 key proteins was significantly different between bleached and unbleached corals. A wide range of proteins was detected and categorized, including transcription factors involved mainly in heat stress/UV responses, immunity, apoptosis, biomineralization, the cytoskeleton, and endo–exophagocytosis. The results suggest that for bleached A. palmata, there was an induced differential protein expression response compared with those colonies that did not bleach under the same environmental conditions.

Ritson-Williams, R., Arnold, S. N., Paul, V. J. & Steneck, R. S. (2014). Larval settlement preferences of Acropora palmata and Montastraea faveolata in response to diverse red algae. *Coral Reefs*, 33(1), 59–66. https://doi.org/10.1007/s00338-013-1113-2 (Ritson-Williams et al. 2014)

Settlement specificity can regulate recruitment but remains poorly understood for coral larvae. We studied larvae of the corals, Acropora palmata and Montastraea faveolata, to determine their rates of settlement and metamorphosis in the presence of ten species of red algae, including eight species of crustose coralline algae, one geniculated coralline and one encrusting peyssonnelid. Twenty to forty percent of larvae of A. palmata settled on coralline surfaces of Hydrolithon boergesenii, Lithoporella atlantica, Neogoniolithon affine, and Titanoderma prototypum, whereas none settled and metamorphosed on Neogoniolithon mamillare. Larvae of M. faveolata had 13–25 % settlement onto the surface of Amphiroa tribulus, H. boergesenii, N. affine, N. munitum, and T. prototypum, but had no settlement on the surface of N. mamillare, Porolithon pachydermum, and a noncoralline crust Peyssonnelia sp. Some of these algal species were common on Belizean reefs, but the species that induced the highest rates of larval settlement and metamorphosis tended to be rare and primarily found in low-light environments. The shallow coral, A. palmata, and the deeper coral, M. faveolata, both had increased larval settlement rates in the presence of only a few species of red algae found at deeper depths suggesting that patterns of coral distribution can only sometimes be related to the distribution of red algae species.

Ritson-Williams, R., Arnold, S. N. & Paul, V. J. (2016). Patterns of larval settlement preferences and post-settlement survival for seven Caribbean corals. *Marine Ecology Progress Series* 548, 127–138. https://doi.org/10.3354/meps11688 (Ritson-Williams et al. 2016)

Caribbean coral reefs continue to decline in coral cover; however, recruitment is a natural process that could increase coral abundance. Benthic habitats that increase coral recruitment are a key factor for coral persistence, but very little is known about habitat selectivity for larvae of most species of corals. The larval settlement preferences and post-settlement survival of 3 brooding and 4 broadcast spawning coral species were compared in this study. The crustose coralline algae Titanoderma prototypum and Hydrolithon boergesenii facilitated larval settlement more than the biofilm control for the broadcast spawning corals but not for the majority of the brooding corals. In paired choice experiments, the larvae of all 7 corals preferred T. prototypum over Paragoniolithon solubile, and 6 of them preferred H. boergesenii over Pa. solubile, the exception being larvae of Porites astreoides. All corals equally preferred T. prototypum and H. boergesenii, except Pseudodiploria strigosa, which preferred T. prototypum, and Acropora palmata, which preferred H. boergesenii. Some recruits from the 3 brooding corals survived longer than 1 yr in the field, but of the 4 spawning corals, only P. strigosa had 2 recruits that survived >1 yr. Corals that spawned their gametes had increased settlement in the presence of a few species of coralline algae, but corals that brooded their larvae settled on biofilms and had much greater post-settlement survival, suggesting that the recruitment of brooding corals will dominate on reefs without facilitating species of crustose coralline algae.

Ritson-Williams, R., Arnold, S. N. & Paul, V. J. (2020). The impact of macroalgae and cyanobacteria on larval survival and settlement of the scleractinian corals Acropora palmata, A. cervicornis and Pseudodiploria strigosa. *Mar Biol*, 167, 31. https://doi.org/10.1007/s00227-019-3639-5 (Ritson-Williams et al. 2020)

Coral reefs are threatened by multiple stressors that degrade these ecosystems and the ecosystem services they provide. Critical to the recovery of coral reefs after a disturbance is coral recruitment, but there is

still little information about the types of benthic habitats that different species of coral larvae require for settlement. Settlement in the presence of different algae and cyanobacteria was tested for three coral species, Acropora palmata, Acropora cervicornis and Pseudodiploria strigosa. The experiments were conducted in larval chambers placed on the reef to ensure that coral larvae were exposed to natural light, seawater temperature and some water flow. Rates of settlement and metamorphosis were assessed by providing these coral larvae with a standard preferred settlement substratum (individuals of the crustose coralline algal species Hydrolithon boergesenii) with an attached treatment of a small piece of live algae or benthic cyanobacteria. The brown algae Dictyota pulchella and D. bartayresiana did not affect the survival or settlement of larvae of A. palmata in 2010, but D. pulchella did reduce larval survival in 2009. Of the cyanobacteria tested, Caldora penicillata decreased A. palmata survival and settlement. For A. cervicornis, neither Dictyota pulchella nor D. bartayresiana reduced survival or settlement in either 2009 or 2010. Algae and cyanobacteria had no effect on Pseudodiploria strigosa larval survival, but there was reduced settlement in the presence of the cyanobacterium Hormothamnion enteromorphoides. These larval experiments show that some macrophytes can reduce coral larval survival and settlement even in the presence of highly preferred substrata.

Sneed, J. M., Sharp, K. H., Ritchie, K. B. & Paul, V. J. (2014). The chemical cue tetrabromopyrrole from a biofilm bacterium induces settlement of multiple Caribbean corals. *Proc. R. Soc. B,* 281(1786), 20133086. https://doi.org/10.1098/rspb.2013.3086 (Sneed et al. 2014)

Microbial biofilms induce larval settlement for some invertebrates, including corals; however, the chemical cues involved have rarely been identified. Here, we demonstrate the role of microbial biofilms in inducing larval settlement with the Caribbean coral Porites astreoides and report the first instance of a chemical cue isolated from a marine biofilm bacterium that induces complete settlement (attachment and metamorphosis) of Caribbean coral larvae. Larvae settled in response to natural biofilms, and the response was eliminated when biofilms were treated with antibiotics. A similar settlement response was elicited by monospecific biofilms of a single bacterial strain, Pseudoalteromonas sp. PS5, isolated from the surface biofilm of a crustose coralline alga. The activity of Pseudoalteromonas sp. PS5 was attributed to the production of a single compound, tetrabromopyrrole (TBP), which has been shown previously to induce metamorphosis without attachment in Pacific acroporid corals. In addition to inducing settlement of brooded larvae (P. astreoides), TBP also induced larval settlement for two broadcast-spawning species, Orbicella (formerly Montastraea) franksi and Acropora palmata, indicating that this compound may have widespread importance among Caribbean coral species.

Vohsen, S. A., Fisher, C. R. & Baums, I. B. (2019). Metabolomic richness and fingerprints of deep-sea coral species and populations. *Metabolomics*, 15(3), 34. https://doi.org/10.1007/s11306-019-1500-y (Vohsen et al. 2019)

From shallow water to the deep sea, corals form the basis of diverse communities with significant ecological and economic value. These communities face many anthropogenic stressors including energy and mineral extraction activities, ocean acidification and rising sea temperatures. Corals and their symbionts produce a diverse assemblage of compounds that may help provide resilience to some of these stressors. Objectives: We aim to characterize the metabolomic diversity of deep-sea corals in an

ecological context by investigating patterns across space and phylogeny. Methods: We applied untargeted Liquid Chromatography-Mass Spectrometry to examine the metabolomic diversity of the deep-sea coral, Callogorgia delta, across three sites in the Northern Gulf of Mexico as well as three other deep-sea corals, Stichopathes sp., Leiopathes glaberrima, and Lophelia pertusa, and a shallow-water species, Acropora palmata. Results: Different coral species exhibited distinct metabolomic fingerprints and differences in metabolomic richness including core ions unique to each species. C. delta was generally least diverse while Lophelia pertusa was most diverse. C. delta from different sites had different metabolomic fingerprints and metabolomic richness at individual and population levels, although no sites exhibited unique core ions. Two core ions unique to C. delta were putatively identified as diterpenes and thus may possess a biologically important function. Conclusion: Deep-sea coral species have distinct metabolomic fingerprints and exhibit high metabolomic diversity at multiple scales which may contribute to their capabilities to respond to both natural and anthropogenic stressors, including climate change.

Abundance, Population, and Demographic Features and Trends

> Bruckner, A. W., Beck, B. & Renaud, P. (2014). The status of coral reefs and associated fishes and invertebrates of commercial importance in Pedro Bank, Jamaica. *Rev. Biol. Trop.*, 62, 11–24. https://doi.org/10.15517/rbt.v62i0.15898 (Bruckner et al. 2014)

The coral reefs located off the north coast of the Jamaican mainland are some of the best and most studied reefs in the world. Coral reefs of Pedro Bank, Jamaica were assessed in March, 2012 as part of the KSLOF Global Reef Expedition using a modified Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol. The main objectives were to: 1) characterize the distribution, structure and health of coral reefs; and 2) evaluate the population status of commercially important reef fishes and invertebrates. This work was conducted to assist in characterizing coral reef habitats within and outside a proposed fishery reserve, and identify other possible conservation zones. Within 20 reefs, live coral cover ranged from 4.9% to 19.2%. Coral communities were dominated by small corals (esp. Agaricia, Porites and Siderastrea) although many sites had high abundances of large colonies of Montastraea annularis and M. faveolata, and these were generally in good condition. A single area, within the proposed fishery reserve, had extensive Acropora cervicornis thickets, and several shallow locations had small, but recovering A. palmata stands. Macroalgal cover at all sites was relatively low, with only three sites having greater than 30% cover; crustose coralline algae (CCA) was high, with eight sites exceeding 20% cover. Fish biomass at all sites near the Cays was low, with a dominance of herbivores (parrotfish and surgeonfish) and a near absence of groupers, snappers and other commercially important species. While parrotfish were the most abundant fish, these were all extremely small (mean size= 12cm; <4% over 29cm), and they were dominated by red band parrotfish (Sparisoma aurofrenatum) followed by striped parrotfish (Scarus iseri). While coral communities remain in better condition than most coastal reefs in Jamaica, intense fishing pressure using fish traps (main target species: surgeonfish) and hookah/spear fishing (main target: parrotfish) is of grave concern to the future persistence of these reefs. The proposed fishery reserve encompasses some of the best coral reef habitat near the Cays, but this MPA should be expanded to encompass other habitats and MPAs should be considered for bank reefs at the northwestern end, as well as Banner Reef and Blowers Rock.

Busch, J., Greer, L., Harbor, D., Wirth, K., Lescinsky, H., Curran, H. A. & de Beurs, K. (2016). Quantifying exceptionally large populations of Acropora spp. corals off Belize using sub-meter satellite imagery classification. *Bulletin of Marine Science*, 92, 265–283. https://doi.org/10.5343/bms.2015.1038 (Busch et al. 2016)

Caribbean coral reefs have experienced dramatic declines in live coral cover in recent decades. Primary branching framework Caribbean corals, Acropora cervicornis (Lamarck, 1816) and Acropora palmata (Lamarck, 1816), have suffered the greatest collapse. Coral Gardens, Belize, is one of few remaining, and perhaps the largest, refugia for abundant, healthy, but undocumented populations of both Acropora species in the Caribbean Sea. In the present study, GeoEye-1 multispectral satellite imagery of a 25 km2 reefal area near Ambergris Caye, Belize, was analyzed to identify live Acropora spp. cover. We used a supervised classification to predict occurrence of areas with live Acropora spp. and to separate them from other benthic cover types, such as sandy bottom, seagrass, and mixed massive coral species. We tested classification accuracy in the field, and new Acropora spp. patches were mapped using differential GPS. Of 11 predicted new areas of Acropora spp., eight were composed of healthy Acropora spp. An unsupervised classification of a red (Band 3):blue (Band 1) ratio calculation of the image successfully separated Acropora corals from other benthic cover, with an overall accuracy of 90%. Our study identified 7.58 ha of reef dominated by Acropora spp. at Coral Gardens, which is one of the largest populations in the Caribbean Sea. We suggest that Coral Gardens may be an important site for the study of modern Acropora spp. resilience. Our technique can be used as an efficient tool for genera-specific identification, monitoring, and conservation of populations of endangered Acropora spp.

Caballero Aragón, H., Armenteros, M., Perera Valderrama, S., Rey Villiers, N., Cobián Rojas, D., Campos Verdecia, K. & Alcolado Menéndez, P. (2019). Ecological condition of coral reef assemblages in the Cuban Archipelago. *Marine Biology Research*, 15(1), 61–73. https://doi.org/10.1080/17451000.2019.1577557 (Caballero Aragón et al. 2019)

The condition of coral reefs in the Cuban Archipelago is poorly known. We aimed to analyse coral assemblages across 199 reef sites belonging to 12 localities. Crest and fore reefs were assessed using six metrics: species richness, density, coral cover, mortality, coral size and reef complexity. The condition of reefs varied across the archipelago from healthy to depleted reefs. The localities with best scores were Cienfuegos, Bahía de Cochinos and Cazones. These reefs have values of living coral cover (>20%) and complexity (>50?cm) similar to the best preserved Caribbean reefs. However, the majority of crest biotopes suffered important deterioration with old mortality of Acropora palmata populations and moderate coral cover (15%); although crest reefs still maintained their structural complexity. Despite moderate levels of coral cover in fore reefs (18%), their condition was alarming because 25% of the sites had cover below the recovery threshold of 10%, accumulated mortality and structural flattening. Compared with the 1980s, the species richness was roughly the same (42) for crest and fore reefs, although dominance has changed to widespread tolerant species. Coral reef assemblages varied at local and regional scales in similar magnitude, suggesting the combined effects of natural and anthropogenic drivers.

Caballero-Aragón, H., Perera-Valderrama, S., Rey-Villiers, N., González-Méndez, J. & Armenteros, M. (2020). Population status of Acropora palmata (Lamarck, 1816) in Cuban coral

reefs. *Regional Studies in Marine Science*, 34, 101029. https://doi.org/10.1016/j.rsma.2019.101029 (Caballero-Aragón et al. 2020)

Acropora palmata is the most important reef-building species in the crest biotopes in the Caribbean Sea. Their populations have been decimated in the last century by disease outbreaks, hurricanes and coral bleaching events. The species has been declared as threatened based on its wide-range decline and poor recovery. We evaluated the status of A. palmata populations across 41 shallow reefs (= sites) around the Cuban archipelago. Density, maximum diameter, and mortality percentage of A. palmata colonies were quantified as main metrics of status. Living coral cover (all species) and reef complexity per site were quantified as well. Metrics of A. palmata varied significantly among sites. A. palmata density was less than 5 colonies 10 m−1 except in one site and only three sites had dominance greater than 50% with respect to the rest of corals. The diameter of A. palmata colonies ranged from 10 to 600 cm, with 70% of sites having a median of less than 200 cm. The mortality was large, with 50% of the sites having more than 50% of mortality, and six sites having 100% mortality. The three sites with better apparent conditions after metric scores were determined were Faro de Cazones, Cayo Fragoso, and Baracoa. A. palmata populations had a bad or regular status in 38 out of 41 studied sites; but, the abundance of erect colonies in many of the sites favored the reef complexity and likely maintained its ecological functions. The low percentage of living coral tissue likely limits the reproductive potential of the species and hence the resiliency of reef crests. In conclusion, the overall status of the species in Cuban archipelago is bad.

Chen, Y. H., K. W. Shertzer, T. S. Viehman, and A. Zhan. 2020. Spatio-temporal dynamics of the threatened elkhorn coral Acropora palmata : Implications for conservation. Diversity and Distributions 26(11):1582-1597. (Chen et al. 2020)

Aim: Species distribution models (SDMs) can be useful for predicting spatial dynamics. For species vulnerable to climate change, much attention has focused on predicting the future range of occurrence. However, predicted range changes provide little information about the potential impacts on population structure. Here, we develop and apply an SDM approach that incorporates population demography of a threatened coral species (U.S. Endangered Species Act) and aim to provide guidance for conservation efforts. We additionally use projected climate change scenarios to predict the potential future range of occurrence and spatial population structure. Location: U.S. Virgin Islands, United States. Methods: We applied process-based dynamic range models to jointly model the spatio- temporal population dynamics and spatial habitat suitability of the threatened elkhorn coral Acropora palmata in the U.S. Virgin Islands. The approach integrates information from multiple data sources under a hierarchical Bayesian framework. The models connect two components: (1) a niche model that correlates environmental predictors with demographic rates and (2) a size-structured population model that describes local population dynamics and dispersal. Results: The model predicts that, under scenarios of elevated sea surface temperature and significant wave height, (a) A. palmata will occur at only a small proportion of its potential habitat (water depth ≤ 20 m) and (b) population structure of the colony will shift from larger towards smaller size classes. Main conclusions: For A. palmata, restricted geographic range and smaller colony sizes, as predicted by the models, would limit future population success. In general, the inclusion of demographic structure into a population range model provides critical information for conservation or restoration efforts in the context of climate change.

Cramer, K. L., Jackson, J. B. C., Donovan, M. K., Greenstein, B. J., Korpanty, C. A., Cook, G. M. & Pandolfi, J. M. (2020). Widespread loss of Caribbean acroporid corals was underway before coral bleaching and disease outbreaks. *Science Advances* 6(17), e9395. https://doi.org/10.1126/sciadv.aax9395 (Cramer et al. 2020)

The mass mortality of acroporid corals has transformed Caribbean reefs from coral- to macroalgal-dominated habitats since systematic monitoring began in the 1970s. Declines have been attributed to overfishing, pollution, sea urchin and coral disease, and climate change, but the mechanisms are unresolved due to the dearth of pre-1970s data. We used paleoecological, historical, and survey data to track Acropora presence and dominance throughout the Caribbean from the prehuman period to present. Declines in dominance from prehuman values first occurred in the 1950s for Acropora palmata and the 1960s for Acropora cervicornis, decades before outbreaks of acroporid disease or bleaching. We compared trends in Acropora dominance since 1950 to potential regional and local drivers. Human population negatively affected and consumption of fertilizer for agriculture positively affected A. palmata dominance, the latter likely due to lower human presence in agricultural areas. The earlier, local roots of Caribbean Acropora declines highlight the urgency of mitigating local human impacts.

Croquer, A., Cavada-Blanco, F., Zubillaga, A. L., Agudo-Adriani, E. A. & Sweet, M. (2016). Is Acropora palmata recovering? A case study in Los Roques National Park, Venezuela. *PeerJ*, 4, e1539. https://doi.org/10.7717/peerj.1539 (Croquer et al. 2016)

Eight years ago (2007), the distribution and status of Acropora palmata was quantified throughout Los Roques archipelago in Venezuela. The aim was to produce a baseline study for this species which combined population genetics with demographic data. The results highlighted that A. palmata had the potential to recover in at least 6 out of 10 sites surveyed. Recovery potential was assumed to be high at sites with a relatively high abundance of the coral, low disease prevalence, high genetic diversity, and high rates of sexual reproduction. However, as noted, Zubillaga et al. (2008) realized recovery was still strongly dependent on local and regional stressors. In 2014 (this study), the status of A. palmata was re-evaluated at Los Roques. We increased the number of sites from 10 in the original baseline study to 106. This allowed us to assess the population status throughout the entirety of the MPA. Furthermore, we also identified local threats that may have hindered population recovery. Here, we show that A. palmata now has a relatively restricted distribution throughout the park, only occurring in 15% of the sites surveyed. Large stands of old dead colonies were common throughout the archipelago; a result which demonstrates that this species has lost almost 50% of its original distribution over the past decades. The majority of corals recorded were large adults (□2 m height), suggesting that these older colonies might be less susceptible or more resilient to local and global threats. However, 45% of these surviving colonies showed evidence of partial mortality and degradation of living tissues. Interestingly, the greatest increase in partial mortality occurred at sites with the lowest levels of protection. This may suggest there is a positive role of small scale marine management in assisting reef recovery. We also recorded a significant reduction in the density of A. palmata in sites that had previously been categorized as having a high potential for recovery. One explanation for this continued decline may be due to the fact that over the past 10 years, two massive bleaching events have occurred throughout the Caribbean with records showing that Los Roques has experienced unprecedented declines in overall coral cover. We therefore conclude

that although local protection could promote recovery, the impacts from global threats such as ocean warming may hamper the recovery of this threatened species.

Devlin-Durante, M. K., Miller, M. W., Precht, W. F. & Baums, I. B. (2016). How old are you? Genet age estimates in a clonal animal. *Molecular Ecology*, 25(22), 5628–5646. https://doi.org/10.1111/mec.13865 (Devlin-Durante et al. 2016)

Foundation species such as redwoods, seagrasses and corals are often long-lived and clonal. Genets may consist of hundreds of members (ramets) and originated hundreds to thousands of years ago. As climate change and other stressors exert selection pressure on species, the demography of populations changes. Yet, because size does not indicate age in clonal organisms, demographic models are missing data necessary to predict the resilience of many foundation species. Here, we correlate somatic mutations with genet age of corals and provide the first, preliminary estimates of genet age in a colonial animal. We observed somatic mutations at five microsatellite loci in rangewide samples of the endangered coral, Acropora palmata (n = 3352). Colonies harboured 342 unique mutations in 147 genets. Genet age ranged from 30 to 838 years assuming a mutation rate of 1.195−04 per locus per year based on colony growth rates and 236 to 6500 years assuming a mutation rate of 1.542−05 per locus per year based on sea level changes to habitat availability. Long-lived A. palmata genets imply a large capacity to tolerate past environmental change, and yet recent mass mortality events in A. palmata suggest that capacity is now being frequently exceeded.

Edmunds, P. J. Large numbers of Acropora palmata grow in shallow water in St. John, US Virgin Islands. (2014). *Bull Mar Sci*, 90(4), 999–1000. https://doi.org/10.5343/bms.2014.1027 (Edmunds 2014)

Fisher, W. S., Fore, L. S., Oliver, L. M., Lobue, C., Quarles, R., Campbell, J., . . . Bradley, P. (2014). Regional status assessment of stony corals in the US Virgin Islands. *Environ Monit Assess*, 186(11), 7165–7181. https://doi.org/10.1007/s10661-014-3918-z (Fisher et al. 2014)

States may protect coral reefs using biological water quality standards outlined by the Clean Water Act. This requires biological assessments with indicators sensitive to human disturbance and regional, probability-based survey designs. Stony coral condition was characterized on a regional scale for the first time in the nearshore waters of the US Virgin Islands (USVI). Coral composition, abundance, size, and health were assessed at 66 stations in the St. Croix region in fall 2007 and at 63 stations in the St. Thomas and St. John region in winter 2009. Indicators were chosen for their sensitivity to human disturbance. Both surveys were probability-based (random) designs with station locations preselected from areas covered by hardbottom and coral reef substrate. Taxa richness was as high as 21 species but more than half the area of both regions exhibited taxa richness of <10 species in the 25 m2 transect area. Coral density was as high as 5 colonies m−2 but more than half the area of both regions had <2 colonies m−2. Both regions showed similar dominant species based on frequency of occurrence and relative abundance. Because of large colony sizes, Montastrea annularis provided more total surface area and live surface area than more abundant species. The surveys establish baseline regional conditions and provide a foundation

for long-term regional monitoring envisioned by the USVI Department of Planning and Natural Resources. The probabilistic sampling design assures the data can be used in Clean Water Act reporting.

García-Sais, J. R., S. Williams, R. Esteves, J. Sabater-Clavell, and M. Carlo. 2017. Final Report Monitoring of Coral Reef Communities from Natural Reserves in Puerto Rico. (García-Sais et al. 2017)

A total of 21 reef stations were scheduled during the 2016-17 coral monitoring cycle to complete the 42-reef station monitoring plan for Puerto Rico, including a set of five (5) stations from south coast sites (Salinas/Guayama and Guayanilla) that were exposed to severe wave and surge conditions during the pass of hurricane Matthew in October, shortly after their initial baseline characterization surveys were completed in 2016. The monitoring sampling protocol includes determinations of reef substrate cover by sessile-benthic and abiotic categories based on a continuous intercept (chain-link) technique on sets of five-10 m long permanent transects at various depths (within the 3 – 30 m range) on each reef. An assessment of the prevalence of infectious diseases on corals was added to the monitoring protocol. Surveys of the taxonomic composition, density, species richness/diversity indices, and size-distribution (selected species) of reef fishes and motile megabenthic invertebrates are also included as tasks of the monitoring protocol. Quantitative/qualitative assessments of reef fishes and motile invertebrates were based on sets of five 3 x 10 m belt-transects for small territorial, non-cryptic species and expanded to a 3 x 20 m belt for assessment of commercially important species, including ecologically important herbivores, such as doctorfishes (Acanthuridae) and parrotfishes (Scaridae). Digital photographic documentation of reef stations was produced for all reef stations. The most important change in the community structure of coral reefs monitored during 2017 in PR was a marked decline (62.7%) of reef substrate cover by live corals, from 13.4% in 2016 to 5.0% in 2017 at the reef crest of Maria Langa 3m in Guayanilla. The drastic reduction of live coral cover was characterized by the disappearance of the dominant coral, Acropora prolifera from permanent transects apparently caused by the detachment and mortality of colonies exposed to conditions of extreme wave and surge action during the pass of Hurricane Matthew across the northern Caribbean and close to the south coast of PR during October 2016. Severe mechanical damage was also observed from Cayo Aurora's Acropora palmata reef biotope in Guanica. The very large Elkhorn Coral colonies were not detached from the base, but many of the large branches (arms) were broken. Survival rates of these fragments will be evaluated from prospective measurements during the next monitoring survey at this reef. Statistically significant reductions of soft coral (gorgonians) were measured at Tres Palmas Reef 3m in Rincon, Resuellos 10 m in Cabo Rojo, Tourmaline 20m in Mayaguez and Media Luna 10 m in La Parguera. Such reductions of gorgonian densities appear to be related to mechanical detachment during exposure to extreme wave and surge energy associated with the pass of Hurricane Matthew. Increasing trends of reef substrate cover by live corals were noted at Tres Palmas 10 and 20m, Tourmaline 10, 20 and 30m, Media Luna 10 and 5m. Boya Vieja 20m, Maria Langa 10 and 20m and Derrumbadero 20m. The main driver of the increasing trend of substrate cover by live corals at all reef stations except Tourmaline 10 (Madracis auretenra) was the consistent increase of cover by Orbicella annularis complex. Coral diseases were observed in 16 out of a total 1,132 coral colonies intercepted by transects during 2017, for a mean disease prevalence of 1.3%. Reefs with the highest disease prevalence were Cayo Caribes 10m in Salinas (4.5%), Boya Vieja 20m in La Parguera (4.1%), Bajo Gallardo in Cabo Rojo (4.0%), and Tres Palmas 3.0m in Rincon (3.0%).

García-Urueña, R. & Garzón-Machado, M. A. (2020). Current status of Acropora palmata and Acropora cervicornis in the Colombian Caribbean: demography, coral cover and condition assessment. *Hydrobiologia*, 847(9), 2141–2153. https://doi.org/10.1007/s10750-020-04238-6 (García-Urueña and Garzón-Machado 2020)

Acropora provides an example of reef degradation, as evidenced by population reductions in Caribbean reefs. However, data on the current status of Acropora populations in Colombia are lacking. In this study, reef habitats were surveyed for Acropora palmata and Acropora cervicornis throughout the Colombian Caribbean, and the size structure, coverage and colony conditions of their populations were evaluated. Acropora palmata size classes were negatively skewed, indicating low recruitment. This species exhibited a patch-type distribution around Tayrona, Isla Fuerte and Isla Arena; these localities exhibited the highest cover among the surveyed regions. The lowest coral cover was recorded for the Rosario Islands. Healthy colonies were dominant; however, disease and damselfish territories were common. The size class data of Acropora cervicornis indicated the persistence of small colonies; however, no recruits were observed. The distribution was dispersed, with important patches and the highest cover observed around the Urabá Gulf and Rosario Islands. Overall, the cover was lower than 10%. Few healthy colonies were observed, and macroalgae and sponges were common. Conservation and management efforts are required for both species; for Acropora palmata, efforts targeting the Rosario Islands are needed, whereas Acropora cervicornis is in critical condition throughout the Colombian Caribbean.

Irwin, A., Greer, L., Humston, R., Devlin-Durante, M., Cabe, P., Lescinsky, H., Wirth, K., . . . Baums, I. B. (2017). Age and intraspecific diversity of resilient Acropora communities in Belize. *Coral Reefs*, 36(4), 1111–1120. https://doi.org/10.1007/s00338-017-1602-9 (Irwin et al. 2017)

The corals Acropora palmata and A. cervicornis are important Caribbean reef-builders that have faced significant mortality in recent decades. While many studies have focused on the recent demise of these species, data from areas where Acropora spp. have continued to thrive are limited. Understanding the genetic diversity, recruitment, and temporal continuity of healthy populations of these threatened Acropora spp. and the hybrid they form ("Acropora prolifera") may provide insights into the demographic processes governing them. We studied three reef sites with abundant A. cervicornis, A. palmata, and hybrid Acropora populations offshore of Ambergris Caye, Belize at Coral Gardens, Manatee Channel, and Rocky Point. Samples were collected from all three Acropora taxa. We used microsatellite markers to determine: (1) genotypic diversity; (2) dominant reproductive mode supporting local recruitment; (3) minimum and maximum genet age estimates for all three acroporids; and (4) the history of hybrid colonization at these sites. We found that Acropora populations were highly clonal with local recruitment primarily occurring through asexual fragmentation. We also estimated the ages of 10 Acropora genets using recent methodology based on somatic mutation rates from genetic data. Results indicate minimum ages of 62–409 yr for A. cervicornis, 187–561 yr for A. palmata, and 156–281 yr for the Acropora hybrids at these sites. Our data indicate that existing A. cervicornis, A. palmata, and Acropora hybrid genets persisted during the 1980s Caribbean-wide Acropora spp. collapse, suggesting that these sites have been a refuge for Caribbean Acropora corals. Additionally, our data suggest that formation of extant hybrid Acropora genets pre-dates the widespread collapse of the parent taxa.

Larson, E. A., Gilliam, D. S., Padiema, M. L. & Walker, B. K. (2014). Possible recovery of Acropora palmata (Scleractinia:Acroporidae) within the Veracruz Reef System, Gulf of Mexico: a survey of 24 reefs to assess the benthic communities. *Rev. Biol. Trop.*, 62, 75–84. https://doi.org/10.15517/rbt.v62i0.15903 (Larson et al. 2014)

Recent evidence shows that Acropora palmata within the Veracruz Reef System, located in the southwestern Gulf of Mexico, may be recovering after the die off from the flooding of the Jamapa River and a dramatic cold water event in the 1970s. Since this decline, few surveys have documented the status of A. palmata. The 28 named reefs in the system are divided into 13 northern and 15 southern groups by the River. Between 2007 and 2013, we surveyed 24 reefs to assess the benthic communities. Seven of the 11 reefs surveyed in the northern group and all in the southern group had A. palmata. Colonies were typically found on the windward side of the reefs in shallow waters along the reef edges or crest. We also recorded colony diameter and condition along belt transects at two reefs in the north (Anegada de Adentro and Verde) and two in the south (Periferico and Sargazo), between 2011 and 2013. In addition, eight permanent transects were surveyed at Rizo (south). A total of 1 804 colonies were assessed; densities ranged from 0.02 to 0.28 colonies/m² (mean (±SD), colony diameter of 58 ± 73cm, and 89 ± 18% live tissue per colony). Total prevalence of predation by damselfish was 5%, by snails 2%, and <1% by fireworms, disease prevalence was <3%. Size frequency distributions indicated that all of the sites had a moderate to high spawning potential, 15-68% of the colonies at each site were mature, measuring over 1 600cm². The presence of these healthy and potentially reproductive colonies is important for species recovery, particularly because much of the greater Caribbean still shows little to no signs of recovery. Conservation and management efforts of these reefs are vital.

Martínez, K., Bone, D., Cróquer, A. & López-Ordaz, A. (2014). Population assessment of Acropora palmata (Scleractinia: Acroporidae): relationship between habitat and reef associated species. *Rev. Biol. Trop.*, 62 (Suppl. 3), 85–93. https://doi.org/10.15517/rbt.v62i0.15904 (Martínez et al. 2014)

Three decades ago, Acropora palmata was one of the main reef-building coral species throughout the Caribbean, forming an essential component of the structural complexity of shallow coral reef habitats. These colonies still provide microhabitats for settlement, food and shelter to many vertebrates and invertebrates. The recent decline of A. palmata has been followed by a significant loss in spatial heterogeneity and possibly in species diversity. Studies addressing whether dead and living stands of Acropora hold different fish and benthic assemblages are scarce. The status of Acropora colonies and their associated species were assessed in October 2012, at two reef zones of Cayo Sombrero, Venezuela. Visual censuses of fish abundance and the number of macrofaunal individuals were recorded for both live and dead zones. Living Acropora colonies had the lowest abundance (<31%). In both zoned the fish community was dominated by damselfishes (<53%) and wrasses (<36%), the benthic macrofauna by peracarid crustaceans (<40%) and polychaetes (<38%). Fish and benthic communities were not correlated with the condition (live or dead) of the Acropora habitats; possibly branching structures provide the necessary shelter and protection no matter if they are dead or alive. More replication is necessary to test this unexpected result.

Miller, M. W., Kerr, K. & Williams, D. E. (2016). Reef-scale trends in Florida Acropora spp. abundance and the effects of population enhancement. *PeerJ*, 4, e2523. https://doi.org/10.7717/peerj.2523 (Miller et al. 2016a)

Since the listing of Acropora palmata and A. cervicornis under the US Endangered Species Act in 2006, increasing investments have been made in propagation of listed corals (primarily A. cervicornis, A. palmata to a much lesser extent) in offshore coral nurseries and outplanting cultured fragments to reef habitats. This investment is superimposed over a spatiotemporal patchwork of ongoing disturbances (especially storms, thermal bleaching, and disease) as well as the potential for natural population recovery. In 2014 and 2015, we repeated broad scale (>50 ha), low precision Acropora spp. censuses (i.e., direct observation by snorkelers documented via handheld GPS) originally conducted in appropriate reef habitats during 2005–2007 to evaluate the trajectory of local populations and the effect of population enhancement. Over the decade-long study, A. palmata showed a cumulative proportional decline of 0.4 – 0.7x in colony density across all sites, despite very low levels of outplanting at some sites. A. cervicornis showed similar proportional declines at sites without outplanting. In contrast, sites that received A. cervicornis outplants showed a dramatic increase in density (over 13x). Indeed, change in A. cervicornis colony density was significantly positively correlated with cumulative numbers of outplants across sites. This study documents a substantive reef-scale benefit of Acropora spp. population enhancement in the Florida Keys, when performed at adequate levels, against a backdrop of ongoing population decline.

Mudge, L., Alves, C., Figueroa-Zavala, B. & Bruno, J. (2019). Assessment of Elkhorn Coral Populations and Associated Herbivores in Akumal, Mexico. *Front. Mar. Sci.*, 6:683. https://doi.org/10.3389/fmars.2019.00683 (Mudge et al. 2019)

Coral decline in the Caribbean is marked by the loss of habitat-forming corals, such as elkhorn coral (Acropora palmata). Elkhorn coral recovery has been isolated and patchy, but recently a "re-sheeting" phenomenon, in which elkhorn tissue grows over standing dead coral skeletons, was observed along the reefs in the Mexican Yucatán peninsula. Little is known about the ecological factors contributing to "re-sheeting", but it is hypothesized that grazing from herbivores provides top-down control of algal growth and promotes coral recovery. The purpose of this study was to evaluate the status of elkhorn populations in Akumal, Mexico and determine if Diadema urchins or parrotfish populations are associated with higher elkhorn abundance and lower algal cover. To achieve this objective, we surveyed 12 spur and groove reef sites in Akumal, where re-sheeting was recently observed, and measured elkhorn coral and herbivore population metrics. We found that both herbivore groups are associated with increasing elkhorn coral presence and cover, and lower macroalgal cover. Additionally, we tested for sampling bias in counting Diadema urchins and found that a significant difference in urchins counts between paired day and night transects on shallow, high complexity reefs Our results suggest that historically important herbivore groups may be contributing to the recovery of elkhorn coral in Akumal by facilitating tissue re-sheeting.

Muller, E. M., Rogers, C. S. & van Woesik, R. (2014). Early signs of recovery of Acropora palmata in St. John, US Virgin Islands. *Mar Biol*, 161(2), 359–365. https://doi.org/10.1007/s00227-013-2341-2 (Muller et al. 2014)

Since the 1980s, diseases have caused significant declines in the population of the threatened Caribbean coral Acropora palmata. Yet it is largely unknown whether the population densities have recovered from these declines and whether there have been any recent shifts in size-frequency distributions toward large colonies. It is also unknown whether colony size influences the risk of disease infection, the most common stressor affecting this species. To address these unknowns, we examined A. palmata colonies at ten sites around St. John, US Virgin Islands, in 2004 and 2010. The prevalence of white-pox disease was highly variable among sites, ranging from 0 to 53 %, and this disease preferentially targeted large colonies. We found that colony density did not significantly change over the 6-year period, although six out of ten sites showed higher densities through time. The size-frequency distributions of coral colonies at all sites were positively skewed in both 2004 and 2010, however, most sites showed a temporal shift toward more large-sized colonies. This increase in large-sized colonies occurred despite the presence of white-pox disease, a severe bleaching event, and several storms. This study provides evidence of slow recovery of the A. palmata population around St. John despite the persistence of several stressors.

Rodríguez-Martínez, R. E., Banaszak, A. T., McField, M. D., Beltrán-Torres, A. U. & Álvarez-Filip, L. (2014). Assessment of Acropora palmata in the Mesoamerican Reef System. *PLOS ONE*, 9(4), e96140. https://doi.org/10.1371/journal.pone.0096140 (Rodriguez-Martinez et al. 2014)

The once-dominant shallow reef-building coral Acropora palmata has suffered drastic geographical declines in the wider Caribbean from a disease epidemic that began in the late 1970s. At present there is a lack of quantitative data to determine whether this species is recovering over large spatial scales. Here, we use quantitative surveys conducted in 107 shallow-water reef sites between 2010 and 2012 to investigate the current distribution and abundance of A. palmata along the Mesoamerican Reef System (MRS). Using historical data we also explored how the distribution and abundance of this species has changed in the northern portion of the MRS between 1985 and 2010–2012. A. palmata was recorded in only a fifth of the surveyed reef sites in 2010–2012. In the majority of these reef sites the presence of A. palmata was patchy and rare. Only one site (Limones reef), in the northernmost portion of the MRS, presented considerably high A. palmata cover (mean: 34.7%, SD: 24.5%). At this site, the size-frequency distribution of A. palmata colonies was skewed towards small colony sizes; 84% of the colonies were healthy, however disease prevalence increased with colony size. A comparison with historical data showed that in the northern portion of the MRS, in 1985, A. palmata occurred in 74% of the 31 surveyed sites and had a mean cover of 7.7% (SD = 9.0), whereas in 2010–2012 this species was recorded in 48% of the sites with a mean cover of 2.9% (SD = 7.5). A. palmata populations along the MRS are failing to recover the distribution and abundance they had prior to the 1980s. Investigating the biological (e.g., population genetics) and environmental conditions (e.g., sources of stress) of the few standing reefs with relatively high A. palmata cover is crucial for the development of informed restoration models for this species.

Rodríguez-Zaragoza, F. A. & Arias-González, J. E. (2015). Coral biodiversity and bio-construction in the northern sector of the mesoamerican reef system. *Front. Mar. Sci.*, 2, 13. https://doi.org/10.3389/fmars.2015.00013 (Rodríguez-Zaragoza and Arias-González 2015)

As the impact of anthropogenic activity and climate change continue to accelerate rates of degradation on Caribbean coral reefs, conservation and restoration faces greater challenges. At at this stage, of particular

importance in coral reefs, is to recognize and to understand the structural spatial patterns of benthic assemblages. We developed a field-based framework of a Caribbean reefscape benthic structure by using hermatypic corals as an indicator group of global biodiversity and bio-construction patterns in eleven reefs of the northern sector of the Mesoamerican Barrier Reef System (nsMBRS). Four hundred and seventy four video-transects (50 m long by 0.4 m wide) were performed throughout a gradient of reef complexity from north to south (□400 km) to identify coral species, families and ensembles of corals. Composition and abundance of species, families and ensembles showed differences among reefs. In the northern zone, the reefs had shallow, partial reef developments with low diversities, dominated by Acropora palmata, Siderastrea spp., Pseudodiploria strigosa and Agaricia tenuifolia. In the central and southern zones, reefs presented extensive developments, high habitat heterogeneity, and the greatest diversity and dominance of Orbicella annularis and Orbicella faveolata. These two species determined the structure and diversity of corals in the central and southern zones of the nsMBRS and their bio-construction in these zones is unique in the Caribbean. Their abundance and distribution depended on the reef habitat area, topographic complexity and species richness. Orbicella species complex were crucial for maintaining the biodiversity and bio-construction of the central and southern zones while A. palmata in the northern zones of the nsMBRS.

Williams, D. E., K. Nedimyer, and M. W. Miller. 2020. Genotypic inventory of Acropora palmata (elkhorn coral) populations in south Florida, NOAA NMFS Southeast Fisheries Science Center, Protected Resources and Biodiversity Division Report: NOAA/SEFSC/PRBD-2020-01, 7pp. https://www.ncei.noaa.gov/data/oceans/coris/library/NOAA/CRCP/NMFS/SEFSC/Projects/1091/Williams2020_Genotypic_Inventory_Of_Acropora_Palmata.pdf (Williams et al. 2020a)

The elkhorn coral, *Acropora palmata*, is the iconic Caribbean reef- building species, and the key constructor of protective reef crest and spur structure. It features as the primary target in the Mission Iconic Reefs plan and was listed under the US Endangered Species Act in 2005. Much of the emerging and emergency efforts toward coral rescue and propagation are currently focused on other species directly affected by Stony Coral Tissue Loss Disease rather than A. palmata. However, this species continues to display precipitous, and perhaps underappreciated, decline in Florida. This document provides a summary of current knowledge, both quantitative and qualitative, regarding the genotypic status of *A. palmata* populations in Florida as of 2019.

Genetic Assessment

Hemond, E. M., Kaluziak, S. T. & Vollmer, S. V. (2014). The genetics of colony form and function in Caribbean Acropora corals. *BMC Genomics*, 15(1), 1–21. https://doi.org/10.1186/1471-2164-15-1133 (Hemond et al. 2014)

Colonial reef-building corals have evolved a broad spectrum of colony morphologies based on coordinated asexual reproduction of polyps on a secreted calcium carbonate skeleton. Though cnidarians have been shown to possess and use similar developmental genes to bilaterians during larval development and polyp formation, little is known about genetic regulation of colony morphology in hard corals. We used RNA-seq to evaluate transcriptomic differences between functionally distinct regions of the coral (apical branch tips and branch bases) in two species of Caribbean Acropora, the staghorn coral, A.

cervicornis, and the elkhorn coral, A. palmata. Transcriptome-wide gene profiles differed significantly between different parts of the coral colony as well as between species. Genes showing differential expression between branch tips and bases were involved in developmental signaling pathways, such as Wnt, Notch, and BMP, as well as pH regulation, ion transport, extracellular matrix production and other processes. Differences both within colonies and between species identify a relatively small number of genes that may contribute to the distinct "staghorn" versus "elkhorn" morphologies of these two sister species. The large number of differentially expressed genes supports a strong division of labor between coral branch tips and branch bases. Genes involved in growth of mature Acropora colonies include the classical signaling pathways associated with development of cnidarian larvae and polyps as well as morphological determination in higher metazoans.

Japaud, A., Bouchon, C., Manceau, J.-L. & Fauvelot, C. (2015). High clonality in Acropora palmata and Acropora cervicornis populations of Guadeloupe, French Lesser Antilles. *Mar. Freshwater Res.*, 66(9), 847–851. https://doi.org/10.1071/MF14181 (Japaud et al. 2015)

Since the 1980s, population densities of Acroporidae have dramatically declined in the Caribbean Sea. Quantitative censuses of Acroporidae provide information on the number of colonies (i.e. ramets), but not on the number of genetically distinct individuals (i.e. genets). In this context, the aim of our study was to provide an overview of the genetic status of Acropora populations in Guadeloupe by examining the genotypic richness of Acropora palmata and Acropora cervicornis. Using 14 microsatellite loci, we found extremely low genotypic richness for both species from Caye-à-Dupont reef (i.e. 0.125 for A. palmata and nearly zero for A. cervicornis). Because genetic diversity contributes to the ability of organisms to evolve and adapt to new environmental conditions, our results are alarming in the context of ongoing global warming as long periods of clonal growth without sexual recruitment may lead to the extinction of these populations.

Japaud, A., Bouchon, C., Magalon, H. & Fauvelot, C. (2019). Geographic distances and ocean currents influence Caribbean Acropora palmata population connectivity in the Lesser Antilles. *Conserv Genet*, 20(3), 447–466. https://doi.org/10.1007/s10592-019-01145-9 (Japaud et al. 2019)

The critically endangered coral species Acropora palmata used to dominate shallow Caribbean reefs but since the early 1980s, populations have dramatically declined. At the Caribbean scale, A. palmata is divided into two genetically divergent lineages and most of previous works investigating population connectivity among populations involved the western lineage (in Florida, the Bahamas, the Mesoamerican Reef System, and the Greater Antilles). Small scale genetic connectivity among A. palmata populations was globally found, possibly enhancing populations' recovery at the local scale. Yet, little is known regarding the genetic connectivity of populations of the eastern lineage, especially those of the Lesser Antilles, a fragmented archipelago located at the edge of the species distribution. Here, we filled this gap by investigating the genetic diversity, population structure and connectivity of A. palmata populations among 36 sampled sites from 11 islands of the Lesser Antilles using 14 hypervariable microsatellite loci. Globally, genetic diversity levels in A. palmata populations from the Lesser Antilles were lower compared to what was previously reported within the Wider Caribbean. The analysis of the genetic

structure, crossed with spatial autocorrelation analysis, revealed an isolation-by-distance pattern at both reef and Lesser Antilles scales. A gene dispersal distance of less than a kilometer, and a northward gene flow direction, in agreement with ocean surface currents in the region were found. Altogether, our results suggest a restricted population connectivity and short distance dispersal of A. palmata larvae within the Lesser Antilles further limited by geographic distances among suitable habitat patches. Additionally, our results suggest that southernmost populations are potential sources of larvae for the most northerly islands and have a key role in reseeding A. palmata populations of the Lesser Antilles.

Mège, P., Schizas, N. V., Reyes, J. G. & Hrbek, T. (2014). Genetic seascape of the threatened Caribbean elkhorn coral, Acropora palmata, on the Puerto Rico Shelf. *Marine Ecology*, 36(2), 195–209. https://doi.org/10.1111/maec.12135 (Mège et al. 2014)

It has been proposed that the elkhorn coral Acropora palmata is genetically separated into two distinct provinces in the Caribbean, an eastern and a western population admixing in Western Puerto Rico and around the Mona Passage. In this study, the genetic structure of A. palmata sampled at 11 Puerto Rican localities and localities from Curaçao, the Bahamas and Guadeloupe were examined. Analyses using five microsatellite markers showed that 75% of sampled colonies had unique genotypes, the rest being clone mates. Genetic diversity among genets was high (HE = 0.761) and consistent across localities (0.685–0.844). FST ranged from −0.011 to 0.047, supporting low but significant genetic differentiation between localities within the previously reported eastern and western genetic provinces. Plots of genetic per geographic distances and significant Mantel tests supported isolation-by-distance (IBD) within Puerto Rico. Analysis with the software STRUCTURE favored a scenario with weak differentiation between two populations, assigning Eastern Puerto Rican locations (Fajardo and Culebra), Guadeloupe and Curaçao to the Caribbean eastern population and Western Puerto Rican locations (west of Vega Baja and Ponce), Mona and the Bahamas to the Caribbean western population. Vieques and San Juan area harbored admixed profiles. Standardized FST per 1000 km unit further supported higher differentiation between localities belonging to different STRUCTURE populations, with IBD being stronger within Puerto Rico than on larger regional scales. This stronger genetic transition seems to separate localities between putative eastern and western provinces in the Eastern Puerto Rican region, but not around the Mona Passage.

Miller, M. W., Baums, I. B., Pausch, R. E., Bright, A. J., Cameron, C. M., Williams, D. E., . . . Woodley, C. M. (2018). Clonal structure and variable fertilization success in Florida Keys broadcast-spawning corals. *Coral Reefs*, 37(1), 239–249. https://doi.org/10.1007/s00338-017-1651-0 (Miller et al. 2018)

Keystone reef-building corals in the Caribbean are predominantly self-incompatible broadcast spawners and a majority are threatened due to both acute adult mortality and poor recruitment. As population densities decline, concerns about fertilization limitation and effective population size in these species increase and would be further exacerbated by either high clonality or gametic incompatibility of parental genotypes. This study begins to address these concerns for two Caribbean broadcasting species by characterizing clonal structure and quantifying experimental pairwise fertilization success. Orbicella faveolata showed surprisingly high and contrasting levels of clonality between two sampled sites;

Acropora palmata was previously known to be highly clonal. Individual pairwise crosses of synchronously spawning genotypes of each species were conducted by combining aliquots of gamete bundles immediately after spawning, and showed high and significant variability in fertilization success. Over half of the individual crosses of O. faveolata and about one-third of A. palmata crosses yielded ≤ 40% fertilization. Total sperm concentration was quantified in only a subset of O. faveolata crosses (range of 1–6 × 107 mL−1), but showed no correlation with fertilization success. We interpret that both parental incompatibility and individual genotypes with low-quality gametes are likely to have contributed to the variable fertilization observed with important implications for conservation. Differential fertilization success implies effective population size may be considerably smaller than hoped and population enhancement efforts need to incorporate many more parental genotypes at the patch scale to ensure successful larval production than indicated by estimates based simply on preserving levels of standing genetic diversity.

> Porto-Hannes, I., Zubillaga, A. L., Shearer, T. L., Bastidas, C., Salazar, C., Coffroth, M. A. & Szmant, A. M. (2015). Population structure of the corals *Orbicella faveolata* and *Acropora palmata* in the Mesoamerican Barrier Reef System with comparisons over Caribbean basin-wide spatial scale. *Marine Biology*, 162(1), 81–98. https://doi.org/10.1007/s00227-014-2560-1 (Porto-Hannes et al. 2015)

Studies of genetic diversity and population genetic structure in marine organisms are relevant to understanding populations' variability, and therefore their ability to withstand environmental perturbations, their potential for resistance to local extinction and their natural rate of recovery. Population structure and genetic diversity were assessed at a regional spatial scale (i.e., Mesoamerican Barrier Reef System, MBRS) in two major reef building coral species Orbicella (formerly Montastraea) faveolata and Acropora palmata, and at a larger spatial scale (i.e., Caribbean-wide; MBRS, Panama, Venezuela and Puerto Rico) for A. palmata only. The most significant findings were as follows: (1) high genetic diversity and low clonality were found for both species, which is expected for O. faveolata but not for A. palmata, (2) both species showed low-to-moderate, yet significant population structure among populations along the MBRS; in particular, O. faveolata and A. palmata from Ambergris (Belize) and O. faveolata from Calabash (Belize) and A. palmata from Puerto Morelos (Mexico) showed some genetic differentiation from the rest of the MBRS populations, and (3) A. palmata from MBRS, Panama, Puerto Rico and Venezuela were grouped into four subregions that could be considered as management units. A more spatially detailed sampling program and the inclusion of recruits will be necessary to get a comprehensive understanding of coral population structure and current gene flow patterns in these two species.

Spatial Distribution

> Hernández-Fernández, L., González de Zayas, R., Olivera, Y. M., Pina Amargós, F., Bustamante López, C., Dulce Sotolongo, L. B., . . . Salmón Moret F. (2019). Distribution and status of living colonies of Acropora spp. in the reef crests of a protected marine area of the Caribbean (Jardines de la Reina National Park, Cuba). *PeerJ*, 7, e6470. https://doi.org/10.7717/peerj.6470 (Hernandez-Fernandez et al. 2019)

The reef crests of the Jardines de la Reina National Park (JRNP) are largely formed by Acropora palmata, but colonies of A. cervicornis and the hybrid A. prolifera are also present. This study shows spatial distribution of colonies, thickets and live fragments of these species in the fore reefs. Snorkeling was used to perform the direct observations. The maximum diameter of 4,399 colonies of A. palmata was measured and the health of 3,546 colonies was evaluated. The same was done to 168 colonies of A. cervicornis and 104 colonies of A. prolifera. The influence of the location and marine currents on a number of living colonies of A. palmata was analyzed. For such purpose, reef crests were divided into segments of 500 m. The marine park was divided into two sectors: East and West. The Caballones Channel was used as the reference dividing line. The park was also divided into five reserve zones. We counted 7,276 live colonies of Acropora spp. 1.4% was A. prolifera, 3.5% A. cervicornis and 95.1% A. palmata. There were 104 thickets of A. palmata, ranging from eight to 12 colonies, and 3,495 fragments; 0.6% was A. cervicornis and the rest A. palmata (99.4%). In the East sector, 263 colonies (3.8% of the total), six thickets (5.8%) and 32 fragments (1%) of A. palmate were recorded. In the same sector, there were 11 fragments (50%) of A.cervicornis and two (2%) colonies of A. prolifera. Health of A. palmata was evaluated as good and not so good in the study area. Health of A. cervicornis was critical and health of A. prolifera was good in all five reserve zones. There was a significant increase in the number of colonies from east to west ($X2 = 11.5$, $gl = 3.0$, $p = 0.009$). This corroborates the existence of an important abundance differences between the eastern and the western region of the JRNP. A negative relationship was observed between the number of colonies and the distance from the channel ($X2 = 65.0$, $df = 3.0$, $p < 0.001$). The influence of the channel, for the live colonies of A. palmata is greater within the first 2,000 m. It then decreases until approximately 6,000 m, and no significant increase beyond. The orientation of the reef crests significantly influenced the abundance of the colonies ($X2 = 15.5$, $df = 2.9$, $p = 0.001$). The results presented here provide a baseline for future research on the status of the populations of Acropora spp., considering that there has been a certain recovery of the species A. palmata during the last 10–16 years. Given the current status of the populations of Acropora spp., conservation actions focusing A. cervicornis should be prioritized.

Kuffner, I. B., A. Stathakopoulos, L. T. Toth, and L. A. Bartlett. 2020. Reestablishing a stepping-stone population of the threatened elkhorn coral Acropora palmata to aid regional recovery. Endangered Species Research 43:461-473. (Kuffner et al. 2020)

Recovery of the elkhorn coral Acropora palmata is critical to reversing coral reef ecosystem collapse in the western Atlantic, but the species is severely threatened. To gauge potential for the species' restoration in Florida, USA, we conducted an assisted migration experiment where 50 coral fragments of 5 nursery-raised genetic strains (genets) from the upper Florida Keys were moved to 5 sites across 350 km of the offshore reef. Additionally, 4 fragments from the 1 remaining colony of A. palmata in Dry Tortugas National Park (DRTO) were added to the 2 DRTO experimental sites to test for local adaptation. To measure coral performance, we tracked coral survival, calcification, growth, and condition from May 2018 to October 2019. All 24 corals relocated to the DRTO sites survived and calcified ~85% faster than the fewer surviving corals transplanted to the 2 upper Keys sites. While coral survival across the entire experiment did not depend on genet, there was a weak but statistically significant genetic effect on calcification rate among the corals relocated to DRTO. The DRTO native genet was among the fastest growing genets, but it was not the fastest, suggesting a lack of local adaptation at this scale. Our results indicate that DRTO, a remote reef system inhabited by the species during the Holocene and located at the

nexus of major ocean currents, may be a prime location for reestablishing A. palmata. Assisted migration of A. palmata to DRTO could restore a sexually reproducing population in <10 yr, thereby promoting the species' regional recovery.

Habitat and Ecosystem Conditions

> Camp, E. F., Smith, D. J., Evenhuis, C., Enochs, I., Manzello, D., Woodcock, S. & Suggett, D. J. (2016). Acclimatization to high-variance habitats does not enhance physiological tolerance of two key Caribbean corals to future temperature and pH. *Proc. R. Soc. B*, 283(1831), 20160442. https://doi.org/10.1098/rspb.2016.0442 (Camp et al. 2016)

Corals are acclimatized to populate dynamic habitats that neighbour coral reefs. Habitats such as seagrass beds exhibit broad diel changes in temperature and pH that routinely expose corals to conditions predicted for reefs over the next 50–100 years. However, whether such acclimatization effectively enhances physiological tolerance to, and hence provides refuge against, future climate scenarios remains unknown. Also, whether corals living in low-variance habitats can tolerate present-day high-variance conditions remains untested. We experimentally examined how pH and temperature predicted for the year 2100 affects the growth and physiology of two dominant Caribbean corals (Acropora palmata and Porites astreoides) native to habitats with intrinsically low (outer-reef terrace, LV) and/or high (neighbouring seagrass, HV) environmental variance. Under present-day temperature and pH, growth and metabolic rates (calcification, respiration and photosynthesis) were unchanged for HV versus LV populations. Superimposing future climate scenarios onto the HV and LV conditions did not result in any enhanced tolerance to colonies native to HV. Calcification rates were always lower for elevated temperature and/or reduced pH. Together, these results suggest that seagrass habitats may not serve as refugia against climate change if the magnitude of future temperature and pH changes is equivalent to neighbouring reef habitats.

> Lopera, L., Cardona, Y. & Zapata-Ramírez, P. A. (2020). Circulation in the Seaflower Reserve and Its Potential Impact on Biological Connectivity. *Front. Mar. Sci.*, 7:385. https://doi.org/10.3389/fmars.2020.00385 (Lopera et al. 2020)

The influence of ocean currents on marine population connectivity is critical to territory planning, and such phenomena should be considered in the design and implementation of marine protected areas (MPAs), marine spatial planning strategies, and restoration plans, among other developments. Knowledge of the influence of currents is also vital in understanding the relationship between oceanographic drivers and ecosystem configurations. However, despite their importance, ocean currents and their role in coral connectivity remain poorly constrained in the Seaflower Marine Reserve, an area that hosts the most productive open-ocean coral reef system in the Caribbean and that was declared a biosphere reserve in 2000. We herein characterize the larva transport patterns associated with surface currents that control connectivity in the reserve. To achieve this aim, we simulated the advection of buoyant coral larvae of Acropora palmata during nine spawning events. Larval dispersal patterns were obtained through offline coupling of a high-spatiotemporal resolution hydrodynamic field and a biophysical Lagrangian model for particle dispersion. Ocean current fields were generated using a Regional Ocean Modeling System (ROMS) that was appropriately configured for the region. Larval dispersion was simulated using an Individual-Based Model (Ichthyop). Our results show that there are heterogeneous connectivity patterns

during the spawning events at seasonal and inter-annual scales. This seems to be associated with high spatiotemporal dynamic variability in the region, such as the Caribbean Current bifurcation close to the Nicaraguan Rise, the intrusion-formation of mesoscale and sub-mesoscale eddies, and the semi-permanent presence of the Panama-Colombia Gyre. We also found that Serranilla, Providencia, Quitasueño, and Serrana act as the most important sinks. In contrast, the northernmost reefs, Serranilla, B. Alicia, and B. Nuevo, seem to be the most important sources of larvae, highlighting that these areas need to be incorporated into the current MPA zonification and that this could lead to the improvement of MPA effectiveness. Our findings also suggest the need to implement MPA networks between Jamaica and Colombia to allow biological populations to become resilient to environmental changes and less prone to local extinctions.

Speare, K. E., Duran, A., Miller, M. W. & Burkepile, D. E. (2019). Sediment associated with algal turfs inhibits the settlement of two endangered coral species. *Marine Pollution Bulletin*, 144, 189–195. https://doi.org/10.1016/j.marpolbul.2019.04.066 (Speare et al. 2019)

Populations of Acropora palmata and Orbicella faveolata, two important reef-building corals, have declined precipitously across the Caribbean region since at least the 1970s. Recruitment failure may be limiting population recovery, possibly due to lack of suitable settlement habitat. Here, we examine the effects of algal turfs and algal turfs + sediment, two widely abundant substrate types across the Florida Keys, on the settlement of these two ecologically-important species. We show that sediment significantly impedes coral settlement, reducing settlement 10- and 13-fold for A. palmata and O. faveolata, respectively, compared to turf algae alone. This result is corroborated by our field survey data that showed a strong, negative relationship between the abundance of turf + sediment and the abundance of juvenile corals. Turf algae alone did not reduce coral settlement. Our results suggest that sediment-laden turf algae are detrimental to settling corals, but that turf algae alone may be relatively benign.

Wirt, K. E., Hallock, P., Palandro, D. & Lunz, K. S. (2015). Potential Habitat of Acropora spp. on Reefs of Florida, Puerto Rico, and the US Virgin Islands. *Global Ecology and Conservation*, 3, 242–255. https://doi.org/10.1016/j.gecco.2014.12.001 (Wirt et al. 2015)

Elkhorn and staghorn corals (Acropora palmata, Acropora cervicornis) were listed in 2006 as threatened under the Endangered Species Act. The goal of this study was to create model potential-habitat maps for A. palmata and A. cervicornis, while identifying areas for possible re-establishment. These maps were created using a database of reported field observations in combination with existing benthic habitat maps. The mapped coral reef and hardbottom classifications throughout Florida, Puerto Rico, and the US Virgin Island reef tracts were used to generate potential-habitat polygons using buffers that incorporated 95% and 99% of reported observations of Acropora spp. Locations of 92% of A. palmata observations and 84% of A. cervicornis observations coincided with mapped coral reef or hard-bottom habitat throughout the study area. These results indicate that potential habitat for A. palmata is currently well defined throughout this region, but that potential habitat for A. cervicornis is more variable and has a wider range than that for A. palmata. This study provides a novel method of combining data sets at various geographic

spatial scales and may be used to inform and refine the current National Oceanic and Atmospheric Administration critical habitat map.

Threat Assessment

Disease

> Bright, A. J., Rogers, C. S., Brandt, M. E., Muller, E. & Smith, T. B. (2016). Disease Prevalence and Snail Predation Associated with Swell-Generated Damage on the Threatened Coral, Acropora palmata (Lamarck). *Front. Mar. Sci.*, 3:77. https://doi.org/10.3389/fmars.2016.00077 (Bright et al. 2016)

Disturbances such as tropical storms cause coral mortality and reduce coral cover as a direct result of physical damage. Storms can be one of the most important disturbances in coral reef ecosystems, and it is crucial to understand their long-term impacts on coral populations. The primary objective of this study was to determine trends in disease prevalence and snail predation on damaged and undamaged colonies of the threatened coral species, Acropora palmata, following an episode of heavy ocean swells in the US Virgin Islands (USVI). At three sites on St. Thomas and St. John, colonies of A. palmata were surveyed monthly over one year following a series of large swells in March 2008 that fragmented 30 to 93% of colonies on monitored reefs. Post-disturbance surveys conducted from April 2008 through March 2009 showed that swell-generated damage to A. palmata caused negative indirect effects that compounded the initial direct effects of physical disturbance. During the 12 months after the swell event, white pox disease prevalence was 41% higher for colonies that sustained damage from the swells than for undamaged colonies ($df = 207$, $p = 0.01$) with greatest differences in disease prevalence occurring during warm water months. In addition, the corallivorous snail, Coralliophila abbreviata, was 46% more abundant on damaged corals than undamaged corals during the 12 months after the swell event ($df = 207$, $p = 0.006$).

> Florida SCTLD Restoration Trials Team. 2020. Are acroporid corals a potential vector of stony coral tissue loss disease? 10pp. (Florida SCTLD Restoration Trials Team 2020)

In April 2019, the Restoration Trials Team created an Action Plan that identified priority research questions to be addressed within the context of conducting restoration within the stony coral tissue loss disease (SCTLD) outbreak. The first question was “Are acroporid corals a potential vector of stony coral tissue loss disease?”. Indeed, most coral restoration along the Florida Reef Tract (FRT) has used acroporids, including both Acropora palmata and A. cervicornis. Acroporid corals have not been observed to exhibit SCTLD despite being subjected to the unknown infectious agents of SCTLD throughout the FRT. These observations, as well as other anecdotal information, suggest that acroporids are not susceptible to SCTLD. However, directed experiments to test susceptibility of acroporids to SCTLD should be conducted. Additionally, concerns have been expressed that acroporid corals could serve as a vector for SCTLD. To address these concerns, the Restoration Trials Team suggested that both field and laboratory experiments should be conducted to determine whether acroporids are indeed resistant to SCTLD and to identify if acroporids may be a vector of SCTLD. In response, two opportunistic experiments were conducted. One included a field experiment conducted by Andrew Bruckner with the Florida Keys National Marine Sanctuary and Erich Bartels at Mote Marine Laboratory. The second

included a laboratory exposure experiment conducted by Erinn Muller with the Coral Health and Disease Program at Mote Marine Laboratory. Results from these two opportunistic experiments are included within this report.

> Joyner, J. L., Sutherland, K. P., Kemp, D. W., Berry, B., Griffin, A., Porter, J. W., . . . Lipp, E. K. (2015). Systematic Analysis of White Pox Disease in Acropora palmata of the Florida Keys and Role of Serratia marcescens. *Appl. Environ. Microbiol.*, 81(13), 4451–4457. https://doi.org/10.1128/AEM.00116-15 (Joyner et al. 2015)

White pox disease (WPD) affects the threatened elkhorn coral, Acropora palmata. Owing in part to the lack of a rapid and simple diagnostic test, there have been few systematic assessments of the prevalence of acroporid serratiosis (caused specifically by Serratia marcescens) versus general WPD signs. Six reefs in the Florida Keys were surveyed between 2011 and 2013 to determine the disease status of A. palmata and the prevalence of S. marcescens. WPD was noted at four of the six reefs, with WPD lesions found on 8 to 40% of the colonies surveyed. S. marcescens was detected in 26.9% (7/26) of the WPD lesions and in mucus from apparently healthy colonies both during and outside of disease events (9%; 18/201). S. marcescens was detected with greater frequency in A. palmata than in the overlying water column, regardless of disease status ($P = 0.0177$). S. marcescens could not be cultured from A. palmata but was isolated from healthy colonies of other coral species and was identified as pathogenic pulsed-field gel electrophoresis type PDR60. WPD lesions were frequently observed on the reef, but unlike in prior outbreaks, no whole-colony death was observed. Pathogenic S. marcescens was circulating on the reef but did not appear to be the primary pathogen in these recent WPD episodes, suggesting that other pathogens or stressors may contribute to signs of WPD. Results highlight the critical importance of diagnostics in coral disease investigations, especially given that field manifestation of disease may be similar, regardless of the etiological agent.

> Miller, M. W., Colburn, P. J., Pontes, E., Williams, D. E., Bright, A. J., Serrano, X. M. & Peters, E. C. (2019). Genotypic variation in disease susceptibility among cultured stocks of elkhorn and staghorn corals. PeerJ, 7, e6751. https://doi.org/10.7717/peerj.6751 (Miller et al. 2019)

Disease mortality has been a primary driver of population declines and the threatened status of the foundational Caribbean corals, Acropora palmata and A. cervicornis. There remain few tools to effectively manage coral disease. Substantial investment is flowing into in situ culture and population enhancement efforts, while disease takes a variable but sometimes high toll in restored populations. If genetic resistance to disease can be identified in these corals, it may be leveraged to improve resistance in restored populations and possibly lead to effective diagnostic tests and disease treatments. Using a standardized field protocol based on replicated direct-graft challenge assays, we quantified this important trait in cultured stocks from three field nurseries in the Florida Keys. Field tests of 12 genotypes of A. palmata and 31 genotypes of A. cervicornis revealed significant genotypic variation in disease susceptibility of both species measured both as risk of transmission (percent of exposed fragments that displayed tissue loss) and as the rate of tissue loss (cm2 d–1) in fragments with elicited lesions. These assay results provide a measure of relative disease resistance that can be incorporated, along with

consideration of other important traits such as growth and reproductive success, into restoration strategies to yield more resilient populations.

> Muller, E. M. & van Woesik, R. (2014). Genetic Susceptibility, Colony Size, and Water Temperature Drive White-Pox Disease on the Coral Acropora palmata. *PLOS ONE*, 9(11), e110759. https://doi.org/10.1371/journal.pone.0110759 (Muller and van Woesik 2014)

Outbreaks of coral diseases are one of the greatest threats to reef corals in the Caribbean, yet the mechanisms that lead to coral diseases are still largely unknown. Here we examined the spatial-temporal dynamics of white-pox disease on Acropora palmata coral colonies of known genotypes. We took a Bayesian approach, using Integrated Nested Laplace Approximation algorithms, to examine which covariates influenced the presence of white-pox disease over seven years. We showed that colony size, genetic susceptibility of the coral host, and high-water temperatures were the primary tested variables that were positively associated with the presence of white-pox disease on A. palmata colonies. Our study also showed that neither distance from previously diseased individuals, nor colony location, influenced the dynamics of white-pox disease. These results suggest that white-pox disease was most likely a consequence of anomalously high water temperatures that selectively compromised the oldest colonies and the most susceptible coral genotypes.

> Randall, C. J. & van Woesik, R. (2015). Contemporary white-band disease in Caribbean corals driven by climate change. *Nature Climate Change*, 5(4), 375–379. https://doi.org/10.1038/nclimate2530 (Randall and van Woesik 2015)

Over the past 40 years, two of the dominant reef-building corals in the Caribbean, Acropora palmata and Acropora cervicornis, have experienced unprecedented declines1,2. That loss has been largely attributed to a syndrome commonly referred to as white-band disease1,3. Climate change-driven increases in sea surface temperature (SST) have been linked to several coral diseases4,5, yet, despite decades of research, the attribution of white-band disease to climate change remains unknown. Here we hindcasted the potential relationship between recent ocean warming and outbreaks of white-band disease on acroporid corals. We quantified eight SST metrics, including rates of change in SST and contemporary thermal anomalies, and compared them with records of white-band disease on A. palmata and A. cervicornis from 473 sites across the Caribbean, surveyed from 1997 to 2004. The results of our models suggest that decades-long climate-driven changes in SST, increases in thermal minima, and the breach of thermal maxima have all played significant roles in the spread of white-band disease. We conclude that white-band disease has been strongly coupled with thermal stresses associated with climate change, which has contributed to the regional decline of these once-dominant reef-building corals.

> Sutherland, K. P., Berry, B., Park, A., Kemp, D. W., Demp, K. M., Lipp, E. K. & Porter, J. W. (2016). Shifting white pox aetiologies affecting Acropora palmata in the Florida Keys, 1994–2014. *Phil. Trans. R. Soc. B*, 371(1689), 20150205. https://doi.org/10.1098/rstb.2015.0205 (Sutherland et al. 2016)

We propose ‘the moving target hypothesis’ to describe the aetiology of a contemporary coral disease that differs from that of its historical disease state. Hitting the target with coral disease aetiology is a complex pursuit that requires understanding of host and environment, and may lack a single pathogen solution. White pox disease (WPX) affects the Caribbean coral Acropora palmata. Acroporid serratiosis is a form of WPX for which the bacterial pathogen (Serratia marcescens) has been established. We used long-term (1994–2014) photographic monitoring to evaluate historical and contemporary epizootiology and aetiology of WPX affecting A. palmata at eight reefs in the Florida Keys. Ranges of WPX prevalence over time (0–71.4%) were comparable for the duration of the 20-year study. Whole colony mortality and disease severity were high in historical (1994–2004), and low in contemporary (2008–2014), outbreaks of WPX. Acroporid serratiosis was diagnosed for some historical (1999, 2003) and contemporary (2012, 2013) outbreaks, but this form of WPX was not confirmed for all WPX cases. Our results serve as a context for considering aetiology as a moving target for WPX and other coral diseases for which pathogens are established and/or candidate pathogens are identified. Coral aetiology investigations completed to date suggest that changes in pathogen, host and/or environment alter the disease state and complicate diagnosis.

Sweet, M. J., Croquer, A. & Bythell, J. C. (2014). Experimental antibiotic treatment identifies potential pathogens of white band disease in the endangered Caribbean coral Acropora cervicornis. *Proceedings of the Royal Society B: Biological Sciences*, 281, 1788. https://doi.org/10.1098/rspb.2014.0094 (Sweet et al. 2014)

Coral diseases have been increasingly reported over the past few decades and are a major contributor to coral decline worldwide. The Caribbean, in particular, has been noted as a hotspot for coral disease, and the aptly named white syndromes have caused the decline of the dominant reef building corals throughout their range. White band disease (WBD) has been implicated in the dramatic loss of Acropora cervicornis and Acropora palmata since the 1970s, resulting in both species being listed as critically endangered on the International Union for Conservation of Nature Red list. The causal agent of WBD remains unknown, although recent studies based on challenge experiments with filtrate from infected hosts concluded that the disease is probably caused by bacteria. Here, we report an experiment using four different antibiotic treatments, targeting different members of the disease-associated microbial community. Two antibiotics, ampicillin and paromomycin, arrested the disease completely, and by comparing with community shifts brought about by treatments that did not arrest the disease, we have identified the likely candidate causal agent or agents of WBD. Our interpretation of the experimental treatments is that one or a combination of up to three specific bacterial types, detected consistently in diseased corals but not detectable in healthy corals, are likely causal agents of WBD. In addition, a histophagous ciliate (Philaster lucinda) identical to that found consistently in association with white syndrome in Indo-Pacific acroporas was also consistently detected in all WBD samples and absent in healthy coral. Treatment with metronidazole reduced it to below detection limits, but did not arrest the disease. However, the microscopic disease signs changed, suggesting a secondary role in disease causation for this ciliate. In future studies to identify a causal agent of WBD via tests of Henle–Koch's postulates, it will be vital to experimentally control for populations of the other potential pathogens identified in this study.

Allgeier, J. E., Andskog, M. A., Hensel, E., Appaldo, R., Layman, C., & Kemp, D. W. (2020). Rewiring coral: Anthropogenic nutrients shift diverse coral–symbiont nutrient and carbon interactions toward symbiotic algal dominance. *Global Change Biology*, 00:1-14. https://doi.org/10.1111/gcb.15230 (Allgeier et al. 2020)

Improving coral reef conservation requires heightened understanding of the mechanisms by which coral cope with changing environmental conditions to maintain optimal health. We used a long-term (10 month) in situ experiment with two phylogenetically diverse scleractinians (Acropora palmata and Porites porites) to test how coral–symbiotic algal interactions changed under real-world conditions that were a priori expected to be beneficial (fish-mediated nutrients) and to be harmful, but non-lethal, for coral (fish + anthropogenic nutrients). Analyzing nine response variables of nutrient stoichiometry and stable isotopes per coral fragment, we found that nutrients from fish positively affected coral growth, and moderate doses of anthropogenic nutrients had no additional effects. While growing, coral maintained homeostasis in their nutrient pools, showing tolerance to the different nutrient regimes. Nonetheless, structural equation models revealed more nuanced relationships, showing that anthropogenic nutrients reduced the diversity of coral–symbiotic algal interactions and caused nutrient and carbon flow to be dominated by the symbiont. Our findings show that nutrient and carbon pathways are fundamentally "rewired" under anthropogenic nutrient regimes in ways that could increase corals' susceptibility to further stressors. We hypothesize that our experiment captured coral in a previously unrecognized transition state between mutualism and antagonism. These findings highlight a notable parallel between how anthropogenic nutrients promote symbiont dominance with the holobiont, and how they promote macroalgal dominance at the coral reef scale. Our findings suggest more realistic experimental conditions, including studies across gradients of anthropogenic nutrient enrichment as well as the incorporation of varied nutrient and energy pathways, may facilitate conservation efforts to mitigate coral loss.

Guzman, H. M., Kaiser, S. & Weil, E. (2020). Assessing the long-term effects of a catastrophic oil spill on subtidal coral reef communities off the Caribbean coast of Panama (1985–2017). *Mar. Biodivers.* 50(3), 28. https://doi.org/10.1007/s12526-020-01057-9 (Guzman et al. 2020)

Accidental oil discharges pose acute and chronic risks on coral communities, but knowledge on the ecological long-term implications is fragmentary. Here, we examine the potential short-, mid-, and long-term effects of a major oil spill on subtidal reef communities over a 30-year period using a multicontrol before-after-control-impact (BACI) approach. In April 1986, 8000 t (~ 9.3 106 L) of crude oil were released from a refinery in Bahia Las Minas (Caribbean Panama) contaminating an area of about 40 km2 consisting of intertidal and subtidal mangrove, seagrass, sandy, and coral reef habitats. Surveys of oiled and unpolluted control sites have been conducted at different times between 1985 and 2017 and changes in community metrics (i.e., percent live cover, diversity, community composition, and recruitment) were compared with pre-spill data. The main focus was on scleractinian corals, but impacts on other major benthic taxa were also considered. Short-term oil effects on scleractinian corals included substantial declines in live cover, and diversity as well as changes in community structure being detectable up to 4 years after the spill, while other benthic taxa were hardly affected. Branching corals, such as Acropora

palmata, seemed to suffer more, but strong incident-related declines could also be seen in two massive species (i.e., Pseudodiploria clivosa and Porites astreoides). Recruitment rates were not significantly different relative to oil exposure, but number of recruits showed strong temporal variation both at the oiled and control sites. While short-term effects (1 year post-spill) could be unequivocally linked to the spill, assessment of mid-term impacts was complicated by cumulative, albeit different stressors (diseases, bleaching, warming, additional accidental oil discharges) that have been driving changes at oiled and control sites respectively and thus ultimately concealing any effects of the spill. Our data did not provide evidence of a long-term (> 10 years) chronic impact of the oil spill, but instead showed that a variety of factors have contributed to reef degradation both at oiled and control sites over the survey period.

Kemp, K. M., Westrich, J. R., Alabady, M. S., Edwards, M. L. & Lipp, E. K. (2018). Abundance and Multilocus Sequence Analysis of Vibrio Bacteria Associated with Diseased Elkhorn Coral (Acropora palmata) of the Florida Keys. *Appl. Environ. Microbiol.*, 84:e01035-17. https://doi.org/10.1128/AEM.01035-17 (Kemp et al. 2018)

The critically endangered elkhorn coral (Acropora palmata) is affected by white pox disease (WPX) throughout the Florida Reef Tract and wider Caribbean. The bacterium Serratia marcescens was previously identified as one etiologic agent of WPX but is no longer consistently detected in contemporary outbreaks. It is now believed that multiple etiologic agents cause WPX; however, to date, no other potential pathogens have been thoroughly investigated. This study examined the association of Vibrio bacteria with WPX occurrence from August 2012 to 2014 at Looe Key Reef in the Florida Keys, USA. The concentration of cultivable Vibrio was consistently greater in WPX samples than in healthy samples. The abundance of Vibrio bacteria relative to total bacteria was four times higher in samples from WPX lesions than in adjacent apparently healthy regions of diseased corals based on quantitative PCR (qPCR). Multilocus sequence analysis (MLSA) was used to assess the diversity of 69 Vibrio isolates collected from diseased and apparently healthy A. palmata colonies and the surrounding seawater. Vibrio species with known pathogenicity to corals were detected in both apparently healthy and diseased samples. While the causative agent(s) of contemporary WPX outbreaks remains elusive, our results suggest that Vibrio spp. may be part of a nonspecific heterotrophic bacterial bloom rather than acting as primary pathogens. This study highlights the need for highly resolved temporal sampling in situ to further elucidate the role of Vibrio during WPX onset and progression.

Norat-Ramírez, J., Méndez-Lázaro, P., Hernández-Delgado, E. A., Mattei-Torres, H. & Cordero-Rivera, L. (2019). A septic waste index model to measure the impact of septic tanks on coastal water quality and coral reef communities in Rincon, Puerto Rico. *Ocean & Coastal Management*, 169, 201–213. https://doi.org/10.1016/j.ocecoaman.2018.12.016 (Norat-Ramírez et al. 2019)

The impact of fecal contamination of coastal waters and coral reefs is a major cause of concern in marine reserves in Puerto Rico. The measurement of the association between septic tank frequency in watersheds of creeks draining into these reserves and coastal water quality and coral reef condition is of importance in configuring pollution control policy. Fecal coliforms and enterococci assays were used to measure the density of fecal contaminants across the Tres Palmas Marine Reserve (TPMR) in Rincon, Puerto Rico. Inshore waters are intermittent creeks, receiving fecal pollution only from faulty septic tanks. Fecal

indicators measurements showed higher densities near the southernmost creek mouth emptying into TPMR, a finding consistent with a larger amount of dwellings with septic tanks within this watershed (Vista Azul creek). A Septic Weight Index was constructed to analyze sewage impact from all watersheds draining into the marine reserve. Linear Regression analyses showed a significant association between these non-point source fecal pollution sources and both coastal water quality and impact on some parameters measuring the condition of Acropora palmata coral reef colonies.

Ross, C., Fogarty, N. D., Ritson-Williams, R. & Paul, V. J. (2017). Interspecific Variation in Coral Settlement and Fertilization Success in Response to Hydrogen Peroxide Exposure. *The Biological Bulletin*, 233(3), 206–218. https://doi.org/10.1086/696215 (Ross et al. 2017)

Hydrogen peroxide (H2O2) is involved in the regulation of numerous reproductive and morphogenic processes across an array of taxa. Extracellular H2O2 can be widespread in oceanic waters, and elevated sea surface temperatures can cause increased levels of intracellular H2O2 within cnidarian tissue, but it remains unclear how this compound affects early life-history processes in corals, such as fertilization, metamorphosis, and settlement. To evaluate the effects of H2O2 on multiple stages of recruitment, experiments were conducted using Caribbean corals with various reproductive modes, including the brooders Porites astreoides and Favia fragum and the broadcast-spawning species Acropora palmata and Orbicella franksi. H2O2 accelerated settlement in all brooding species tested. Concentrations of 1000 µmol l−1 H2O2 caused close to 100% settlement in all larval age classes, regardless of exposure duration. As larvae aged, the required threshold of H2O2 capable of inducing settlement decreased. In contrast, H2O2 concentrations of 100 µmol l−1 or greater caused a significant reduction in metamorphosis and settlement in the larvae of spawners. Furthermore, fertilization of their gametes was inhibited in the presence of H2O2 concentrations as low as 100 µmol l−1. In Porites astreoides larvae, internal levels of H2O2 reached a maximal value of 75 µmol l−1 following 48 h of incubation at 31 °C. This concentration was found to significantly alter settlement rates in both brooding coral species and likely induced a cellular cascade in the settlement signaling pathway. The results of this study suggest that temperature stress influences H2O2 production, which in turn impacts coral settlement. While it is unlikely that the current levels of externally derived concentrations of oceanic H2O2 are affecting coral larvae, internal concentrations (produced under heat stress) have the capacity to impact recruitment under a changing climate.

Williams, D. E., Miller, M. W., Bright, A. J., Pausch, R. E. & Valdivia, A. (2017). Thermal stress exposure, bleaching response, and mortality in the threatened coral Acropora palmata. *Marine Pollution Bulletin*, 124(1), 189–197. https://doi.org/10.1016/j.marpolbul.2017.07.001 (Williams et al. 2017)

Demographic data for Elkhorn coral, Acropora palmata, and in situ water temperature data from seven upper Florida Keys (USA) reefs revealed three warm thermal stress events between 2010 and 2016. During a mild bleaching event in 2011, up to 59% of colonies bleached, but no mortality resulted. In both 2014 and 2015, severe and unprecedented bleaching was observed with up to 100% of colonies bleached. A. palmata live tissue cover declined by one-third following the 2014–2015 events. Colony mortality of mildly- and non-bleached colonies did not differ but increased significantly with more severe bleaching.

Increased bleaching prevalence corresponded to maximum daily average water temperatures above 31.3°C. However, the cumulative days with daily average exceeding 31.0°C provided a better predictor of bleaching response. The bleaching response of surviving colonies in 2015 was not consistent with acclimatization as most individual colonies bleached at least as badly as in 2014.

> Yuan, J., Liu, L., Zhang, Y., Shen, C. & Lin, S. (2019). Molecular Processes and Hub Genes of Acropora Palmata in Response to Thermal Stress And Bleaching. *Journal of Coastal Research*, 35(1), 26–32. https://doi.org/10.2112/JCOASTRES-D-18-00053.1 (Yuan et al. 2019)

Among many environmental factors, high temperature is the main factor that causes coral bleaching. Thus, analyses of the bleaching mechanism and important genes involved in coral responses to thermal stress and bleaching are important. This study explored the gene expression profiling data (GSE16151) from the Gene Expression Omnibus database by using bioinformatics analysis to study the molecular processes and hub genes involved in the thermal stress and bleaching responses of the coral Acropora palmata. The results suggest that thermal stress down-regulated the snoRNP genes, which led to a reduction of some ribosomal proteins, and then decreased biosynthesis, resulting in disruption of a series of biological processes such as the glyoxylate cycle and vitamin metabolic processes. Moreover, the coral cytoskeleton showed breakdown because the CCT7 gene was down-regulated and because of insufficient adenosine triphosphate production caused by the thermal stress. All these responses will destroy the P53 pathway and initiate apoptosis and ultimately necrosis. In addition, 107 differentially expressed genes were detected between the normal and bleached corals, indicating that snoRNPs, CCT7, RPL37, and RPS27A may be the hub genes responsible for thermal stress and bleaching responses. These genes can be used as new biomarkers to help solve the problem of coral bleaching.

Predation

> Bright, A. J., Cameron, C. M. & Miller, M. W. (2015). Enhanced susceptibility to predation in corals of compromised condition. *PeerJ*, 3, e1239. https://doi.org/10.7717/peerj.1239 (Bright et al. 2015)

The marine gastropod, Coralliophila abbreviata, is an obligate corallivore that causes substantial mortality in Caribbean Acropora spp. Considering the imperiled status of Acropora cervicornis and A. palmata, a better understanding of ecological interactions resulting in tissue loss may enable more effective conservation strategies. We examined differences in susceptibility of A. cervicornis to C. abbreviata predation based on coral tissue condition. Coral tissue condition was a strong determinant of snail prey choice, with snails preferring A. cervicornis fragments that were diseased or mechanically damaged over healthy fragments. In addition, snails always chose fragments undergoing active predation by another snail, while showing no preference for a non-feeding snail when compared with an undisturbed prey fragment. These results indicate that the condition of A. cervicornis prey influenced foraging behavior of C. abbreviata, creating a potential feedback that may exacerbate damage from predation in coral populations compromised by other types of disturbance.

Marulanda-Gómez, Á., López-Victoria, M. & Zea, S. (2017). Current status of coral takeover by an encrusting excavating sponge in a Caribbean reef. *Marine Ecology*, 38:e12379. https://doi.org/10.1111/maec.12379 (Marulanda-Gómez et al. 2017)

On Caribbean reefs, the excavating sponge Cliona tenuis opportunistically colonized dead skeletons of the elkhorn coral Acropora palmata after its massive die-off in the 1980s. Further C. tenuis population increase occurred by colonization of other coral species, causing coral tissue death through undermining of live tissue and lateral growth. To follow up on a previous (2001) characterization of the abundance and size structure of C. tenuis at Islas del Rosario (Colombia), these factors were again estimated in 2014, along with its substratum utilization. The fate of sponge individuals colonizing massive coral colonies marked in 2001–2004 was also followed. By 2014 C. tenuis was still disproportionally occupying dead A. palmata branches, but its abundance and density, and the cover of other benthic elements, had not significantly changed over the 13-year period, suggesting that a stasis has been reached. Cliona tenuis was thus initially favored in the 1980s, but substratum monopolization did not occur. From 2001 to 2014, small individuals increased in number and very large ones decreased, suggesting not only that new recruitment is occurring, but also that larger sponges are shrinking or fragmenting. Marked sponges continued killing corals over the first few years, but over longer times they retreated or died, allowing corals to resume upward growth. However, it could not be ascertained whether the sponge retreat was age-related or the result of some environmental effect. The apparent preference for recently dead clean coral by larvae of C. tenuis and its current dynamics of recruitment, growth, fragmentation and mortality have stabilized its space occupation at Islas del Rosario.

Rivera-Sosa, A., Muñiz-Castillo, A. I., McField, M. & Arias-González, J. E. (2018). Unusual "Knob-Like Chimney" Growth Forms on Acropora Species in the Caribbean. *Front. Mar. Sci.*, 5:41. https://doi.org/10.3389/fmars.2018.00041 (Rivera-Sosa et al. 2018)

This manuscript provides new insights on an unusual morphological plasticity growth form on Acropora spp. in the Caribbean. This abnormal knob-shaped growth is thought to be a progression from the damselfish "chimneys" that are commonly seen in coral-algal farms. However, the diameters of the observed knobs tend to be much larger on Acropora palmata, where they range from 1.37 to 5.44 cm in diameter, and they tend to be slightly smaller on A. prolifera, where they range from 1.1 to 2.72 cm in diameter. These knob-like chimney growths can affect entire colonies. The knobs are mostly covered with live tissue, while some knobs compete with turf algae. We hypothesize that these growths may be linked to stress from multiple predation and environmental conditions. Local stressors could synergistically influence the regeneration of scarred tissue and skeleton that result from predatory lesions, possibly leading to the formation of the knobs. Therefore, we provide preliminary data from a shallow reef site in coastal Honduras located within the Mesoamerican region where we found the knobs. To the best of our knowledge, the conditions that drive the occurrence of these unusual "knob-like chimneys" on Acropora spp. have not been previously assessed. Thus, we propose a series of guidelines to research the coral morphological plasticity that may be linked to this knob-like chimney phenomenon.

Restoration and Conservation Methods

Chamberland, V. F., Vermeij, M. J. A., Brittsan, M., Carl, M., Schick, M., Snowden, S., . . . Petersen, D. (2015). Restoration of critically endangered elkhorn coral (Acropora palmata) populations using larvae reared from wild-caught gametes. *Global Ecology and Conservation*, 4, 526–537. https://doi.org/10.1016/j.gecco.2015.10.005 (Chamberland et al. 2015)

Elkhorn coral (Acropora palmata) populations provide important ecological functions on shallow Caribbean reefs, many of which were lost when a disease reduced their abundance by more than 95% beginning in the mid-1970s. Since then, a lack of significant recovery has prompted rehabilitation initiatives throughout the Caribbean. Here, we report the first successful outplanting and long-term survival of A. palmata settlers reared from gametes collected in the field. A. palmata larvae were settled on clay substrates (substrate units) and either outplanted on the reef two weeks after settlement or kept in a land-based nursery. After 2.5 years, the survival rate of A. palmata settlers outplanted two weeks after settlement was 6.8 times higher (3.4%) than that of settlers kept in a land-based nursery (0.5%). Furthermore, 32% of the substrate units on the reef still harbored one or more well-developed recruit compared to 3% for substrate units kept in the nursery. In addition to increasing survival, outplanting A. palmata settlers shortly after settlement reduced the costs to produce at least one 2.5-year-old A. palmata individual from $325 to $13 USD. Thus, this study not only highlights the first successful long-term rearing of this critically endangered coral species, but also shows that early outplanting of sexually reared coral settlers can be more cost-effective than the traditional approach of nursery rearing for restoration efforts aimed at rehabilitating coral populations.

Cummings, K., Zuke, A., Stasio, B. D. & Krumholz, J. (2015). Coral Growth Assessment on an Established Artificial Reef in Antigua. *Ecological Rest.*, 33(1), 90–95. https://doi.org/10.3368/er.33.1.90 (Cummings et al. 2015)

Anthropogenic pressure on coral reef ecosystems has increased the need for effective restoration and rehabilitation as a management tool. However, quantifying the success of restoration projects can be difficult, and adequate monitoring data are scarce. This study compared growth rates over a six-year period of three Caribbean coral species, staghorn coral (Acropora cervicornis), elkhorn coral (Acropora palmata), and thick finger coral (Porites porites), transplanted on an artificial reef off Maiden Island, Antigua, to literature values for the same species growing on naturally formed reefs in the Caribbean region. The average growth rate of staghorn coral was considerably lower than growth rates reported in the literature, while elkhorn and finger corals showed growth rates similar to literature values. The observed inter- and intraspecific differences may be caused by species-specific growth requirements and/or restoration site conditions, factors that should be taken into account when planning future projects involving coral transplant or rescue. This study also determined the analytical precision of a ‘low tech’ monitoring method using a basic underwater digital camera and the software program ImageJ to measure growth rates of corals. Measurement error between volunteer analysts receiving only minimal training was shown to be very small, ranging from 0.37–1.40% depending on the coral species. This confirms the validity of this basic technique, particularly in cases where data are sparse and resources for monitoring are extremely limited.

Devlin-Durante, M. K. & Baums, I. B. (2017). Genome-wide survey of single-nucleotide polymorphisms reveals fine-scale population structure and signs of selection in the threatened Caribbean elkhorn coral, Acropora palmata. *PeerJ*, 5:e4077. https://doi.org/10.7717/peerj.4077 (Devlin-Durante and Baums 2017)

The advent of next-generation sequencing tools has made it possible to conduct fine-scale surveys of population differentiation and genome-wide scans for signatures of selection in non-model organisms. Such surveys are of particular importance in sharply declining coral species, since knowledge of population boundaries and signs of local adaptation can inform restoration and conservation efforts. Here, we use genome-wide surveys of single-nucleotide polymorphisms in the threatened Caribbean elkhorn coral, Acropora palmata, to reveal fine-scale population structure and infer the major barrier to gene flow that separates the eastern and western Caribbean populations between the Bahamas and Puerto Rico. The exact location of this break had been subject to discussion because two previous studies based on microsatellite data had come to differing conclusions. We investigate this contradiction by analyzing an extended set of 11 microsatellite markers including the five previously employed and discovered that one of the original microsatellite loci is apparently under selection. Exclusion of this locus reconciles the results from the SNP and the microsatellite datasets. Scans for outlier loci in the SNP data detected 13 candidate loci under positive selection, however there was no correlation between available environmental parameters and genetic distance. Together, these results suggest that reef restoration efforts should use local sources and utilize existing functional variation among geographic regions in ex situ crossing experiments to improve stress resistance of this species.

Forrester, G. E., Ferguson, M. A., O'Connell-Rodwell, C. E. & Jarecki, L. L. (2014). Long-term survival and colony growth of Acropora palmata fragments transplanted by volunteers for restoration. *Aquatic Conserv: Mar. Freshw. Ecosyst.*, 24(1), 81–91. https://doi.org/10.1002/aqc.2374 (Forrester et al. 2014)

Many branching corals are fragmented by storms, which can serve as a mechanism of asexual reproduction for species that are able to reattach themselves to the substratum and form new colonies. Fragments can also be manually reattached as a means of reef restoration. The growth and survival of 832 fragments of Elkhorn coral, Acropora palmata, that were transplanted for a restoration project in the British Virgin Islands was modelled. Mortality was higher in the first year after transplanting than in subsequent years, perhaps reflecting stress from handling or failure of the attachment method. Survival also varied with the year of transplantation (from 2005–2011), and was lowest in years with major storms (2007 and 2010). Fragment survival increased with increasing initial size, with the largest fragments (surface area roughly 1000 cm2) faring substantially better than the smallest (roughly 10 cm2) and average sized fragments (roughly 100 cm2). Colony size (surface area of live tissue) tended to decrease slightly in the first 3 months after being reattached, presumably due to stress from transplanting. Subsequently, the surface area of surviving colonies tended to progressively increase over time, with fragments typically reaching 3000 cm2 after 7 years. Colony growth was, however, extremely variable and largely independent of initial colony size. Despite initial reductions in growth and survival due to transplanting, long-term survival of transplanted fragments was roughly comparable with that of natural colonies. Transplanting fragments is thus a promising tool for grass-roots restoration projects.

Pausch, R. E., Williams, D. E. & Miller, M. W. (2018). Impacts of fragment genotype, habitat, and size on outplanted elkhorn coral success under thermal stress. *Marine Ecology Progress Series*, 592, 109–117. https://doi.org/10.3354/meps12488 (Pausch et al. 2018)

Active coral restoration through coral 'gardening' aims to remediate some of the drastic coral cover lost on Caribbean reefs, with increasing attention to the imperiled, iconic foundation species elkhorn coral Acropora palmata. We documented 2 experiments quantifying effects of A. palmata outplant characteristics and habitat on outplant success. Two thermal stress events (summer 2014 and 2015) occurred while the experiments were underway and thus lend insight into environmental interactions and coral restoration outcomes under projected thermal regimes. In the first experiment comparing 2 size classes of a single genotype, smaller fragments produced significantly more live tissue area, experienced less bleaching, and demonstrated equal survivorship compared to larger fragments. The second experiment compared 4 genotypes outplanted to both fore reef and mid-channel patch reef habitats. Genotypes varied significantly in survivorship, bleaching severity, and net change in size, with one (CN2g) performing well in all 3 metrics, and another (SLg) exhibiting poor survivorship, the most bleaching, and smaller changes in size. Overall, bleaching was less severe and survivorship less varied between genotypes in fore reef versus patch reef habitats. Fragments returned to the site of genotype origin did not consistently outperform 'foreign' genotypes from a different habitat type. Recognizing unique attributes associated with size and specific genotypes may improve the efficacy of active coral restoration in the face of future climate scenarios.

Viehman, T.S., M. Nemeth, S.H. Groves, C.A. Buckel, S. Griffin, D. Field, T.D. Moore, J. Moore. 2020. Coral assessment and restoration in the U.S. Caribbean after 2017 hurricanes. NOAA National Ocean Service, National Centers for Coastal Ocean Science. NOAA Technical Memorandum 278. Silver Spring, MD. 64 pp. doi: 10.25923/7r0b-wc52. Data archive doi:10.25921/a1c4-bg06 for NCEI accession 0221189. (Viehman et al. 2020)

In September 2017, major Hurricanes Irma and Maria impacted Puerto Rico and the U.S. Virgin Islands (USVI) and caused considerable damage to shallow coral reefs. In February 2018, at the request of the Puerto Rico Department of Natural and Environmental Resources (PRDNER), the Federal Emergency Management Agency (FEMA) assigned the National Oceanic and Atmospheric Administration (NOAA) to conduct coral reef assessments and emergency coral stabilization activities in Puerto Rico as part of the Hurricane Maria response under the National Disaster Recovery Framework Natural and Cultural Resources Recovery Support Function. A total of 414,354 m2 of coral reef area, including over 87,000 corals, were assessed at 150 sites across Puerto Rico between February 27 and May 7, 2018. More than 8,700 corals were reattached at 35 reef sites in Puerto Rico. Prior to the FEMA effort, coral stabilization efforts were supported by NOAA and the National Fish and Wildlife Foundation (NFWF) in Puerto Rico and St. Thomas, USVI and reattached more than 7,500 corals at 28 additional sites. In total, coral stabilization efforts in PR and the USVI reattached 16,000 corals at 63 sites. Hurricane damage of destabilized, broken, and loose corals was observed at approximately 12% of shallow reefs assessed in Puerto Rico. Damage varied between geographic regions, sites, and species. The most severely impacted coral species include four listed as Threatened under the Endangered Species Act (ESA): Dendrogyra cylindrus (pillar coral), Acropora palmata (elkhorn coral), Orbicella annularis (lobed star coral), and

Acropora cervicornis (staghorn coral). Considerable variability was observed between assessment sites in the extent of wave impacts to corals and reefs, likely due to reef exposure to the dominant wave energy and coral species, abundance, size, and morphology.

> Williams, D. E., Miller, M. W., Bright, A. J. & Cameron, C. M. (2014). Removal of corallivorous snails as a proactive tool for the conservation of acroporid corals. *PeerJ*, 2, e680. https://doi.org/10.7717/peerj.680 (Williams et al. 2014)

Corallivorous snail feeding is a common source of tissue loss for the threatened coral, Acropora palmata, accounting for roughly one-quarter of tissue loss in monitored study plots over seven years. In contrast with larger threats such as bleaching, disease, or storms, corallivory by Coralliophila abbreviata is one of the few direct sources of partial mortality that may be locally managed. We conducted a field experiment to explore the effectiveness and feasibility of snail removal. Long-term monitoring plots on six reefs in the upper Florida Keys were assigned to one of three removal treatments: (1) removal from A. palmata only, (2) removal from all host coral species, or (3) no-removal controls. During the initial removal in June 2011, 436 snails were removed from twelve 150 m2 plots. Snails were removed three additional times during a seven month "removal phase", then counted at five surveys over the next 19 months to track recolonization. At the conclusion, snails were collected, measured and sexed. Before-After-Control-Impact analysis revealed that both snail abundance and feeding scar prevalence were reduced in removal treatments compared to the control, but there was no difference between removal treatments. Recolonization by snails to baseline abundance is estimated to be 3.7 years and did not differ between removal treatments. Recolonization rate was significantly correlated with baseline snail abundance. Maximum snail size decreased from 47.0 mm to 34.6 mm in the removal treatments. The effort required to remove snails from A. palmata was 30 diver minutes per 150 m2 plot, compared with 51 min to remove snails from all host corals. Since there was no additional benefit observed with removing snails from all host species, removals can be more efficiently focused on only A. palmata colonies and in areas where C. abbreviata abundance is high, to effectively conserve A. palmata in targeted areas.

PILLAR CORAL (DENDROGYRA CYLINDRUS)

Biology and Life History Characteristics

> Cruz-Ortega, I., Cabral-Tena, R. A., Carpizo-Ituarte, E., Grosso-Becerra, V. & Carricart-Ganivet, J. P. (2020). Sensitivity of calcification to thermal history differs between sexes in the gonochoric reef-building corals Dichocoenia stokesi and Dendrogyra cylindrus. *Mar Biol*, 167, 101. https://doi.org/10.1007/s00227-020-03713-x (Cruz-Ortega et al. 2020)

Calcification and sexual reproduction in corals are energy consuming metabolic processes. In symbiotic corals, calcification is a daily process and depends on the ability of the coral colony to produce energy, through the photosynthesis of symbiotic algae or heterotrophy, while sexual reproduction in several broadcast spawning species is carried out once a year and depends on the amount of energy stored as lipids within the coral tissue. Calcification and reproduction are influenced by environmental parameters, such as light irradiance and sea surface temperature (SST). Reproduction may be inhibited by thermal

stress and coral calcification rate decreases as SST increases above a certain threshold. However, it is unknown if there is a sex-related response of calcification rate to thermal history. Here, we test the differential sensitivities of calcification rates to thermal history by examining its recent historical variation in females and males of two common Caribbean gonochoric reef-building coral species, Dichocoenia stokesi and Dendrogyra cylindrus. Colony sex was determined by histological techniques, and sclerochronology was measured using densitometry from digitized X-ray images. Calcification rates were higher in male colonies than in females of both species, as previously reported in other gonochoric corals, and can be explained in terms of disparity in energy availability for calcification among sexes due to the differential energetic costs of eggs and sperm. Calcification rates of both species were negatively related to SST when data of both sexes were pooled together. When data were analyzed separately by sex, only female colonies, of both species, showed a significant dependence of calcification rate to SST. The fact that SST differentially affects coral calcification in female and male colonies, will have repercussions on population dynamics of the studied coral species in a global warming scenario.

Lewis, C., Neely, K. & Rodriguez-Lanetty, M. (2019). Recurring Episodes of Thermal Stress Shift the Balance From a Dominant Host-Specialist to a Background Host-Generalist Zooxanthella in the Threatened Pillar Coral, Dendrogyra cylindrus. *Front. Mar.*, *Sci.* 6:5. https://doi.org/10.3389/fmars.2019.00005 (Lewis et al. 2019)

Most scleractinian corals form obligate symbioses with photosynthetic dinoflagellates (family Symbiodiniaceae), which provide differential tolerances to their host. Previously, research has focused on the influence of symbiont composition and the dynamic processes of symbiont repopulation during single episodes of hyperthermal events, followed by years of less-stressful conditions. In contrast, this study characterized for the first time, the role of Symbiodiniaceae species changes in response to annually recurring hyperthermal events, a scenario soon expected to become the norm. Consecutive hyperthermal events during summer 2014 and 2015 along the Florida Reef Tract offered a unique opportunity to study bleaching susceptibility and recovery under recurrent annual hyperthermal scenarios. We utilized Illumina amplicon sequencing of the chloroplast 23S DNA region to assess with fine resolution the Symbiodiniaceae diversity associated with pillar coral, Dendrogyra cylindrus. Our findings show diverse assemblages of Symbiodiniaceae species and that some cryptic members are not transient associates but persistent and ecologically relevant, especially during recurrent annual warming events. This was evidenced by changes in relative abundance from the typically dominant host-specialist endosymbiont, Breviolum dendrogyrum, to B. meandrinium a host-generalist species common to corals in the family Meandrinidae but occurs at background densities in most coral colonies of D. cylindrus. The rise in abundance of B. meandrinium associated strongly with bleaching resistance in the coral host during two consecutive hyperthermal events. In some cases, host-compatible background symbionts can rapidly increase in abundance during episodes of stress and may impart physiological resilience to rapid environmental change; and thus, represents a potentially important ecological process by which symbiotic corals acclimatize to changing ocean conditions.

Marhaver, K. L., Vermeij, M. J. & Medina, M. M. (2015). Reproductive natural history and successful juvenile propagation of the threatened Caribbean Pillar Coral Dendrogyra cylindrus.

BMC Ecol, 15, 1–12.
https://doi.org/10.1186/s12898-015-0039-7 (Marhaver et al. 2015)

The Caribbean pillar coral Dendrogyra cylindrus was recently listed as a threatened species under the United States Endangered Species Act. One of the major threats to this species is its low, virtually undetectable recruitment rate. To our knowledge, sexually-produced recruits have never been found in over 30 years of surveys of Caribbean reefs. Until recently, the reproductive behavior of D. cylindrus was uncharacterized, limiting efforts to study its early life history, identify population bottlenecks, and conduct outplanting projects with sexually-produced offspring. In Curaçao, we observed the spawning behavior of this species over three years and five lunar cycles. We collected gametes from spawning individuals on three occasions and attempted to rear larvae and primary polyp settlers. Here we describe successful fertilization methods for D. cylindrus and we document rapid embryonic development. We describe the successful propagation of embryos to the swimming larvae stage, the first settlement of larvae in the laboratory, and the survival of primary polyp settlers for over seven months. We show that spawning times are highly predictable from year to year relative to the lunar cycle and local sunset times. We use colony-level data to confirm that males begin spawning before females. We also provide the first reports of split-spawning across months in this species. Together, our findings of consistent spawning times, split-spawning, rapid embryonic development, and remarkable robustness of larvae and settlers now enable expanded research on the early life history and settlement ecology of D. cylindrus. This will help biologists to identify the population bottlenecks in nature that underlie low recruitment rates. Further, the settlement of D. cylindrus larvae in the laboratory now makes out-planting for restoration more feasible. Asynchronous spawning times and rapid embryonic development may have important consequences for population biology, connectivity, and management, by affecting fertilization dynamics and larval dispersal distances. We argue that a precautionary approach to conservation is warranted, given this species' peculiar life history traits and still-unresolved population structure. Overall, the natural history and husbandry contributions presented here should facilitate accelerated research and conservation of this threatened coral.

Neely, K. L., Lewis, C., Chan, A. N. & Baums, I. B. (2018). Hermaphroditic spawning by the gonochoric pillar coral Dendrogyra cylindrus. *Coral Reefs; Heidelberg*, 37(4), 1087–1092.
https://doi.org/10.1007/s00338-018-1730-x (Neely et al. 2018)

Scleractinian corals typically reproduce sexually as either gonochoric (separate male and female) or hermaphroditic (producing both eggs and sperm) colonies. The Caribbean pillar coral Dendrogyra cylindrus has been classified as gonochoric, but multi-year spawning observations at a Florida Keys site revealed incidences of hermaphroditism. Separate clonal colonies (ramets) of a single genet released either male or female gametes. Furthermore, 22% of observed ramets produced both eggs and sperm within different regions of a single colony. Over multiple years, one ramet switched from female to hermaphrodite, one from male to hermaphrodite, and one from hermaphrodite to male. Proposed evolutionary mechanisms include size- or age-based energy allocation, environmental energy allocation, or chemically induced change in a single-sex region. Because of the low population density of D. cylindrus in the Florida Keys, sexual partners are scarce, and hermaphroditism may be a strategy to yield higher rates of successful sexual reproduction. The findings also have implications for future restoration efforts aiming to strategically outplant individuals to maximize in situ fertilization.

Abundance, Population, and Demographic Features and Trends

Bernal-Sotelo, K., Acosta, A. & Cortés, J. (2019). Decadal Change in the Population of Dendrogyra cylindrus (Scleractinia: Meandrinidae) in Old Providence and St. Catalina Islands, Colombian Caribbean. *Front. Mar. Sci.*, 5:513. https://doi.org/10.3389/fmars.2018.00513 (Bernal-Sotelo et al. 2019)

The IUCN considers the stony coral Dendrogyra cylindrus as vulnerable. However, there is insufficient information on its population structure and dynamics, conservation status, or extinction risk and population decreases have been inferred from observations of habitat degradation. In 2002 and 2012, surveys using manta tows, circular plots and satellite images were performed in Old Providence and Santa Catalina Islands (Seaflower Biosphere Reserve) to determine changes in the condition and structure of a local population of D. cylindrus and its habitat. Size-frequency histograms were asymmetric and leptokurtic, showing positive distribution induced by colony fragmentation, which is indicative of reef degradation. Signs of degradation were more evident in 2012, when partial mortality of living tissue in the parent colony yielded 96.6% of the asexually produced fragments. Most of the fragments were from larger colonies (≥115cm), which exhibited the highest partial and total mortality (>50%). Three of the four benthic habitats used by the species in 2002 were seen in 2012, but with reduced areas. The results suggest that the reduction of living tissue, the dominance of colonies produced asexually, and reduced size of fragments limit population growth and species viability in an unfavorable and changing habitat within this marine protected area (MPA) of the southwestern Caribbean. In the west of the reef complex of Old Providence, a synergy of multiple stressors could cause the habitat degradation and the fragmentation of colonies, limiting the potential recovery of the species and therefore the ability to create a healthy, genetically diverse and resilient population. Thus, these stressors must be minimized to prevent local extinction. Monitoring the population trends and recording sexual recruitment continues to be vital to understand the larvae's habitat selection and determine whether these habitats are suitable for the survival of coral recruits. Other stressors to be monitored include anchor damage, diseases and bleaching. We recommend the MPA management program to include specific plans of conservation, recovery and restoration for coral reef builders species like D. cylindrus.

Chan, A. N., Lewis, C. L., Neely, K. L. & Baums, I. B. (2019). Fallen Pillars: The Past, Present, and Future Population Dynamics of a Rare, Specialist Coral–Algal Symbiosis. *Front. Mar. Sci.*, 6. https://doi.org/10.3389/fmars.2019.00218 (Chan et al. 2019)

With ongoing changes in climate, rare and ecologically specialized species are at increased risk of extinction. In sessile foundation fauna that reproduce asexually via fragmentation of existing colonies, the number of colonies does not reflect the number of genets and thus can obscure genotypic diversity. Colonies that are the product of fragmentation are not visually distinguishable from colonies that stem from sexual recruits. For this reason, molecular markers are necessary to assess genotypic variation and population structure in clonal organisms such as reef-building corals and their endosymbiotic dinoflagellates. For the rare Caribbean pillar coral, Dendrogyra cylindrus, and its endosymbiotic dinoflagellate, Breviolum dendrogyrum, we use de novo microsatellite markers to infer past demographic changes, describe modern population structure, and quantify the frequency of asexual reproduction. Our analyses show that D. cylindrus comprises three distinct populations across the Greater Caribbean

whereas the symbiont could be differentiated into four populations, indicating barriers to gene flow differ between host and symbiont. In Florida, host and symbiont populations reproduced mainly asexually, yielding lower genotypic diversity than predicted from census size. When multiple coral ramets were present, they often associated with the same clonal strain of B. dendrogyrum, pointing to the high fidelity of this relationship. Models of past demographic events revealed no evidence for historical changes in population sizes, consistent with the paleontological record of D. cylindrus indicating it has been rare for hundreds of thousands of years. The most recent global thermal stress event triggered a severe disease outbreak among D. cylindrus in Florida, resulting in a severe population decline. Projections indicate a high likelihood that this species will become extinct in the Northern Greater Caribbean within a few decades. The ecosystem consequences of losing rare coral species and their symbionts with increasingly frequent extreme warming events are not known but require urgent study.

Threat Assessment

> Lewis, C. L., Neely, K. L., Richardson, L. L. & Rodriguez-Lanetty, M. (2017). Temporal dynamics of black band disease affecting pillar coral (Dendrogyra cylindrus) following two consecutive hyperthermal events on the Florida Reef Tract. *Coral Reefs*, 36, 427–431. https://doi.org/10.1007/s00338-017-1545-1 (Lewis et al. 2017)

Black band disease (BBD) affects many coral species worldwide and is considered a major contributor to the decline of reef-building coral. On the Florida Reef Tract BBD is most prevalent during summer and early fall when water temperatures exceed 29 °C. BBD is rarely reported in pillar coral (Dendrogyra cylindrus) throughout the Caribbean, and here we document for the first time the appearance of the disease in this species on Florida reefs. The highest monthly BBD prevalence in the D. cylindrus population were 4.7% in 2014 and 6.8% in 2015. In each year, BBD appeared immediately following a hyperthermal bleaching event, which raises concern as hyperthermal seawater anomalies become more frequent.

> Neely, K. 2018. Surveying the Florida Keys Southern Coral Disease Boundary. Florida DEP, Miami, FL. Pp 1-15 (Neely 2018)

Since 2014, multi-year, multi-species disease outbreak has progressed geographically along the Florida Reef Tract from an origin near Virginia Key. From fall 2017 to spring 2018, 134 reef sites were surveyed to identify the geographic boundary of the disease as well as provide information on rates of progression, cross-reef prevalence differences, and differences in responses of impacted species. Roving diver surveys were conducted during two reef-tract wide assessments in fall 2017 and spring 2018, and roving diver and belt transect surveys were conducted in a targeted effort near the southern disease boundary in winter 2017-18 between Long Key and Marathon. Surveys confirmed prevalence of the disease on 15 coral species, including the primary reef builders and five ESA-listed species. Disease was conspicuously absent on some other species, including the *Acropora* and *Porites* spp. Disease hotspots and geographic differences in disease prevalence showed that tissue loss begins on different species at different times. Broadly, the brain corals (particularly *Meandrina meandrites*) are the first to show tissue loss. Boulder coral infections generally appear shortly thereafter, with *Montastraea cavernosa* in particular often a later species to exhibit tissue loss.

Rosales, S. M., Clark, A. S., Huebner, L. K., Ruzicka, R. R. & Muller, E. M. (2020). Rhodobacterales and Rhizobiales Are Associated With Stony Coral Tissue Loss Disease and Its Suspected Sources of Transmission. *Front. Microbiol.*, 11:681. https://doi.org/10.3389/fmicb.2020.00681 (Rosales et al. 2020)

In 2014, Stony Coral Tissue Loss Disease (SCTLD) was detected off the coast of Miami, Florida, USA, and continues to persist. Along the Florida Reef Tract (FRT), coral reefs have previously succumbed to disease outbreaks. However, SCTLD can have up to a 99% mortality rate and has affected 23 species of scleractinian corals. In addition to its high mortality rate, its fast spread through the FRT has led to the regional near-extinction of at least one coral species, Dendrogya cylindrus. Although the disease has persisted for over 5 years, the etiology of SCTLD is unknown. As a means to characterize potential SCTLD pathogens, we collected tissue samples from four affected coral species: Stephanocoenia intersepta, Diploria labyrinthiformis, Dichocoenia stokesii, and Meandrina meandrites. Tissue samples were from apparently healthy (AH) corals, and unaffected tissue (DU) and lesion tissue (DL) on diseased corals. Samples were collected from three zones: (1) Lower Florida Keys (ahead of the SCTLD disease boundary, "vulnerable zone"), (2) Upper Florida Keys (post-SCTLD outbreak, "endemic zone"), and (3) Middle Florida Keys (SCTLD was active and prevalent, "epidemic zone"). From each zone, sediment and water samples were also collected to identify potential reservoirs of the SCTLD pathogen. We used 16S rRNA gene amplicon high-throughput sequencing methods to characterize the microbiomes of the coral, water, and sediment samples. We identified a relatively higher abundance of the bacteria orders Rhodobacterales and Rhizobiales in DL compared to AH and DU tissue. Also, our results showed relatively higher abundances of Rhodobacterales in water from the endemic and epidemic zones compared to the vulnerable zone. However, potential Rhodobacterales and Rhizobiales pathogens identified from DL were detected in sediment samples, but not in water samples. Our data indicate that Rhodobacterales and Rhizobiales may play a role in SCTLD and that sediment may be a disease reservoir.

Rough Cactus Coral (Mycetophyllia ferox)

Genetic Assessment

Wirshing, H. H. & Baker, A. C. (2014). Molecular evolution of calcification genes in morphologically similar but phylogenetically unrelated scleractinian corals. *Molecular Phylogenetics and Evolution*, 77, 281–295. https://doi.org/10.1016/j.ympev.2014.04.015 (Wirshing and Baker 2014)

Molecular phylogenies of scleractinian corals often fail to agree with traditional phylogenies derived from morphological characters. These discrepancies are generally attributed to non-homologous or morphologically plastic characters used in taxonomic descriptions. Consequently, morphological convergence of coral skeletons among phylogenetically unrelated groups is considered to be the major evolutionary process confounding molecular and morphological hypotheses. A strategy that may help identify cases of convergence and/or diversification in coral morphology is to compare phylogenies of existing "neutral" genetic markers used to estimate genealogic phylogenetic history with phylogenies

generated from non-neutral genes involved in calcification (biomineralization). We tested the hypothesis that differences among calcification gene phylogenies with respect to the "neutral" trees may represent convergent or divergent functional strategies among calcification gene proteins that may correlate to aspects of coral skeletal morphology. Partial sequences of two nuclear genes previously determined to be involved in the calcification process in corals, "Cnidaria-III" membrane-bound/secreted α-carbonic anhydrase (CIII-MBSα-CA) and bone morphogenic protein (BMP) 2/4, were PCR-amplified, cloned and sequenced from 31 scleractinian coral species in 26 genera and 9 families. For comparison, "neutral" gene phylogenies were generated from sequences from two protein-coding "non-calcification" genes, one nuclear (β-tubulin) and one mitochondrial (cytochrome b), from the same individuals. Cloned CIII-MBSα-CA sequences were found to be non-neutral, and phylogenetic analyses revealed CIII-MBSα-CAs to exhibit a complex evolutionary history with clones distributed between at least 2 putative gene copies. However, for several coral taxa only one gene copy was recovered. With CIII-MBSα-CA, several recovered clades grouped taxa that differed from the "non-calcification" loci. In some cases, these taxa shared aspects of their skeletal morphology (i.e., convergence or diversification relative to the "non-calcification" loci), but in other cases they did not. For example, the "non-calcification" loci recovered Atlantic and Pacific mussids as separate evolutionary lineages, whereas with CIII-MBSα-CA, clones of two species of Atlantic mussids (Isophyllia sinuosa and Mycetophyllia sp.) and two species of Pacific mussids (Acanthastrea echinata and Lobophyllia hemprichii) were united in a distinct clade (except for one individual of Mycetophyllia). However, this clade also contained other taxa which were not unambiguously correlated with morphological features. BMP2/4 also contained clones that likely represent different gene copies. However, many of the sequences showed no significant deviation from neutrality, and reconstructed phylogenies were similar to the "non-calcification" tree topologies with a few exceptions. Although individual calcification genes are unlikely to precisely explain the diverse morphological features exhibited by scleractinian corals, this study demonstrates an approach for identifying cases where morphological taxonomy may have been misled by convergent and/or divergent molecular evolutionary processes in corals. Studies such as this may help illuminate our understanding of the likely complex evolution of genes involved in the calcification process, and enhance our knowledge of the natural history and biodiversity within this central ecological group.

Threat Assessment

Neely, K. 2018. Surveying the Florida Keys Southern Coral Disease Boundary. Florida DEP, Miami, FL. Pp 1-15 (Neely 2018)

Since 2014, multi-year, multi-species disease outbreak has progressed geographically along the Florida Reef Tract from an origin near Virginia Key. From fall 2017 to spring 2018, 134 reef sites were surveyed to identify the geographic boundary of the disease as well as provide information on rates of progression, cross-reef prevalence differences, and differences in responses of impacted species. Roving diver surveys were conducted during two reef-tract wide assessments in fall 2017 and spring 2018, and roving diver and belt transect surveys were conducted in a targeted effort near the southern disease boundary in winter 2017-18 between Long Key and Marathon. Surveys confirmed prevalence of the disease on 15 coral species, including the primary reef builders and five ESA-listed species. Disease was conspicuously absent on some other species, including the *Acropora* and *Porites* spp. Disease hotspots and geographic differences in disease prevalence showed that tissue loss begins on different species at different times.

Broadly, the brain corals (particularly *Meandrina meandrites*) are the first to show tissue loss. Boulder coral infections generally appear shortly thereafter, with *Montastraea cavernosa* in particular often a later species to exhibit tissue loss.

LOBED STAR CORAL (ORBICELLA ANNULARIS)

Biology and Life History Characteristics

> Cetz-Navarro, N. P., Carpizo-Ituarte, E. J., Espinoza-Avalos, J. & Chee-Barragán, G. (2015). The Effect of Filamentous Turf Algal Removal on the Development of Gametes of the Coral Orbicella annularis. *PLOS ONE* 10(2), e0117936. https://doi.org/10.1371/journal.pone.0117936 (Cetz-Navarro et al. 2015)

Macroalgae and filamentous turf algae (FTA) are abundant on degraded coral reefs, and the reproductive responses of corals may indicate sub-lethal stress under these conditions. The percentage of gametogenic stages (PGS) and the maximum diameter of eggs (MDE; or egg size) of Orbicella annularis were used to evaluate the effect of long- (7–10 months) and short-term (2.5 months) FTA removal (treatments T1 and T2, respectively) at both the beginning (May) and the end (August) of gametogenesis. Ramets (individual lobes of a colony) surrounded by FTA (T3) or crustose coralline algae (CCA; T4) were used as controls. The removal of FTA enhanced the development of gametes (i.e., a larger and higher percentage of mature gametes (PMG)) of O. annularis for T1 vs. T3 ramets in May and T1 and T2 vs. T3 ramets in August. Similar values of PGS and MDE between gametes from T3 and T4 in both May and August were unexpected because a previous study had shown that the same ramets of T4 (with higher tissue thickness, chlorophyll a cm-2 and zooxanthellae density and lower mitotic index values) were less stressed than ramets of T3. Evaluating coral stress through reproduction can reveal more sensitive responses than other biological parameters; within reproductive metrics, PGS can be a better stress indicator than egg size. The presence of turf algae strongly impacted the development of gametes and egg size (e.g., PMG in ramets with FTA removal increased almost twofold in comparison with ramets surrounded by FTA in August), most likely exerting negative chronic effects in the long run due to the ubiquity and permanence of turf algae in the Caribbean. These algae can be considered a stressor that affects coral sexual reproduction. Although the effects of turf algae on O. annularis are apparently less severe than those of other stressors, the future of this species is uncertain because of the combined impacts of these effects, the decline of O. annularis populations and the almost complete lack of recruitment.

> Edmunds, P. J., Pochon, X., Levitan, D.R., Yost, D.M., Belcaid, M., Putnam, H.M., & Gates, R.D. (2014). Long-term changes in Symbiodinium communities in Orbicella annularis in St. John, US Virgin Islands. *Marine Ecology Progress Series,* **506**, 129–144. https://doi.org/10.3354/meps10808 (Edmunds et al. 2014)

Efforts to monitor coral reefs rarely combine ecological and genetic tools to provide insight into the processes driving patterns of change. We focused on a coral reef at 14 m depth in St. John, US Virgin Islands, and used both sets of tools to examine 12 colonies of Orbicella (formerly Montastraea) annularis in 2 photoquadrats that were monitored for 16 yr and sampled genetically at the start and end of the study. Coral cover and colony growth were assessed annually, microsatellites were used to genetically

identify coral hosts in 2010, and their Symbiodinium were genotyped using chloroplastic 23S (cloning) and nuclear ITS2 (cloning and pyrosequencing) in 1994 and 2010. Coral cover declined from 40 to 28% between 1994 and 2010, and 3 of the 12 sampled colonies increased in size, while 9 decreased in size. The relative abundance of Symbiodinium clades varied among corals over time, and patterns of change differed between photoquadrats but not among host genotypes. Symbiodinium communities in 8 corals in 1 photoquadrat differed among colonies and changed over time, with a trend towards reduced abundance of clade C and increased abundance of clade B. Symbiodinium communities in 4 corals in the second photoquadrat were similar among colonies, dominated by clade C, and remained relatively constant in clade composition over time. Based on an analysis that sampled only a small number of corals, but is unique in the long temporal scale and the combination of techniques employed, this study demonstrates that the processes underlying shifts in coral cover are complex and difficult to predict. Meter-scale variation in reef microhabitats affected Symbiodinium communities in O. annularis, and host genotype coupled with variation in Symbiodinium communities appeared to mediate colony success.

Kennedy, E. V., Foster, N. L., Mumby, P. J. & Stevens, J. R. (2015). Widespread prevalence of cryptic Symbiodinium D in the key Caribbean reef builder, Orbicella annularis. *Coral Reefs; Heidelberg*, **34**, 519–531. https://doi.org/10.1007/s00338-015-1264-4 (Kennedy et al. 2015)

Symbiodinium D, a relatively rare clade of algal endosymbiont with a global distribution, has attracted interest as some of its sub-cladal types induce increased thermal tolerance and associated trade-offs, including reduced growth rate in its coral hosts. Members of Symbiodinium D are increasingly reported to comprise low-abundance 'cryptic' (<10 %) proportions of mixed coral endosymbiont communities, with unknown ecological implications. Real-time PCR (RT-PCR) targeted to specific types is sufficiently sensitive to detect these background symbiont levels. In this study, RT-PCR was employed to screen 552 colonies of the key Caribbean reef builder Orbicella annularis sampled across a 5.4 million km^sup 2^ range for the presence of cryptic Symbiodinium 'D1' (i.e., the principal Caribbean ITS2 variants, D1 and D1-4). All but one out of 33 populations analysed were shown to host low abundances of Symbiodinium D1, with an average of >30 % of corals per site found to harbour the symbiont. When the same samples were analysed using the conventional screening technique, denaturing gradient gel electrophoresis, Symbiodinium D1 was only detected in 12 populations and appeared to be hosted by <12 % of colonies where present (in agreement with other reported low prevalence/absences in O. annularis). Cryptic Symbiodinium D1 showed a mainly uniform distribution across the wider Caribbean region, although significantly more Mesoamerican Barrier Reef corals hosted cryptic Symbiodinium D1 than might be expected by chance, possibly as a consequence of intense warming in the region in 1998. Widespread prevalence of thermally tolerant Symbiodinium in O. annularis may potentially reflect a capacity for the coral to temporarily respond to warming events through symbiont shuffling. However, association with reduced coral calcification means that the ubiquitous nature of Symbiodinium D1 in O. annularis populations is unlikely to prevent long-term declines in reef health, at a time when maintaining reef growth is vital to sustain reef ecosystem function. [PUBLICATION ABSTRACT] Erratum DOI: 10.1007/s00338-015-1264-4

Kennedy, E. V., Tonk, L., Foster, N.L., Chollett, I. Ortiz, J., Dove, S., . . . Stevens, J.R. (2016). Symbiodinium biogeography tracks environmental patterns rather than host genetics in a key Caribbean reef-builder, Orbicella annularis. *Proceedings of the Royal Society B: Biological Sciences*, 283(1842), 20161938. http://dx.doi.org/10.1098/rspb.2016.1938 (Kennedy et al. 2016)

The physiological performance of a reef-building coral is a combined outcome of both the coral host and its algal endosymbionts, Symbiodinium. While Orbicella annularis—a dominant reef-building coral in the Wider Caribbean—is known to be a flexible host in terms of the diversity of Symbiodinium types it can associate with, it is uncertain how this diversity varies across the Caribbean, and whether spatial variability in the symbiont community is related to either O. annularis genotype or environment. Here, we target the Symbiodinium-ITS2 gene to characterize and map dominant Symbiodinium hosted by O. annularis at an unprecedented spatial scale. We reveal northwest–southeast partitioning across the Caribbean, both in terms of the dominant symbiont taxa hosted and in assemblage diversity. Multivariate regression analyses incorporating a suite of environmental and genetic factors reveal that observed spatial patterns are predominantly explained by chronic thermal stress (summer temperatures) and are unrelated to host genotype. Furthermore, we were able to associate the presence of specific Symbiodinium types with local environmental drivers (for example, Symbiodinium C7 with areas experiencing cooler summers, B1j with nutrient loading and B17 with turbidity), associations that have not previously been described.

Kennedy, E. V., Tonk, L., Foster, N. L., Mumby, P. J. & Stevens, J. R. (2019). Temporal stability of Orbicella annularis symbioses: a case study in The Bahamas. *Bulletin of Marine Science*, 95, 289–304. https://doi.org/10.5343/bms.2018.0064 (Kennedy et al. 2019)

Orbicella annularis (Ellis and Solander, 1786), a key reef building species, is unusual among Caribbean corals in the flexibility it displays in its symbioses with dinoflagellates in the family Symbiodiniaceae. This variability has been documented at a range of spatial scales; from within and between colonies to scales spanning the entire species range. However, temporal variability in Symbiodiniaceae communities found within O. annularis colonies is not well understood. Evidence suggests that symbiont communities in this coral species fluctuate temporally in response to environmental stressors (sporadic changes in abundance and in community composition). In this study, we investigated temporal stability of symbiont communities in O. annularis at four sites in The Bahamas over a period spanning 6 yrs. While the dominant symbiont species, Breviolum minutum (LaJeunesse et al.) J. E. Parkinson & LaJeunesse (formerly ITS2-type B1), remained stable across four patch-reef study sites, finer resolution molecular techniques revealed inter-annual variability in the presence/absence of cryptic species Durusdinium trenchii (LaJeunesse) LaJeunesse (formerly ITS2-type D1a). Durusdinium trenchii is known to play a role in resistance to environmental stress and may have a protective effect under warm conditions. These results suggest that, while it might take an extreme environmental perturbation to trigger a long-term shift in the dominant symbiont, at background levels, less prevalent symbiont taxa are likely to be continually shuffling their relative abundances as they change in response to seasonal or environmental changes.

Pochon, X., Gates, R. D., Vik, D. & Edmunds, P. J. (2014). Molecular characterization of symbiotic algae (Symbiodinium spp.) in soritid foraminifera (Soritesorbiculus) and a scleractinian coral (Orbicella annularis) from St John, US Virgin Islands. *Mar Biol*, 161, 2307–2318.
https://doi.org/10.1007/s00227-014-2507-6 (Pochon et al. 2014)

The exchange of Symbiodinium symbionts among scleractinian and soritid hosts could facilitate acclimatization to changing conditions by establishing novel symbiotic unions better tuned to prevailing conditions. In this study, we compare the communities of Symbiodinium spp. in neighboring populations of Orbicella annularis and Sorites orbiculus from St. John, US Virgin Islands, using operational taxonomic unit (OTU) clustering of cloned internal transcribed spacer 2 (ITS-2) rDNA sequences. We tested for partitioning of Symbiodinium OTUs by host and depth within and between two sites to explore the potential for symbiont exchange between hosts and light-dependent microhabitat specialization. An apparent lack of overlap in Symbiodinium communities (13 OTUs representing 7 clades) hosted by O. annularis and S. orbiculus suggests that exchange among these hosts does not occur. A low number of novel clade G ITS-2 sequences were found in one O. annularis and one S. orbiculus. A phylogenetic analysis of these sequences revealed them to be sub-clade G2 Symbiodinium, which are most commonly hosted by excavating clionid sponges. A permutational MANOVA revealed within host differences in the partitioning of Symbiodinium OTUs by site but not depth. This finding highlights the potential roles of either dissimilar environmental conditions between sites, or at least partial separation between populations, in determining the types of Symbiodinium contained in different hosts on a spatial scale of a few kilometers.

Abundance, Population, and Demographic Features and Trends

Edmunds, P. J. (2015). A quarter-century demographic analysis of the Caribbean coral, Orbicella annularis, and projections of population size over the next century. *Limnology and Oceanography*, 60(3), 840–855.
https://doi.org/10.1002/lno.10075 (Edmunds 2015)

In this study, size-based matrix models for the reef-building coral Orbicella annularis at 14-m depth on the Tektite reef in St. John, U.S. Virgin Islands, were used to: (1) explore the demography of changing coral cover over 25 yr, (2) test for spatial homogeneity in demographic properties through a contrast with a previous study (at Yawzi Point, Edmunds and Elahi 2007), and (3) evaluate the potential for future population stability. During three, five year intervals from 1988 to 2002, St. John was affected by hurricanes and bleaching, yet coral cover at Tektite increased from 33% to 49%; from 2002 to 2007, it declined to 27%; and from 2010 to 2013, it stabilized at 28%. Over a quarter-century, colonies > 50 cm2 became rare, the abundance of colonies ≤ 50 cm2 increased from 58% (1988) to 92% (2013), and population density doubled to 67 colonies m-2 by 2013. Population growth (λ) was greater at Tektite ($1.152 \geq \lambda \geq 1.018$) than Yawzi Point ($0.679 \geq \lambda \geq 0.586$), and while population size at Tektite declined due to bleaching and disease in 2005 ($\lambda = 0.753$ over 2003–2008), it recovered between 2008 and 2013 ($\lambda = 0.966$); the population at Yawzi Point declined from 1988 to 2003 without signs of recovery. Projections suggest a continuation of recent conditions could allow O. annularis at Tektite to retain 9% cover after 100 yr, but with a return to the rates of growth and survival of 1993–1998, it could attain coverage similar to that of 1988 (33%) in 15 yr.

Edmunds, P. J. (2019). The demography of hurricane effects on two coral populations differing in dynamics. *Ecosphere*, 10(9), e02836. https://doi.org/10.1002/ecs2.2836 (Edmunds 2019)

On most tropical coral reefs, decades of disturbances have ratcheted down coral cover to create low abundance communities. In such a state, the reefs of St. John, US Virgin Islands, were hit by two Category 5 hurricanes in September 2017, yet the effects on two sites dominated by Orbicella annularis were minor in terms of coral cover. To explore the implications of this outcome, the fates of O. annularis colonies were determined from photoquadrats and used to prepare size-based matrix models for the year preceding the storms and the four months bracketing the storms. The populations displayed contrasting dynamics from 1988 to July 2017, with coral cover declining from 43% to 5% at Yawzi Point but remaining at 30% at Tektite. Over this period, colony sizes declined, with ≥82% having planar areas ≤50 cm2 (i.e., the smallest size class) by July 2017, and while densities declined from 47 to 8 colonies/m2 at Yawzi Point, they increased from 36 to 51 colonies/m2 at Tektite. Hurricanes Irma and Maria depressed coral cover by 1–4%, transitioned colonies into the smallest size class (>87% by November), killed 27% and 5% of the colonies in the smallest size class at Yawzi Point and Tektite, respectively, and depressed the 5-yr intrinsic rate of population growth (λ) to 0.53–0.87. Twenty-year projections suggested these demographic effects will not have ecologically meaningful impacts on population size, at least compared to projections initiated assuming Hurricanes Irma and Maria had not occurred. With low cover of O. annularis distributed among many small colonies, future disturbances may play more important roles in winnowing the few remaining host genotypes rather than further depressing coral cover.

García-Sais, J. R., S. Williams, R. Esteves, J. Sabater-Clavell, and M. Carlo. 2017. Final Report Monitoring of Coral Reef Communities from Natural Reserves in Puerto Rico. (García-Sais et al. 2017)

A total of 21 reef stations were scheduled during the 2016-17 coral monitoring cycle to complete the 42-reef station monitoring plan for Puerto Rico, including a set of five (5) stations from south coast sites (Salinas/Guayama and Guayanilla) that were exposed to severe wave and surge conditions during the pass of hurricane Matthew in October, shortly after their initial baseline characterization surveys were completed in 2016. The monitoring sampling protocol includes determinations of reef substrate cover by sessile-benthic and abiotic categories based on a continuous intercept (chain-link) technique on sets of five-10 m long permanent transects at various depths (within the 3 – 30 m range) on each reef. An assessment of the prevalence of infectious diseases on corals was added to the monitoring protocol. Surveys of the taxonomic composition, density, species richness/diversity indices, and size-distribution (selected species) of reef fishes and motile megabenthic invertebrates are also included as tasks of the monitoring protocol. Quantitative/qualitative assessments of reef fishes and motile invertebrates were based on sets of five 3 x 10 m belt-transects for small territorial, non-cryptic species and expanded to a 3 x 20 m belt for assessment of commercially important species, including ecologically important herbivores, such as doctorfishes (Acanthuridae) and parrotfishes (Scaridae). Digital photographic documentation of reef stations was produced for all reef stations. The most important change in the community structure of coral reefs monitored during 2017 in PR was a marked decline (62.7%) of reef substrate cover by live corals, from 13.4% in 2016 to 5.0% in 2017 at the reef crest of Maria Langa 3m in Guayanilla. The drastic reduction of live coral cover was characterized by the disappearance of the

dominant coral, Acropora prolifera from permanent transects apparently caused by the detachment and mortality of colonies exposed to conditions of extreme wave and surge action during the pass of Hurricane Matthew across the northern Caribbean and close to the south coast of PR during October 2016. Severe mechanical damage was also observed from Cayo Aurora's Acropora palmata reef biotope in Guanica. The very large Elkhorn Coral colonies were not detached from the base, but many of the large branches (arms) were broken. Survival rates of these fragments will be evaluated from prospective measurements during the next monitoring survey at this reef. Statistically significant reductions of soft coral (gorgonians) were measured at Tres Palmas Reef 3m in Rincon, Resuellos 10 m in Cabo Rojo, Tourmaline 20m in Mayaguez and Media Luna 10 m in La Parguera. Such reductions of gorgonian densities appear to be related to mechanical detachment during exposure to extreme wave and surge energy associated with the pass of Hurricane Matthew. Increasing trends of reef substrate cover by live corals were noted at Tres Palmas 10 and 20m, Tourmaline 10, 20 and 30m, Media Luna 10 and 5m. Boya Vieja 20m, Maria Langa 10 and 20m and Derrumbadero 20m. The main driver of the increasing trend of substrate cover by live corals at all reef stations except Tourmaline 10 (Madracis auretenra) was the consistent increase of cover by Orbicella annularis complex. Coral diseases were observed in 16 out of a total 1,132 coral colonies intercepted by transects during 2017, for a mean disease prevalence of 1.3%. Reefs with the highest disease prevalence were Cayo Caribes 10m in Salinas (4.5%), Boya Vieja 20m in La Parguera (4.1%), Bajo Gallardo in Cabo Rojo (4.0%), and Tres Palmas 3.0m in Rincon (3.0%).

García-Sais, J. R., Williams, S. M. & Amirrezvani, A. (2017). Mortality, recovery, and community shifts of scleractinian corals in Puerto Rico one decade after the 2005 regional bleaching event. *PeerJ* 5, e3611. https://doi.org/10.7717/peerj.3611 (Garcia-Sais et al. 2017)

This work analyzes the mortality, recovery, and shifts in the composition of scleractinian corals from Puerto Rico one decade after the 2005 regional coral bleaching event. Temporal and spatial patterns of coral community structure were examined using a stratified, non-random sampling approach based on five permanent transects per reef at 16 reef stations. A negative correlation between percent coral cover loss and light attenuation coefficient (Kd490) was observed, suggesting that light attenuation, as influenced by water turbidity and depth, played a major role in coral protection during the bleaching event ("sunblock effect"). Responses of coral assemblages varied after the bleaching event, including shifts of cover from massive corals (Orbicella spp.) to opportunistic (Porites astreoides) and branching corals (Madracis auretenra, P. porites) and/or turf algae; partial recovery of reef substrate cover by O. annularis complex; and no measurable changes in coral assemblages before and after the event.

Hernández-Delgado, E. A., González-Ramos, C. M. & Alejandro-Camis, P. J. (2014). Large-scale coral recruitment patterns on Mona Island, Puerto Rico: evidence of a transitional community trajectory after massive coral bleaching and mortality. *Rev. Biol. Trop.*, 62(3), 283–298. http://www.scielo.sa.cr/scielo.php?script=sci_arttext&pid=S0034-77442014000700012&lng=en&nrm=iso (Hernández-Delgado et al. 2014a)

Coral reefs have largely declined across the northeastern Caribbean following the 2005 massive bleaching event. Climate change-related sea surface warming and coral disease outbreaks of a white plague-like syndrome and of yellow band disease (YBD) have caused significant coral decline affecting massive reef

building species (i.e., Orbicella annularis species complex) which show no apparent signs of recovery through larval sexual recruitment. We addressed coral recruit densities across three spur and groove reef locations along the western shelf of remote Mona Island, Puerto Rico: Punta Capitán (PCA), Pasa de Las Carmelitas (PLC), and Las Carmelitas-South (LCS). Data were collected during November 2012 along 93 haphazard transects across three depth zones (<5m, 5-10m, 10-15m). A total of 32 coral species (9 octocorals, 1 hydrocoral, 22 scleractinians) were documented among the recruit community. Communities had low densities and dominance by short-lived brooder species seven years after the 2005 event. Mean coral recruit density ranged from 1.2 to 10.5/m2 at PCA, 6.3 to 7.2/m2 at LCS, 4.5 to 9.5/m2 at PLC. Differences in coral recruit community structure can be attributed to slight variation in percent macroalgal cover and composition as study sites had nearly similar benthic spatial heterogeneity. Dominance by ephemeral coral species was widespread. Recovery of largely declining massive reef-building species such as the O. annularis species complex was limited or non-existent. The lack of recovery could be the combined result of several mechanisms involving climate change, YBD disease, macroalgae, fishing, urchins and Mona Island's reefs limited connectivity to other reef systems. There is also for rehabilitation of fish trophic structure, with emphasis in recovering herbivore guilds and depleted populations of D. antillarum. Failing to recognize the importance of ecosystem-based management and resilience rehabilitation may deem remote coral reefs recovery unlikely.

Rodriguez-Zaragoza, F. A. & Arias-Gonzalez, J. E. (2015). Coral biodiversity and bio-construction in the northern sector of the mesoamerican reef system. *Frontiers in Marine Science*, 2, 1–16. https://doi.org/10.3389/fmars.2015.00013 (Rodríguez-Zaragoza and Arias-González 2015)

As the impact of anthropogenic activity and climate change continue to accelerate rates of degradation on Caribbean coral reefs, conservation and restoration faces greater challenges. At this stage, it is of particular importance in coral reefs to recognize and to understand the structural spatial patterns of benthic assemblages. We developed a field-based framework of a Caribbean reefscape benthic structure by using hermatypic corals as an indicator group of global biodiversity and bio-construction patterns in 11 reefs of the northern sector of the mesoamerican barrier reef system (nsMBRS). Four hundred and seventy four video-transects (50 m long by 0.4 m wide) were performed throughout a gradient of reef complexity from north to south (~400 km) to identify coral species, families and ensembles of corals. Composition and abundance of species, families and ensembles showed differences among reefs. In the northern zone, the reefs had shallow, partial reef developments with low diversities, dominated by Acropora palmata, Siderastrea spp., Pseudodiploria strigosa, and Agaricia tenuifolia. In the central and southern zones, reefs presented extensive developments, high habitat heterogeneity, and the greatest diversity and dominance of Orbicella annularis and Orbicella faveolata. These two species determined the structure and diversity of corals in the central and southern zones of the nsMBRS and their bio-construction in these zones is unique in the Caribbean. Their abundance and distribution depended on the reef habitat area, topographic complexity and species richness. Orbicella species complex were crucial for maintaining the biodiversity and bio-construction of the central and southern zones while A. palmata in the northern zones of the nsMBRS.

Soto-Santiago, F. J., Mercado-Molina, A., Reyes-Maldonado, K., Vélez, Y., Ruiz-Díaz, C.P., & Sabat, A. (2017). Comparative demography of two common scleractinian corals: Orbicella annularis and Porites astreoides. *PeerJ* **5**, e3906. https://doi.org/10.7717/peerj.3906 (Soto-Santiago et al. 2017)

Background Studies directed at understanding the demography and population dynamics of corals are relatively scarce. This limits our understanding of both the dynamics of coral populations and our capacity to develop management and conservation initiatives directed at conserving such ecosystems. Methods From 2012 to 2014, we collected data on the growth, survival, and recruitment rates of two common Caribbean coral species, the stress-tolerant Orbicella annularis and the weedy Porites astreoides. A set of size-based population matrix model was developed for two localities in Northeastern Puerto Rico and used to estimate population growth rates (λ) and determine the life cycle transition(s) that contribute the most to spatiotemporal differences in λs. The model was parameterized by following the fate of 100 colonies of each species at the two sites for two years. Results Our data indicate that spatial variability in vital rates of both species was higher than temporal variability. During the first year, populations of O. annularis exhibited λs below equilibrium at Carlos Rosario (0.817) and Palomino (0.694), followed by a considerable decline at both sites during the second year (0.700 and 0.667). Populations of P. astreoides showed higher λs than O. annularis during the first census period at Carlos Rosario (0.898) and Palomino (0.894) with a decline at one of the sites (0.681 and 0.893) during the second census period. Colony fate in both species exhibited a significant interaction with respect to location but not to time (G2 = 20.96; df = 3 for O. annularis and G2 = 9.55; df = 3 for P. astreoides). Discussion The similar variability of λs as well as the similar survival rates for both species during the two-year census period (2012–2014) show similar variability on demographic patterns in space and time. Our results suggest that location rather than time is important for the resiliency in coral colonies. Also, P. astreoides will show higher resistance to disturbance in the future than O. annularis.

Genetic Assessment

Olsen, K. C., Moscoso, J. A. & Levitan, D. R. (2019). Somatic Mutation Is a Function of Clone Size and Depth in Orbicella Reef-Building Corals. *The Biological Bulletin*, 236(1), 1–12. https://doi.org/10.1086/700261 (Olsen et al. 2019)

In modular organisms, the propagation of genetic variability within a clonal unit can alter the scale at which ecological and evolutionary processes operate. Genetic variation within an individual primarily arises through the accretion of somatic mutations over time, leading to genetic mosaicism. Here, we assess the prevalence of intraorganismal genetic variation and potential mechanisms influencing the degree of genetic mosaicism in the reef corals Orbicella franksi and Orbicella annularis. Colonies of both species, encompassing a range of coral sizes and depths, were sampled multiple times and genotyped at the same microsatellite loci to detect intraorganismal genetic variation. Genetic mosaicism was detected in 38% of corals evaluated, and mutation frequency was found to be positively related with clonal size and negatively associated with coral depth. We suggest that larger clones experience a greater number of somatic cell divisions and consequently have an elevated potential to accumulate mutations. Furthermore, corals at shallower depths may be exposed to abiotic conditions such as elevated thermal regimes, which promote increased mutation rates. The results highlight the pervasiveness of intraorganismal genetic

variation in reef-building corals and emphasize potential mechanisms generating somatic mutations in modular organisms.

Habitat and Ecosystem Conditions

> Oliver, L. M., Smith, A., Fore, L., Bradley, P. & Fisher, W. S. (2018). Assessing land use, sedimentation, and water quality stressors as predictors of coral reef condition in St. Thomas, U.S. Virgin Islands. *Environ Monit Assess*, 190(4), 213. https://doi.org/10.1007/s10661-018-6562-1 (Oliver et al. 2018)

Coral reef condition on the south shore of St. Thomas, U.S. Virgin Islands, was assessed at various distances from Charlotte Amalie, the most densely populated city on the island. Human influence in the area includes industrial activity, wastewater discharge, cruise ship docks, and impervious surfaces throughout the watershed. Anthropogenic activity was characterized using a landscape development intensity (LDI) index, sedimentation threat (ST) estimates, and water quality (WQ) impairments in the near-coastal zone. Total three-dimensional coral cover, reef rugosity, and coral diversity had significant negative coefficients for LDI index, as did densities of dominant species Orbicella annularis, Orbicella franksi, Montastraea cavernosa, Orbicella faveolata, and Porites porites. However, overall stony coral colony density was not significantly correlated with stressors. Positive relationships between reef rugosity and ST, between coral diversity and ST, and between coral diversity and WQ were unexpected because these stressors are generally thought to negatively influence coral growth and health. Sponge density was greater with higher disturbance indicators (ST and WQ), consistent with reports of greater resistance by sponges to degraded water quality compared to stony corals. The highest FoRAM (Foraminifera in Reef Assessment and Monitoring) indices indicating good water quality were found offshore from the main island and outside the harbor. Negative associations between stony coral metrics and LDI index have been reported elsewhere in the Caribbean and highlight LDI index potential as a spatial tool to characterize land-based anthropogenic stressor gradients relevant to coral reefs. Fewer relationships were found with an integrated stressor index but with similar trends in response direction.

> Roff, G., Zhao, J. & Mumby, P. J. (2015). Decadal-scale rates of reef erosion following El Niño-related mass coral mortality. *Global Change Biology*, 21(12), 4415–4424. https://doi.org/10.1111/gcb.13006 (Roff et al. 2015)

As the frequency and intensity of coral mortality events increase under climate change, understanding how declines in coral cover may affect the bioerosion of reef frameworks is of increasing importance. Here, we explore decadal-scale rates of bioerosion of the framework building coral Orbicella annularis by grazing parrotfish following the 1997/1998 El Niño-related mass mortality event at Long Cay, Belize. Using high-precision U-Th dating and CT scan analysis, we quantified in situ rates of external bioerosion over a 13-year period (1998-2011). Based upon the error-weighted average U-Th age of dead O. annularis skeletons, we estimate the average external bioerosion between 1998 and 2011 as 0.92 ± 0.55 cm depth. Empirical observations of herbivore foraging, and a nonlinear numerical response of parrotfish to an increase in food availability, were used to create a model of external bioerosion at Long Cay. Model estimates of external bioerosion were in close agreement with U-Th estimates (0.85 ± 0.09 cm). The model was then used to quantify how rates of external bioerosion changed across a gradient of coral

mortality (i.e., from few corals experiencing mortality following coral bleaching to complete mortality). Our results indicate that external bioerosion is remarkably robust to declines in coral cover, with no significant relationship predicted between the rate of external bioerosion and the proportion of O. annularis that died in the 1998 bleaching event. The outcome was robust because the reduction in grazing intensity that follows coral mortality was compensated for by a positive numerical response of parrotfish to an increase in food availability. Our model estimates further indicate that for an O. annularis-dominated reef to maintain a positive state of reef accretion, a necessity for sustained ecosystem function, live cover of O. annularis must not drop below a ~5-10% threshold of cover.

Sabine, A. M., Smith, T. B., Williams, D. E. & Brandt, M. E. (2015). Environmental conditions influence tissue regeneration rates in scleractinian corals. *Marine Pollution Bulletin*, 95, 253–264. https://doi.org/10.1016/j.marpolbul.2015.04.006 (Sabine et al. 2015)

Natural and anthropogenic factors may influence corals' ability to recover from partial mortality. To examine how environmental conditions affect lesion healing, we assessed several water quality parameters and tissue regeneration rates in corals at six reefs around St. Thomas, US Virgin Islands. We hypothesized that sites closer to developed areas would have poor water quality due to proximity to anthropogenic stresses, which would impede tissue regeneration. We found that water flow and turbidity most strongly influenced lesion recovery rates. The most impacted site, with high turbidity and low flow, recovered almost three times slower than the least impacted site, with low turbidity, high flow, and low levels of anthropogenic disturbance. Our results illustrate that in addition to lesion-specific factors known to affect tissue regeneration, environmental conditions can also control corals' healing rates. Resource managers can use this information to protect low-flow, turbid nearshore reefs by minimizing sources of anthropogenic stress.

Vega-Rodriguez, M., Müller-Karger, F.E., Hallock, P., Quiles-Perez, G.A., Eakin, C.M., Colella, M., . . . Ruzicka, R. (2015). Influence of water-temperature variability on stony coral diversity in Florida Keys patch reefs. *Marine Ecology Progress Series*, 528, 173–186. https://doi.org/10.2307/24895884 (Vega-Rodriguez et al. 2015)

Annual surveys conducted by the Coral Reef Evaluation and Monitoring Project (CREMP) reported that average benthic cover of stony corals in the Florida Keys National Marine Sanctuary, USA declined from ~13% in 1996 to 8% in 2009. Keys-wide, mean species richness (SR) declined by ~2.3 species per station. Stress due to temperature extremes is suspected to be a major driver of this trend. We tested the potential for sea surface temperature (SST) variability and acute warm-temperature events (assessed with Degree Heating Weeks) to affect stony coral diversity in the Florida Keys. Benthic cover of 43 stony coral species was examined with respect to SST variability and habitat type (patch, offshore shallow, and offshore deep reefs). For each CREMP site, SST annual variance was classified as low (<7.0°C_2), intermediate (7.0 to 10.9°C_2), or high (≥11.0°C_2). Nonparametric MANOVA analyses showed that in the Upper, Middle, and Lower Keys regions, massive-type stony coral species (e.g. Siderastrea siderea, Pseudodiploria strigosa, Orbicella annularis complex, Montastraea cavernosa, and Colpophyllia natans) were prevalent in the patch reef habitats exposed to intermediate to high SST variability. Intermediate SST variability was also correlated with higher Shannon diversity means in patch reefs in the Upper Keys and higher SR means in the Middle Keys, indicating either that the stony coral species in these habitats

are adapted to an intermediate temperature range or that individual colonies have acclimatized to that range. No significant relationships were found between stony coral diversity and SST variability in the Dry Tortugas region.

Threat Assessment

Disease

> Clemens, E. & Brandt, M. E. (2015). Multiple mechanisms of transmission of the Caribbean coral disease white plague. *Coral Reefs*, 34(4), 1179–1188. http://dx.doi.org.libproxy.smith.edu:2048/10.1007/s00338-015-1327-6 (Clemens and Brandt 2015)

White plague is one of the most devastating coral diseases in the Caribbean, and yet important aspects of its epidemiology, including how the disease transmits, remain unknown. This study tested potential mechanisms and rates of transmission of white plague in a laboratory setting. Transmission mechanisms including the transport of water, contact with macroalgae, and predation via corallivorous worms and snails were tested on the host species Orbicella annularis. Two of the tested mechanisms were shown to transmit disease: water transport and the corallivorous snail Coralliophila abbreviata. Between these transmission mechanisms, transport of water between a diseased coral and a healthy coral resulted in disease incidence significantly more frequently in exposed healthy corals. Transmission via water transport also occurred more quickly and was associated with higher rates of tissue loss (up to 3.5 cm d^sup -1^) than with the corallivorous snail treatment. In addition, water that was in contact with diseased corals but was filtered with a 0.22-[mu]m filter prior to being introduced to apparently healthy corals also resulted in the transmission of disease signs, but at a much lower rate than when water was not filtered. This study has provided important information on the transmission potential of Caribbean white plague disease and highlights the need for a greater understanding of how these processes operate in the natural environment.

> Meyer, J. L., Rodgers, J. M., Dillard, B. A., Paul, V. J. & Teplitski, M. (2016). Epimicrobiota Associated with the Decay and Recovery of Orbicella Corals Exhibiting Dark Spot Syndrome. *Frontiers in Microbiology*, 7:893. https://doi.org/10.3389/fmicb.2016.00893 (Meyer et al. 2016)

Dark Spot Syndrome (DSS) is one of the most common diseases of boulder corals in the Caribbean. It presents as sunken brown lesions in coral tissue, which can spread quickly over coral colonies. With this study, we tested the hypothesis that similar to other coral diseases, DSS is a dysbiosis characterized by global shifts in the coral microbiome. Because Black Band Disease (BBD) was sometimes found following DSS lesions, we also tested the hypothesis that DSS is a precursor of BBD. To track disease initiation and progression 24 coral colonies were tagged. Of them five Orbicella annularis corals and three O. faveolata corals exhibited DSS lesions at tagging. Microbiota of lesions and apparently healthy tissues from DSS-affected corals over the course of 18 months were collected. Final visual assessment showed that five of eight corals incurred substantial tissue loss while two corals remained stable and one appeared to recover from DSS lesions. Illumina sequencing of the V6 region of bacterial 16S rRNA genes

demonstrated no significant differences in bacterial community composition associated with healthy tissue or DSS lesions. The epimicrobiomes of both healthy tissue and DSS lesions contained high relative abundances of Operational Taxonomic Units assigned to Halomonas, an unclassified gammaproteobacterial genus, Moritella, an unclassified Rhodobacteraceae genus, Renibacterium, Pseudomonas, and Acinetobacter. The relative abundance of bacterial taxa was not significantly different between samples when grouped by tissue type (healthy tissue vs. DSS lesion), coral species, collection month, or the overall outcome of DSS-affected corals (substantial tissue loss vs. stable/recovered). Two of the tagged corals with substantial tissue loss also developed BBD during the 18-month sampling period. The bacterial community of the BBD layer was distinct from both healthy tissue and DSS lesions, with high relative abundances of the presumed BBD pathogen Roseofilum reptotaenium and an unclassified Bacteroidales genus, similar to previous results. Roseofilum was detected in all samples from this study, with the highest relative abundance in healthy tissue from DSS-affected corals sampled in August, suggesting that while DSS is not a precursor to BBD, DSS-affected corals are in a weakened state and therefore more susceptible to additional infections.

Neely, K. 2018. Surveying the Florida Keys Southern Coral Disease Boundary. Florida DEP, Miami, FL. Pp 1-15 (Neely 2018)

Since 2014, multi-year, multi-species disease outbreak has progressed geographically along the Florida Reef Tract from an origin near Virginia Key. From fall 2017 to spring 2018, 134 reef sites were surveyed to identify the geographic boundary of the disease as well as provide information on rates of progression, cross-reef prevalence differences, and differences in responses of impacted species. Roving diver surveys were conducted during two reef-tract wide assessments in fall 2017 and spring 2018, and roving diver and belt transect surveys were conducted in a targeted effort near the southern disease boundary in winter 2017-18 between Long Key and Marathon. Surveys confirmed prevalence of the disease on 15 coral species, including the primary reef builders and five ESA-listed species. Disease was conspicuously absent on some other species, including the *Acropora* and *Porites* spp. Disease hotspots and geographic differences in disease prevalence showed that tissue loss begins on different species at different times. Broadly, the brain corals (particularly *Meandrina meandrites*) are the first to show tissue loss. Boulder coral infections generally appear shortly thereafter, with *Montastraea cavernosa* in particular often a later species to exhibit tissue loss.

Precht, W. F., Gintert, B. E., Robbart, M. L., Fura, R. & van Woesik, R. (2016). Unprecedented Disease-Related Coral Mortality in Southeastern Florida. *Scientific Reports*, 6:31374. https://doi.org/10.1038/srep31374 (Precht et al. 2016)

Anomalously high water temperatures, associated with climate change, are increasing the global prevalence of coral bleaching, coral diseases, and coral-mortality events. Coral bleaching and disease outbreaks are often inter-related phenomena, since many coral diseases are a consequence of opportunistic pathogens that further compromise thermally stressed colonies. Yet, most coral diseases have low prevalence (<5%), and are not considered contagious. By contrast, we document the impact of an extremely high-prevalence outbreak (61%) of white-plague disease at 14 sites off southeastern Florida. White-plague disease was observed near Virginia Key, Florida, in September 2014, and after 12 months had spread 100 km north and 30 km south. The disease outbreak directly followed a high temperature

coral-bleaching event and affected at least 13 coral species. Eusmilia fastigiata, Meandrina meandrites, and Dichocoenia stokesi were the most heavily impacted coral species, and were reduced to <3% of their initial population densities. A number of other coral species, including Colpophyllia natans, Pseudodiploria strigosa, Diploria labyrinthiformis, and Orbicella annularis were reduced to <25% of their initial densities. The high prevalence of disease, the number of susceptible species, and the high mortality of corals affected suggests this disease outbreak is arguably one of the most lethal ever recorded on a contemporary coral reef.

Verde, A., Bastidas, C. & Croquer, A. (2016). Tissue mortality by Caribbean ciliate infection and white band disease in three reef-building coral species. *PeerJ* 4:e2196. https://dx.doi.org/10.7717%2Fpeerj.2196 (Verde et al. 2016)

Caribbean ciliate infection (CCI) and white band disease (WBD) are diseases that affect a multitude of coral hosts and are associated with rapid rates of tissue losses, thus contributing to declining coral cover in Caribbean reefs. In this study we compared tissue mortality rates associated to CCI in three species of corals with different growth forms: Orbicella faveolata (massive-boulder), O. annularis (massive-columnar) and Acropora cervicornis (branching). We also compared mortality rates in colonies of A. cervicornis bearing WBD and CCI. The study was conducted at two locations in Los Roques Archipelago National Park between April 2012 and March 2013. In A. cervicornis, the rate of tissue loss was similar between WBD (0.8 ± 1 mm/day, mean ± SD) and CCI (0.7 ± 0.9 mm/day). However, mortality rate by CCI in A. cervicornis was faster than in the massive species O. faveolata (0.5 ± 0.6 mm/day) and O. annularis (0.3 ± 0.3 mm/day). Tissue regeneration was at least fifteen times slower than the mortality rates for both diseases regardless of coral species. This is the first study providing coral tissue mortality and regeneration rates associated to CCI in colonies with massive morphologies, and it highlights the risks of further cover losses of the three most important reef-building species in the Caribbean.

Walker, B. 2018. Southeast Florida reef-wide Post-Irma coral disease surveys. Florida DEP, Miami, FL. Pp. 1-37. (Walker 2018)

Florida's coral reefs are currently experiencing a multi-year outbreak of coral disease that have resulted in the mortality of millions of corals across southeast Florida, Biscayne National Park, and the Upper and Middle Florida Keys. In early September 2017, Hurricane Irma impacted the entire FRT. The purpose of this project was to conduct field surveys to identify the current state of the coral reefs in southeast Florida and coordinate with other concomitant reef tract efforts to improve the regional understanding of the extent of the disease outbreak and identify recent hurricane injury to direct future restoration. Through a broader partner network, 62 sites from Key Biscayne to St. Lucie Reef were targeted for survey. Twenty-nine sites were chosen based on previous data that indicated high coral values of richness, density, and/or cover at those locations. Thirty-three sites were chosen with FDEP reef managers where there were previous data gaps. A new protocol was developed, which was a modification of the Florida Reef Resilience Program (FRRP) Disturbance Response Monitoring (DRM) methodology. This included collecting additional disease and injury metrics in transects and by rover diver to prioritize sites for triage and restoration activities.

Williams, L., Smith, T. B., Burge, C. A. & Brandt, M. E. (2020). Species-specific susceptibility to white plague disease in three common Caribbean corals. *Coral Reefs*, 39(1), 27–31. https://doi.org/10.1007/s00338-019-01867-9 (Williams et al. 2020b)

White plague disease has caused widespread coral mortality and affects over 30 Caribbean coral species, yet how different coral species respond to disease exposure has not been tested experimentally. This study quantified white plague transmission from Orbicella franksi to three susceptible and abundant coral species in the U.S. Virgin Islands: Orbicella annularis, Siderastrea siderea, and Porites astreoides. White plague was observed in 83% of tested O. annularis corals within 5.8 ± 1.1 (mean ± SE) d, 42% of S. siderea corals within 9.1 ± 1.4 d, and 17% of P. astreoides corals within 12 ± 0.87 d. Results from this study indicate that: (1) O. annularis is significantly more susceptible to white plague than S. siderea and P. astreoides, and (2) white plague infection occurs more rapidly in O. annularis than in P. astreoides. These results are important for understanding how multi-species diseases may impact coral species assemblages.

Pollution, Acidification, and Thermal Stress

Kemp, D. W., Colella, M.A., Bartlett, L.A. Ruzicka, R.R., Porter, J.W., & Fitt, W.K. (2016). Life after cold death: reef coral and coral reef responses to the 2010 cold water anomaly in the Florida Keys. *Ecosphere,* 7:e01373. https://doi.org/10.1002/ecs2.1373 (Kemp et al. 2016)

Organismal and community-wide responses of reef-building corals are documented before and after a severe cold-water thermal anomaly that occurred in 2010 in the Florida Keys, USA. In January 2010 seawater temperatures dropped far below the normal minima (to <11°C), resulting in the largest documented coral mass mortality event ever recorded in the Florida Keys. Physiological measurements demonstrated species-specific thermal sensitivities to this environmental perturbation. Four common corals with narrow thermal tolerance, Acropora cervicornis, Orbicella annularis, O. faveolata, and Porites astreoides, sustained high mortality (>80%) on inshore reefs. In contrast, another common coral with a wide thermal tolerance, Siderastrea siderea, was not affected by this cold anomaly. We measured biomass, symbiotic algal densities (genus: Symbiodinium), chlorophyll a content, and maximum quantum efficiency of photosystem II for reef-building corals on a seasonal basis before and after the 2010 cold anomaly. Our data document a clear correspondence between physiological response, biomass levels, and survivorship among these five scleractinian coral species. These physiological findings are mirrored by in-shore benthic community monitoring data, which show the dramatic loss of the three cold-sensitive species and continued survival of the cold-tolerant species. Finally, we document recruitment and survival rates of newly settled reef-building corals on four inshore reefs, which experienced high coral mortality during the 2010 cold-kill. Interestingly, both a cold-tolerant species, S. siderea, and a cold-intolerant species, P. astreoides, were the most abundant species recruiting to these postdisturbance reefs.

Levitan, D. R., Boudreau, W., Jara, J. & Knowlton, N. (2014). Long-term reduced spawning in Orbicella coral species due to temperature stress. *Marine Ecology Progress Series*, 515, 1–10. https://doi.org/10.3354/meps11063 (Levitan et al. 2014)

We examined the long-term reproductive consequence of bleaching stress on Caribbean corals in the Orbicella (formerly Montastraea) species complex (O. annularis, O. faveolata, and O. franksi). Over 2000 observations of spawning in 526 tagged corals in Panama were made from 2002 through 2013. Bleaching events were noted in 2005 and 2010. At the population level, a reduction in spawning persisted for several years following each bleaching event. In 2010, (1) the bleaching event did not alter the timing of spawning, nor coral survivorship or tissue loss; (2) both bleached and unbleached corals had a reduced probability of spawning for several years following the bleaching event, and corals that visibly bleached were less likely to spawn than corals that did not visibly bleach; (3) the species that was affected most by the bleaching event (O. annularis) recovered the ability to spawn in fewer years compared to the species least affected by the bleaching event (O. franksi); and (4) in O. franksi, the species with the widest depth distribution, recovery in the likelihood to spawn was not depth related, although individuals at greater depths were less likely to bleach. In sum, corals that recover from bleaching events can experience long-term reduction in reproduction, over time scales that can bridge the interval between subsequent bleaching events. This may be catastrophic for the long-term maintenance of the population.

Scheufen, T., Krämer, W. E., Iglesias-Prieto, R. & Enríquez, S. (2017). Seasonal variation modulates coral sensibility to heat-stress and explains annual changes in coral productivity. *Scientific Reports*, 7:4937. https://doi.org/10.1038/s41598-017-04927-8 (Scheufen et al. 2017b)

The potential effects of seasonal acclimatization on coral sensitivity to heat-stress, has received limited attention despite differing bleaching thresholds for summer and winter. In this study, we examined the response of two contrasting phenotypes, termed winter and summer, of four Caribbean reef corals to similar light and heat-stress levels. The four species investigated were categorized into two groups: species with the ability to harbour large number of symbionts, Orbicella annularis and O. faveolata, and species with reduced symbiont density (Montastraea cavernosa and Pseudodiploria strigosa). The first group showed higher capacity to enhance photosynthetic rates per area (Pmax), while Pmax enhancement in the second group was more dependent on Symbiodinium performance (Psym). In summer all four species presented higher productivity, but also higher sensitivity to lose coral photosynthesis under heat-stress. In contrast, corals in winter exhibit symbionts with higher capacity to photoacclimate to the increased levels of light-stress elicited by heat-stress. Overall, our study supports the importance of the acclimatory coral condition in addition to the previous thermal history, to determine the severity of the impact of heat-stress on coral physiology, but also the dependence of this response on the particular structural and functional traits of the species.

van Woesik, R. & McCaffrey, K. R. (2017). Repeated Thermal Stress, Shading, and Directional Selection in the Florida Reef Tract. *Frontiers in Marine Science*, 4:182. https://doi.org/10.3389/fmars.2017.00182 (van Woesik and McCaffrey 2017)

Over the last three decades reef corals have been subjected to an unprecedented frequency and intensity of thermal-stress events, which have led to extensive coral bleaching, disease, and mortality. Over the next century, the climate is predicted to drive sea-surface water temperatures to even higher levels, consequently increasing the risk of mass bleaching and disease outbreaks. Yet, there is considerable temporal and spatial variation in coral bleaching and in disease prevalence. Using data collected from

2398 sites along the Florida reef tract from 2005 to 2015, this stuy examined the temporal and spatial patterns of coral bleaching and disease in relation to coral-colony size, depth, temperature, and chlorophyll-a concentrations. The results show that coral bleaching was most prevalent during the warmest years in 2014 and 2015, and disease was also most prevalent in 2010, 2014, and 2015. Although the majority of the corals surveyed, independent of their size, were found in habitats with low chlorophyll-a concentrations, and high irradiance, these same habitats showed the highest prevalence of coral bleaching and disease outbreaks during thermal-stress events. These results suggest that directional selection in a warming ocean may favor corals able to tolerate inshore, shaded environments with high turbidity and productivity.

MOUNTAINOUS STAR CORAL (ORBICELLA FAVEOLATA)

Biology and Life History Characteristics

> Alvarado-Chacon, E. M., L. A. Gómez-Lemos, N. P. Sierra-Sabalza, A. M. Hernández-Chamorro, J. P. Lozano-Peña, C. A. Valcárcel-Castellanos, V. Pizarro, R. García-Ureña, J. C. Zárate-Arévalo, and J. A. Rojas. 2020. Early life history of the Caribbean coral *Orbicella faveolata* (Scleractinia: Merulinidae). Revista de Biología Tropical 68(4):1262-1274. (Alvarado-Chacon et al. 2020)

Introduction: Rehabilitation of hermatypic coral species that have declined in the Caribbean in recent decades is a priority. Production of sexual recruits is considered the best restoration method to aid affected populations. Objective: To gain knowledge of early life stages of Orbicella faveolata and to enhance production of new sexual recruits. Methods: Gamete bundles from the coral species O. faveolata were collected over two years (2018 and 2019) from Los Corales del Rosario y de San Bernardo Natural National Park, Cartagena, Colombia. Assisted fertilization, larval rearing, settlement (onto crustose coralline algae, CCA) and post settlement survival in laboratory conditions were monitored. Results: Embryonic and larval development were documented over 55 hours after the first cleavage, when larvae were fully developed and started pre-settlement behavior. Settlement began 7 days after first cleavage and after 37 days polyps had acquired zooxanthellae. Larval settlement was higher on Lythophyllum congestum and Titanoderma prototypum than in response to Porolithon pachydermum, Neogoniolithon sp., Hydrolithon sp., and Lythophyllum sp. Larvae did not settle on dead coral or on the negative control (sterilized seawater). After the first week post settlement survival was 59% amongst O. faveolata recruits. During the second week, survival dropped to 42 %, and was further reduced to 0% at the end of the third week. Conclusions: O. faveolata larvae require cues from certain CCA species to settle, they do not settle in absence of CCA. Increased larvae availability is possible through assisted fertilization in the laboratory, however, due to the high mortality in early post-settlement phases, additional research needs to be conducted in order to scale up larvae production and improve understanding of the cues that enhance settlement and the factors which cause post-settlement mortality.

Cunning, R., Silverstein, R. N. & Baker, A. C. (2015). Investigating the causes and consequences of symbiont shuffling in a multi-partner reef coral symbiosis under environmental change. *Proceedings of the Royal Society B: Biological Sciences*, 282:20141725. https://doi.org/10.1098/rspb.2014.1725 (Cunning et al. 2015)

Dynamic symbioses may critically mediate impacts of climate change on diverse organisms, with repercussions for ecosystem persistence in some cases. On coral reefs, increases in heat-tolerant symbionts after thermal bleaching can reduce coral susceptibility to future stress. However, the relevance of this adaptive response is equivocal owing to conflicting reports of symbiont stability and change. We help reconcile this conflict by showing that change in symbiont community composition (symbiont shuffling) in Orbicella faveolata depends on the disturbance severity and recovery environment. The proportion of heat-tolerant symbionts dramatically increased following severe experimental bleaching, especially in a warmer recovery environment, but tended to decrease if bleaching was less severe. These patterns can be explained by variation in symbiont performance in the changing microenvironments created by differentially bleached host tissues. Furthermore, higher proportions of heat-tolerant symbionts linearly increased bleaching resistance but reduced photochemical efficiency, suggesting that any change in community structure oppositely impacts performance and stress tolerance. Therefore, even minor symbiont shuffling can adaptively benefit corals, although fitness effects of resulting trade-offs are difficult to predict. This work helps elucidate causes and consequences of dynamism in symbiosis, which is critical to predicting responses of multi-partner symbioses such as O. faveolata to environmental change.

Fisch, J., Drury, C., Towle, E. K., Winter, R. N. & Miller, M. W. (2019). Physiological and reproductive repercussions of consecutive summer bleaching events of the threatened Caribbean coral Orbicella faveolata. *Coral Reefs,* 38(4), 863–876. https://doi.org/10.1007/s00338-019-01817-5 (Fisch et al. 2019)

Thermal stress is a major contributor to loss of coral cover, significantly impacting reefs during the third global bleaching event between 2014 and 2017. The long-term persistence of coral reefs depends on acclimatization and adaptation to changing climate, which are influenced greatly by the interactions between bleaching and reproductive success. We observed a genotypically diverse population of Orbicella faveolata before, during, and after consecutive bleaching events in 2014 and 2015 in the Florida Keys. We documented less bleaching during the second event despite 40% more time above local bleaching thresholds and an association between bleaching severity and subsequent spawning. Approximately 75% of colonies experienced the same or less severe bleaching in the second event despite being metabolically compromised, with a substantial minority (~ 35%) faring better in the second event. The second bleaching event also resulted in smaller decreases in chlorophyll content per symbiont cell and symbiont-to-host cell ratio reef-wide, representing less damage to the coral–algal symbiosis. All colonies that recovered quickly (~ 1 month) or did not bleach in 2014 released gametes in 2015, while only 60% of colonies that recovered more slowly did. Bleaching also impacted the amount of gametes released, with more severe bleaching significantly associated with gamete release from < 50% of the colony surface area. Bleaching and spawning outcomes were supported by dynamic physiological changes during bleaching and recovery. Lipid concentration and symbiont-to-host cell ratios collected from the bottom edge of the colony in the middle of the recovery period (February and April) were most

important for predicting spawning the following year, highlighting the dynamic interaction between micro-habitats and time in recovery and gametogenesis. This study finds signals of physiological acclimatization in an important reef-building coral and underscores the importance of recovery post-bleaching and reproduction for the persistence of coral reefs.

Fuess, L. E., Butler, C. C., Brandt, M. E. & Mydlarz, L. D. (2020). Investigating the roles of transforming growth factor-beta in immune response of Orbicella faveolata, a scleractinian coral. *Developmental & Comparative Immunology*, 107, 103639. https://doi.org/10.1016/j.dci.2020.103639 (Fuess et al. 2020a)

Symbiotic relationships range from parasitic to mutualistic, yet all endosymbionts face similar challenges, including evasion of host immunity. Many symbiotic organisms have evolved similar mechanisms to face these challenges, including manipulation of the host's transforming growth factor-beta (TGFβ) pathway. Here we investigate the TGFβ pathway in scelaractinian corals which are dependent on symbioses with dinoflagellates from the family Symbiodiniaceae. Using the Caribbean coral, Orbicella faveolata, we explore the effects of enhancement and inhibition of the TGFβ pathway on host gene expression. Following transcriptomic analyses, we demonstrated limited effects of pathway manipulation in absence of immune stimulation. However, manipulation of the TGFβ pathway significantly affects the subsequent ability of host corals to mount an immune response. Enhancement of the TGFβ pathway eliminates transcriptomic signatures of host coral immune response, while inhibition of the pathway maintains the response. This is, to our knowledge, the first evidence of an immunomodulatory role for TGFβ in a scelaractinian coral. These findings suggest variation in TGFβ signaling may have implications in the face of increasing disease prevelance. Our results suggest that the TGFβ pathway can modulate tradeoffs between symbiosis and immunity. Further study of links between symbiosis, TGFβ, and immunity is needed to better understand the ecological implications of these findings.

Limer, B. D., Bloomberg, J. & Holstein, D. M. (2020). The Influence of Eddies on Coral Larval Retention in the Flower Garden Banks. *Front. Mar. Sci.*, 7:372. https://doi.org/10.3389/fmars.2020.00372 (Limer et al. 2020)

While coral larval exchange among reef patches is crucial to the persistence of coral metapopulations, larval retention within patches is critical for local population maintenance. In isolated systems such as the Flower Garden Banks (FGB) of the NW Gulf of Mexico (GoM), local retention is thought to play an important role in maintaining high levels of coral cover. Numerous mesoscale cyclonic and anticyclonic features (eddies) are known to spin off from the GoM's Loop Current, many of which pass over the FGB. We developed a biophysical model of coral larval dispersal (2004–2018) to investigate the extent to which eddies may facilitate coral larval exchange between and within the East and West FGB. Virtual larvae of the broadcast spawning Orbicella faveolata and the brooding Porites astreoides were released and tracked with species-specific reproductive and larval behaviors to investigate differences in retention and connectivity in corals with contrasting life histories. Eddies were detected and tracked using sea surface altimetry and compared with larval trajectories to assess the retentive characteristics of these features. Results suggest consistently high, but species-specific, levels of local retention and cross-bank connectivity in both coral species. High local retention is possible early in the dispersal of P. astreoides, and both species routinely experience retention due to recirculation in eddy features as late as 30 days

after planulation or spawning. Eddies passing over the FGB were associated with pulses of between- and within-bank retention, indicating that larvae are capable of dispersing from and returning to coral reefs in the NW GoM. Although opportunities for retention are inherently ephemeral and stochastic due to the nature of Loop Current eddy shedding, eddy propagation should serve as a reliable reseeding mechanism for FGB coral populations. In particular, peaks in late summer eddy propagation correspond with mass coral spawning and may enhance larval retention. These findings support the assertions that healthy FGB reefs may be largely self-sustaining, and that persistent, self-sustaining populations at the FGB may supply downstream reefs with larvae and behave as a remote climate change refugium.

Lizcano-Sandoval, L. D., Marulanda-Gómez, Á., López-Victoria, M. & Rodriguez-Ramirez, A. (2019). Climate Change and Atlantic Multidecadal Oscillation as Drivers of Recent Declines in Coral Growth Rates in the Southwestern Caribbean. *Front. Mar. Sci.*, 6:38. https://doi.org/10.3389/fmars.2019.00038 (Lizcano-Sandoval et al. 2019)

Historical records of growth rates of the key Caribbean reef framework-building coral Orbicella faveolata can be fundamental not only to understand how these organisms respond to environmental changes but also to infer future responses of reef ecosystems in a changing world. While coral growth rates have been widely documented throughout the Caribbean, the drivers of coral growth variability remain poorly understood. Here we provide a record spanning 53 years (1963–2015) of the coral growth parameters for five O. faveolata core samples collected at Serrana Atoll, inside the Seaflower Biosphere Reserve, Colombian Caribbean. Coral cores were extracted from reefs isolated from direct anthropogenic impacts, and growth estimations were derived using computerized tomography. Master records of coral growth parameters were evaluated to identify long-term trends and to relate growth responses with sea surface temperature (SST), the Atlantic Multi-decadal Oscillation (AMO), North Atlantic Oscillation (NAO) and Southern Oscillation indexes, aragonite saturation state (Ωarag), and degree heating months (DHM). Mean density, linear extension and calcification rates were 1.08 g cm-3, 0.96 cm yr-1 and 1.02 g cm-2 yr-1, respectively. We found significant negative relationships between density and mean SST, maximum SST, AMO, and DHM. Moreover, density showed significant positive correlations with NAO and Ωarag. Extension rate did not show significant correlations with any environmental variable; however, there were significant negative correlations between calcification and maximum SST, AMO, and DHM. Trends of coral growth indicated a significant reduction in density and calcification over time, which were best explained by changes in Ωarag. Inter-annual declines in calcification and density up to 25% (relative to historical mean) were associated to the impacts of previously recorded mass bleaching events (1998, 2005 and 2010). Our study provides further evidence that AMO and Ωarag are important drivers affecting coral growth rates in the Southwestern Caribbean. Therefore, we suggest upcoming variations of AMO and future trajectories of Ωarag in the Anthropocene could have a substantial influence on future disturbances, ecological process and responses of the Caribbean reefs.

McIlroy, S. E., Gillette, P., Cunning, R., Klueter, A., Capo, T., Baker, A.C. & Coffroth, M.A. (2016). The effects of Symbiodinium (Pyrrhophyta) identity on growth, survivorship, and thermal tolerance of newly settled coral recruits. *Journal of Phycology*, 52, 1114–1124. https://doi.org/10.1111/jpy.12471 (McIlroy et al. 2016)

For many coral species, the obligate association with phylogenetically diverse algal endosymbiont species is dynamic in time and space. Here, we used controlled laboratory inoculations of newly settled, aposymbiotic corals (Orbicella faveolata) with two cultured species of algal symbiont (Symbiodinium microadriaticum and S. minutum) to examine the role of symbiont identity on growth, survivorship, and thermal tolerance of the coral holobiont. We evaluated these data in the context of Symbiodinium photophysiology for 9 months post-settlement and also during a 5-d period of elevated temperatures Our data show that recruits that were inoculated with S. minutum grew significantly slower than those inoculated with S. microadriaticum (occasionally co-occurring with S. minutum), but that there was no difference in survivorship of O. faveolata polyps infected with Symbiodinium. However, photophysiological metrics (ΔFv/F′m, the efficiency with which available light is used to drive photosynthesis and α, the maximum light utilization coefficient) were higher in those slower growing recruits containing S. minutum. These findings suggest that light use (i.e., photophysiology) and carbon acquisition by the coral host (i.e., host growth) are decoupled, but did not distinguish the source of this difference. Neither Symbiodinium treatment demonstrated a significant negative effect of a 5-d exposure to temperatures as high as 32°C under low light conditions similar to those measured at settlement habitats.

McIlroy, S. E. & Coffroth, M. A. (2017). Coral ontogeny affects early symbiont acquisition in laboratory-reared recruits. *Coral Reefs*, 36, 927–932. https://doi.org/10.1007/s00338-017-1584-7 (McIlroy and Coffroth 2017)

In most coral species, the critical association with a subset of genetically diverse algal endosymbionts, Symbiodinium, is re-established anew each generation in early coral ontogeny. Yet little is known about the window during which these associations are established or the potential for altering symbiont associations through early exposure to non-native, and/or ecologically beneficial (e.g., stress tolerant), symbiont strains. This study examined the ontogenetic window of symbiont uptake in a restoration target species. Orbicella faveolata recruits, maintained aposymbiotic in laboratory tanks for 4 months, showed a significant decrease in symbiont acquisition upon exposure to natural seawater. Recruits initially inoculated with cultured Symbiodinium readily acquired additional strains from environmental symbiont populations upon exposure, but exogenous uptake also decreased in frequency after 4 months of laboratory rearing. Early exposure to Symbiodinium may benefit laboratory-reared recruits (e.g., enhance growth), but the potential for establishing long-term novel symbiotic associations may be limited.

Miller, M. W. (2014). Post-settlement survivorship in two Caribbean broadcasting corals. *Coral Reefs*, 33, 1041–1046. https://doi.org/10.1007/s00338-014-1177-7 (Miller 2014)

The post-settlement phase of broadcast-spawned coral life histories is poorly known due to its almost complete undetectability and, hence, presumed low abundance in the field. We used lab-cultured settled polyps of two important Caribbean reef-building species with negligible larval recruitment to quantify early post-settlement survivorship (6–9 weeks) over multiple years/cohorts and differing orientation on a reef in the Florida Keys. Orbicella faveolata showed significantly and consistently better survivorship in vertical rather than horizontal orientation, but no discernable growth overall. Meanwhile, Acropora palmata showed no significant difference in survivorship between orientations, but significantly greater

growth in the horizontal orientation. Both species showed significant variation in mean survivorship between cohorts of different years; 0–47 % for O. faveolata and 12–49 % for A. palmata over the observed duration. These results demonstrate wide variation in success of cohorts and important differences in the larval recruitment capacities of these two important but imperiled reef-building species.

Miller, M. W., A. J. Bright, R. E. Pausch, and D. E. Williams. 2020. Larval longevity and competency patterns of Caribbean reef-building corals. PeerJ 8:e9705. https://peerj.com/articles/9705/ (Miller et al. 2020a)

The potential for long-distance larval dispersal depends on the longevity of planktonic, free-swimming larvae and their capacity to successfully recruit to reef habitat. We present multi-year laboratory observations of the persistence of planular larvae and settlement competency over time for cohorts derived from the same parental populations of the most important Caribbean reef building coral species, Orbicella faveolata and Acropora spp. Despite variability among years/cohorts, larvae of both species display capacity for extended longevity (up to 83 d) and competency (demonstrated at up to 48 d). Both species also displayed significantly reduced survivorship and lower realized settlement under elevated temperatures. Although the observed levels of settlement in 24 h competency assays was extremely variable, the timing of onset of competence were highly consistent among years/cohorts but distinct between species. Orbicella faveolata displayed onset of competence during day 3-5 or 4-7 (with or without exposure to positive settlement cue) after spawning; whereas, onset for Acropora spp. was day 7-8 or day 10-11 (with or without cue, respectively). This longer pre-competency period for Acropora spp. nonetheless corresponded to a greater persistence of A. palmata larvae to this age of competence (71-83% of initial cohort compared to 54-55% for O. faveolata). Such life history variation implies meaningful differences in likely dispersal potential between these imperiled reef-building species.

Rico-Esenaro, S. D., Sanchez-Cabeza, J.-A., Carricart-Ganivet, J. P., Montagna, P. & Ruiz-Fernández, A. C. (2019). Uncertainty and variability of extension rate, density and calcification rate of a hermatypic coral (Orbicella faveolata). *Science of The Total Environment*, 650, 1576–1581. https://doi.org/10.1016/j.scitotenv.2018.08.397 (Rico-Esenaro et al. 2019)

Skeleton growth variables of hermatypic corals, such as extension rate, density and calcification rate, are widely used to study coral response to environmental stressors, establish chronological age models and reconstruct the evolution of key climate variables. In this work, we addressed methodological aspects of the measurement of coral growth variables and the implications of their variability. A core of Orbicella faveolata was collected from the Puerto Morelos coral reef, in the Mexican Caribbean, and we measured and analysed 10 parallel transects of a core slab, covering 30 years. Density calibration was performed by measuring a high-quality and well-characterised wedge of Tridacna maxima, and the interval of interest was adjusted to the measured coral optical densities. The measurement uncertainties of extension rate, density and calcification rate were 0.011%, 1.1% and 1.6%, respectively. However, for density and calcification rate, overall variability was 29% and 33%, respectively, of which about half was attributed to intra-band growth variability. The intra-band variability of extension rate was only 0.68%, indicating the suitability of extension rate as a precise environmental proxy. These results likely differ by coral species, environments and experimental conditions, such as the exact location of the core within the colony and

the method used to determine density. Uncertainties of coral growth variables should be carefully considered when reconstructing past environmental conditions.

Abundance, Population, and Demographic Features and Trends

> Bruckner, A. W., Beck, B. & Renaud, P. (2014). The status of coral reefs and associated fishes and invertebrates of commercial importance in Pedro Bank, Jamaica. *Rev. Biol. Trop.*, 62, 11–24. https://doi.org/10.15517/rbt.v62i0.15898 (Bruckner et al. 2014)

The coral reefs located off the north coast of the Jamaican mainland are some of the best and most studied reefs in the world. Coral reefs of Pedro Bank, Jamaica were assessed in March, 2012 as part of the KSLOF Global Reef Expedition using a modified Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol. The main objectives were to: 1) characterize the distribution, structure and health of coral reefs; and 2) evaluate the population status of commercially important reef fishes and invertebrates. This work was conducted to assist in characterizing coral reef habitats within and outside a proposed fishery reserve, and identify other possible conservation zones. Within 20 reefs, live coral cover ranged from 4.9% to 19.2%. Coral communities were dominated by small corals (esp. Agaricia, Porites and Siderastrea) although many sites had high abundances of large colonies of Montastraea annularis and M. faveolata, and these were generally in good condition. A single area, within the proposed fishery reserve, had extensive Acropora cervicornis thickets, and several shallow locations had small, but recovering A. palmata stands. Macroalgal cover at all sites was relatively low, with only three sites having greater than 30% cover; crustose coralline algae (CCA) was high, with eight sites exceeding 20% cover. Fish biomass at all sites near the Cays was low, with a dominance of herbivores (parrotfish and surgeonfish) and a near absence of groupers, snappers and other commercially important species. While parrotfish were the most abundant fish, these were all extremely small (mean size= 12cm; <4% over 29cm), and they were dominated by red band parrotfish (Sparisoma aurofrenatum) followed by striped parrotfish (Scarus iseri). While coral communities remain in better condition than most coastal reefs in Jamaica, intense fishing pressure using fish traps (main target species: surgeonfish) and hookah/spear fishing (main target: parrotfish) is of grave concern to the future persistence of these reefs. The proposed fishery reserve encompasses some of the best coral reef habitat near the Cays, but this MPA should be expanded to encompass other habitats and MPAs should be considered for bank reefs at the northwestern end, as well as Banner Reef and Blowers Rock.

> Holstein, D. M., Smith, T. B., Gyory, J. & Paris, C. B. (2015). Fertile fathoms: Deep reproductive refugia for threatened shallow corals. *Sci. Rep.*, 5, 12407. https://doi.org/10.1038/srep12407 (Holstein et al. 2015)

The persistence of natural metapopulations may depend on subpopulations that exist at the edges of species ranges, removed from anthropogenic stress. Mesophotic coral ecosystems (30-150 m) are buffered from disturbance by depth and distance, and are potentially massive reservoirs of coral diversity and fecundity; yet we know little about the reproductive capabilities of their constituent species and the potential for these marginal environments to influence patterns of coral reef persistence. We investigated the reproductive performance of the threatened depth-generalist coral Orbicella faveolata over the extent

of its vertical range to assess mesophotic contributions to regional larval pools. Over equal habitat area, mesophotic coral populations were found to produce over an order of magnitude more eggs than nearby shallow populations. Positive changes with depth in both population abundance and polyp fecundity contributed to this discrepancy. Relative larval pool contributions of deeper living corals will likely increase as shallow habitats further degrade due to climate change and local habitat degradation. This is a compelling example of the potential for marginal habitat to be critical to metapopulation persistence as reproductive refugia.

Genetic Assessment

> Anderson, D. A., Walz, M. E., Weil, E., Tonellato, P. & Smith, M. C. (2016). RNA-Seq of the Caribbean reef-building coral Orbicella faveolata (Scleractinia-Merulinidae) under bleaching and disease stress expands models of coral innate immunity. *PeerJ*, 4:e1616. https://doi.org/10.7717/peerj.1616 (Anderson et al. 2016)

Climate change-driven coral disease outbreaks have led to widespread declines in coral populations. Early work on coral genomics established that corals have a complex innate immune system, and whole-transcriptome gene expression studies have revealed mechanisms by which the coral immune system responds to stress and disease. The present investigation expands bioinformatic data available to study coral molecular physiology through the assembly and annotation of a reference transcriptome of the Caribbean reef-building coral, Orbicella faveolata. Samples were collected during a warm water thermal anomaly, coral bleaching event and Caribbean yellow band disease outbreak in 2010 in Puerto Rico. Multiplex sequencing of RNA on the Illumina GAIIx platform and de novo transcriptome assembly by Trinity produced 70,745,177 raw short-sequence reads and 32,463 O. faveolata transcripts, respectively. The reference transcriptome was annotated with gene ontologies, mapped to KEGG pathways, and a predicted proteome of 20,488 sequences was generated. Protein families and signaling pathways that are essential in the regulation of innate immunity across Phyla were investigated in-depth. Results were used to develop models of evolutionarily conserved Wnt, Notch, Rig-like receptor, Nod-like receptor, and Dicer signaling. O. faveolata is a coral species that has been studied widely under climate-driven stress and disease, and the present investigation provides new data on the genes that putatively regulate its immune system.

> Barfield, S., Aglyamova, G. V. & Matz, M. V. (2016). Evolutionary origins of germline segregation in Metazoa: evidence for a germ stem cell lineage in the coral Orbicella faveolata (Cnidaria, Anthozoa). *Proceedings of the Royal Society B: Biological Sciences*, 283:20152128. https://doi.org/10.1098/rspb.2015.2128 (Barfield et al. 2016)

The ability to segregate a committed germ stem cell (GSC) lineage distinct from somatic cell lineages is a characteristic of bilaterian Metazoans. However, the occurrence of GSC lineage specification in basally branching Metazoan phyla, such as Cnidaria, is uncertain. Without an independently segregated GSC lineage, germ cells and their precursors must be specified throughout adulthood from continuously dividing somatic stem cells, generating the risk of propagating somatic mutations within the individual and its gametes. To address the potential for existence of a GSC lineage in Anthozoa, the sister-group to all remaining Cnidaria, we identified moderate- to high-frequency somatic mutations and their potential

for gametic transfer in the long-lived coral Orbicella faveolata (Anthozoa, Cnidaria) using a 2b-RAD sequencing approach. Our results demonstrate that somatic mutations can drift to high frequencies (up to 50%) and can also generate substantial intracolonial genetic diversity. However, these somatic mutations are not transferable to gametes, signifying the potential for an independently segregated GSC lineage in O. faveolata. In conjunction with previous research on germ cell development in other basally branching Metazoan species, our results suggest that the GSC system may be a Eumetazoan characteristic that evolved in association with the emergence of greater complexity in animal body plan organization and greater specificity of stem cell functions.

Dimos, B. A., Butler, C. C., Ricci, C. A., MacKnight, N. J. & Mydlarz, L. D. (2019). Responding to Threats Both Foreign and Domestic: NOD-Like Receptors in Corals. *Integrative and Comparative Biol*ogy, 59, 819–829. https://doi.org/10.1093/icb/icz111 (Dimos et al. 2019)

Historically mechanisms with which basal animals such as reef-building corals use to respond to changing and increasingly stressful environments have remained elusive. However, the increasing availability of genomic and transcriptomic data from these organisms has provided fundamental insights into the biology of these critically important ecosystem engineers. Notably, insights into cnidarians gained in the post-genomics age have revealed a surprisingly complex immune system which bears a surprising level of similarity with the vertebrate innate immune system. This system has been critically linked to how corals respond to the two most prominent threats on a global scale, emerging coral diseases and increasing water temperature, which are recognized cellularly as either foreign or domestic threats, respectively. These threats can arise from pathogenic microbes or internal cellular dysfunction, underscoring the need to further understand mechanisms corals use to sense and respond to threats to their cellular integrity. In this investigation and meta-analysis, we utilize resources only recently available in the post-genomic era to identify and characterize members of an underexplored class of molecules known as NOD-like receptors in the endangered Caribbean coral Orbicella faveolata. We then leverage these data to identify pathways possibly mediated by NLRs in both O. faveolata and the ecologically important branching coral Acropora digitifera. Overall, we find support that this class of proteins may provide a mechanistic link to how reef-building corals respond to threats both foreign and domestic.

Dziedzic, K. E., Elder, H., Tavalire, H. & Meyer, E. (2019). Heritable variation in bleaching responses and its functional genomic basis in reef-building corals (Orbicella faveolata). *Molecular Ecology*, 28(9), 2238–2253. https://doi.org/10.1111/mec.15081 (Dziedzic et al. 2019)

Reef-building corals are highly sensitive to rising ocean temperatures, and substantial adaptation will be required for corals and the ecosystems they support to persist in changing ocean conditions. Genetic variation that might support adaptive responses has been measured in larval stages of some corals, but these estimates remain unavailable for adult corals and the functional basis of this variation remains unclear. In this study, we focused on the potential for adaptation in Orbicella faveolata, a dominant reef-builder in the Caribbean. We conducted thermal stress experiments using corals collected from natural populations in Bocas del Toro, Panama, and used multilocus SNP genotypes to estimate genetic relatedness among samples. This allowed us to estimate narrow-sense heritability of variation in

bleaching responses, revealing that variation in these responses was highly heritable (h2 = 0.58). This suggests substantial potential for adaptive responses to warming by natural populations of O. faveolata in this region. We further investigated the functional basis for this variation using genomic and transcriptomic approaches. We used a publicly available genetic linkage map and genome assembly to map markers associated with bleaching responses, identifying twelve markers associated with variation in bleaching responses. We also profiled gene expression in corals with contrasting bleaching phenotypes, uncovering substantial differences in transcriptional stress responses between heat-tolerant and heat-susceptible corals. Together, our findings contribute to the growing body of evidence that natural populations of corals possess genetic variation in thermal stress responses that may potentially support adaptive responses to rising ocean temperatures.

Green, E. A., Davies, S. W., Matz, M. V. & Medina, M. (2014). Quantifying cryptic *Symbiodinium* diversity within *Orbicella faveolata* and *Orbicella franksi* at the Flower Garden Banks, Gulf of Mexico. *PeerJ*, 2:e386. https://doi.org/10.7717/peerj.386 (Green et al. 2014)

The genetic composition of the resident Symbiodinium endosymbionts can strongly modulate the physiological performance of reef-building corals. Here, we used quantitative metabarcoding to investigate Symbiodinium genetic diversity in two species of mountainous star corals, Orbicella franksi and Orbicella faveolata, from two reefs separated by 19 km of deep water. We aimed to determine if the frequency of different symbiont genotypes varied with respect to coral host species or geographic location. Our results demonstrate that across the two reefs both coral species contained seven haplotypes of Symbiodinium, all identifiable as clade B and most closely related to type B1. Five of these haplotypes have not been previously described and may be endemic to the Flower Garden Banks. No significant differences in symbiont composition were detected between the two coral species. However, significant quantitative differences were detected between the east and west banks for three background haplotypes comprising 0.1%–10% of the total. The quantitative metabarcoding approach described here can help to sensitively characterize cryptic genetic diversity of Symbiodinium and potentially contribute to the understanding of physiological variations among coral populations.

Manzello, D. P., Matz, M. V., Enochs, I. C., Valentino, L., Carlton, R. D., Kolodziej, G., . . . Jankulak, M. (2019). Role of host genetics and heat-tolerant algal symbionts in sustaining populations of the endangered coral *Orbicella faveolata* in the Florida Keys with ocean warming. *Global Change Biology*, 25(3), 1016–1031. https://doi.org/10.1111/gcb.14545 (Manzello et al. 2019)

Identifying which factors lead to coral bleaching resistance is a priority given the global decline of coral reefs with ocean warming. During the second year of back-to-back bleaching events in the Florida Keys in 2014 and 2015, we characterized key environmental and biological factors associated with bleaching resilience in the threatened reef-building coral Orbicella faveolata. Ten reefs (five inshore, five offshore, 179 corals total) were sampled during bleaching (September 2015) and recovery (May 2016). Corals were genotyped with 2bRAD and profiled for algal symbiont abundance and type. O. faveolata at the inshore sites, despite higher temperatures, demonstrated significantly higher bleaching resistance and better recovery compared to offshore. The thermotolerant Durusdinium trenchii (formerly Symbiondinium

trenchii) was the dominant endosymbiont type region-wide during initial (78.0% of corals sampled) and final (77.2%) sampling; >90% of the nonbleached corals were dominated by D. trenchii. 2bRAD host genotyping found no genetic structure among reefs, but inshore sites showed a high level of clonality. While none of the measured environmental parameters were correlated with bleaching, 71% of variation in bleaching resistance and 73% of variation in the proportion of D. trenchii was attributable to differences between genets, highlighting the leading role of genetics in shaping natural bleaching patterns. Notably, D. trenchii was rarely dominant in O. faveolata from the Florida Keys in previous studies, even during bleaching. The region-wide high abundance of D. trenchii was likely driven by repeated bleaching associated with the two warmest years on record for the Florida Keys (2014 and 2015). On inshore reefs in the Upper Florida Keys, O. faveolata was most abundant, had the highest bleaching resistance, and contained the most corals dominated by D. trenchii, illustrating a causal link between heat tolerance and ecosystem resilience with global change.

Miller, M. W., Baums, I. B., Pausch, R. E., Bright, A. J., Cameron, C. M., Williams, D. E., . . . Woodley, C. M. (2018). Clonal structure and variable fertilization success in Florida Keys broadcast-spawning corals. *Coral Reefs*, 37, 239–249. https://doi.org/10.1007/s00338-017-1651-0 (Miller et al. 2018)

Keystone reef-building corals in the Caribbean are predominantly self-incompatible broadcast spawners and a majority are threatened due to both acute adult mortality and poor recruitment. As population densities decline, concerns about fertilization limitation and effective population size in these species increase and would be further exacerbated by either high clonality or gametic incompatibility of parental genotypes. This study begins to address these concerns for two Caribbean broadcasting species by characterizing clonal structure and quantifying experimental pairwise fertilization success. Orbicella faveolata showed surprisingly high and contrasting levels of clonality between two sampled sites; Acropora palmata was previously known to be highly clonal. Individual pairwise crosses of synchronously spawning genotypes of each species were conducted by combining aliquots of gamete bundles immediately after spawning, and showed high and significant variability in fertilization success. Over half of the individual crosses of O. faveolata and about one-third of A. palmata crosses yielded ≤ 40% fertilization. Total sperm concentration was quantified in only a subset of O. faveolata crosses (range of 1–6 × 107 mL−1), but showed no correlation with fertilization success. We interpret that both parental incompatibility and individual genotypes with low-quality gametes are likely to have contributed to the variable fertilization observed with important implications for conservation. Differential fertilization success implies effective population size may be considerably smaller than hoped and population enhancement efforts need to incorporate many more parental genotypes at the patch scale to ensure successful larval production than indicated by estimates based simply on preserving levels of standing genetic diversity.

Porto-Hannes, I., Zubillaga, A. L., Shearer, T. L., Bastidas, C., Salazar, C., Coffroth, M. A. & Szmant, A. M. (2015). Population structure of the corals *Orbicella faveolata* and *Acropora palmata* in the Mesoamerican Barrier Reef System with comparisons over Caribbean basin-wide spatial scale. *Marine Biology*, 162(1), 81–98. https://doi.org/10.1007/s00227-014-2560-1 (Porto-Hannes et al. 2015)

Studies of genetic diversity and population genetic structure in marine organisms are relevant to understanding populations' variability, and therefore their ability to withstand environmental perturbations, their potential for resistance to local extinction and their natural rate of recovery. Population structure and genetic diversity were assessed at a regional spatial scale (i.e., Mesoamerican Barrier Reef System, MBRS) in two major reef building coral species Orbicella (formerly Montastraea) faveolata and Acropora palmata, and at a larger spatial scale (i.e., Caribbean-wide; MBRS, Panama, Venezuela and Puerto Rico) for A. palmata only. The most significant findings were as follows: (1) high genetic diversity and low clonality were found for both species, which is expected for O. faveolata but not for A. palmata, (2) both species showed low-to-moderate, yet significant population structure among populations along the MBRS; in particular, O. faveolata and A. palmata from Ambergris (Belize) and O. faveolata from Calabash (Belize) and A. palmata from Puerto Morelos (Mexico) showed some genetic differentiation from the rest of the MBRS populations, and (3) A. palmata from MBRS, Panama, Puerto Rico and Venezuela were grouped into four subregions that could be considered as management units. A more spatially detailed sampling program and the inclusion of recruits will be necessary to get a comprehensive understanding of coral population structure and current gene flow patterns in these two species.

Rippe, J. P., Matz, M. V., Green, E. A., Medina, M., Khawaja, N. Z., Pongwarin, T., . . . Davies, S. W. (2017). Population structure and connectivity of the mountainous star coral, Orbicella faveolata, throughout the wider Caribbean region. *Ecology and Evolution* **7**, 9234–9246. https://doi.org/10.1002/ece3.3448 (Rippe et al. 2017)

As coral reefs continue to decline worldwide, it becomes ever more necessary to understand the connectivity between coral populations to develop efficient management strategies facilitating survival and adaptation of coral reefs in the future. Orbicella faveolata is one of the most important reef-building corals in the Caribbean and has recently experienced severe population reductions. Here, we utilize a panel of nine microsatellite loci to evaluate the genetic structure of O. faveolata and to infer connectivity across ten sites spanning the wider Caribbean region. Populations are generally well-mixed throughout the basin (FST = 0.038), although notable patterns of substructure arise at local and regional scales. Eastern and western populations appear segregated with a genetic break around the Mona Passage in the north, as has been shown previously in other species; however, we find evidence for significant connectivity between Curaçao and Mexico, suggesting that the southern margin of this barrier is permeable to dispersal. Our results also identify a strong genetic break within the Mesoamerican Barrier Reef System associated with complex oceanographic patterns that promote larval retention in southern Belize. Additionally, the diverse genetic signature at Flower Garden Banks suggests its possible function as a downstream genetic sink. The findings reported here are relevant to the ongoing conservation efforts for this important and threatened species, and contribute to the growing understanding of large-scale coral reef connectivity throughout the wider Caribbean.

Ulmo-Díaz, G., Casane, D., Bernatchez, L., González-Díaz, P., Appril, A., Castellanos-Gell, J., . . . García-Machado, E. (2018). Genetic differentiation in the mountainous star coral Orbicella faveolata around Cuba. *Coral Reefs*, 37(4), 1217–1227. https://doi.org/10.1007/s00338-018-1722-x (Ulmo-Díaz et al. 2018)

Caribbean coral reefs are biodiversity-rich habitats which provide numerous ecosystem services with both ecological and economical values, but nowadays they are severely degraded. In particular, populations of the major framework-building coral Orbicella faveolata have declined sharply, and therefore, understanding how these threatened coral populations are interconnected and how demographic changes have impacted their genetic diversity is essential for their management and conservation. Previous population genetic surveys showed that gene flow in this species is sometimes locally restricted in the Caribbean; however, little genetic data are available for Cuban populations. Here, we analyzed the variation at the mitochondrial DNA control region and six microsatellite loci from O. faveolata colonies from five distant localities representing most of the main coral reefs around Cuba. Both genetic markers showed evidence of genetic differentiation between the northwestern area (Colorados Archipelago) and the other reefs. Colonies from the Colorados Archipelago harbored the largest number of unique mtDNA haplotypes and microsatellite alleles, which suggests long-term large population size or gene flow from other areas of the Caribbean. These results indicate that the Colorados Archipelago area is particularly important for O. faveolata populations and it is well suited for reef management and restoration efforts.

Williams, L. M., Fuess, L. E., Brennan, J. J., Mansfield, K. M., Salas-Rodriguez, E., Welsh, J., . . . Gilmore, T. D. (2018). A conserved Toll-like receptor-to-NF-κB signaling pathway in the endangered coral Orbicella faveolata. *Developmental & Comparative Immunology*, 79, 128–136. https://doi.org/10.1016/j.dci.2017.10.016 (Williams et al. 2018)

Herein, we characterize the Toll-like receptor (TLR)-to-NF-κB innate immune pathway of Orbicella faveolata (Of), which is an ecologically important, disease-susceptible, reef-building coral. As compared to human TLRs, the intracellular TIR domain of Of-TLR is most similar to TLR4, and it can interact in vitro with the human TLR4 adapter MYD88. Treatment of O. faveolata tissue with lipopolysaccharide, a ligand for mammalian TLR4, resulted in gene expression changes consistent with NF-κB pathway mobilization. Biochemical and cell-based assays revealed that Of-NF-κB resembles the mammalian non-canonical NF-κB protein p100 in that C-terminal truncation results in translocation of Of-NF-κB to the nucleus and increases its DNA-binding and transcriptional activation activities. Moreover, human IκB kinase (IKK) and Of-IKK can both phosphorylate conserved residues in Of-NF-κB in vitro and induce C-terminal processing of Of-NF-κB in vivo. These results are the first characterization of TLR-to-NF-κB signaling proteins in an endangered coral, and suggest that these corals have conserved innate immune pathways.

Wright, R. M., Correa, A. M. S., Quigley, L. A., Santiago-Vázquez, L. Z., Shamberger, K. E. F. & Davies, S. W. (2019). Gene Expression of Endangered Coral (*Orbicella* spp.) in Flower Garden Banks National Marine Sanctuary After Hurricane Harvey. *Frontiers in Marine Science.* 6:672. https://doi.org/10.3389/fmars.2019.00672 (Wright et al. 2019)

About 190 km south of the Texas–Louisiana border, the East and West Flower Garden Banks (FGB) have maintained >50% coral cover with infrequent and minor incidents of disease or bleaching since monitoring began in the 1970s. However, a mortality event, affecting 5.6 ha (2.6% of the area) of the East FGB, occurred in late July 2016 and coincided with storm-generated freshwater runoff extending offshore and over the reef system. To capture the immediate effects of storm-driven freshwater runoff on coral and

symbiont physiology, we leveraged the heavy rainfall associated with Hurricane Harvey in late August 2017 by sampling FGB corals at two time points: September 2017, when surface water salinity was reduced (~34 ppt); and one month later when salinity had returned to typical levels (~36 ppt in October 2017). Tissue samples (N = 47) collected midday were immediately preserved for gene expression profiling from two congeneric coral species (Orbicella faveolata and Orbicella franksi) from the East and West FGB to determine the physiological consequences of storm-derived runoff. In the coral, differences between host species and sampling time points accounted for the majority of differentially expressed genes. Gene ontology enrichment for genes differentially expressed immediately after Hurricane Harvey indicated increases in cellular oxidative stress responses. Although tissue loss was not observed on FGB reefs following Hurricane Harvey, our results suggest that poor water quality following this storm caused FGB corals to experience sub-lethal stress. We also found dramatic expression differences across sampling time points in the coral's algal symbiont, Breviolum minutum. Some of these differentially expressed genes may be involved in the symbionts' response to changing environments, including a group of differentially expressed post-transcriptional RNA modification genes. In this study, we cannot disentangle the effects of reduced salinity from the collection time point, so these expression patterns could also be related to seasonality. These findings highlight the urgent need for continued monitoring of these reef systems to establish a baseline for gene expression of healthy corals in the FGB system across seasons, as well as the need for integrated solutions to manage stormwater runoff in the Gulf of Mexico.

Spatial Distribution

> Rodríguez-Zaragoza, F. A. & Arias-González, J. E. (2015). Coral biodiversity and bio-construction in the northern sector of the mesoamerican reef system. *Front. Mar. Sci.*, 2:13. https://doi.org/10.3389/fmars.2015.00013 (Rodríguez-Zaragoza and Arias-González 2015)

As the impact of anthropogenic activity and climate change continue to accelerate rates of degradation on Caribbean coral reefs, conservation and restoration faces greater challenges. At at this stage, of particular importance in coral reefs, is to recognize and to understand the structural spatial patterns of benthic assemblages. We developed a field-based framework of a Caribbean reefscape benthic structure by using hermatypic corals as an indicator group of global biodiversity and bio-construction patterns in eleven reefs of the northern sector of the Mesoamerican Barrier Reef System (nsMBRS). Four hundred and seventy four video-transects (50 m long by 0.4 m wide) were performed throughout a gradient of reef complexity from north to south (□400 km) to identify coral species, families and ensembles of corals. Composition and abundance of species, families and ensembles showed differences among reefs. In the northern zone, the reefs had shallow, partial reef developments with low diversities, dominated by Acropora palmata, Siderastrea spp., Pseudodiploria strigosa and Agaricia tenuifolia. In the central and southern zones, reefs presented extensive developments, high habitat heterogeneity, and the greatest diversity and dominance of Orbicella annularis and Orbicella faveolata. These two species determined the structure and diversity of corals in the central and southern zones of the nsMBRS and their bio-construction in these zones is unique in the Caribbean. Their abundance and distribution depended on the reef habitat area, topographic complexity and species richness. Orbicella species complex were crucial for maintaining the biodiversity and bio-construction of the central and southern zones while A. palmata in the northern zones of the nsMBRS.

Habitat and Ecosystem Conditions

> Kemp, D. W., Thornhill, D.J., Rotjan, R.D., Iglesias-Prieto, R., Fitt, W.K. & Schmidt, G.W. (2015). Spatially distinct and regionally endemic Symbiodinium assemblages in the threatened Caribbean reef-building coral Orbicella faveolata. *Coral Reefs*, 34(2), 535–547. https://doi.org/10.1007/s00338-015-1277-z (Kemp et al. 2015)

Recently, the Caribbean reef-building coral Orbicella faveolata was listed as "threatened" under the U.S. Endangered Species Act. Despite attention to this species' conservation, the extent of geographic variation within O. faveolata warrants further investigation. O. faveolata is unusual in that it can simultaneously harbor multiple genetically distinct and co-dominant species of endosymbiotic dinoflagellates in the genus Symbiodinium. Here, we investigate the geographic and within-colony complexity of Symbiodinium-O. faveolata associations from Florida Keys, USA; Exuma Cays, Bahamas; Puerto Morelos, Mexico; and Carrie Bow Cay, Belize. We collected coral samples along intracolony axes, and Symbiodinium within O. faveolata samples was analyzed using the nuclear ITS2 region and chloroplast 23S rDNA genotyping. O. faveolata associated with species of Symbiodinium in clades A (type A3), B (B1 and B17), C (C3, C7, and C7a), and D (D1a/Symbiodinium trenchii). Within-colony distributions of Symbiodinium species correlated with light availability, cardinal direction, and depth, resulting in distinct zonation patterns of endosymbionts within a host. Symbiodinium species from clades A and B occurred predominantly in the light-exposed tops, while species of clade C generally occurred in the shaded sides of colonies or in deeper-water habitats. Furthermore, geographic comparisons of host–symbiont associations revealed regional differences in Symbiodinium associations. Symbiodinium A3 was detected in Mesoamerican coral colonies, but not in colonies from the Florida Keys or Bahamas. Likewise, Symbiodinium B17 was unique to Mesoamerican O. faveolata, whereas Symbiodinium B1 was found at all localities sampled. However, using cp23S genotyping paired with ITS2 analysis revealed geographically endemic haplotypes among Symbiodinium clades A, B, and C. Since Symbiodinium spatial heterogeneity among this coral species is greater than most corals, a question arises as to whether all western Atlantic populations of O. faveolata should be considered equally "threatened"? Alternatively, geographically and spatially distinct coral–symbiont associations may benefit from specialized management protocols.

> Lillis, A., Bohnenstiehl, D., Peters, J. W. & Eggleston, D. (2016). Variation in habitat soundscape characteristics influences settlement of a reef-building coral. *PeerJ*, 4:e2557. https://doi.org/10.7717/peerj.2557 (Lillis et al. 2016)

Coral populations, and the productive reef ecosystems they support, rely on successful recruitment of reef-building species, beginning with settlement of dispersing larvae into habitat favourable to survival. Many substrate cues have been identified as contributors to coral larval habitat selection; however, the potential for ambient acoustic cues to influence coral settlement responses is unknown. Using in situ settlement chambers that excluded other habitat cues, larval settlement of a dominant Caribbean reef-building coral, Orbicella faveolata, was compared in response to three local soundscapes, with differing acoustic and habitat properties. Differences between reef sites in the number of larvae settled in chambers isolating acoustic cues corresponded to differences in sound levels and reef characteristics, with sounds at the loudest reef generating significantly higher settlement during trials compared to the quietest site (a

29.5 % increase). These results suggest that soundscapes could be an important influence on coral settlement patterns and that acoustic cues associated with reef habitat may be related to larval settlement. This study reports an effect of soundscape variation on larval settlement for a key coral species, and adds to the growing evidence that soundscapes affect marine ecosystems by influencing early life history processes of foundational species.

Manzello, D. P., Enochs, I. C., Kolodziej, G. & Carlton, R. (2015). Recent decade of growth and calcification of Orbicella faveolata in the Florida Keys: an inshore-offshore comparison. *Marine Ecology Progress Series* 521, 81–89. https://doi.org/10.3354/meps11085 (Manzello et al. 2015)

Coral reefs along the Florida Keys portion of the Florida Reef Tract (FRT) have undergone a dramatic decline since the 1980s. Since the 1997-1998 El Niño event, coral cover on offshore reefs of the FRT has been ≤5% and continues to decline. Mortality of the framework-constructing coral in the Orbicella (formerly Montastraea) annularis species complex has driven this recent loss in overall coral cover. One exception to this decline occurred on the inshore patch reefs of the Florida Keys, where coral cover has remained relatively high. We examined the growth and calcification of Orbicella faveolata, an ecologically important subspecies of the O. annularis complex, at both an inshore and an offshore reef site representing this dichotomy of present-day coral cover. The period examined (2004 to 2013) encompasses the Caribbean-wide 2005 mass coral bleaching, the 2009-2010 catastrophic cold-water bleaching, and a warm-water bleaching event in 2011. Extension and calcification rates were higher inshore every year from 2004 to 2013 except when there were thermal stress events that solely impacted inshore reefs (as in 2009-2010 and 2011). Inshore growth rates recovered quickly from cold and warm-water stress. These higher calcification rates and their quick recovery after thermal stress are likely important factors in the persistence of high coral cover inshore.

Oliver, L. M., Fisher, W. S., Fore, L., Smith, A. & Bradley, P. (2018). Assessing land use, sedimentation, and water quality stressors as predictors of coral reef condition in St. Thomas, U.S. Virgin Islands. *Environ Monit Assess*, 190(4), 213. https://doi.org/10.1007/s10661-018-6562-1 (Oliver et al. 2018)

Coral reef condition on the south shore of St. Thomas, U.S. Virgin Islands, was assessed at various distances from Charlotte Amalie, the most densely populated city on the island. Human influence in the area includes industrial activity, wastewater discharge, cruise ship docks, and impervious surfaces throughout the watershed. Anthropogenic activity was characterized using a landscape development intensity (LDI) index, sedimentation threat (ST) estimates, and water quality (WQ) impairments in the near-coastal zone. Total three-dimensional coral cover, reef rugosity, and coral diversity had significant negative coefficients for LDI index, as did densities of dominant species Orbicella annularis, Orbicella franksi, Montastraea cavernosa, Orbicella faveolata, and Porites porites. However, overall stony coral colony density was not significantly correlated with stressors. Positive relationships between reef rugosity and ST, between coral diversity and ST, and between coral diversity and WQ were unexpected because these stressors are generally thought to negatively influence coral growth and health. Sponge density was greater with higher disturbance indicators (ST and WQ), consistent with reports of greater resistance by sponges to degraded water quality compared to stony corals. The highest FoRAM (Foraminifera in Reef

Assessment and Monitoring) indices indicating good water quality were found offshore from the main island and outside the harbor. Negative associations between stony coral metrics and LDI index have been reported elsewhere in the Caribbean and highlight LDI index potential as a spatial tool to characterize land-based anthropogenic stressor gradients relevant to coral reefs. Fewer relationships were found with an integrated stressor index but with similar trends in response direction.

Speare, K. E., Duran, A., Miller, M. W. & Burkepile, D. E. (2019). Sediment associated with algal turfs inhibits the settlement of two endangered coral species. *Mar. Pollut. Bull.,* 144, 189–195. https://doi.org/10.1016/j.marpolbul.2019.04.066 (Speare et al. 2019)

Populations of Acropora palmata and Orbicella faveolata, two important reef-building corals, have declined precipitously across the Caribbean region since at least the 1970s. Recruitment failure may be limiting population recovery, possibly due to lack of suitable settlement habitat. Here, we examine the effects of algal turfs and algal turfs + sediment, two widely abundant substrate types across the Florida Keys, on the settlement of these two ecologically-important species. We show that sediment significantly impedes coral settlement, reducing settlement 10- and 13-fold for A. palmata and O. faveolata, respectively, compared to turf algae alone. This result is corroborated by our field survey data that showed a strong, negative relationship between the abundance of turf + sediment and the abundance of juvenile corals. Turf algae alone did not reduce coral settlement. Our results suggest that sediment-laden turf algae are detrimental to settling corals, but that turf algae alone may be relatively benign.

Towle, E. K., Palacio-Castro, A. M., Baker, A. C. & Langdon, C. (2017). Source location and food availability determine the growth response of Orbicella faveolata to climate change stressors. *Regional Studies in Marine Science*, 10, 107–115. https://doi.org/10.1016/j.rsma.2017.01.007 (Towle et al. 2017)

The local environment shapes coral physiology through acclimatization and also selects for genotypes best suited to a particular site. Both acclimatization and selection likely affect the response of corals to future climate change. The local environment is therefore an important factor to consider for restoration ecology. In this study, we exposed Orbicella faveolata from two different locations in Florida (Emerald Reef, near Key Biscayne in the upper Florida Keys, and Truman Harbor near Key West in the lower Florida Keys) that were common-gardened for one month prior to experimentation to four temperature, CO2, and food availability treatments (26°C/390 ppm, 26°C/1000 ppm, 31°C/390 ppm, and 31°C/1000 ppm where each of these treatments had fed and unfed components). The goal was to determine how the same species of coral from different locations would respond to projected climate change scenarios. We found that growth (measured as changes in buoyant weight) was highly correlated to source location (i.e., whether the corals came from Emerald Reef or Truman Harbor) and not to parent colony, and growth, symbiont density, chlorophyll a content, and lipid content were highly correlated to feeding regime. These findings show that within a single reef tract, (i.e. the Florida Reef Tract), source location and food availability matter for the physiological outcome of a coral's stress response, and suggest that an explicit consideration of these effects may be important for management activities such as coral restoration, transplantation, and MPA placement.

Threat Assessment

Disease

> Closek, C. J., Sunagawa, S., DeSalvo, M. K., Piceno, Y. M., DeSantis, T. Z., Brodie, E. L., . . . Medina, M. (2014). Coral transcriptome and bacterial community profiles reveal distinct Yellow Band Disease states in Orbicella faveolata. *The ISME Journal*, 8(12), 2411–2422. https://doi.org/10.1038/ismej.2014.85 (Closek et al. 2014)

Coral diseases impact reefs globally. Although we continue to describe diseases, little is known about the etiology or progression of even the most common cases. To examine a spectrum of coral health and determine factors of disease progression we examined Orbicella faveolata exhibiting signs of Yellow Band Disease (YBD), a widespread condition in the Caribbean. We used a novel combined approach to assess three members of the coral holobiont: the coral-host, associated Symbiodinium algae, and bacteria. We profiled three conditions: (1) healthy-appearing colonies (HH), (2) healthy-appearing tissue on diseased colonies (HD), and (3) diseased lesion (DD). Restriction fragment length polymorphism analysis revealed health state-specific diversity in Symbiodinium clade associations. 16S ribosomal RNA gene microarrays (PhyloChips) and O. faveolata complimentary DNA microarrays revealed the bacterial community structure and host transcriptional response, respectively. A distinct bacterial community structure marked each health state. Diseased samples were associated with two to three times more bacterial diversity. HD samples had the highest bacterial richness, which included components associated with HH and DD, as well as additional unique families. The host transcriptome under YBD revealed a reduced cellular expression of defense- and metabolism-related processes, while the neighboring HD condition exhibited an intermediate expression profile. Although HD tissue appeared visibly healthy, the microbial communities and gene expression profiles were distinct. HD should be regarded as an additional (intermediate) state of disease, which is important for understanding the progression of YBD.

> Daniels, C., Baumgarten, S., Yum, L. K., Michell, C. T., Bayer, T., Arif, C., . . . Vool, C. R. (2015). Metatranscriptome analysis of the reef-building coral Orbicella faveolata indicates holobiont response to coral disease. *Frontiers in Marine Science*, 2:62. https://doi.org/10.3389/fmars.2015.00062 (Daniels et al. 2015)

White Plague Disease (WPD) is implicated in coral reef decline in the Caribbean and is characterized by microbial community shifts in coral mucus and tissue. Studies thus far have focused on assessing microbial communities or the identification of specific pathogens, yet few have addressed holobiont response across metaorganism compartments in coral disease. Here, we report on the first metatranscriptomic assessment of the coral host, algal symbiont, and microbial compartment in order to survey holobiont structure and function in healthy and diseased samples from Orbicella faveolata collected at reef sites off Puerto Rico. Our data indicate metaorganism-wide as well as compartment-specific responses to WPD. Gene expression changes in the diseased coral host involved proteins playing a role in innate immunity, cytoskeletal integrity, cell adhesion, oxidative stress, chemical defense, and retroelements. In contrast, the algal symbiont showed comparatively few expression changes, but of large magnitude, of genes related to stress, photosynthesis, and metal transport. Concordant with the coral host response, the bacterial compartment showed increased abundance of heat shock proteins, genes related to

oxidative stress, DNA repair, and potential retroelement activity. Importantly, analysis of the expressed bacterial gene functions establishes the participation of multiple bacterial families in WPD pathogenesis and also suggests a possible involvement of viruses and/or phages in structuring the bacterial assemblage. In this study, we implement an experimental approach to partition the coral holobiont and resolve compartment- and taxa-specific responses in order to understand metaorganism function in coral disease.

Fuess, L. E., A. M. Palacio-Castro, C. C. Butler, A. C. Baker, and L. D. Mydlarz. 2020. Increased Algal Symbiont Density Reduces Host Immunity in a Threatened Caribbean Coral Species, Orbicella faveolata. Frontiers in Ecology and Evolution 8. (Fuess et al. 2020b)

Scleractinian corals are the principal builders of coral reefs. These megadiverse ecosystems are declining due to coral mortality from a variety of stressors, including disease. Corals are dependent upon symbiotic dinoflagellates in the family Symbiodiniaceae for phototrophic contributions to their energy budgets. However, suppression of host immunity may be necessary to maintain these intracellular symbioses. To explore the consequences of symbiosis on host immunity, we manipulated symbiont density by increasing nitrogen availability. Replicate cores from four colonies of the Caribbean coral, Orbicella faveolata, were reared in seawater treated with ammonium for 1 month to increase symbiont density. Corals were then immunestimulated using lipopolysaccharide and poly I:C. Gene expression was analyzed using RNAseq and symbiont density was quantified (as symbiont:host cell ratio) using quantitative PCR (qPCR). Ammonium treatment had limited positive effects on host immunity. In contrast, increases in symbiont density had large negative effects on host expression of immune-related transcripts. These results suggest links between nutrient enrichment and coral disease may be the result of the effect of increased symbiont density on host immunity, rather than the direct effect of the nutrients. Further study of the trade-offs between symbiont density and immunity may help understand how decreasing water quality and increasing disease will shape future reef communities.

Grottoli, A. G., Warner, M. E., Levas, S. J., Aschaffenburg, M. D., Schoepf, V., McGinley, M., . . . Matsui, Y. (2014). The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Global Change Biology*, 20, 3823–3833. https://doi.org/10.1111/gcb.12658 (Grottoli et al. 2014)

Mass coral bleaching events caused by elevated seawater temperatures result in extensive coral loss throughout the tropics, and are projected to increase in frequency and severity. If bleaching becomes an annual event later in this century, more than 90% of coral reefs worldwide may be at risk of long-term degradation. While corals can recover from single isolated bleaching and can acclimate to recurring bleaching events that are separated by multiple years, it is currently unknown if and how they will survive and possibly acclimatize to annual coral bleaching. Here, we demonstrate for the first time that annual coral bleaching can dramatically alter thermal tolerance in Caribbean corals. We found that high coral energy reserves and changes in the dominant algal endosymbiont type (Symbiodinium spp.) facilitated rapid acclimation in Porites divaricata, whereas low energy reserves and a lack of algal phenotypic plasticity significantly increased susceptibility in Porites astreoides to bleaching the following year. Phenotypic plasticity in the dominant endosymbiont type of Orbicella faveolata did not prevent repeat bleaching, but may have facilitated rapid recovery. Thus, coral holobiont response to an isolated single bleaching event is not an accurate predictor of its response to bleaching the following year. Rather, the

cumulative impact of annual coral bleaching can turn some coral species ‘winners’ into ‘losers’, and can also facilitate acclimation and turn some coral species ‘losers’ into ‘winners’. Overall, these findings indicate that cumulative impact of annual coral bleaching could result in some species becoming increasingly susceptible to bleaching and face a long-term decline, while phenotypically plastic coral species will acclimatize and persist. Thus, annual coral bleaching and recovery could contribute to the selective loss of coral diversity as well as the overall decline of coral reefs in the Caribbean.

Guerra, M., López, M. A., Estéves, I., Zubillaga, A. L. & Cróquer, A. (2014). Fourier-transformed infrared spectroscopy: a tool to identify gross chemical changes from healthy to yellow band disease tissues. *Dis. Aquat. Org.*, 107, 249–258 . https://doi.org/10.3354/dao02680 (Guerra et al. 2014)

Yellow band disease (YBD) is a common and wide-spread Caribbean syndrome that affects the genus Orbicella, a group of species that constitute the framework of Caribbean coral reefs. Previous studies have shown that the structure and function of bacterial assemblages vary between healthy tissues and YBD lesions; however, how the molecular composition of tissues varies as tissues transition from healthy to YBD has not been determined before. The present study provides the first survey of macromolecules found from healthy (H), apparently healthy (AH), transition (TR) and YBD tissues of Orbicella faveolata. For this, we used Fourier-transformed mid-infrared spectroscopy (FTIR) to compare absorption profiles as a proxy for the gross molecular composition of decalcified H, AH and YBD tissues. We found a significantly higher level of infrared absorption for bands assigned to lipids in H tissues compared to YBD tissues, suggesting that lipid compounds are more abundant in compromised tissues in relation to other macromolecules. We also found a lower level of intensity of bands assigned to carbohydrates and proteins in YBD tissues, compared to H and AH tissues. A similar pattern was observed for phospholipidic compounds in relation to fatty acids. This study is the first to show that healthy and YBD-compromised tissues have different infrared absorption profiles, suggesting that alterations in the biochemical composition occur during pathogenesis. Future studies should focus on determining the actual concentration of these compounds in H, AH, TR and YBD tissues and on testing the role of translocation of photoassimilates from H tissues and/or from endolithic algae to YBD tissues.

Meyer, J. L., Rodgers, J. M., Dillard, B. A., Paul, V. J. & Teplitski, M. (2016). Epimicrobiota Associated with the Decay and Recovery of Orbicella Corals Exhibiting Dark Spot Syndrome. *Frontiers in Microbiology*, 7, 893. https://doi.org/10.3389/fmicb.2016.00893 (Meyer et al. 2016)

Dark Spot Syndrome (DSS) is one of the most common diseases of boulder corals in the Caribbean. It presents as sunken brown lesions in coral tissue, which can spread quickly over coral colonies. With this study, we tested the hypothesis that similar to other coral diseases, DSS is a dysbiosis characterized by global shifts in the coral microbiome. Because Black Band Disease (BBD) was sometimes found following DSS lesions, we also tested the hypothesis that DSS is a precursor of BBD. To track disease initiation and progression 24 coral colonies were tagged. Of them five Orbicella annularis corals and three O. faveolata corals exhibited DSS lesions at tagging. Microbiota of lesions and apparently healthy tissues from DSS-affected corals over the course of 18 months were collected. Final visual assessment showed that five of eight corals incurred substantial tissue loss while two corals remained stable and one appeared

to recover from DSS lesions. Illumina sequencing of the V6 region of bacterial 16S rRNA genes demonstrated no significant differences in bacterial community composition associated with healthy tissue or DSS lesions. The epimicrobiomes of both healthy tissue and DSS lesions contained high relative abundances of Operational Taxonomic Units assigned to Halomonas, an unclassified gammaproteobacterial genus, Moritella, an unclassified Rhodobacteraceae genus, Renibacterium, Pseudomonas, and Acinetobacter. The relative abundance of bacterial taxa was not significantly different between samples when grouped by tissue type (healthy tissue vs. DSS lesion), coral species, collection month, or the overall outcome of DSS-affected corals (substantial tissue loss vs. stable/recovered). Two of the tagged corals with substantial tissue loss also developed BBD during the 18-month sampling period. The bacterial community of the BBD layer was distinct from both healthy tissue and DSS lesions, with high relative abundances of the presumed BBD pathogen Roseofilum reptotaenium and an unclassified Bacteroidales genus, similar to previous results. Roseofilum was detected in all samples from this study, with the highest relative abundance in healthy tissue from DSS-affected corals sampled in August, suggesting that while DSS is not a precursor to BBD, DSS-affected corals are in a weakened state and therefore more susceptible to additional infections.

> Meyer, J. L., Castellanos-Gell, J., Aeby, G. S., Häse, C. C., Ushijima, B. & Paul, V. J. (2019). Microbial Community Shifts Associated With the Ongoing Stony Coral Tissue Loss Disease Outbreak on the Florida Reef Tract. *Frontiers in Microbiology*, 10:2244. https://doi.org/10.3389/fmicb.2019.02244 (Meyer et al. 2019)

As many as 22 of the 45 coral species on the Florida Reef Tract are currently affected by stony coral tissue loss disease (SCTLD). The ongoing disease outbreak was first observed in 2014 in Southeast Florida near Miami and as of early 2019 has been documented from the northernmost reaches of the reef tract in Martin County down to Key West. We examined the microbiota associated with disease lesions and apparently healthy tissue on diseased colonies of Montastraea cavernosa, Orbicella faveolata, Diploria labyrinthiformis, and Dichocoenia stokesii. Analysis of differentially abundant taxa between disease lesions and apparently healthy tissue identified five unique amplicon sequence variants enriched in the diseased tissue in three of the coral species (all expect O. faveolata), namely an unclassified genus of Flavobacteriales and sequences identified as Fusibacter (Clostridiales), Planktotalea (Rhodobacterales), Algicola (Alteromonadales), and Vibrio (Vibrionales). In addition, several groups of likely opportunistic or saprophytic colonizers such as Epsilonbacteraeota, Patescibacteria, Clostridiales, Bacteroidetes, and Rhodobacterales were also enriched in SCTLD disease lesions. This work represents the first microbiological characterization of SCTLD, as an initial step toward identifying the potential pathogen(s) responsible for SCTLD.

> Montilla, L. M., Ramos, R., García, E. & Cróquer, A. (2016). Caribbean yellow band disease compromises the activity of catalase and glutathione S-transferase in the reef-building coral Orbicella faveolata exposed to anthracene. *Diseases of Aquatic Organisms*, 119(2), 153–161. https://doi.org/10.3354/dao02980 (Montilla et al. 2016)

Healthy and diseased corals are threatened by different anthropogenic sources, such as pollution, a problem expected to become more severe in the near future. Despite the fact that coastal pollution and coral diseases might represent a serious threat to coral reef health, there is a paucity of controlled

experiments showing whether the response of diseased and healthy corals to xenobiotics differs. In this study, we exposed healthy and Caribbean yellow band disease (CYBD)-affected Orbicella faveolata colonies to 3 sublethal concentrations of anthracene to test if enzymatic responses to this hydrocarbon were compromised in CYBD-affected tissues. For this, a 2-factorial fully orthogonal design was used in a controlled laboratory bioassay, using tissue condition (2 levels: apparently healthy and diseased) and pollutant concentration (4 levels: experimental control, 10, 30 and 100 ppb concentration) as fixed factors. A permutation-based ANOVA (PERMANOVA) was used to test the effects of condition and concentration on the specific activity of 3 enzymatic biomarkers: catalase, glutathione S-transferase, and glutathione peroxidase. We found a significant interaction between the concentration of anthracene and the colony condition for catalase (Pseudo-F = 3.84, df = 3, $p < 0.05$) and glutathione S-transferase (Pseudo-F = 3.29, df = 3, $p < 0.05$). Moreover, our results indicated that the enzymatic response to anthracene in CYBD-affected tissues was compromised, as the activity of these enzymes decreased 3- to 4-fold compared to healthy tissues. These results suggest that under a potential scenario of increasing hydrocarbon coastal pollution, colonies of O. faveolata affected with CYBD might become more vulnerable to the deleterious effects of chemical pollution.

Morgan, M., Goodner, K., Ross, J., Poole, A. Z., Stepp, E., Stuart, C. H., . . . Weil, E. (2015). Development and application of molecular biomarkers for characterizing Caribbean Yellow Band Disease in Orbicella faveolata. *PeerJ*, 3:e1371. https://doi.org/10.7717/peerj.1371 (Morgan et al. 2015)

Molecular stress responses associated with coral diseases represent an under-studied area of cnidarian transcriptome investigations. Caribbean Yellow Band Disease (CYBD) is considered a disease of Symbiodinium within the tissues of the coral host Orbicella faveolata. There is a paucity of diagnostic tools to assist in the early detection and characterization of coral diseases. The validity of a diagnostic test is determined by its ability to distinguish host organisms that have the disease from those that do not. The ability to detect and identify disease-affected tissue before visible signs of the disease are evident would then be a useful diagnostic tool for monitoring and managing disease outbreaks. Representational Difference Analysis (RDA) was utilized to isolate differentially expressed genes in O. faveolata exhibiting CYBD. Preliminary screening of RDA products identified a small number of genes of interest (GOI) which included an early growth response factor and ubiquitin ligase from the coral host as well as cytochrome oxidase from the algal symbiont. To further characterize the specificity of response, quantitative real-time PCR (qPCR) was utilized to compare the expression profiles of these GOIs within diseased tissues (visible lesions), tissues that precede visible lesions by 2–4 cm (transition area), and tissues from healthy-looking colonies with no signs of disease. Results show there are distinctive differences in the expression profiles of these three GOIs within each tissue examined. Collectively, this small suite of GOIs can provide a molecular “finger print” which is capable of differentiating between infected and uninfected colonies on reefs where CYBD is known to occur.

Muller, E. M., Leporacci, N. M., Macartney, K. J., Shea, A. G., Crane, R. E., Hall, E. R. & Ritchie, K. B. (2017). Low pH reduces the virulence of black band disease on Orbicella faveolata. *PLOS ONE*. 12:e0178869. https://doi.org/10.1371/journal.pone.0178869 (Muller et al. 2017)

Black band is a deadly coral disease found worldwide, which may become more virulent as oceanic conditions continue to change. To determine the effects of climate change and ocean acidification on black band disease virulence, Orbicella faveolata corals with black band were exposed to different temperature and pH conditions. Results showed a significant decrease in disease progression under low pH (7.7) conditions. Low pH also altered the relative abundance of the bacterial community of the black band disease consortium. Here, there was a significant decrease in Roseofilum, the cyanobacterium that typically dominates the black band mat. These results indicate that as oceanic pH decreases so may the virulence of a worldwide coral disease.

Neely, K. 2018. Surveying the Florida Keys Southern Coral Disease Boundary. Florida DEP, Miami, FL. Pp 1-15 (Neely 2018)

Since 2014, multi-year, multi-species disease outbreak has progressed geographically along the Florida Reef Tract from an origin near Virginia Key. From fall 2017 to spring 2018, 134 reef sites were surveyed to identify the geographic boundary of the disease as well as provide information on rates of progression, cross-reef prevalence differences, and differences in responses of impacted species. Roving diver surveys were conducted during two reef-tract wide assessments in fall 2017 and spring 2018, and roving diver and belt transect surveys were conducted in a targeted effort near the southern disease boundary in winter 2017-18 between Long Key and Marathon. Surveys confirmed prevalence of the disease on 15 coral species, including the primary reef builders and five ESA-listed species. Disease was conspicuously absent on some other species, including the *Acropora* and *Porites* spp. Disease hotspots and geographic differences in disease prevalence showed that tissue loss begins on different species at different times. Broadly, the brain corals (particularly *Meandrina meandrites*) are the first to show tissue loss. Boulder coral infections generally appear shortly thereafter, with *Montastraea cavernosa* in particular often a later species to exhibit tissue loss.

Neely, K. L., Macaulay, K. A., Hower, E. K. & Dobler, M. A. (2020). Effectiveness of topical antibiotics in treating corals affected by Stony Coral Tissue Loss Disease. *PeerJ*, 8:e9289. https://doi.org/10.7717/peerj.9289 (Neely et al. 2020)

Since 2014, Stony Coral Tissue Loss Disease (SCTLD) has led to mass mortality of the majority of hard coral species on the Florida Reef Tract. Following the successful treatment of SCTLD lesions on laboratory corals using water dosed with antibiotics, two topical pastes were developed as vehicles to directly apply antibiotic treatments to wild corals. These pastes were tested as placebos and with additions of amoxicillin on active SCTLD lesions on multiple coral species. The effectiveness of the pastes without antibiotics (placebo treatments) was 4% and 9%, no different from untreated controls. Adding amoxicillin to both pastes significantly increased effectiveness to 70% and 84%. Effectiveness with this method was seen across five different coral species, with success rates of the more effective paste ranging from 67% (Colpophyllia natans) to 90% (Orbicella faveolata and Montastraea cavernosa). Topical antibiotic application is a viable and effective tool for halting disease lesions on corals affected by SCTLD.

Randall, C. J., Whitcher, E. M., Code, T., Pollock, C., Lundgren, I., Hillis-Starr, Z. & Muller, E. M. (2018). Testing methods to mitigate Caribbean yellow-band disease on Orbicella faveolata.

PeerJ, 6:e4800.
https://doi.org/10.7717/peerj.4800 (Randall et al. 2018)

Outbreaks of coral diseases continue to reduce global coral populations. In the Caribbean, yellow band is a severe and wide-spread disease that commonly affects corals of the Orbicella spp. complex, significantly impeding coral reproduction, and hindering the natural recovery of Orbicella spp. populations. Caribbean yellow-band disease (CYBD) lesions may be severe, and often result in the complete loss of coral tissue. The slow spread of CYBD, however, provides an opportunity to test methods to mitigate the disease. Here we report the results of in situ experiments, conducted within Buck Island Reef National Monument in St. Croix, USVI, to test the effectiveness of three techniques to minimize disease impact on Orbicella faveolata: (1) shading, (2) aspirating, and (3) chiseling a "firebreak" to isolate the lesion. Neither shading nor aspirating the diseased tissue significantly reduced CYBD tissue loss. However, chiseling reduced the rate and amount of tissue lost by 31%. While 30–40% of the chiseled lesions appeared to be free of disease signs 12–16 months after treatment, success significantly and steadily declined over 23 months, indicating a possible lack of long-term viability of the technique. The results of this study demonstrate that creating a "firebreak" between diseased and healthy-appearing tissue slows the spread of the disease and may prolong the life of O. faveolata colonies. The firebreak method yielded the best results of all the techniques tested, and also required the least amount of effort and resources. However, we do not recommend that this treatment alone be used for long-term disease mitigation. Rather, we propose that modifications of this and other treatment options be sought. The results also highlight the need for extended monitoring of CYBD after any treatment, due to the slow but variable rate and pattern of tissue loss in this disease.

Roder, C., Arif, C., Daniels, C., Weil, E. & Voolstra, C. R. (2014). Bacterial profiling of White Plague Disease across corals and oceans indicates a conserved and distinct disease microbiome. *Molecular Ecology*, 23, 965–974.
https://doi.org/10.1111/mec.12638 (Roder et al. 2014)

Coral diseases are characterized by microbial community shifts in coral mucus and tissue, but causes and consequences of these changes are vaguely understood due to the complexity and dynamics of coral-associated bacteria. We used 16S rRNA gene microarrays to assay differences in bacterial assemblages of healthy and diseased colonies displaying White Plague Disease (WPD) signs from two closely related Caribbean coral species, Orbicella faveolata and Orbicella franksi. Analysis of differentially abundant operational taxonomic units (OTUs) revealed strong differences between healthy and diseased specimens, but not between coral species. A subsequent comparison to data from two Indo-Pacific coral species (Pavona duerdeni and Porites lutea) revealed distinct microbial community patterns associated with ocean basin, coral species and health state. Coral species were clearly separated by site, but also, the relatedness of the underlying bacterial community structures resembled the phylogenetic relationship of the coral hosts. In diseased samples, bacterial richness increased and putatively opportunistic bacteria were consistently more abundant highlighting the role of opportunistic conditions in structuring microbial community patterns during disease. Our comparative analysis shows that it is possible to derive conserved bacterial footprints of diseased coral holobionts that might help in identifying key bacterial species related to the underlying etiopathology. Furthermore, our data demonstrate that similar-appearing disease phenotypes produce microbial community patterns that are consistent over coral species and oceans,

irrespective of the putative underlying pathogen. Consequently, profiling coral diseases by microbial community structure over multiple coral species might allow the development of a comparative disease framework that can inform on cause and relatedness of coral diseases.

Schoepf, V., Grottoli, A. G., Levas, S. J., Aschaffenburg, M. D., Baumann, J. H., Matsui, Y. & Warner, M. E. (2015). Annual coral bleaching and the long-term recovery capacity of coral. *Proc. Biol. Sci.* 282:1819). https://doi.org/10.1098/rspb.2015.1887 (Schoepf et al. 2015)

Mass bleaching events are predicted to occur annually later this century. Nevertheless, it remains unknown whether corals will be able to recover between annual bleaching events. Using a combined tank and field experiment, we simulated annual bleaching by exposing three Caribbean coral species (Porites divaricata, Porites astreoides and Orbicella faveolata) to elevated temperatures for 2.5 weeks in 2 consecutive years. The impact of annual bleaching stress on chlorophyll a, energy reserves, calcification, and tissue C and N isotopes was assessed immediately after the second bleaching and after both short- and long-term recovery on the reef (1.5 and 11 months, respectively). While P. divaricata and O. faveolata were able to recover from repeat bleaching within 1 year, P. astreoides experienced cumulative damage that prevented full recovery within this time frame, suggesting that repeat bleaching had diminished its recovery capacity. Specifically, P. astreoides was not able to recover protein and carbohydrate concentrations. As energy reserves promote bleaching resistance, failure to recover from annual bleaching within 1 year will likely result in the future demise of heat-sensitive coral species.

Verde, A., Bastidas, C. & Croquer, A. (2016). Tissue mortality by Caribbean ciliate infection and white band disease in three reef-building coral species. *PeerJ*, 4:e2196. https://doi.org/10.7717/peerj.2196 (Verde et al. 2016)

Caribbean ciliate infection (CCI) and white band disease (WBD) are diseases that affect a multitude of coral hosts and are associated with rapid rates of tissue losses, thus contributing to declining coral cover in Caribbean reefs. In this study we compared tissue mortality rates associated to CCI in three species of corals with different growth forms: Orbicella faveolata (massive-boulder), O. annularis (massive-columnar) and Acropora cervicornis (branching). We also compared mortality rates in colonies of A. cervicornis bearing WBD and CCI. The study was conducted at two locations in Los Roques Archipelago National Park between April 2012 and March 2013. In A. cervicornis, the rate of tissue loss was similar between WBD (0.8 ± 1 mm/day, mean ± SD) and CCI (0.7 ± 0.9 mm/day). However, mortality rate by CCI in A. cervicornis was faster than in the massive species O. faveolata (0.5 ± 0.6 mm/day) and O. annularis (0.3 ± 0.3 mm/day). Tissue regeneration was at least fifteen times slower than the mortality rates for both diseases regardless of coral species. This is the first study providing coral tissue mortality and regeneration rates associated to CCI in colonies with massive morphologies, and it highlights the risks of further cover losses of the three most important reef-building species in the Caribbean.

Hankins, C., Duffy, A. & Drisco, K. (2018). Scleractinian coral microplastic ingestion: Potential calcification effects, size limits, and retention. *Marine Pollution Bulletin*, 135, 587–593. https://doi.org/10.1016/j.marpolbul.2018.07.067 (Hankins et al. 2018)

The impact that microplastics (<5 mm) have on scleractinian coral is largely unknown. This study investigated calcification effects, size limits, and retention times of microbeads and microfibers in two Caribbean species, Montastraea cavernosa and Orbicella faveolata, in a series of three experiments. No calcification effects were seen in the two-day exposure to a microbead concentration of 30 mg L−1. M. cavernosa and O. faveolata actively ingested microbeads ranging in size from 425 µm–2.8 mm, however, a 212–250 µm size class did not elicit a feeding response. The majority of microbeads were expelled within 48 h of ingestion. There was no difference in ingestion or retention times of 425–500 µm microbeads versus 3–5 mm long microfibers. M. cavernosa and O. faveolata have the ability to recognize and reject indigestible material, yet, there is still a need to study effects of energetics and microplastic contamination as a result of ingestion and egestion.

Horta-Puga, G. & Carriquiry, J. D. (2014). The Last Two Centuries of Lead Pollution in the Southern Gulf of Mexico Recorded in the Annual Bands of the Scleractinian Coral Orbicella faveolata. *Bull Environ Contam Toxicol*, 92(5), 567–573. https://doi.org/10.1007/s00128-014-1222-9 (Horta-Puga and Carriquiry 2014)

Lead (Pb) pollution history (1855–2001 A.D.) of the southern Gulf of Mexico (SGM) was reconstructed from the geochemical record contained in the annual bands of the hermatypic coral Orbicella faveolata from the Veracruz Reef System, Mexico. Pb concentrations ranged from 5.5 µg/g in 1889–23.6 µg/g in 1992, with an average of 10.0 ± 4.1 µg/g. These high concentrations are evidence of a highly polluted environment. High statistical correlations were observed between the annual Pb coral time-series and both, the production of alkyl-lead gasoline in Mexico during the second half of the twentieth century ($r = 0.86$, $p < 0.001$), and the industrial production of lead in North America for the 1900–1940 years period ($r = 0.73$, $p < 0.001$). Hence, this research provides evidence that these two processes generated Pb-rich aerosols that were atmospherically transported, increasing the environmental levels of Pb in the SGM.

Jovanović, B. & Guzmán, H. M. (2014). Effects of titanium dioxide (TiO2) nanoparticles on caribbean reef-building coral (Montastraea faveolata). *Environmental Toxicology and Chemistry*, 33(6), 1346–1353. https://doi.org/10.1002/etc.2560 (Jovanovic and Guzman 2014)

Increased use of manufactured titanium dioxide nanoparticles (nano-TiO2) is causing a rise in their concentration in the aquatic environment, including coral reef ecosystems. Caribbean mountainous star coral (Montastraea faveolata) has frequently been used as a model species to study gene expression during stress and bleaching events. Specimens of M. faveolata were collected in Panama and exposed for 17 d to nano-TiO2 suspensions (0.1 mg L−1 and 10 mg L−1). Exposure to nano-TiO2 caused significant zooxanthellae expulsion in all the colonies, without mortality. Induction of the gene for heat-shock protein 70 (HSP70) was observed during an early stage of exposure (day 2), indicating acute stress.

However, there was no statistical difference in HSP70 expression on day 7 or 17, indicating possible coral acclimation and recovery from stress. No other genes were significantly upregulated. Inductively coupled plasma mass spectrometry analysis revealed that nano-TiO2 was predominantly trapped and stored within the posterior layer of the coral fragment (burrowing sponges, bacterial and fungal mats). The bioconcentration factor in the posterior layer was close to 600 after exposure to 10 mg L−1 of nano-TiO2 for 17 d. The transient increase in HSP70, expulsion of zooxanthellae, and bioaccumulation of nano-TiO2 in the microflora of the coral colony indicate the potential of such exposure to induce stress and possibly contribute to an overall decrease in coral populations.

Kemp, D. W., Colella, M. A., Bartlett, L. A., Ruzicka, R. R., Porter, J. W. & Fitt, W. K. (2016). Life after cold death: reef coral and coral reef responses to the 2010 cold water anomaly in the Florida Keys. *Ecosphere*, 7:e01373. https://doi.org/10.1002/ecs2.1373 (Kemp et al. 2016)

Recently, the Caribbean reef-building coral Orbicella faveolata was listed as "threatened" under the U.S. Endangered Species Act. Despite attention to this species' conservation, the extent of geographic variation within O. faveolata warrants further investigation. O. faveolata is unusual in that it can simultaneously harbor multiple genetically distinct and co-dominant species of endosymbiotic dinoflagellates in the genus Symbiodinium. Here, we investigate the geographic and within-colony complexity of Symbiodinium-O. faveolata associations from Florida Keys, USA; Exuma Cays, Bahamas; Puerto Morelos, Mexico; and Carrie Bow Cay, Belize. We collected coral samples along intracolony axes, and Symbiodinium within O. faveolata samples was analyzed using the nuclear ITS2 region and chloroplast 23S rDNA genotyping. O. faveolata associated with species of Symbiodinium in clades A (type A3), B (B1 and B17), C (C3, C7, and C7a), and D (D1a/Symbiodinium trenchii). Within-colony distributions of Symbiodinium species correlated with light availability, cardinal direction, and depth, resulting in distinct zonation patterns of endosymbionts within a host. Symbiodinium species from clades A and B occurred predominantly in the light-exposed tops, while species of clade C generally occurred in the shaded sides of colonies or in deeper-water habitats. Furthermore, geographic comparisons of host–symbiont associations revealed regional differences in Symbiodinium associations. Symbiodinium A3 was detected in Mesoamerican coral colonies, but not in colonies from the Florida Keys or Bahamas. Likewise, Symbiodinium B17 was unique to Mesoamerican O. faveolata, whereas Symbiodinium B1 was found at all localities sampled. However, using cp23S genotyping paired with ITS2 analysis revealed geographically endemic haplotypes among Symbiodinium clades A, B, and C. Since Symbiodinium spatial heterogeneity among this coral species is greater than most corals, a question arises as to whether all western Atlantic populations of O. faveolata should be considered equally "threatened"? Alternatively, geographically and spatially distinct coral–symbiont associations may benefit from specialized management protocols.

Baker, D. M., Freeman, C. J., Wong, J. C. Y., Fogel, M. L. & Knowlton, N. (2018). Climate change promotes parasitism in a coral symbiosis. *ISME J*, 12, 921–930. https://doi.org/10.1038/s41396-018-0046-8 (Baker et al. 2018)

Coastal oceans are increasingly eutrophic, warm and acidic through the addition of anthropogenic nitrogen and carbon, respectively. Among the most sensitive taxa to these changes are scleractinian

corals, which engineer the most biodiverse ecosystems on Earth. Corals' sensitivity is a consequence of their evolutionary investment in symbiosis with the dinoflagellate alga, Symbiodinium. Together, the coral holobiont has dominated oligotrophic tropical marine habitats. However, warming destabilizes this association and reduces coral fitness. It has been theorized that, when reefs become warm and eutrophic, mutualistic Symbiodinium sequester more resources for their own growth, thus parasitizing their hosts of nutrition. Here, we tested the hypothesis that sub-bleaching temperature and excess nitrogen promotes symbiont parasitism by measuring respiration (costs) and the assimilation and translocation of both carbon (energy) and nitrogen (growth; both benefits) within Orbicella faveolata hosting one of two Symbiodinium phylotypes using a dual stable isotope tracer incubation at ambient (26 °C) and sub-bleaching (31 °C) temperatures under elevated nitrate. Warming to 31 °C reduced holobiont net primary productivity (NPP) by 60% due to increased respiration which decreased host %carbon by 15% with no apparent cost to the symbiont. Concurrently, Symbiodinium carbon and nitrogen assimilation increased by 14 and 32%, respectively while increasing their mitotic index by 15%, whereas hosts did not gain a proportional increase in translocated photosynthates. We conclude that the disparity in benefits and costs to both partners is evidence of symbiont parasitism in the coral symbiosis and has major implications for the resilience of coral reefs under threat of global change.

Enzor, L. A., Hankins, C., Vivian, D. N., Fisher, W. S. & Barron, M. G. (2018). Calcification in Caribbean reef-building corals at high pCO2 levels in a recirculating ocean acidification exposure system. *J Exp Mar Bio Ecol*, 499, 9–16. https://doi.org/10.1016/j.jembe.2017.12.008 (Enzor et al. 2018)

Projected increases in ocean pCO2 levels are anticipated to affect calcifying organisms more rapidly and to a greater extent than other marine organisms. The effects of ocean acidification (OA) have been documented in numerous species of corals in laboratory studies, largely tested using flow-through exposure systems. We developed a recirculating ocean acidification exposure system that allows precise pCO2 control using a combination of off-gassing measures including aeration, water retention devices, venturi injectors, and CO2 scrubbing. We evaluated the recirculating system performance in off-gassing effectiveness and maintenance of target pCO2 levels over an 84-day experiment. The system was used to identify changes in calcification and tissue growth in response to elevated pCO2 (1000 µatm) in three reef-building corals of the Caribbean: Pseudodiploria clivosa, Montastraea cavernosa, and Orbicella faveolata. All three species displayed an overall increase in net calcification over the 84-day exposure period regardless of pCO2 level (control +0.28- 1.12 g, elevated pCO2 +0.18- 1.16 g), and the system was effective at both off-gassing acidified water to ambient pCO2 levels, and maintaining target elevated pCO2 levels over the 3-month experiment.

Langdon, C., Albright, R., Baker, A. C. & Jones, P. (2018). Two threatened Caribbean coral species have contrasting responses to combined temperature and acidification stress. *Limnology and Oceanography*, 63(6), 2450–2464. https://doi.org/10.1002/lno.10952 (Langdon et al. 2018)

There is growing evidence that different coral species and algal symbionts (Symbiodinium spp.) can vary greatly in their response to rising temperatures and also ocean acidification. In a fully crossed factorial experimental design, two threatened Caribbean reef-building coral species, Acropora cervicornis hosting

a mixture of Symbiodinium clades A and C and Orbicella faveolata hosting Symbiodinium D, were exposed to combinations of a normal (26°C) and elevated (32°C) temperature and normal (380 ppm) and elevated (800 ppm) CO2 for 62 d and then recovered at 26°C and 380 ppm or 32°C and 380 ppm for an additional 56 d. CO2 enrichment did not confer enhanced thermal tolerance as had been suggested in other studies. A. cervicornis was more sensitive to heat stress (maximum monthly mean + 1.5°C) experiencing 100% mortality after 25 d while all O. faveolata survived. Conversely, O. faveolata was more sensitive to high CO2 experiencing a 47% reduction in growth while A. cervicornis experienced no significant reduction. It is predicted that A. cervicornis is unlikely to survive past 2035. O. faveolata with D symbionts might survive to 2060 and later but its abundance will be impacted by CO2 effects on recruitment potential.

Levitan, D. R., Boudreau, W., Jara, J. & Knowlton, N. (2014). Long-term reduced spawning in Orbicella coral species due to temperature stress. *Marine Ecology Progress Series*, 515, 1–10. https://doi.org/10.3354/meps11063 (Levitan et al. 2014)

We examined the long-term reproductive consequence of bleaching stress on Caribbean corals in the Orbicella (formerly Montastraea) species complex (O. annularis, O. faveolata, and O. franksi). Over 2000 observations of spawning in 526 tagged corals in Panama were made from 2002 through 2013. Bleaching events were noted in 2005 and 2010. At the population level, a reduction in spawning persisted for several years following each bleaching event. In 2010, (1) the bleaching event did not alter the timing of spawning, nor coral survivorship or tissue loss; (2) both bleached and unbleached corals had a reduced probability of spawning for several years following the bleaching event, and corals that visibly bleached were less likely to spawn than corals that did not visibly bleach; (3) the species that was affected most by the bleaching event (O. annularis) recovered the ability to spawn in fewer years compared to the species least affected by the bleaching event (O. franksi); and (4) in O. franksi, the species with the widest depth distribution, recovery in the likelihood to spawn was not depth related, although individuals at greater depths were less likely to bleach. In sum, corals that recover from bleaching events can experience long-term reduction in reproduction, over time scales that can bridge the interval between subsequent bleaching events. This may be catastrophic for the long-term maintenance of the population.

Okazaki, R. R., Towle, E. K., van Hooidonk, R., Mor, C., Winter, R. N., Piggot, A. M., . . . Langdon, C. (2017). Species-specific responses to climate change and community composition determine future calcification rates of Florida Keys reefs. *Glob Chang Biol*, 23, 1023–1035. https://doi.org/10.1111/gcb.13481 (Okazaki et al. 2017)

Anthropogenic climate change compromises reef growth as a result of increasing temperatures and ocean acidification. Scleractinian corals vary in their sensitivity to these variables, suggesting species composition will influence how reef communities respond to future climate change. Because data are lacking for many species, most studies that model future reef growth rely on uniform scleractinian calcification sensitivities to temperature and ocean acidification. To address this knowledge gap, calcification of twelve common and understudied Caribbean coral species was measured for two months under crossed temperatures (27, 30.3 °C) and CO2 partial pressures (pCO2) (400, 900, 1300 µatm). Mixed-effects models of calcification for each species were then used to project community-level scleractinian calcification using Florida Keys reef composition data and IPCC AR5 ensemble climate

model data. Three of the four most abundant species, Orbicella faveolata, Montastraea cavernosa, and Porites astreoides, had negative calcification responses to both elevated temperature and pCO2 . In the business-as-usual CO2 emissions scenario, reefs with high abundances of these species had projected end-of-century declines in scleractinian calcification of >50% relative to present-day rates. Siderastrea siderea, the other most common species, was insensitive to both temperature and pCO2 within the levels tested here. Reefs dominated by this species had the most stable end-of-century growth. Under more optimistic scenarios of reduced CO2 emissions, calcification rates throughout the Florida Keys declined <20% by 2100. Under the most extreme emissions scenario, projected declines were highly variable among reefs, ranging 10-100%. Without considering bleaching, reef growth will likely decline on most reefs, especially where resistant species like S. siderea are not already dominant. This study demonstrates how species composition influences reef community responses to climate change and how reduced CO2 emissions can limit future declines in reef calcification.

Parker, K. E., Ward, J.O., Eggleston, E.M., Fedorov, E., Parkinson, J.E., Dahlgren, C.P. & Cunning, R. (2020). Characterization of a thermally tolerant Orbicella faveolata reef in Abaco, The Bahamas. *Coral Reefs,* 39(3), 675–685. https://doi.org/10.1007/s00338-020-01948-0 (Parker et al. 2020)

Increased ocean temperatures from anthropogenic climate change induce coral bleaching, the breakdown of symbioses between corals and photosynthetic dinoflagellates. However, some corals thrive in marginal, warm environments that exceed typical bleaching thresholds. Their survival may be mediated by specific genes within the coral host, association with heat-tolerant algal symbionts, and/or distinct bacterial communities. At Mermaid Reef in Great Abaco, The Bahamas, Orbicella faveolata colonies did not bleach during a warming event that reached 33.0 °C, while at Sandy Cay Reef (~ 18 km south), which reached only 32.0 °C, O. faveolata bleached extensively. To investigate abiotic and biotic factors contributing to Mermaid Reef's higher thermal tolerance, we compared temperature, depth, and coral composition at each site and used microsatellite genotyping, quantitative PCR, and 16S rRNA metabarcoding to examine host genotype diversity, Symbiodiniaceae composition, and bacterial communities in O. faveolata. All O. faveolata colonies at the tolerant Mermaid Reef were clonemates and hosted exclusively Durusdinium symbionts, while colonies at Sandy Cay Reef comprised diverse genotypes and hosted varying proportions of four Symbiodiniaceae genera, which were primarily structured by depth. Mermaid Reef colonies also tended to have higher bacterial family richness than Sandy Cay Reef. These findings suggest that shallow, warm environments like Mermaid Reef may select for few, putatively heat-tolerant genotypes of corals and symbionts, and that while warming may greatly reduce genetic diversity, certain individuals may thrive. Such individuals existing today can provide valuable biological insights and resources for intervention conservation aimed at boosting reef resilience under climate change.

Pitts, K. A., Campbell, J. E., Figueiredo, J. & Fogarty, N. D. (2020). Ocean acidification partially mitigates the negative effects of warming on the recruitment of the coral, Orbicella faveolata. *Coral Reefs,* 39(2), 281–292. https://doi.org/10.1007/s00338-019-01888-4 (Pitts et al. 2020)

Ocean acidification and ocean warming constitute major threats to many calcifying reef organisms, including scleractinian corals. The combined effects of these two environmental stressors on the earliest life history stages of reef calcifiers remain poorly studied, particularly for Atlantic corals. Here, we investigate how acidification and warming influence the fertilization success, larval survivorship, and larval settlement of the threatened Atlantic coral, Orbicella faveolata. Gametes and larvae from O. faveolata were subjected to a factorial combination of warming (ambient versus + 1.5 °C) and acidification (ambient versus − 0.2 pH units) projected to occur by the year 2050. O. faveolata individuals were maintained in the same treatments throughout all early life history stages investigated. The fertilization success of O. faveolata was not affected by acidification, warming, or their combination. However, during larval development, warming caused complete mortality and prevented any subsequent settlement. Interestingly, these negative effects of warming were mitigated when combined with ocean acidification, such that both larval survivorship and settlement increased by 41% in the combined treatment relative to the isolated warming treatment. Our research suggests that temperature-induced increases in larval metabolism may be counterbalanced by acidification, which serves to reduce larval metabolism. Notwithstanding, larval survivorship and settlement were still reduced by 50% under combined acidification and warming relative to the ambient treatment, indicating that climate change will continue to serve as major stressor during the early life history stages of corals, jeopardizing the resilience of Caribbean reefs.

Scheufen, T., Iglesias-Prieto, R. & Enríquez, S. (2017). Changes in the Number of Symbionts and Symbiodinium Cell Pigmentation Modulate Differentially Coral Light Absorption and Photosynthetic Performance. *Frontiers in Marine Science; Lausanne*, 4:309. https://doi.org/10.3389/fmars.2017.00309 (Scheufen et al. 2017a)

In order to understand the contribution of pigmented coral tissues to the extraordinary optical properties of the coral-symbiont-skeleton unit, we analyzed the associations between structural and optical traits for four coral species, which broadly differ in skeleton morphology, tissue thickness and in the variation of coral pigmentation, symbiont content, Symbiodinium dominant type and Symbiodinium cell pigmentation (Ci). Significant differences among species were found for the maximum capacity of light absorption (Amax) and for the minimum pigmentation required to reach that maximum. The meandroid morphotype represented by Pseudodiploria strigosa showed a slightly lower Amax than the other three chalice-type species, while the thickest species, Montastraea cavernosa, required 2 to 3.5 times higher pigmentation to reach Amax. In contrast, Orbicella faveolata and O. annularis, which were able to harbour high number of symbionts and achieve the highest photosynthetic rates per area, showed the largest abilities for light collection at decreasing symbiont densities, leading to a more fragile photophysiological condition under light and heat-stress. Holobiont photosynthesis was more dependent on Symbiodinium performance in the less populated organisms. At reduced pigmentation, we observed a similar non-linear increase in holobiont light absorption efficiency (a*Chla), which was differentially modulated by reductions in the number of symbionts and Symbiodinium Ci. For similar pigmentation, larger symbiont losses relative to Ci declines resulted in smaller increases in a*Chla. Two additional optical traits were used to characterize light absorption efficiency of Symbiodinium (a*sym) and coral host (a*M). Optimization of a*sym was well represented by P. strigosa, whereas a*M was better optimized by O. annularis. The species with the largest symbiont content, O. faveolata, and with the thickest tissues, M. cavernosa, represented, respectively, less efficient solutions for both coral traits. Our comparison demonstrates the utility of

optical traits to characterize inter-specific differences in coral acclimatization and performance. Furthermore, holobiont light absorption efficiency (a*Chla) appeared as a better proxy for the "bleached phenotype" than simple reductions in coral color. The analysis of a putative coordinated variation in the number of symbionts and in Symbiodinium cell pigmentation deserves special attention to understand holobiont optimization of energy collection (a*Chla) and photosynthetic performance.

> Serrano, X. M., Miller, M. W., Hendee, J. C., Jensen, B. A., Gapayao, J. Z., Pasparakis, C., . . . Baker, A. C. (2018). Effects of thermal stress and nitrate enrichment on the larval performance of two Caribbean reef corals. *Coral Reefs*, 37, 173–182. https://doi.org/10.1007/s00338-017-1645-y (Serrano et al. 2018)

The effects of multiple stressors on the early life stages of reef-building corals are poorly understood. Elevated temperature is the main physiological driver of mass coral bleaching events, but increasing evidence suggests that other stressors, including elevated dissolved inorganic nitrogen (DIN), may exacerbate the negative effects of thermal stress. To test this hypothesis, we investigated the performance of larvae of Orbicella faveolata and Porites astreoides, two important Caribbean reef coral species with contrasting reproductive and algal transmission modes, under increased temperature and/or elevated DIN. We used a fluorescence-based microplate respirometer to measure the oxygen consumption of coral larvae from both species, and also assessed the effects of these stressors on P. astreoides larval settlement and mortality. Overall, we found that (1) larvae increased their respiration in response to different factors (O. faveolata in response to elevated temperature and P. astreoides in response to elevated nitrate) and (2) P. astreoides larvae showed a significant increase in settlement as a result of elevated nitrate, but higher mortality under elevated temperature. This study shows how microplate respirometry can be successfully used to assess changes in respiration of coral larvae, and our findings suggest that the effects of thermal stress and nitrate enrichment in coral larvae may be species specific and are neither additive nor synergistic for O. faveolata or P. astreoides. These findings may have important consequences for the recruitment and community reassembly of corals to nutrient-polluted reefs that have been impacted by climate change.

Predation

> Johnston, L. & Miller, M. W. (2014). Negative indirect effects of neighbors on imperiled scleractinian corals. *Coral Reefs*, 33(4), 1047–1056. https://doi.org/10.1007/s00338-014-1176-8 (Johnston and Miller 2014)

Predation pressure on an individual may be influenced by spatial associations with other organisms. In the case of rare and imperiled species, such indirect interactions may affect the persistence and recovery of local populations. This study examined the effects of coral neighborhood composition on the foraging behavior and impact of the corallivorous gastropod, Coralliophila abbreviata. We conducted a manipulative field experiment in which focal colonies of the threatened scleractinian coral Acropora cervicornis had no neighbors, conspecific neighbors, alternative prey (Orbicella faveolata) neighbors, or non-prey (Porites asteroides) neighbors. Individually tagged C. abbreviata were then seeded into the study area and allowed to colonize the experimental plots. Initial colonization was significantly affected by the species of neighboring corals and snail abundance after colonization was negatively correlated with focal

colony growth. Snails exhibited a strong prey preference for A. cervicornis over O. faveolata and responded numerically to neighborhood quality (i.e., relative preference for neighboring corals). Thus, conspecific neighbors had the greatest predator-mediated negative effect on focal colony performance followed by O. faveolata neighbors. The results suggest that C. abbreviata mediate apparent competition between O. faveolata and A. cervicornis as both species contributed to the local abundance of their shared predator. Additionally, home range estimates for tagged C. abbreviata were calculated, compared among sexes, and found to be significantly greater for males than for females. Overall, this study sheds light on the foraging behavior of an important coral predator and highlights the potential importance of consumer-mediated indirect interactions in the dynamics of severely reduced populations. The results also have direct implications for conservation and population enhancement efforts.

Restoration and Conservation Methods

> Forsman, Z. H., Page, C. A., Toonen, R. J. & Vaughan, D. (2015). Growing coral larger and faster: micro-colony-fusion as a strategy for accelerating coral cover. *PeerJ*, 3:e1313. https://doi.org/10.7717/peerj.1313 (Forsman et al. 2015)

Fusion is an important life history strategy for clonal organisms to increase access to shared resources, to compete for space, and to recover from disturbance. For reef building corals, fragmentation and colony fusion are key components of resilience to disturbance. Observations of small fragments spreading tissue and fusing over artificial substrates prompted experiments aimed at further characterizing Atlantic and Pacific corals under various conditions. Small (□1–3 cm2) fragments from the same colony spaced regularly over ceramic tiles resulted in spreading at rapid rates (e.g., tens of square centimeters per month) followed by isogenic fusion. Using this strategy, we demonstrate growth, in terms of area encrusted and covered by living tissue, of Orbicella faveolata, Pseudodiploria clivosa, and Porites lobata as high as 63, 48, and 23 cm2 per month respectively. We found a relationship between starting and ending size of fragments, with larger fragments growing at a faster rate. Porites lobata showed significant tank effects on rates of tissue spreading indicating sensitivity to biotic and abiotic factors. The tendency of small coral fragments to encrust and fuse over a variety of surfaces can be exploited for a variety of applications such as coral cultivation, assays for coral growth, and reef restoration.

> Page, C. A., Muller, E. M. & Vaughan, D. E. (2018). Microfragmenting for the successful restoration of slow growing massive corals. *Ecological Engineering*, 123, 86–94. https://doi.org/10.1016/j.ecoleng.2018.08.017 (Page et al. 2018)

Slow growing, massive stony corals have often been overlooked in reef-restoration activities, despite their resilience to climate change and contribution to reef framework. Techniques to effectively propagate and outplant these species have proven challenging. However, advancement in methodology may increase rates of success. In 2013, Orbicella faveolata and Montastrea cavernosa fragments were outplanted on reefs in the Florida Keys at a nearshore and offshore location, to determine whether “microfragmenting” corals, the process of creating □1 cm2 fragments, increased outplant survival and growth compared with larger fragments (16–64 cm2). Arrays of eight microfragments were planted near one larger fragment of similar size at each location. Six replicate pairs were haphazardly placed within each □700 m2 study site. Fragments at both sites were monitored for growth and survival over 31 months, spanning two bleaching

events. Initial predation occurred on microfragments, but was absent in the larger fragments. Survival and growth differed between sites, but did not differ between the larger fragments and microfragment arrays. However, excluding plots with >40% predation at the nearshore site showed that O. faveolata microfragment arrays produced 10 times more tissue than traditionally used larger fragments. Results from this study suggest that if predation events are reduced, massive corals can be successfully grown and outplanted for restoration purposes.

Rivas, N. I. 2020. Developing Best Practices for the Propagation and Restoration of Massive Corals: The Influence of Predation, Colony Size and Genotype. Masters. University of Miami, Coral Gables, FL. https://scholarship.miami.edu/discovery/delivery/01UOML_INST:ResearchRepository/12367569120002976?l#13367569110002976 (Rivas 2020)

Coral reefs have undergone drastic declines due to a combination of human and natural disturbances. In response, restoration efforts were developed to recover lost ecosystem services. Over the past decade, reef restoration in Florida has focused almost exclusively on branching Acropora corals but declines in the abundance of corals with massive morphologies highlighted the need to expand our restoration toolbox and develop a holistic "multi-species" approach. Recent studies incorporating corals with massive morphologies into restoration have reported high mortality rates (>50%) because of predation by fish in the first few weeks following outplanting. To address this challenge, I conducted a series of experiments aimed at mitigating predation and understanding factors driving fish predation. I found limiting physical access to newly outplanted corals using colonies of the branching coral Acropora cervicornis, metal spikes, and cages to be highly effective at reducing predation impacts while in place but that cage and spike protective benefits declined immediately after their removal. I identified a size threshold where larger colonies (25 cm2) are less susceptible to predation than smaller coral fragments (5 cm2). I also found coral genotype to play a role in an outplant's probability of being consumed or removed from the reef by fish, with the most susceptible genotype experiencing 86% mortality after 4 weeks compared to the least susceptible genotype that experienced 26% mortality over the same period. Finally, I found evidence that the observed fish impacts are likely driven by consumption activities and not territorial behavior as dead coral controls were not impacted by fish while adjacent live corals experienced 100% mortality. These results suggest that preventing access by fish to coral outplants by planting them in close proximity to large, complex coral colonies, outplanting larger fragments, and utilizing multiple coral genotypes in restored reefs can be an effective way to limit predation impacts and improve the overall efficiency of reef restoration activities.

Rodríguez-Martínez, R. E., Jordán-Garza, A. G. & Jordán-Dahlgren, E. (2016). Low regeneration of lesions produced by coring in Orbicella faveolata. *PeerJ*, 4:e1596. https://doi.org/10.7717/peerj.1596 (Rodriguez-Martinez et al. 2016)

The extraction of tissue-skeleton cores from coral colonies is a common procedure to study diverse aspects of their biology, water quality or to obtain environmental proxies. Coral species preferred for such studies in Caribbean reefs belong to the genera Orbicella. The long term effects of coring in the coral colony are seldom evaluated and in many Caribbean countries this practice is not regulated. We monitored 50 lesions produced on Orbicella faveolata colonies by the extraction of two centimeter-

diameter cores to determine if they were able to heal after a four year period. At the end of the study 4% of the lesions underwent full regeneration, 52% underwent partial regeneration, 14% suffered additional tissue loss but remained surrounded by live tissue, and 30% merged with dead areas of the colonies. Given the low capacity of Orbicella faveolata to regenerate tissue-skeleton lesions, studies that use coring should be regulated and mitigation actions, such as using less destructive techniques and remediation measures after extraction, should be conducted to facilitate tissue regeneration.

> Vanegas, M. J. & Pizarro, V. (2018). Preliminary studies of sperm traits and cryopreservation of the Caribbean reef building coral Orbicella Faveolata. *Bulletin of Marine and Coastal Research*, 47(2), 25–36. http://dx.doi.org/10.25268/bimc.invemar.2018.47.2.745 (Vanegas and Pizarro 2018)

Cryopreservation has been recently applied to coral gametes and tissue with successful results that can be applied for different purposes on coral conservation and restoration. In this study, we decided to determine the sperm morphology of the coral Orbicella faveolata and assess the feasibility of sperm cryopreservation using a combination of intracellular (1,2-Propadiol) and extracellular (milk) cryoprotectants, and two frozen treatments for 24 h. Mature spermatozoa had a triangular-like head shape measuring 4.10 ± 0.69 μm(mean ± SD) and long flagellum (43.24 ± 7.99 μm). Fresh sperm remained viable and mobile for more than five hours after being released from the gamete bundles. After cryopreservation, all post-thaw sperm components assessed (morphology, motility and viability) showed no difference in contrast to fresh sperm. This study is the first report of cryopreservation of O. faveolata sperm, however further research is needed to increase the success of the cryopreservation protocol for broad-scale application.

BOULDER STAR CORAL (ORBICELLA FRANKSI)

Biology and Life History Characteristics

> Courtney, T. A., Andersson, A. J., Bates, N. R., Collins, A., Cyronak, T., de Putron, S. J., . . . Tribollet, A. (2016). Comparing Chemistry and Census-Based Estimates of Net Ecosystem Calcification on a Rim Reef in Bermuda. *Front. Mar. Sci.*, 3:181. https://doi.org/10.3389/fmars.2016.00181 (Courtney et al. 2016)

Coral reef net ecosystem calcification (NEC) has decreased for many Caribbean reefs over recent decades primarily due to a combination of declining coral cover and changing benthic community composition. Chemistry-based approaches to calculate NEC utilize the drawdown of seawater total alkalinity (TA) combined with residence time to calculate an instantaneous measurement of NEC. Census-based approaches combine annual growth rates with benthic cover and reef structural complexity to estimate NEC occurring over annual timescales. Here, NEC was calculated for Hog Reef in Bermuda using both chemistry and census-based NEC techniques to compare the mass-balance generated by the two methods and identify the dominant biocalcifiers at Hog Reef. Our findings indicate close agreement between the annual 2011 census-based NEC 2.35±1.01 kg CaCO3•m-2•y-1 and the chemistry-based NEC 2.23±1.02

kg CaCO3•m-2•y-1 at Hog Reef. An additional record of Hog Reef TA data calculated from an autonomous CO2 mooring measuring pCO2 and modeled pHtotal every 3-hours highlights the dynamic temporal variability in coral reef NEC. This ability for chemistry-based NEC techniques to capture higher frequency variability in coral reef NEC allows the mechanisms driving NEC variability to be explored and tested. Just four coral species, Diploria labyrinthiformis, Pseudodiploria strigosa, Millepora alcicornis, and Orbicella franksi, were identified by the census-based NEC as contributing to 94±19% of the total calcium carbonate production at Hog Reef suggesting these species should be highlighted for conservation to preserve current calcium carbonate production rates at Hog Reef. As coral cover continues to decline globally, the agreement between these NEC estimates suggest that either method, but ideally both methods, may serve as a useful tool for coral reef managers and conservation scientists to monitor the maintenance of coral reef structure and ecosystem services.

Genetic Assessment

> Olsen, K. C., Moscoso, J. A. & Levitan, D. R. (2019). Somatic Mutation Is a Function of Clone Size and Depth in Orbicella Reef-Building Corals. *The Biological Bulletin*, 236, 1–12. https://doi.org/10.1086/700261 (Olsen et al. 2019)

In modular organisms, the propagation of genetic variability within a clonal unit can alter the scale at which ecological and evolutionary processes operate. Genetic variation within an individual primarily arises through the accretion of somatic mutations over time, leading to genetic mosaicism. Here, we assess the prevalence of intraorganismal genetic variation and potential mechanisms influencing the degree of genetic mosaicism in the reef corals Orbicella franksi and Orbicella annularis. Colonies of both species, encompassing a range of coral sizes and depths, were sampled multiple times and genotyped at the same microsatellite loci to detect intraorganismal genetic variation. Genetic mosaicism was detected in 38% of corals evaluated, and mutation frequency was found to be positively related with clonal size and negatively associated with coral depth. We suggest that larger clones experience a greater number of somatic cell divisions and consequently have an elevated potential to accumulate mutations. Furthermore, corals at shallower depths may be exposed to abiotic conditions such as elevated thermal regimes, which promote increased mutation rates. The results highlight the pervasiveness of intraorganismal genetic variation in reef-building corals and emphasize potential mechanisms generating somatic mutations in modular organisms.

> Wright, R. M., Correa, A. M. S., Quigley, L. A., Santiago-Vázquez, L. Z. Shamberger, K. E. F. & Davies, S. W. (2019). Gene Expression of Endangered Coral (Orbicella spp.) in Flower Garden Banks National Marine Sanctuary After Hurricane Harvey. *Front. Mar. Sci.*, 6:672. https://doi.org/10.3389/fmars.2019.00672 (Wright et al. 2019)

About 190 km south of the Texas–Louisiana border, the East and West Flower Garden Banks (FGB) have maintained >50% coral cover with infrequent and minor incidents of disease or bleaching since monitoring began in the 1970s. However, a mortality event, affecting 5.6 ha (2.6% of the area) of the East FGB, occurred in late July 2016 and coincided with storm-generated freshwater runoff extending offshore and over the reef system. To capture the immediate effects of storm-driven freshwater runoff on coral and symbiont physiology, we leveraged the heavy rainfall associated with Hurricane Harvey in late August

2017 by sampling FGB corals at two time points: September 2017, when surface water salinity was reduced (~34 ppt); and one month later when salinity had returned to typical levels (~36 ppt in October 2017). Tissue samples (N = 47) collected midday were immediately preserved for gene expression profiling from two congeneric coral species (Orbicella faveolata and Orbicella franksi) from the East and West FGB to determine the physiological consequences of storm-derived runoff. In the coral, differences between host species and sampling time points accounted for the majority of differentially expressed genes. Gene ontology enrichment for genes differentially expressed immediately after Hurricane Harvey indicated increases in cellular oxidative stress responses. Although tissue loss was not observed on FGB reefs following Hurricane Harvey, our results suggest that poor water quality following this storm caused FGB corals to experience sub-lethal stress. We also found dramatic expression differences across sampling time points in the coral's algal symbiont, Breviolum minutum. Some of these differentially expressed genes may be involved in the symbionts' response to changing environments, including a group of differentially expressed post-transcriptional RNA modification genes. In this study, we cannot disentangle the effects of reduced salinity from the collection time point, so these expression patterns could also be related to seasonality. These findings highlight the urgent need for continued monitoring of these reef systems to establish a baseline for gene expression of healthy corals in the FGB system across seasons, as well as the need for integrated solutions to manage stormwater runoff in the Gulf of Mexico.

Spatial Distribution

Davies, S. W., Strader, M. E., Kool, J. T., Kenkel, C. D. & Matz, M. V. (2017). Modeled differences of coral life-history traits influence the refugium potential of a remote Caribbean reef. *Coral Reefs* 36(3), 913–925. https://doi.org/10.1007/s00338-017-1583-8 (Davies et al. 2017)

Remote populations can influence connectivity and may serve as refugia from climate change. We investigated two reef-building corals (Pseudodiploria strigosa and Orbicella franksi) from the Flower Garden Banks (FGB), the most isolated, high-latitude Caribbean reef system, which, until recently, retained high coral cover. We characterized coral size-frequency distributions, quantified larval mortality rates and onset of competence ex situ, estimated larval production, and created detailed biophysical models incorporating these parameters to evaluate the source–sink dynamics at the FGB from 2009 to 2012. Estimated mortality rates were similar between species, but pre-competency differed dramatically; P. strigosa was capable of metamorphosis within 2.5 d post-fertilization (dpf) and was competent at least until 8 dpf, while O. franksi was not competent until >20 dpf and remained competent up to 120 dpf. To explore the effect of such contrasting life histories on connectivity, we modeled larval dispersal from the FGB assuming pelagic larval durations (PLD) of either 3–20 d, approximating laboratory-measured pre-competency of P. strigosa, or 20–120 d, approximating pre-competency observed in O. franksi. Surprisingly, both models predicted similar probabilities of local retention at the FGB, either by direct rapid reseeding or via long-term persistence in the Loop Current with larvae returning to the FGB within a month. However, our models predicted that short PLDs would result in complete isolation from the rest of the Caribbean, while long PLDs allowed for larval export to more distant northern Caribbean reefs, highlighting the importance of quantifying larval pre-competency dynamics when parameterizing biophysical models to predict larval connectivity. These simulations suggest that FGB coral populations

are likely to be largely self-sustaining and highlight the potential of long-PLD corals, such as endangered Orbicella, to act as larval sources for other degraded Caribbean reefs.

Habitat and Ecosystem Conditions

> Groves, S. H., Holstein, D. M., Enochs, I. C., Kolodzeij, G., Manzello, D. P, Brandt, M. E. & Smith, T. B. (2018). Growth rates of Porites astreoides and Orbicella franksi in mesophotic habitats surrounding St. Thomas, US Virgin Islands. *Coral Reefs*, 37, 345–354. https://doi.org/10.1007/s00338-018-1660-7 (Groves et al. 2018)

Mesophotic coral ecosystems (MCEs) are deep (> 30 m), light-dependent communities that are abundant in many parts of the global ocean. MCEs are potentially connected to shallow reefs via larval exchange and may act as refuges for reef organisms. However, MCE community level recovery after disturbance, and thus, community resilience, are poorly understood components of their capacity as refuges. To assess the potential for disturbance and growth to drive community structure on MCEs with differential biophysical conditions and coral communities, we collected colonies of Orbicella franksi and Porites astreoides and used computerized tomography to quantify calcification. The divergence of coral growth rates in MCEs with different environmental conditions may be species specific; habitat-forming O. franksi have slow and consistent growth rates of ~ 0.2 cm yr−1 below 30 m, regardless of mesophotic habitat, compared to ~ 1.0 cm yr−1 in shallow-water habitats. Slow skeletal growth rates in MCEs suggest that rates of recovery from disturbance will likely also be slow. Localized buffering of MCEs from the stressors affecting shallow reefs is therefore crucial to the long-term capacity of these sites to serve as refugia, given that skeletal extension and recovery from disturbance in MCEs will be significantly slower than on shallow reefs.

> Oliver, L. M., Fisher, W. S., Fore, L., Smith, A. & Bradley, P. (2018). Assessing land use, sedimentation, and water quality stressors as predictors of coral reef condition in St. Thomas, U.S. Virgin Islands. *Environ Monit Assess*, 190(4), 213. https://doi.org/10.1007/s10661-018-6562-1 (Oliver et al. 2018)

Coral reef condition on the south shore of St. Thomas, U.S. Virgin Islands, was assessed at various distances from Charlotte Amalie, the most densely populated city on the island. Human influence in the area includes industrial activity, wastewater discharge, cruise ship docks, and impervious surfaces throughout the watershed. Anthropogenic activity was characterized using a landscape development intensity (LDI) index, sedimentation threat (ST) estimates, and water quality (WQ) impairments in the near-coastal zone. Total three-dimensional coral cover, reef rugosity, and coral diversity had significant negative coefficients for LDI index, as did densities of dominant species Orbicella annularis, Orbicella franksi, Montastraea cavernosa, Orbicella faveolata, and Porites porites. However, overall stony coral colony density was not significantly correlated with stressors. Positive relationships between reef rugosity and ST, between coral diversity and ST, and between coral diversity and WQ were unexpected because these stressors are generally thought to negatively influence coral growth and health. Sponge density was greater with higher disturbance indicators (ST and WQ), consistent with reports of greater resistance by sponges to degraded water quality compared to stony corals. The highest FoRAM (Foraminifera in Reef Assessment and Monitoring) indices indicating good water quality were found offshore from the main

island and outside the harbor. Negative associations between stony coral metrics and LDI index have been reported elsewhere in the Caribbean and highlight LDI index potential as a spatial tool to characterize land-based anthropogenic stressor gradients relevant to coral reefs. Fewer relationships were found with an integrated stressor index but with similar trends in response direction.

Threat Assessment

Disease

> Neely, K. 2018. Surveying the Florida Keys Southern Coral Disease Boundary. Florida DEP, Miami, FL. Pp 1-15 (Neely 2018)

Since 2014, multi-year, multi-species disease outbreak has progressed geographically along the Florida Reef Tract from an origin near Virginia Key. From fall 2017 to spring 2018, 134 reef sites were surveyed to identify the geographic boundary of the disease as well as provide information on rates of progression, cross-reef prevalence differences, and differences in responses of impacted species. Roving diver surveys were conducted during two reef-tract wide assessments in fall 2017 and spring 2018, and roving diver and belt transect surveys were conducted in a targeted effort near the southern disease boundary in winter 2017-18 between Long Key and Marathon. Surveys confirmed prevalence of the disease on 15 coral species, including the primary reef builders and five ESA-listed species. Disease was conspicuously absent on some other species, including the *Acropora* and *Porites* spp. Disease hotspots and geographic differences in disease prevalence showed that tissue loss begins on different species at different times. Broadly, the brain corals (particularly *Meandrina meandrites*) are the first to show tissue loss. Boulder coral infections generally appear shortly thereafter, with *Montastraea cavernosa* in particular often a later species to exhibit tissue loss.

> Roder, C., Arif, C., Daniels, C., Weil, E. & Voolstra, C. R. (2014). Bacterial profiling of White Plague Disease across corals and oceans indicates a conserved and distinct disease microbiome. *Molecular Ecology*, 23, 965–974. https://doi.org/10.1111/mec.12638 (Roder et al. 2014)

Coral diseases are characterized by microbial community shifts in coral mucus and tissue, but causes and consequences of these changes are vaguely understood due to the complexity and dynamics of coral-associated bacteria. We used 16S rRNA gene microarrays to assay differences in bacterial assemblages of healthy and diseased colonies displaying White Plague Disease (WPD) signs from two closely related Caribbean coral species, Orbicella faveolata and Orbicella franksi. Analysis of differentially abundant operational taxonomic units (OTUs) revealed strong differences between healthy and diseased specimens, but not between coral species. A subsequent comparison to data from two Indo-Pacific coral species (Pavona duerdeni and Porites lutea) revealed distinct microbial community patterns associated with ocean basin, coral species and health state. Coral species were clearly separated by site, but also, the relatedness of the underlying bacterial community structures resembled the phylogenetic relationship of the coral hosts. In diseased samples, bacterial richness increased and putatively opportunistic bacteria were consistently more abundant highlighting the role of opportunistic conditions in structuring microbial community patterns during disease. Our comparative analysis shows that it is possible to derive conserved

bacterial footprints of diseased coral holobionts that might help in identifying key bacterial species related to the underlying etiopathology. Furthermore, our data demonstrate that similar-appearing disease phenotypes produce microbial community patterns that are consistent over coral species and oceans, irrespective of the putative underlying pathogen. Consequently, profiling coral diseases by microbial community structure over multiple coral species might allow the development of a comparative disease framework that can inform on cause and relatedness of coral diseases.

> Williams, L., Smith, T. B., Burge, C. A. & Brandt, M. E. (2020). Species-specific susceptibility to white plague disease in three common Caribbean corals. *Coral Reefs*, 39, 27–31. https://doi.org/10.1007/s00338-019-01867-9 (Williams et al. 2020b)

White plague disease has caused widespread coral mortality and affects over 30 Caribbean coral species, yet how different coral species respond to disease exposure has not been tested experimentally. This study quantified white plague transmission from Orbicella franksi to three susceptible and abundant coral species in the U.S. Virgin Islands: Orbicella annularis, Siderastrea siderea, and Porites astreoides. White plague was observed in 83% of tested O. annularis corals within 5.8 ± 1.1 (mean ± SE) d, 42% of S. study indicate that: (1) O. annularis is significantly more susceptible to white plague than S. siderea and P. astreoides, and (2) white plague infection occurs more rapidly in O. annularis than in P. astreoides. These results are important for understanding how multi-species diseases may impact coral species assemblages.

Pollution, Acidification, and Thermal Stress

> Levitan, D. R., Boudreau, W., Jara, J. & Knowlton, N. (2014). Long-term reduced spawning in Orbicella coral species due to temperature stress. *Marine Ecology Progress Series*, 515, 1–10. https://doi.org/10.3354/meps11063 (Levitan et al. 2014)

We examined the long-term reproductive consequence of bleaching stress on Caribbean corals in the Orbicella (formerly Montastraea) species complex (O. annularis, O. faveolata, and O. franksi). Over 2000 observations of spawning in 526 tagged corals in Panama were made from 2002 through 2013. Bleaching events were noted in 2005 and 2010. At the population level, a reduction in spawning persisted for several years following each bleaching event. In 2010, (1) the bleaching event did not alter the timing of spawning, nor coral survivorship or tissue loss; (2) both bleached and unbleached corals had a reduced probability of spawning for several years following the bleaching event, and corals that visibly bleached were less likely to spawn than corals that did not visibly bleach; (3) the species that was affected most by the bleaching event (O. annularis) recovered the ability to spawn in fewer years compared to the species least affected by the bleaching event (O. franksi); and (4) in O. franksi, the species with the widest depth distribution, recovery in the likelihood to spawn was not depth related, although individuals at greater depths were less likely to bleach. In sum, corals that recover from bleaching events can experience long-term reduction in reproduction, over time scales that can bridge the interval between subsequent bleaching events. This may be catastrophic for the long-term maintenance of the population.

> Neal, B. P., Khen, A., Treibitz, T., Beijbom, O., O'Connor, G., Coffroth, M. A., . . . Kline, D. I. (2017). Caribbean massive corals not recovering from repeated thermal stress events during

2005–2013. *Ecology and Evolution*, 7(5), 1339–1353. https://doi.org/10.1002/ece3.2706 (Neal et al. 2017)

Massive coral bleaching events associated with high sea surface temperatures are forecast to become more frequent and severe in the future due to climate change. Monitoring colony recovery from bleaching disturbances over multiyear time frames is important for improving predictions of future coral community changes. However, there are currently few multiyear studies describing long-term outcomes for coral colonies following acute bleaching events. We recorded colony pigmentation and size for bleached and unbleached groups of co-located conspecifics of three major reef-building scleractinian corals (Orbicella franksi, Siderastrea siderea, and Stephanocoenia michelini; n = 198 total) in Bocas del Toro, Panama, during the major 2005 bleaching event and then monitored pigmentation status and changes live tissue colony size for 8 years (2005–2013). Corals that were bleached in 2005 demonstrated markedly different response trajectories compared to unbleached colony groups, with extensive live tissue loss for bleached corals of all species following bleaching, with mean live tissue losses per colony 9 months postbleaching of 26.2% (±5.4 SE) for O. franksi, 35.7% (±4.7 SE) for S. michelini, and 11.2% (±3.9 SE) for S. siderea. Two species, O. franksi and S. michelini, later recovered to net positive growth, which continued until a second thermal stress event in 2010. Following this event, all species again lost tissue, with previously unbleached colony species groups experiencing greater declines than conspecific sample groups, which were previously bleached, indicating a possible positive acclimative response. However, despite this beneficial effect for previously bleached corals, all groups experienced substantial net tissue loss between 2005 and 2013, indicating that many important Caribbean reef-building corals will likely suffer continued tissue loss and may be unable to maintain current benthic coverage when faced with future thermal stress forecast for the region, even with potential benefits from bleaching-related acclimation.

Silbiger, N. J., Goodbody-Gringley, G., Bruno, J. F. & Putnam, H. M. (2019). Comparative thermal performance of the reef-building coral Orbicella franksi at its latitudinal range limits. *Mar Biol*, 166, 126. https://doi.org/10.1007/s00227-019-3573-6 (Silbiger et al. 2019)

Temperature drives biological responses that scale from the cellular to ecosystem levels and thermal sensitivity will shape organismal functions and population dynamics as the world warms. Reef-building corals are sensitive to temperature due to their endosymbiotic relationship with single-celled dinoflagellates, with mass mortality events increasing in frequency and magnitude. The purpose of this study was to quantify the thermal sensitivity of important physiological functions of a Caribbean reef-building coral, Orbicella franksi, through the measurement of thermal performance curves (TPCs). We compared TPC metrics (thermal optimum, critical maximum, activation energy, deactivation energy, and rate at a standardized temperature) between two populations at the northern and southern extents of the geographic range of O. franksi. We further compared essential coral organismal processes (gross photosynthesis, respiration, and calcification) within a site to determine which function is most sensitive to thermal stress using a hierarchical Bayesian-modeling approach. We found evidence for differences in thermal performance, which could be due to thermal adaptation or acclimatization, with higher TPC metrics (thermal optimum and critical maximum) in warmer Panama, compared to cooler Bermuda. We also documented the hierarchy in thermal sensitivity of essential organismal functions within a population: respiration was less sensitive than photosynthesis, which was less sensitive than calcification.

Understanding thermal performance of corals is essential for projecting coral reef futures, given that key biological functions necessary to sustain coral reef ecosystems are thermally mediated.

Predation

> Maher, R. L., Johnston, M. A., Brandt, M. E., Smith, T. B. & Correa, A. M. S. (2018). Depth and coral cover drive the distribution of a coral macroborer across two reef systems. *PLOS ONE*, 13(6), e0199462. https://doi.org/10.1371/journal.pone.0199462 (Maher et al. 2018)

Bioerosion, the removal of calcium carbonate from coral frameworks by living organisms, influences a variety of reef features, from their topographic complexity to the net balance of carbonate budgets. Little is known, however, about how macroborers, which bore into reef substrates leaving traces greater than 0.1 mm diameter, are distributed across coral reefs, particularly reef systems with high (>50%) stony coral cover or at mesophotic depths (≥30 m). Here, we present an accurate and efficient method for quantifying macroborer densities from stony coral hosts via image analysis, using the bioeroding barnacle, Lithotrya dorsalis, and its host coral, Orbicella franksi, as a case study. We found that in 2014, L. dorsalis densities varied consistently with depth and host percent cover in two Atlantic reef systems: the Flower Garden Banks (FGB, northwest Gulf of Mexico) and the U.S. Virgin Islands (USVI). Although average barnacle density was nearly 4.5 times greater overall in the FGB than in the USVI, barnacle density decreased with depth in both reef regions. Barnacle density also scaled negatively with increasing coral cover in the study areas, suggesting that barnacle populations are not strictly space-limited in their distribution and settlement opportunities. Our findings suggest that depth and host coral cover, and potentially, local factors may strongly influence the abundance of macroborers, and thus the rate of CaCO3 loss, in a given reef system. Our image analysis method for quantifying macroborers can be standardized across historical and modern reef records to better understand how borers impact host growth and reef health.

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