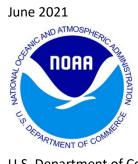
Coral Critical Habitat

Bibliography

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Background & Scope

In 2020 and 2021, the National Marine Fisheries Service (NMFS) proposed rules to designate critical habitat for threatened corals in U.S. waters of the Indo-Pacific and the Caribbean: Proposed Rule to Designate Critical Habitat for the Threatened Indo-Pacific Corals and Proposed Rule to Designate Critical Habitat for the Threatened Caribbean Corals. The NOAA Central Library created this bibliography to provide NMFS with the most up-to-date scientific literature concerning the habitat features and threats to the corals named in the two proposed rules linked above. The literature included here is from 2018 forward and organized into sections relating to the physical and biological features essential for coral conservation. These sections appear in the same order that they appear in the NMFS reports and rules.

Section 1: Substrate

Section 2: Trophic Effects of Reef Fishing

Section 3: Invasive Species and Algae

Section 4: Sedimentation

Section 5: Ocean Warming

Section 6: Ocean Acidification

Section 7: Nutrient Enrichment

Section 8: Water Clarity

Section 9: Contaminants

Section 10: Symbiotic Species

Section 11: Disease

Section 12: Ocean Deoxygenation

Section 13: General Habitat Information

Sources Reviewed

The following literature sources and databases were searched in order to create this bibliography: Clarivate's Web of Science, ProQuest's Aquatic Science Fisheries Abstracts, Google Scholar, Dimensions, JSTOR, EBSCO's Academic Search Premier and Elsevier's ScienceDirect, BioOne Complete, Science.gov, and open web searching.

Section 1: Substrate

Barnhill, K. A., & Bahr, K. D. (2019). Coral Resilience at Malauka`a Fringing Reef, Kāne'ohe Bay, O'ahu after 18 years. *Journal of Marine Science and Engineering*, 7(9). https://doi.org/10.3390/jmse7090311

Globally, coral reefs are under threat from climate change and increasingly frequent bleaching events. However, corals in Kāne'ohe Bay, Hawai'i have demonstrated the ability to acclimatize and resist increasing temperatures. Benthic cover (i.e., coral, algae, other) was compared over an 18 year period (2000 vs. 2018) to estimate species composition changes. Despite a climate change induced 0.96 °C temperature increase and two major bleaching events within the 18-year period, the fringing reef saw no significant change in total coral cover (%) or relative coral species composition in the two dominant reef-building corals, Porites compressa and Montipora capitata. However, the loss of two coral species (Pocillopora meandrina and Porites lobata) and the addition of one new coral species (Leptastrea purpurea) between surveys indicates that while the fringing reef remains intact, a shift in species composition has occurred. While total non-coral substrate cover (%) increased from 2000 to 2018, two species of algae (Gracilaria salicornia and Kappaphycus alvarezii) present in the original survey were absent in 2018. The previously dominant algae Dictyosphaeria spp. significantly decreased in percent cover between surveys. The survival of the studied fringing reef indicates resilience and suggests these Hawaiian corals are capable of acclimatization to climate change and bleaching events.

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. <u>https://doi.org/10.1111/gcb.14800</u>

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 CaCO3 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 CaCO3 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.

Januchowski-Hartley, F. A., Bauman, A. G., Morgan, K. M., Seah, J. C. L., Huang, D., & Todd, P. A. (2020). Accreting coral reefs in a highly urbanized environment. *Coral Reefs*, 39(3), 717-731. <u>https://doi.org/10.1007/s00338-020-01953-3</u>

Globally, many coral reefs have fallen into negative carbonate budget states, where biological erosion exceeds carbonate production. The compounding effects of urbanization and climate change have caused reductions in coral cover and shifts in community composition that may limit the ability of reefs to maintain rates of vertical accretion in line with rising sea levels. Here we report on coral reef carbonate budget surveys across seven coral reefs in Singapore, which persist under chronic turbidity and in highly disturbed environmental conditions, with less than 20% light penetration to 2 m depth. Results show that mean net carbonate budgets across Singapore's reefs were relatively low, at 0.63 ± 0.27 kg CaCO3 m-2 yr-1 (mean ± 1 SE) with a range from - 1.56 to 1.97, compared with the mean carbonate budgets across the Indo-Pacific of 1.4 ± 0.15 kg CaCO3 m-2 yr-1, and isolated Indian Ocean reefs pre-2016 bleaching (~ 3.7 kg CaCO3 m-2 yr-1). Of the seven reefs surveyed, only one reef had a net negative, or erosional budget, due to near total loss of coral cover (< 5% remaining coral). Mean gross carbonate production on Singapore's reefs was dominated by stress-tolerant and generalist species, with low-profile morphologies, and was \sim 3 kg m-2 yr-1 lower than on reefs with equivalent coral cover elsewhere in the Indo-Pacific. While overall these reefs are maintaining and adding carbonate structure, their mean vertical accretion potential is below both current rates of sea level rise (1993–2010), and future predictions under RCP 4.5 and RCP 8.5 scenarios. This is likely to result in an increase of 0.2–0.6 m of water above Singapore's reefs in the next 80 yr, further narrowing the depth range over which these reefs can persist.

Jiang, M., Pan, C., Barbero, L., Reed, J., Salisbury, J. E., VanZwieten, J. H., & Wanninkhof, R. (2020). Variability of bottom carbonate chemistry over the deep coral reefs in the Florida Straits and the impacts of mesoscale processes. *Ocean Modelling*, 147, 101555. <u>https://doi.org/10.1016/j.ocemod.2019.101555</u>

Abundant and diverse cold-water coral and fish communities can be found in the deep waters of the Florida Straits, which are believed to be living under suboptimal conditions impacted by increasing oceanic CO2 levels. Yet, little is known regarding the spatial-temporal variability of bottom carbonate chemistry parameters and their dynamic drivers in this area. To address this issue, we present results from numerical simulations of a coupled physical-biogeochemical model for the south Florida shelf and Florida Straits. Our exploratory analysis focuses on two well-known deep-coral habitats: Pourtalès Terrace (200–450 m) and Miami Terrace (270–600 m). Results suggest that bottom waters along the northern/western slope of the Straits are comprised primarily of the North Atlantic Central Water

(NWCW) and Antarctic Intermediate Water (AAIW), driven by upwelling associated with the bottom Ekman transport of the Florida Current. Over the Pourtalès Terrace, both the meandering of the Florida Current and mesoscale eddies modulate the upwelling (downwelling) of cold (warm) waters. In contrast, Florida Current makes a sharp turn at the southern end of the Miami Terrace leading to persistent island wakes, frequent occurrences of a transient eddy, and strong upwelling of deep waters toward the platform of the terrace. Passage of the transient eddy often accompanies strong downwelling of warm waters and a return (southward) flow on top of the platform. Overall, bottom water properties including temperature (T), dissolved inorganic carbon (DIC) and total alkalinity (TA) show strong variability on weekly to monthly time-scales over entire Pourtalès Terrace and on the platform of Miami Terrac, mostly driven by physics. In deeper areas (>400 m), bottom water properties are fairly stable with both DIC and TA showing narrow ranges. Interestingly, waters over the southeastern portion of the Pourtalès Terrace show consistently warmer temperature, lower DIC, and higher TA than those on top of this terrace. The aragonite saturation state (Ω) ranges 1.2-2 on top of the Pourtalès Terrace and 1.2-1.7 both on top of Miami Terrace and on the upper slope of Pourtalès Terrace. In the deeper slope areas (>400 m), it is nearly constant at 1.2-1.3. This modeling effort suggests that remote forcing and biogeochemical processes along the transport paths, from the Gulf of Mexico to the Straits, are significant but second-order contributors to the variability of bottom carbonate chemistry. The impacts of benthic biogeochemical processes along the transit paths are not resolved.

Kellogg, C. A., Moyer, R. P., Jacobsen, M., & Yates, K. (2020). Identifying mangrove-coral habitats in the Florida Keys. *Peerj*, 8. <u>https://doi.org/10.7717/peerj.9776</u>

Coral reefs are degrading due to many synergistic stressors. Recently there have been a number of global reports of corals occupying mangrove habitats that provide a supportive environment or refugium for corals, sheltering them by reducing stressors such as oxidative light stress and low pH. This study used satellite imagery and manual ground-truthing surveys to search for mangrove-coral habitats in the Florida Keys National Marine Sanctuary and then collected basic environmental parameters (temperature, salinity, dissolved oxygen, pH(NBS), turbidity) at identified sites using a multi-parameter water quality sonde. Two kinds of mangrove-coral habitats were found in both the Upper and Lower Florida Keys: (1) prop-root corals, where coral colonies were growing directly on (and around) mangrove prop roots, and (2) channel corals, where coral colonies were growing in mangrove channels under the shade of the mangrove canopy, at deeper depths and not in as close proximity to the mangroves. Coral species found growing on and directly adjacent to prop roots included Porites porites (multiple morphs, including P. divaricata and P. furcata), Siderastrea radians, and Favia fragum. Channel coral habitats predominantly hosted S. radians and a few S. siderea, although single colonies of Solenastrea bournoni and Stephanocoenia intersepta were observed. Although clear, low-turbidity water was a consistent feature of these mangrove-coral habitats, the specific combination of environmental factors that determine which mangrove habitats are favorable for coral recruitment remains to be defined. Circumstantial evidence suggests additional coral communities existed on mangrove shorelines of oceanside and backcountry islands until destroyed, likely by Hurricane Irma. These mangrove-coral habitats may be climate refugia for corals and could be included in ecosystem management plans and considered for their applications in coral restoration.

Keyes, A., Perry, J., & Johnson, D. H. (2019). Effects of mangrove deforestation on near-shore coral reefs. BIOS, 90(1), 8-13. <u>https://doi.org/10.1893/0005-3155-90.1.8</u>

Mangrove forests are among the world's most vulnerable subtropical and tropical habitats. With global losses already in excess of 50%, mangroves are being lost more rapidly than tropical rainforests. Those losses are critical to society because mangroves filter terrestrial contaminants, protecting coral reefs from eutrophication, sedimentation, and resulting degradation. Utila is a small island northeast of Honduras, well known for its diving opportunities. Anthropogenic development reduces the island's mangrove forests, threatening the health of surrounding coral reefs. We examined the effects of mangrove deforestation on coral reefs using shoreline mangrove density, near-shore nitrate levels, and algal coverage on adjacent reefs. These variables were measured offshore of both developed and undeveloped coast. Mangrove density was significantly lower along the developed than the undeveloped coast (mean 0.27 stems/m2 vs. 3.01 stems/m2, respectively, p < 0.0001). Nitrate levels were significantly higher along the developed coast than along the undeveloped coast (mean 22.7 mg/L vs. 7.9 mg/L, respectively, p < 0.0001), as was algal cover (mean 48.1% vs. 32.4%, respectively, p < 0.0001). These results support arguments to reduce mangrove deforestation and encourage reforestation, which will protect not only mangroves and corals, but also avoid negative impacts to the local economy, which often is heavily reliant on dive tourism and fisheries.

Masucci, G. D., Acierno, A., & Reimer, J. D. (2020). Eroding diversity away: Impacts of a tetrapod breakwater on a subtropical coral reef. *Aquatic Conservation-Marine and Freshwater Ecosystems*, 30(2), 290-302. https://doi.org/10.1002/aqc.3249

Artificial barriers for coastal protection have been deployed across numerous tropical and subtropical islands in the Pacific, including Okinawa Island, southern Japan, where artificial defences have been installed along a large part of the coastline. Although artificial barriers can lead to beach narrowing or loss and can exacerbate erosion, their effects on coral reef ecosystems remain understudied. This study investigated the impact of a tetrapod breakwater in Ogimi Village, Okinawa Island, Japan, comparing the area affected by the presence of the barrier with a nearby natural coastline, and examining differences in physical parameters (depth profiles, sediment granulometry, and erosion on plaster balls) and benthic community composition. Significant differences in depth profiles, sediment granulometry, and erosion were found, suggestive of alterations in water energy levels (lower than controls on the landward side of the barrier, and higher on the seaward side). The benthic community was also clearly affected, with almost no living corals growing over the blocks or in their proximity. Overall, the data show how breakwaters can affect the physical environment and benthic communities in a subtropical coral reef ecosystem, with negative consequences for coral survival.

Ortiz-Rosa, S., Hernandez, W. J., Williams, S. M., & Armstrong, R. A. (2020). Water Quality Anomalies following the 2017 Hurricanes in Southwestern Puerto Rico: Absorption of Colored Detrital and Dissolved Material. *Remote Sensing*, 12(21). <u>https://doi.org/10.3390/rs12213596</u>

Absorption of colored dissolved organic matter or detrital gelbstoff (aCDOM/ADG) and light attenuation coefficient (K(d)490) parameters were studied at La Parguera Natural Reserve in southwestern Puerto Rico, before and following Hurricanes Irma (6-7 September) and Maria (20-21 September) in 2017. Water quality assessments involving Sentinel 3A ocean color products and field sample data was

performed. The estimated mean of ADG in surface waters was calculated at >0.1 m(-1) with a median of 0.05 m(-1) and aCDOM443 ranged from 0.0023 to 0.1121 m(-1) in field samples (n=21) in 2017. Mean ADG443 values increased from July to August at 0.167 to 0.353 m(-1) in September-October over Turrumote reef (LP6) with a maximum value of 0.683 m(-1). Values above 0.13 m(-1) persisted at offshore waters off Guanica Bay and over coral reef areas at La Parguera for over four months. The ADG443 product presented values above the median and the second standard deviation of 0.0428 m(-1) from September to October 2017 and from water sample measurement on 19 October 2017. Mean K(d)490 values increased from 0.16 m(-1) before hurricanes to 0.28 right after Hurricane Irma. The value remained high, at 0.34 m(-1), until October 2017, a month after Hurricane Maria. Analysis of the Sentinel (S3) OLCI products showed a significant positive correlation (r(s) = 0.71, p = 0.0005) between K(d)490_M07 and ADG_443, indicating the influence of ADG on light attenuation. These significant short-term changes could have ecological impacts on benthic habitats highly dependent on light penetration, such as coral reefs, in southwestern Puerto Rico.

Skinner, L. F. (2018). Record of Tubastraea coccinea on Xestospongia barrel sponge: a new threat to Caribbean and Gulf of Mexico reefs? *Coral Reefs*, 37(3), 809-809. https://doi.org/10.1007/s00338-018-1706-x

Over the last 30 years, Tubastraea spp. has acquired the status of one of the most effective invasive species in the western Atlantic Ocean causing impacts in community structure, mortality of native corals, and the predation of both fish and invertebrate larva, with presumed effects on fishing yields (Creed et al. 2017; Miranda et al. 2018).

During sampling for the Marine Biodiversity of Yucatan (BDMY) project, seventy-nine sites on six reef areas at Cayos Oeste were surveyed during more than 320 team dives. One 10 polyp colony of Tubastraea coccinea Lesson, 1829 was recorded at Banco Obispo Sur; (20.42535 N/92.22692 W) at a depth of approximately 15 m. It was recorded deeply encrusted on the vertical outer wall of the barrel sponge Xestopongia muta (Schmidt, 1870) without any visible indication of necrosis on the sponge surface due to Tubastraea cnidocytes (Fig. 1). As T. coccinea could become very invasive in just few years after initial establishment (Creed et al. 2017), the colony was completely removed. To our knowledge, it is the first record of T. coccinea growing on living animals. The possibility of T. coccinea to colonize X. muta in the absence of other suitable substrates could favor its spread along reefs both on Gulf of Mexico and Caribbean, representing a threat to these areas.

Section 2: Trophic Effects of Reef Fishing

Bo, M., Montgomery, A. D., Opresko, D. M., Wagner, D., & Bavestrello, G. (2019). Antipatharians of the Mesophotic Zone: Four Case Studies (Vol. 12). https://doi.org/10.1007/978-3-319-92735-0_37

About 63% of the known antipatharian genera occur at mesophotic depths (30-150 m), with the majority extending into the deep sea. Along the continental shelf and offshore sites, antipatharians tend to increase in diversity and abundance with depth, reaching a peak at mesophotic depths due to favorable environmental factors enhancing their settlement and growth and biotic factors associated with lower levels of competition for space. A review of taxonomic and ecological studies for shallow and mesophotic antipatharians is presented for four regionally based case studies, three in the tropics (1) Central Indo-Pacific, plus adjacent sections of the Western Indo-Pacific, (2) Eastern Indo-Pacific (primarily Hawai'i), and (3) the Caribbean Sea) and one at temperate latitudes in the Mediterranean Sea and adjacent sections of the Northeast Atlantic. The mesophotic fauna is mainly represented by the families Antipathidae, Aphanipathidae, and Myriopathidae. The most diverse community is found in the Central/Western Indo-Pacific, followed by the Caribbean Sea. The tropical antipatharians are represented by shallow species that extend their distribution into the upper mesophotic zone (30-60 m), while the temperate antipatharians consist of deepwater (> 150 m) species that extend upward into the lower part of the mesophotic zone. Black corals in mesophotic coral ecosystems can be habitat-forming components of benthic assemblages on hard substratum. They have an enormous potential for hidden biodiversity and play an important ecological role for the broader marine ecosystem. The threats to antipatharians consist of demersal fishing activities and coral harvesting, which may be highly destructive to these poorly understood systems.

Chagaris, D., Patterson, W. F., & Allen, M. S. (2020). Relative Effects of Multiple Stressors on Reef Food Webs in the Northern Gulf of Mexico Revealed via Ecosystem Modeling. *Frontiers in Marine Science*. <u>https://doi.org/10.3389/fmars.2020.00513</u>

Since 2010, the northern Gulf of Mexico (NGoM) has experienced two unique environmental stressors. First, the 2010 Deepwater Horizon oil spill (DWH) impacted a broad range of taxa and habitats and resulted in declines of small demersal reef fish over the study area (88.5–85.5°W and 29–30.5°N). Then, from 2011 to 2014 the invasive Indo-Pacific lionfish (Pterois volitans) underwent exponential population growth, leading to some of the highest densities in their invaded range. The primary objective of this study was to evaluate the effect of these stressors on reef ecosystems, and specifically how invasive lionfish and fishing may have impacted recovery following DWH. Site-specific datasets on fish density and diet composition were synthesized into an Ecopath with Ecosim food web model of a NGoM reef ecosystem. The model consisted of 63 biomass groups and was calibrated to time series of abundance from 2009 to 2016. The model accounted for mortality from the DWH using forcing functions derived from logistic dose-response curves and oil concentrations. Eight stressor scenarios were simulated, representing all combinations of DWH, lionfish, and fishing. Simulated biomass differed across model groups due to singular and cumulative impacts of stressors and direct and indirect effects arising through food web interactions. Species with high exploitation rates were influenced by fishing more than lionfish following DWH. Several small demersal fish groups were predicted to be strongly influenced by either the cumulative effects of lionfish and DWH or by lionfish alone. A second group of small demersal fish benefited in the stressor scenarios due to reduced top-down predation and competition in the combined stressor scenarios. We conclude that lionfish had a major impact on this

ecosystem, based on both empirical data and simulation results. This caused slower recoveries following DWH and lower fish biomass and diversity. Additionally, the lack of recovery for some groups in the absence of lionfish suggests system reorganization may be preventing return to a pre-DWH state. We intended for this work to improve our understanding of how temperate reef ecosystems, like those in the NGoM, respond to broad scale stressors and advance the state of applied ecosystem modeling for resource damage assessment and restoration planning.

Robinson, J. P. W., McDevitt-Irwin, J. M., Dajka, J. C., Hadj-Hammou, J., Howlett, S., Graba-Landry, A., . . . Graham, N. A. J. (2020). Habitat and fishing control grazing potential on coral reefs. *Functional Ecology*, 34(1), 240-251. <u>https://doi.org/10.1111/1365-2435.13457</u>

Herbivory is a key process on coral reefs, which, through grazing of algae, can help sustain coraldominated states on frequently disturbed reefs and reverse macroalgal regime shifts on degraded ones. Our understanding of herbivory on reefs is largely founded on feeding observations at small spatial scales, yet the biomass and structure of herbivore populations is more closely linked to processes which can be highly variable across large areas, such as benthic habitat turnover and fishing pressure. Though our understanding of spatiotemporal variation in grazer biomass is well developed, equivalent macroscale approaches to understanding bottom-up and top-down controls on herbivory are lacking. Here, we integrate underwater survey data of fish abundances from four Indo-Pacific island regions with herbivore feeding observations to estimate grazing rates for two herbivore functions, cropping (which controls turf algae) and scraping (which promotes coral settlement by clearing benthic substrate), for 72 coral reefs. By including a range of reef states, from coral to algal dominance and heavily fished to remote wilderness areas, we evaluate the influences of benthic habitat and fishing on the grazing rates of fish assemblages. Cropping rates were primarily influenced by benthic condition, with cropping maximized on structurally complex reefs with high substratum availability and low macroalgal cover. Fishing was the primary driver of scraping function, with scraping rates depleted at most reefs relative to remote, unfished reefs, though scraping did increase with substratum availability and structural complexity. Ultimately, benthic and fishing conditions influenced herbivore functioning through their effect on grazer biomass, which was tightly correlated to grazing rates. For a given level of biomass, we show that grazing rates are higher on reefs dominated by small-bodied fishes, suggesting that grazing pressure is greatest when grazer size structure is truncated. Stressors which cause coral declines and clear substrate for turf algae will likely stimulate increases in cropping rates, in both fished and protected areas. In contrast, scraping functions are already impaired at reefs inhabited by people, particularly where structural complexity has collapsed, indicating that restoration of these key processes will require scraper biomass to be rebuilt towards wilderness levels. A free Plain Language Summary can be found within the Supporting Information of this article.

Suka, R., Huntington, B., Morioka, J., O'Brien, K., & Acoba, T. (2020). Successful application of a novel technique to quantify negative impacts of derelict fishing nets on Northwestern Hawaiian Island reefs. *Marine Pollution Bulletin*, 157, 111312. <u>https://doi.org/10.1016/j.marpolbul.2020.111312</u>

The remote and uninhabited Northwestern Hawaiian Islands (NWHI) contain 70% of the shallow water coral reefs in the United States and are regularly exposed to derelict fishing nets. These nets snag on the shallow reefs, damaging or killing benthic communities. However, no data exist to quantify this impact.

Here we use a novel application of photogrammetry, Structure-from-Motion (SfM), to calculate benthic cover from mosaic images at net-impact and control sites. Net-impact sites had significantly higher cover of bare substrate, sand, and crustose coralline algae and significantly lower coral and macroalgae cover compared to control sites. These differences were unrelated to net size and fouling. Our study demonstrates the utility of using SfM to efficiently quantify impacts of derelict fishing nets. Revisiting these sites will be essential to document how the reef recovers to further our understanding of the lasting impacts of derelict fishing nets on coral reef habitats.

Section 3: Invasive Species and Algae

Anderson, D. M., Fensin, E., Gobler, C. J., Hoeglund, A. E., Hubbard, K. A., Kulis, D. M., . . . Trainer, V. L. (2021). Marine harmful algal blooms (HABs) in the United States: History, current status and future trends. *Harmful Algae*, 101975. <u>https://doi.org/10.1016/j.hal.2021.101975</u>

Harmful algal blooms (HABs) are diverse phenomena involving multiple. species and classes of algae that occupy a broad range of habitats from lakes to oceans and produce a multiplicity of toxins or bioactive compounds that impact many different resources. Here, a review of the status of this complex array of marine HAB problems in the U.S. is presented, providing historical information and trends as well as future perspectives. The study relies on thirty years (1990–2019) of data in HAEDAT - the IOC-ICES-PICES Harmful Algal Event database, but also includes many other reports. At a qualitative level, the U.S. national HAB problem is far more extensive than was the case decades ago, with more toxic species and toxins to monitor, as well as a larger range of impacted resources and areas affected. Quantitatively, no significant trend is seen for paralytic shellfish toxin (PST) events over the study interval, though there is clear evidence of the expansion of the problem into new regions and the emergence of a species that produces PSTs in Florida – Pyrodinium bahamense. Amnesic shellfish toxin (AST) events have significantly increased in the U.S., with an overall pattern of frequent outbreaks on the West Coast, emerging, recurring outbreaks on the East Coast, and sporadic incidents in the Gulf of Mexico. Despite the long historical record of neurotoxic shellfish toxin (NST) events, no significant trend is observed over the past 30 years. The recent emergence of diarrhetic shellfish toxins (DSTs) in the U.S. began along the Gulf Coast in 2008 and expanded to the West and East Coasts, though no significant trend through time is seen since then. Ciguatoxin (CTX) events caused by Gambierdiscus dinoflagellates have long impacted tropical and subtropical locations in the U.S., but due to a lack of monitoring programs as well as underreporting of illnesses, data on these events are not available for time series analysis. Geographic expansion of Gambierdiscus into temperate and non-endemic areas (e.g., northern Gulf of Mexico) is apparent, and fostered by ocean warming. HAB-related marine wildlife morbidity and mortality events appear to be increasing, with statistically significant increasing trends observed in marine mammal poisonings caused by ASTs along the coast of California and NSTs in Florida. Since their first occurrence in 1985 in New York, brown tides resulting from high-density blooms of Aureococcus have spread south to Delaware, Maryland, and Virginia, while those caused by Aureoumbra have spread from the Gulf Coast to the east coast of Florida. Blooms of Margalefidinium polykrikoides occurred in four locations in the U.S. from 1921–2001 but have appeared in more than 15 U.S. estuaries since then, with ocean warming implicated as a causative factor. Numerous blooms of toxic cyanobacteria have been documented in all 50 U.S. states and the transport of cyanotoxins from freshwater systems into marine coastal waters is a recently identified and potentially significant threat to public and ecosystem health. Taken together, there is a significant increasing trend in all HAB events in HAEDAT over the 30-year study interval. Part of this observed HAB expansion simply reflects a better realization of the true or historic scale of the problem, long obscured by inadequate monitoring. Other contributing factors include the dispersion of species to new areas, the discovery of new HAB poisoning syndromes or impacts, and the stimulatory effects of human activities like nutrient pollution, aquaculture expansion, and ocean warming, among others. One result of this multifaceted expansion is that many regions of the U.S. now face a daunting diversity of species and toxins, representing a significant and growing challenge to resource managers and public health officials in terms of toxins, regions, and time intervals to monitor, and necessitating new approaches to monitoring and management. Mobilization of funding and resources for research, monitoring and management of HABs requires accurate information on the

scale and natu e of the national problem. HAEDAT and other databases can be of great value in this regard but efforts are needed to expand and sustain the collection of data regionally and nationally.

Derouen, Z. C., Peterson, M. R., Wang, H.-H., & Grant, W. E. (2020). Determinants of Tubastraea coccinea invasion and likelihood of further expansion in the northern Gulf of Mexico. *Marine Biodiversity*, 50(6), 101. https://doi.org/10.1007/s12526-020-01126-z

Invasive species have large economic and ecological impacts and are the leading driver of extinction for both plants and animals worldwide. In the USA, coral reefs, which provide \$3.4 billion per year in ecosystem services, are impacted by invasive marine species. One such species is Tubastraea coccinea, which was the first scleractinia to invade the western Atlantic and recently has spread to natural reefs within the northern Gulf of Mexico (GoM). We document this recent invasion by compiling occurrence records, develop a species distribution model identifying important determinants of invasion, and project potential range expansion. Our results indicate T. coccinea currently is distributed along the GoM coast from the Florida Keys to southern Texas, with documented localities clustered ≈ 100 km off the Louisiana coast and \approx 200 km off the Texas coast, and sparsely distributed elsewhere. Our species distribution model identified five environmental factors that together contribute > 99% to the overall model. These factors include two surface variables (mean pH and mean calcite, contributing \approx 40%) and three benthic variables (maximum current velocity, minimum iron, and minimum dissolved oxygen, contributing \approx 60%). Our model suggests potential habitat for range expansion is distributed mainly within the western portion of the northern GoM, with the highest probabilities of occurrence (0.8 < P < 1.0) clustered along the Texas and Louisiana coasts between 88 and 97° W (near the border between states).

Edmunds, P. J., Zimmermann, S. A., & Bramanti, L. (2019). A spatially aggressive peyssonnelid algal crust (PAC) threatens shallow coral reefs in St. John, US Virgin Islands. *Coral Reefs*, 38(6), 1329-1341. <u>https://doi.org/10.1007/s00338-019-01846-0</u>

In recent decades, many Caribbean reefs have experienced large declines in abundance of scleractinian corals, and blooms of fleshy macroalgae have often accompanied these trends. In 2010 a new macroalgal threat emerged in Lac Bay, Bonaire, where peyssonnelid algal crusts (PAC) rapidly spread in shallow water and overgrew corals and sponges. Similar growths have been reported in Puerto Rico and the Virgin Islands, and here, we describe the spread of PAC on the shallow reefs of St. John, US Virgin Islands, ~ 760 km northeast of Bonaire. In 2015, PAC covered 0.2–20.6% of hard benthic surfaces at \leq 7 m depth. By August 2017, at the same sites, PAC had increased to 3.2–61.0% cover, at 5 m depth at 10 other sites along 5 km of shore, it covered 1.4–61.6% of reef surfaces, and at 9 m depth at five sites, it covered 0.8–41.0% of reef surfaces. At 5 m depth in August 2017, scleractinians and octocorals were frequently contacting PAC (42–47% of colonies), and more scleractinians (74%) than octocorals (39%) were overgrown by PAC. Following surveys in August 2017, St. John was hit by two Category 5 hurricanes, yet the shore-wide mean cover of PAC at 5 m depth was only reduced from 26 to 23%. Our results suggest PAC is poised to cause significant ecological change on the reefs of St. John and potentially will promote a community shift favoring octocorals over scleractinians. PAC constitutes an emerging regional threat on shallow Caribbean reefs to which researchers and resource managers will need to quickly respond.

Figueroa, D. F., McClure, A., Figueroa, N. J., & Hicks, D. W. (2019). Hiding in plain sight: invasive coral Tubastraea tagusensis (Scleractinia:Hexacorallia) in the Gulf of Mexico. *Coral Reefs*, 38(3), 395-403. <u>https://doi.org/10.1007/s00338-019-01807-7</u>

Our research presents the first record of Tubastraea tagusensis (Wells, Notes on Indo-Pacific scleractinian corals. Part 9. New corals from the Galapagos Islands, 1982) in the Gulf of Mexico. Specimens of Tubastraea were collected from various artificial reefs. Morphological analyses of these specimens show that there are three distinct lineages of Tubastraea that have remained cryptic due to similar morphology in the field: Tubastraea coccinea (Lesson, 1829), T. tagusensis, and a third clade containing a mix of characters of the former two. These results based on morphology are corroborated by phylogenetic and haplotype analyses using a partial sequence of the mitochondrial genes ATP8 and cytochrome oxidase I (mtCOI). The negative effects on natural habitats by invasive species of Tubastraea have been documented worldwide. Therefore, it is imperative to implement management policies that will help prevent the expansion of these species into natural habitats in the Gulf of Mexico. The essential first step is accurate identification to determine possible sources, vectors, and current expansion rates. We present a clear set of morphological characters and a genetic marker to help distinguish between these three cryptic lineages.

Ford, A. K., Bejarano, S., Nugues, M. M., Visser, P. M., Albert, S., & Ferse, S. C. A. (2018). Reefs under Siege—the Rise, Putative Drivers, and Consequences of Benthic Cyanobacterial Mats. *Frontiers in Marine Science*. <u>https://doi.org/10.3389/fmars.2018.00018</u>

Benthic cyanobacteria have commonly been a small but integral component of coral reef ecosystems, fulfilling the critical function of introducing bioavailable nitrogen to an inherently oligotrophic environment. Though surveys may have previously neglected benthic cyanobacteria, or grouped them with more conspicuous benthic groups, emerging evidence strongly indicates that they are becoming increasingly prevalent on reefs worldwide. Some species can form mats comprised by a diverse microbial consortium which allows them to exist across a wide range of environmental conditions. This review evaluates the putative driving factors of increasing benthic cyanobacterial mats, including climate change, declining coastal water quality, iron input, and overexploitation of key consumer and ecosystem engineer species. Ongoing global environmental change can increase growth rates and toxin production of physiologically plastic benthic cyanobacterial mats, placing them at a considerable competitive advantage against reef-building corals. Once established, strong ecological feedbacks (e.g. inhibition of coral recruitment, release of dissolved organic carbon) reinforce reef degradation. The review also highlights previously overlooked implications of mat proliferation, which can extend beyond reef health and affect human health and welfare. Though identifying (opportunistic) consumers of mats remains a priority, their perceived low palatability implies that herbivore management alone may be insufficient to control their proliferation and must be accompanied by local measures to improve water quality and watershed management.

Haywood, M. D. E., Thomson, D. P., Babcock, R. C., Pillans, R. D., Keesing, J. K., Miller, M., . . . Field, S. N. (2019). Crown-of-thorns starfish impede the recovery potential of coral reefs following bleaching. *Marine Biology*, 166(7), 99. <u>https://doi.org/10.1007/s00227-019-3543-z</u>

High densities of the corallivorous crown-of-thorns starfish (CoTS; Acanthaster sp.) have occurred throughout the Indo-Pacific often resulting in widespread coral loss. Whilst CoTS have previously been recorded at Barrow and the Montebello Islands, in the Pilbara offshore bioregion of northwestern Australia, their densities were relatively low. Outbreak densities of CoTS have been described as the level at which the rate of coral consumption by the starfish is equal to or greater than rate at which the coral grows. In 2014, we recorded densities as high as 320 ± 58 CoTS ha–1 in the region which is well above recognised outbreak densities. Whilst there is little terrestrial runoff and agriculture in the Pilbara region, both temperature and chlorophyll- α levels appear to be sufficient to allow a high degree of CoTS larval success in most years. The region was subjected to anomalously high water temperatures during the summers of 2010–2011 and particularly 2012–2013 which resulted in the mortality of almost 70% of live coral. We hypothesise that the high densities of CoTS observed are a result of CoTS responding to a reduced food supply and aggregating around the remaining live coral resulting in outbreak densities rather than a significant increase in the number of CoTS in the area. The small amount of remaining live coral is concentrated in a few areas and this, combined with high densities of CoTS in these areas, suggest that CoTS represent a significant threat to the recovery of the coral communities of the region.

Joy, L. S., & Brian, N. P. (2020). Assessment of an Invasive Tropical Sponge on Coral Reefs in Hawai'i. Pacific Science, 74(2), 175-187. <u>https://doi.org/10.2984/74.2.7</u>

Sponges are ecologically important components of many marine ecosystems and are abundant benthic fauna on coral reefs. Mycale grandis is an alien invasive sponge found on many partially degraded shallow water coral ecosystems in Hawai'i. Mycale grandis is known to compete spatially with dominant native reef building coral such as Montipora capitata and Porites compressa. Since its appearance in the late 1990s, M. grandis has established itself in a number of coral reef ecosystems around the main Hawaiian Islands. Within south Kāne'ohe Bay, sponge coverage in 2014–2017 ranged from 2.1% on fringing reefs to 32.3% within the mangrove habitat along the northern edge of Coconut Island, which is similar to coverage found in 2006–2007 surveys. Sponges are prolific filter feeders and pump seawater for the dual purpose of obtaining resources and removing metabolic wastes, and thus process large amounts of water in their environment. Mycale grandis pumps 0.0027 L seawater s–1 L–1 sponge, equivalent to 115 times its own volume per day. These pumping rates were combined with biomass estimates, depth, and circulation parameters in south Kāne'ohe Bay to show that M. grandis can cycle a substantial amount of the overlying water column and therefore has the potential to influence the biogeochemistry of overlying reef water in south Kāne'ohe Bay.

Neilson, B. J., Wall, C. B., Mancini, F. T., & Gewecke, C. A. (2018). Herbivore biocontrol and manual removal successfully reduce invasive macroalgae on coral reefs. *Peerj*, 6, e5332. <u>https://doi.org/10.7717/peerj.5332</u>

Invasive macroalgae pose a serious threat to coral reef biodiversity by monopolizing reef habitats, competing with native species, and directly overgrowing, and smothering reef corals. Several invasive macroalgae (Eucheuma clade E, Kappaphycus clade A and B, Gracilaria salicornia, and Acanthophora

spicifera) are established within Kane'ohe Bay (O'ahu, Hawai'i, USA), and reducing invasive macroalgae cover is a coral reef conservation and management priority. Invasive macroalgae control techniques, however, are limited and few successful large-scale applications exist. Therefore, a two-tiered invasive macroalgae control approach was designed, where first, divers manually remove invasive macroalgae (Eucheuma and Kappaphycus) aided by an underwater vacuum system ("The Super Sucker"). Second, hatchery-raised juvenile sea urchins (Tripneustes gratilla), were outplanted to graze and control invasive macroalgae regrowth. To test the effectiveness of this approach in a natural reef ecosystem, four discrete patch reefs with high invasive macroalgae cover (15–26%) were selected, and macroalgae removal plus urchin biocontrol (treatment reefs, n = 2), or no treatment (control reefs, n = 2), was applied at the patch reef-scale. In applying the invasive macroalgae treatment, the control effort manually removed ~19,000 kg of invasive macroalgae and ~99,000 juvenile sea urchins were outplanted across to two patch reefs, totaling ~24,000 m2 of reef area. Changes in benthic cover were monitored over 2 years (five sampling periods) before-and-after the treatment was applied. Over the study period, removal and biocontrol reduced invasive macroalgae cover by 85% at treatment reefs. Our results show manual removal in combination with hatchery raised urchin biocontrol to be an effective management approach in controlling invasive macroalgae at reef-wide spatial scales and temporal scales of months to years.

Soares, M. d. O., Salani, S., Paiva, S. V., & Braga, M. D. A. (2020). Shipwrecks help invasive coral to expand range in the Atlantic Ocean. *Marine Pollution Bulletin*, 158, 111394. https://doi.org/10.1016/j.marpolbul.2020.111394

The invasive coral Tubastraea tagusensis (sun coral) is a habitat-forming species currently increasing its geographical range into the Atlantic Ocean, thereby causing negative ecological and socioeconomic impacts. Scuba divers observed this coral in the western equatorial Atlantic in January 2020, growing at high densities on a shipwreck from World War II (sunk in 1943) at a depth of approximately 32 m. Available footage from the beginning of the decade (2012–2018) shows no obvious signs of sun coral on this shipwreck, suggesting recent colonization and range expansion. The recent evidence of expansion was found 200 km east of the last record, which was also found on a WWII shipwreck (sunk in 1942) in 2016. We have identified hundreds of overlooked WWII shipwrecks, as well as new wrecks in shallow and mesophotic waters, that may provide stepping-stone habitats for this coral to expand its distribution in the Atlantic. We discuss the role of shipwrecks as a network of stepping stones for the sun coral spread, creating complementary paths for the invasiveness by overcoming physiological traits and the short lifespan of the coral larvae. Previous research underestimates the importance of these artificial stepping-stone patches in sustaining crucial dispersal events and range expansion of invasive species. These results are a call to action to manage the invasive Tubastraea corals at a national and international scale in the Atlantic basin.

Veazey, L., Williams, O., Wade, R., Toonen, R., & Spalding, H. L. (2019). Present-Day Distribution and Potential Spread of the Invasive Green Alga Avrainvillea amadelpha Around the Main Hawaiian Islands. *Frontiers in Marine Science*, 6. <u>https://doi.org/10.3389/fmars.2019.00402</u>

Algal assemblages are critical components of marine ecosystems from the intertidal to mesophotic depths; they act as primary producers, nutrient cyclers, and substrate providers. Coral reef ecosystems

can be disrupted by stressors such as storm events, effluent inundation, sudden temperature shifts, and non-native invaders. Avrainvillea amadelpha is an invasive green alga that was first recorded in the main Hawaiian Islands on the west shore of Oahu and has continued to be of concern due to its extreme competitiveness with native algae and seagrasses. It has spread rapidly across the island of Oahu, decreasing the biodiversity of the benthos from shorelines to similar to 90 m depth. We employed a boosted regression tree modeling framework to identify highly vulnerable regions prone to invasion. Our model indicated that regions exposed to minimal bottom currents and at least five degree heating weeks are particularly susceptible to A. amadelpha colonization. Additionally, we extrapolated our model to the main Hawaiian Islands and forecasted how a 25% increase in statewide annual maximum degree heating weeks may change habitat suitability for A. amadelpha. Across all islands, we identified particularly vulnerable "hotspot" regions of concern for resource managers and conservationists. This manuscript demonstrates the utility of this approach for identifying priority regions for invasive species management in the face of a changing climate.

Williams, S. M., & Garcia-Sais, J. R. (2020). A potential new threat on the coral reefs of Puerto Rico: The recent emergence of Ramicrusta spp. *Marine Ecology-an Evolutionary Perspective*, 41(4). <u>https://doi.org/10.1111/maec.12592</u>

The rapid appearance of Ramicrusta spp. is described and analyzed from 40 permanent monitoring coral reef stations in Puerto Rico. Before 2016, Ramicrusta had not been observed from any of the reef monitoring stations. By 2018, it was present at 76% of all the monitoring stations. Ramicrusta was the dominant substrata type at all of the shallow reef sites sampled on the east coast (e.g., Fajardo, Culebra, and Vieques), reaching a cover (+/- SE) as high as 63.0 +/- 5.8%. The spread of Ramicrusta occurred at the expense of historically resilient living benthic elements, such as turf algae. Since its detection in 2016, colonization of hard substrata by Ramicrusta remained constant, with the exception of two shallow reefs in Fajardo and Culebra, where the cover was significantly reduced by the scouring and or abrasive effects of two major hurricanes. The ecological implications of Ramicrusta prevalence on Puerto Rican reefs remain unclear; however, increasing herbivory might be a useful mitigation tool in the reduction of Ramicrusta abundance on coral reefs.

Section 4: Sedimentation

Bourque, J. R., & Demopoulos, A. W. J. (2018). The influence of different deep-sea coral habitats on sediment macrofaunal community structure and function. *Peerj*, 6, e5276. <u>https://doi.org/10.7717/peerj.5276</u>

Deep-sea corals can create a highly complex, three-dimensional structure that facilitates sediment accumulation and influences adjacent sediment environments through altered hydrodynamic regimes. Infaunal communities adjacent to different coral types, including reef-building scleractinian corals and individual colonies of octocorals, are known to exhibit higher macrofaunal densities and distinct community structure when compared to non-coral soft-sediment communities. However, the coral types have different morphologies, which may modify the adjacent sediment communities in discrete ways. Here we address: (1) how infaunal communities and their associated sediment geochemistry compare among deep-sea coral types (Lophelia pertusa, Madrepora oculata, and octocorals) and (2) do infaunal communities adjacent to coral habitats exhibit typical regional and depth-related patterns observed in the Gulf of Mexico (GOM). Sediment push cores were collected to assess diversity, composition, numerical abundance, and functional traits of macrofauna (>300 μm) across 450 kilometers in the GOM at depths ranging from 263–1,095 m. Macrofaunal density was highest in L. pertusa habitats, but similar between M. oculata and octocorals habitats. Density overall exhibited a unimodal relationship with depth, with maximum densities between 600 and 800 m. Diversity and evenness were highest in octocoral habitats; however, there was no relationship between diversity and depth. Infaunal assemblages and functional traits differed among coral habitats, with L. pertusa habitats the most distinct from both M. oculata and octocorals. These patterns could relate to differences in sediment geochemistry as L. pertusa habitats contained high organic carbon content but low proportions of mud compared to both M. oculata and octocoral habitats. Distance-based linear modeling revealed depth, mud content, and organic carbon as the primary factors in driving coral infaunal community structure, while geographic location (longitude) was the primary factor in functional trait composition, highlighting both the location and ecological differences of L. pertusa habitats from other coral habitats. Enhanced habitat structural complexity associated with L. pertusa and differences in localized hydrodynamic flow may contribute to the dissimilarities in the communities found among the coral types. Our results suggest a decoupling for infaunal coral communities from the typical depthrelated density and diversity patterns present throughout soft-sediment habitats in the GOM, highlighting the importance of deep-sea corals in structuring unique communities in the nearby benthos.

Browning, T. N., Sawyer, D. E., Brooks, G. R., Larson, R. A., Ramos-Scharrón, C. E., & Canals-Silander, M. (2019). Widespread Deposition in a Coastal Bay Following Three Major 2017 Hurricanes (Irma, Jose, and Maria). *Scientific Reports*, 9(1), 7101. <u>https://doi.org/10.1038/s41598-019-43062-4</u>

In 2017, three major hurricanes (Irma, Jose, and Maria) impacted the Northeastern Caribbean within a 2-week span. Hurricane waves can cause physical damage to coastal ecosystems, re-suspend and transport antecedent seafloor sediment, while the associated intense rainfall can yield large influxes of land-derived sediment to the coast (e.g. burial of ecosystems). To understand sedimentation provenance (terrestrial or marine) and changes induced by the hurricanes, we collected bathymetry surveys and sediment samples of Coral Bay, St. John, US Virgin Islands in August 2017, (pre-storms) and repeated it in November 2017 (post-storms). Comparison reveals morphologic seafloor changes and

widespread aggradation with an average of ~25 cm of sediment deposited over a 1.28 km2 benthic zone. Despite an annual amount of precipitation between surveys, sediment yield modeling suggests watersheds contributed <0.2% of the total depositional volume. Considering locally established accumulation rates, this multi-hurricane event equates to ~1–3 centuries of deposition. Critical benthic communities (corals, seagrasses) can be partially or fully buried by deposits of this thickness and previous studies demonstrate that prolonged burial of similar organisms often leads to mortality. This study illuminates how storm events can result in major sediment deposition, which can significantly impact seafloor morphology and composition and benthic ecosystems.

Medina-Valmaseda, A. E., Rodríguez-Martínez, R. E., Alvarez-Filip, L., Jordan-Dahlgren, E., & Blanchon, P. (2020). The role of geomorphic zonation in long-term changes in coral-community structure on a Caribbean fringing reef. *Peerj*, 8, e10103. <u>https://doi.org/10.7717/peerj.10103</u>

Ecological processes on coral reefs commonly have limited spatial and temporal scales and may not be recorded in their long-term geological history. The widespread degradation of Caribbean coral reefs over the last 40 years therefore provides an opportunity to assess the impact of more significant ecological changes on the geological and geomorphic structure of reefs. Here, we document the changing ecology of communities in a coral reef seascape within the context of its geomorphic zonation. By comparing basic ecological indices between historical and modern data we show that in 35 years the reef-front zone was transformed from a complex coral assemblage with a three-dimensional structure, to a sizehomogenized and flattened one that is guasi indistinguishable from the adjacent non-accretional coralground zone. Today coral assemblages at Punta Maroma are characterized by the dominance of opportunistic species which are either tolerant to adverse environmental conditions, including sedimentation, or are known to be the first scleractinian species to recruit on disturbed reefs, implying they reflect a post-hurricane stage of adjustment. Despite an increase in similarity in ecological indices, the reef-front and coral-ground geomorphic zones still retain significant differences in coral assemblages and benthic habitat and are not homogeneous. The partial convergence of coral assemblages certainly has important consequences for the ecology and geological viability of the reef and its role in coastal protection, but environmental physical drivers continue to exert a fundamental role in the character and zonation of benthic communities of this reef seascape.

Morgan, K. M., Moynihan, M. A., Sanwlani, N., & Switzer, A. D. (2020). Light Limitation and Depth-Variable Sedimentation Drives Vertical Reef Compression on Turbid Coral Reefs. *Frontiers in Marine Science*. <u>https://doi.org/10.3389/fmars.2020.571256</u>

Turbid coral reefs experience high suspended sediment loads and low-light conditions that vertically compress the maximum depth of reef growth. Although vertical reef compression is hypothesized to further decrease available coral habitat as environmental conditions on reefs change, its causative processes have not been fully quantified. Here, we present a high-resolution time series of environmental parameters known to influence coral depth distribution (light, turbidity, sedimentation, currents) within reef crest (2–3 m) and reef slope (7 m) habitats on two turbid reefs in Singapore. Light levels on reef crests were low [mean daily light integral (DLI): 13.9 ± 5.6 and 6.4 ± 3.0 mol photons m–2 day–1 at Kusu and Hantu, respectively], and light differences between reefs were driven by a 2-fold increase in turbidity at Hantu (typically 10–50 mg l–1), despite its similar distance offshore. Light

attenuation was rapid (KdPAR: 0.49–0.57 m–1) resulting in a shallow euphotic depth of <11 m, and daily fluctuations of up to 8 m. Remote sensing indicates a regional west-to-east gradient in light availability and turbidity across southern Singapore attributed to spatial variability in suspended sediment, chlorophyll-a and colored dissolved organic matter. Net sediment accumulation rates were ~5% of gross rates on reefs (9.8–22.9 mg cm–2 day–1) due to the resuspension of sediment by tidal currents, which contribute to the ecological stability of reef crest coral communities. Lower current velocities on the reef slope deposit ~4 kg m2 more silt annually, and result in high soft-sediment benthic cover. Our findings confirm that vertical reef compression is driven from the bottom-up, as the photic zone contracts and fine silt accumulates at depth, reducing available habitat for coral growth. Assuming no further declines in water quality, future sea level rise could decrease the depth distribution of these turbid reefs by a further 8–12%. This highlights the vulnerability of deeper coral communities on turbid reefs to the combined effects of both local anthropogenic inputs and climate-related impacts.

Otaño-Cruz, A., Montanez-Acuna, A. A., Garcia-Rodriguez, N. M., Diaz-Morales, D. M., Benson, E., Cuevas, E., . . . Hernandez-Delgado, E. A. (2019). Caribbean Near-Shore Coral Reef Benthic Community Response to Changes on Sedimentation Dynamics and Environmental Conditions. *Frontiers in Marine Science*, 6. <u>https://doi.org/10.3389/fmars.2019.00551</u>

Coral reefs are facing unprecedented global, regional and local threats that continue to degrade nearshore habitats. Water quality degradation, due to unsustainable development practices at coastal watersheds, is one of the greatest stressors across multiple spatial scales. The goal of this study was to assess near-shore coral reef benthic community spatio-temporal response to sedimentation patterns, weather, and oceanographic dynamics at Bahfa Tamarindo and Punta Soldado in Culebra Island, Puerto Rico. Benthic data were collected across a distance gradient from the shore through high-resolution images at marked belt transects. Environmental data were assessed and contrasted with benthic assemblages using multivariate correlations and multiple linear regression. Coral colony abundance and coral recruit assemblages showed significant variation among seasons, sites and distance zones (PERMANOVA, p < 0.01). Species diversity (H 'n) increased at both study sites with distance from shore, and the most conspicuous coral recruit species were stress-tolerant Porites astreoidec, P porites, and Siderastrea radians. Difference in coral abundance and coral recruits per site had a strong significant negative relationship with sediment characteristics and depth (p < 0.05). Near-shore coral reef benthic community structure was significantly different between sites and distance zones from shore, with depth having an important role in shaping reef zonation. Changes in benthic community structure were associated with local sediment distribution patterns emerging from human alteration of coastal watersheds and natural events that cause terrigenous sediment deposition and sand resuspension across the reef. Coral cover was significantly lower at zones more exposed to recurrent sedimentation stress (p < 0.01). It was also correlated with sediment texture (p = 0.006) and terrigenous sediment deposition (p = 0.016). Scleractinian coral cover had an inverse relationship with gorgonian and macroalgae cover. In a short-term period, a pattern of increased dominance of encrusting calcareous algae Ramicrusta textills and invasive sponge Dictyonella funicularis were documented. Changing land use and increased frequency of extreme weather events, as a consequence of global patterns of climate change, may play an important role shaping near-shore coral reefs benthic communities and could threaten the resilience of coastal regions. Therefore, collaborative and trans-disciplinary ecosystembased management efforts are urgently needed to effectively reduce land-based stressors and foster near-shore coral reef recovery.

Ramos-Scharron, C. E. (2018). Land disturbance effects of roads in runoff and sediment production on dry tropical settings. *Geoderma*, 310, 107-119. <u>https://doi.org/10.1016/j.geoderma.2017.08.035</u>

Accelerated soil loss due to human land use is still one the most critical environmental problems as it can degrade both soils and downstream resources. Major gaps still exist in our knowledge of erosion, particularly in the dry tropics that make up about a fourth of the world's tropical landmass. The Insular Caribbean presents a particular need because erosion here has deleterious effects on soils, nearshore coral reefs, and their associated myriad of ecosystem services. Through plot-scale monitoring of runoff and sediment production over an eleven month period, this study quantified the impacts of land disturbance on runoff development and sediment production relative to background rates on disturbed surfaces (i.e., roads) in a dry tropical area of Puerto Rico. Results demonstrate that unpaved road surfaces have the potential to generate runoff two to three-and-a-half times more frequently than under natural conditions and that they can produce sediment at rates that are between six to twohundred times greater than background. These results suggest that land development in small drytropical coastal watersheds can potentially induce an increase in the frequency of runoff and sediment delivery into coastal waters even when a relatively small percentage of the land is disturbed. Soil formation simply cannot keep up with accelerated erosion, which implies a net exhaustion of the soil mantle and a decay of the ecological services it provides. Offsetting these soil losses will require implementing proven conservation practices to protect soils and coral reef ecosystems in this and other dry tropical settings.

Shore-Maggio, A., Aeby, G. S., & Callahan, S. M. (2018). Influence of salinity and sedimentation on Vibrio infection of the Hawaiian coral Montipora capitata. *Diseases of Aquatic Organisms*, 128(1), 63-71. <u>https://doi.org/10.3354/dao03213</u>

Environmental cofactors alter host-pathogen interactions and influence disease dynamics by impairing host resistance and/or increasing pathogen virulence. Terrestrial runoff is recognized as a major threat to coral reef health. However, the direct links between runoff and coral disease are not clear. Montipora white syndrome (MWS) is a coral disease that occurs in the Hawaiian archipelago, can be caused by various bacterial pathogens, including Vibrio species, and is linked to conditions associated with heavy rainfall and runoff. The objective of this study was to determine whether a short-term hyposalinity stress (20 ppt for 24 h) or sedimentation stress (1000 g m-2 d-1) would influence bacterial infection of the coral Montipora capitata. Hyposalinity increased M. capitata susceptibility to infection by 2 MWS pathogens, Vibrio corallilyticus strain OCN008 and Vibrio owensii strain OCN002. Specifically, hyposalinity allowed OCN008 to infect at lower doses (106 CFU ml-1 compared with 108 CFU ml-1) and reduced the amount of time before onset of OCN002 infection at high doses (108 CFU ml-1). In contrast, short-term sedimentation stress did not affect M. capitata infection by either of these 2 pathogens. Although several studies have found a correlation between runoff and increased coral disease prevalence in field studies, this is the first study to show that one aspect of runoff (reduced salinity) enhances bacterial infection of coral using manipulative experiments.

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. <u>https://doi.org/10.1016/j.marpolbul.2019.04.066</u>

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.

Tebbett, S. B., & Bellwood, D. R. (2019). Algal turf sediments on coral reefs: what's known and what's next. *Marine Pollution Bulletin*, 149, 110542. <u>https://doi.org/10.1016/j.marpolbul.2019.110542</u>

Algal turfs are likely to rise in prominence on coral reefs in the Anthropocene. In these ecosystems the sediments bound within algal turfs will shape ecosystem functions and the services humanity can obtain from reefs. However, while interest is growing in the role of algal turf sediments, studies remain limited. In this review we provide an overview of our knowledge to-date concerning algal turf sediments on coral reefs. Specifically, we highlight what algal turf sediments are, their role in key ecosystem processes, the potential importance of algal turf sediments on Anthropocene reefs, and key knowledge gaps for future research. The evidence suggests that the management of algal turf sediments will be critically important if we are to sustain key functions and services on highly-altered, Anthropocene coral reef configurations.

Tebbett, S. B., Bellwood, D. R., & Purcell, S. W. (2018). Sediment addition drives declines in algal turf yield to herbivorous coral reef fishes: implications for reefs and reef fisheries. *Coral Reefs*, 37(3), 929-937. <u>https://doi.org/10.1007/s00338-018-1718-6</u>

Coral reefs around the world are changing rapidly, with overfishing of herbivorous fishes and increased sediment inputs being two of the major local-scale stressors. We therefore assessed the effects of sediment loads and overfishing on the nutritional quality and yield to grazing fishes of algal turfs, within the epilithic algal matrix, on a coral reef at Lizard Island, Australia. Low, ambient and high sediment loads were maintained on turf-covered coral tiles, with and without grazer exclusion cages, for 1 month. Subsequently, algal turfs were removed and analysed for organic carbon and nitrogen content. Under grazer exclusion, sediment additions decreased algal turf biomass by approximately 63%, while algal turf biomass was the highest on tiles with sediments removed. In the presence of grazing fishes, algal turfs in all treatments were cropped by grazers to similar low biomass levels. Nitrogen content of algal turfs followed a similar trend. Effectively, added sediments decreased the potential yield of algal turf biomass and nitrogen to grazing fishes by an average of 2000 and 3300%, respectively. Sediments profoundly affect algal turf yield to grazing herbivorous fishes and, therefore, the productivity of algal turf-based food chains, potentially diminishing reef-based fisheries.

Section 5: Ocean Warming

Bahr, K. D., Tran, T., Jury, C. P., & Toonen, R. J. (2020). Abundance, size, and survival of recruits of the reef coral Pocillopora acuta under ocean warming and acidification. *PLOS ONE*, 15(2), e0228168. https://doi.org/10.1371/journal.pone.0228168

Ocean warming and acidification are among the greatest threats to coral reefs. Massive coral bleaching events are becoming increasingly common and are predicted to be more severe and frequent in the near future, putting corals reefs in danger of ecological collapse. This study quantified the abundance, size, and survival of the coral Pocillopora acuta under future projections of ocean warming and acidification. Flow-through mesocosms were exposed to current and future projections of ocean warming or acidification, nor their combination, influenced the size or abundance of P. acuta recruits, but heating impacted subsequent health and survival of the recruits. During annual maximum temperatures, coral recruits in heated tanks experienced higher levels of bleaching and subsequent mortality. Results of this study indicate that P. acuta is able to recruit under projected levels of ocean warming and acidification but are susceptible to bleaching and mortality during the warmest months.

 Baird, A. H., Madin, J. S., Alvarez-Noriega, M., Fontoura, L., Kerry, J. T., Kuo, C. Y., . . . Hughes, T. P. (2018). A decline in bleaching suggests that depth can provide a refuge from global warming in most coral taxa. *Marine Ecology Progress Series*, 603, 257-264. https://doi.org/10.3354/meps12732

Coral reefs are under increasing threat from increasing warm temperature stress. Coral bleaching is caused by a combination of heat and light anomalies and therefore fewer corals should bleach in areas where either heat or light anomalies are ameliorated, such as in turbid waters or at depth. Here, we explore the overall response of the coral assemblage and of 16 individual taxa to a thermal anomaly along a depth gradient during the 2016 mass bleaching event at sites on the outer shelf of the northern Great Barrier Reef. Across all taxa, there was a curvilinear decline in the percentage of colonies bleached with depth that was consistent among sites and reflected the attenuation of light in the ocean. The percentage of colonies bleached was also higher on reefs with higher levels of temperature stress. In 10 taxa, including the abundant and ecologically significant Acropora, Pocillopora and Porites, the percentage of colonies bleached declined with depth. In 4 taxa, the percentage of colonies bleached peaked at intermediate depth. In 2 taxa, there was no effect of depth because bleaching was uniformly low. These data suggest that deeper areas of reef can provide a refuge from mass bleaching for many colonies of most taxa.

Barker, V. (2018). Exceptional Thermal Tolerance of Coral Reefs in American Samoa: a Review. *Current Climate Change Reports*, 4(4), 417-427. <u>https://doi.org/10.1007/s40641-018-0112-3</u>

As climate change poses an ever increasing threat to coral reefs globally, understanding why particular corals are resistant to bleaching is paramount to their continued survival. The coral reefs of Ofu Island, American Samoa, provide a living laboratory to examine mechanisms of coral adaptation to extreme thermal conditions and serve as an analog for a future environment impacted by climate change. Three

backreef pools exhibit remarkably different temperature regimes, which consequently results in varying levels of coral thermal tolerance. In pool 300, temperatures can reach 35 °C and fluctuate up to 6 °C throughout the day. Pools 400 and 500 are less variable, with temperatures rarely exceeding 32 °C. Yet, the pools contain a highly diverse community of corals, including an abundance of thermally sensitive species. This review summarizes the results of nearly two decades of research into the mechanisms contributing to differential bleaching resistance among pools. Factors examined include the effects of intermittent water flow, previous exposure to subbleaching temperatures, Symbiodinium genotype, modifications of genetic expression within the polyp, and the associated bacterial microbiome. Corals within the highly variable pool 300 appear to be more adequately adapted to thermal extremes by retaining chlorophyll concentrations during frequent heat pulses, associating with thermally tolerant endosymbionts, upregulating gene expression associated with heat acclimatization, and potentially possessing an advantageous microbiome composition. Though encompassing a small geographic area, the findings from Ofu's reefs have widespread implications for coral conservation as they serve to elucidate the impacts of these many confounding factors and their contributions to bleaching resistance.

Barkley, H. C., Cohen, A. L., Mollica, N. R., Brainard, R. E., Rivera, H. E., DeCarlo, T. M., . . . Luu, V. H. (2018). Repeat bleaching of a central Pacific coral reef over the past six decades (1960-2016). *Communications Biology*, 1. https://doi.org/10.1038/s42003-018-0183-7

The oceans are warming and coral reefs are bleaching with increased frequency and severity, fueling concerns for their survival through this century. Yet in the central equatorial Pacific, some of the world's most productive reefs regularly experience extreme heat associated with El Nino. Here we use skeletal signatures preserved in long-lived corals on Jarvis Island to evaluate the coral community response to multiple successive heatwaves since 1960. By tracking skeletal stress band formation through the 2015-16 El Nino, which killed 95% of Jarvis corals, we validate their utility as proxies of bleaching severity and show that 2015-16 was not the first catastrophic bleaching event on Jarvis. Since 1960, eight severe (>30% bleaching) and two moderate (<30% bleaching) events occurred, each coinciding with El Nino. While the frequency and severity of bleaching on Jarvis did not increase over this time period, 2015-16 was unprecedented in magnitude. The trajectory of recovery of this historically resilient ecosystem will provide critical insights into the potential for coral reef resilience in a warming world.

Barshis, D. J., Birkeland, C., Toonen, R. J., Gates, R. D., & Stillman, J. H. (2018). High-frequency temperature variability mirrors fixed differences in thermal limits of the massive coral Porites lobata. *Journal of Experimental Biology*, 221(24). <u>https://doi.org/10.1242/jeb.188581</u>

Spatial heterogeneity in environmental characteristics can drive adaptive differentiation when contrasting environments exert divergent selection pressures. This environmental and genetic heterogeneity can substantially influence population and community resilience to disturbance events. Here, we investigated corals from the highly variable back-reef habitats of Ofu Island in American Samoa that thrive in thermal conditions known to elicit widespread bleaching and mortality elsewhere. To investigate the relative importance of acclimation versus site of origin in shaping previously observed differences in coral tolerance limits at Ofu Island, specimens of the common Indo-Pacific coral Porites lobata from locations with differing levels of thermal variability were acclimated to low and high thermal variation in controlled common garden aquaria. Overall, there were minimal effects of the acclimation

exposure. Corals native to the site with the highest level of daily variability grew fastest, regardless of acclimation treatment. When exposed to lethal thermal stress, corals native to both variable sites contained elevated levels of heat shock proteins and maintained photosynthetic performance for 1-2 days longer than corals from the stable environment. Despite being separated by <5 km, there was significant genetic differentiation among coral colonies (F-ST=0.206, P<0.0001; nuclear ribosomal DNA), whereas Symbiodiniaceae were all Cladocopium sp. (ITS type C15). Our study demonstrates consistent signatures of adaptation in growth and stress resistance in corals from naturally thermally variable habitats, suggesting that differences in the amount of thermal variability may be an important contributor to adaptive differentiation in reef-building corals.

Baumann, J. H., Ries, J. B., Rippe, J. P., Courtney, T. A., Aichelman, H. E., Westfield, I., & Castillo, K. D. (2019). Nearshore coral growth declining on the Mesoamerican Barrier Reef System. *Global Change Biology*, 25(11), 3932-3945. <u>https://doi.org/10.1111/gcb.14784</u>

Anthropogenic global change and local stressors are impacting coral growth and survival worldwide, altering the structure and function of coral reef ecosystems. Here, we show that skeletal extension rates of nearshore colonies of two abundant and widespread Caribbean corals (Siderastrea siderea, Pseudodiploria strigosa) declined across the Belize Mesoamerican Barrier Reef System (MBRS) over the past century, while offshore coral conspecifics exhibited relatively stable extension rates over the same temporal interval. This decline has caused nearshore coral extension rates to converge with those of their historically slower growing offshore coral counterparts. For both species, individual mass coral bleaching events were correlated with low rates of skeletal extension rates across all reef environments. We postulate that the decline in skeletal extension rates for nearshore corals is driven primarily by the combined effects of long-term ocean warming and increasing exposure to higher levels of land-based anthropogenic stressors, with acute thermally induced bleaching events playing a lesser role. If these declining trends in skeletal growth of nearshore S. siderea and P. strigosa continue into the future, the structure and function of these critical nearshore MBRS coral reef systems is likely to be severely impaired.

 Bove, C. B., Ries, J. B., Davies, S. W., Westfield, I. T., Umbanhowar, J., & Castillo, K. D. (2019). Common Caribbean corals exhibit highly variable responses to future acidification and warming. *Proceedings of the Royal Society B-Biological Sciences*, 286(1900), 20182840. https://doi.org/10.1098/rspb.2018.2840

We conducted a 93-day experiment investigating the independent and combined effects of acidification (280-3300 µatm pCO(2)) and warming (28°C and 31°C) on calcification and linear extension rates of four key Caribbean coral species (Siderastrea siderea, Pseudodiploria strigosa, Porites astreoides, Undaria tenuifolia) from inshore and offshore reefs on the Belize Mesoamerican Barrier Reef System. All species exhibited nonlinear declines in calcification rate with increasing pCO(2). Warming only reduced calcification in Ps. strigosa. Of the species tested, only S. siderea maintained positive calcification in the aragonite-undersaturated treatment. Temperature and pCO(2) had no effect on the linear extension of S. siderea and Po. astreoides, and natal reef environment did not impact any parameter examined. Results suggest that S. siderea is the most resilient of these corals to warming and acidification owing to

its ability to maintain positive calcification in all treatments, Ps. strigosa and U. tenuifolia are the least resilient, and Po. astreoides falls in the middle. These results highlight the diversity of calcification responses of Caribbean corals to projected global change.

Bruno, J. F., Cote, I. M., & Toth, L. T. (2019). Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience? Annual Review of Marine Science, 11, 307-334. <u>https://doi.org/10.1146/annurev-marine-010318-095300</u>

Scientists have advocated for local interventions, such as creating marine protected areas and implementing fishery restrictions, as ways to mitigate local stressors to limit the effects of climate change on reef-building corals. However, in a literature review, we find little empirical support for the notion of managed resilience. We outline some reasons for why marine protected areas and the protection of herbivorous fish (especially parrotfish) have had little effect on coral resilience. One key explanation is that the impacts of local stressors (e.g., pollution and fishing) are often swamped by the much greater effect of ocean warming on corals. Another is the sheer complexity (including numerous context dependencies) of the five cascading links assumed by the managed-resilience hypothesis. If reefs cannot be saved by local actions alone, then it is time to face reef degradation head-on, by directly addressing anthropogenic climate change-the root cause of global coral decline.

Ceccherelli, G., Pinna, F., Pansini, A., Piazzi, L., & La Manna, G. (2020). The constraint of ignoring the subtidal water climatology in evaluating the changes of coralligenous reefs due to heating events. *Scientific Reports,* 10(1). <u>https://doi.org/10.1038/s41598-020-74249-9</u>

Predicting community-level responses to seawater warming is a pressing goal of global change ecologists. How far such predictions can be derived from a fine gradient of thermal environments needs to be explored, even if ignoring water climatology does not allow estimating subtidal marine heat waves. In this study insights about the influence of the thermal environment on the coralligenous community structure were gained by considering sites (Sardinia, Italy) at different temperature conditions. Heating events were measured (by loggers at 18 m, 23 m, 28 m, 33 m and 38 m deep) and proxies for their duration (the maximum duration of events warmer than the 90th percentile temperature), intensity (the median temperature) and variability (the number of daily Delta T larger than the mean daily Delta T, and the number of heating events larger in Delta T than the 90th percentile Delta T) were selected by GAM models. Reliable predictions of decrease in coralligenous richness of taxa/morphological groups, with relevant increment in turfs and encrusting coralline algae abundance at the expenses of bryozoans were made. Associations to the different types of heating descriptor have highlighted the aspect (intensity, duration or variability) of the heating events and the threshold for each of them responsible for the trajectories of change.

Coles, S. L., Bahr, K. D., Rodgers, K. u. S., May, S. L., McGowan, A. E., Tsang, A., . . . Han, J. H. (2018). Evidence of acclimatization or adaptation in Hawaiian corals to higher ocean temperatures. *Peerj*, 6, e5347. <u>https://doi.org/10.7717/peerj.5347</u>

Ocean temperatures have been accelerating at an alarming rate mainly due to anthropogenic fossil fuel emissions. This has led to an increase in the severity and duration of coral bleaching events. Predicted projections for the state of reefs do not take into account the rates of adaptation or acclimatization of corals as these have not as yet been fully documented. To determine any possible changes in thermal tolerances, manipulative experiments were conducted to precisely replicate the initial, pivotal research defining threshold temperatures of corals nearly five decades ago. Statistically higher calcification rates, survivorship, and lower mortality were observed in Montipora capitata, Pocillopora damicornis, and Lobactis scutaria in the present study at 31 °C compared to the original 1970 findings. First whole colony mortality was also observed to occur sooner in 1970 than in 2017 in M. capitata (3 d vs. 15 d respectively), L. scutaria (3 d vs. 17 d), and in P. damicornis (3 d vs. 13 d). Additionally, bleaching occurred sooner in 1970 compared to the 2017 experiment across species. Irradiance was an important factor during the recovery period for mortality but did not significantly alter calcification. Mortality was decreased by 17% with a 50% reduction in irradiance during the recovery period. These findings provide the first evidence of coral acclimatization or adaptation to increasing ocean temperatures for corals collected from the same location and using close replication of the experiment conducted nearly 50 years earlier. An important factor in this increased resistance to elevated temperature may be related to removal of the discharge of treated sewage into Kane'ohe Bay and resulting decrease in nitrification and eutrophication. However, this level of increased temperature tolerance may not be occurring rapidly enough to escape the projected increased intensity of bleaching events, as evidenced by the recent 2014 and 2015 high coral mortality in Hawai'i (34%) and in the tropics worldwide.

Drury, C. (2020). Resilience in reef-building corals: The ecological and evolutionary importance of the host response to thermal stress. *Molecular Ecology*, 29(3), 448-465. <u>https://doi.org/10.1111/mec.15337</u>

Coral reefs are under extreme threat due to a number of stressors, but temperature increases due to changing climate are the most severe. Rising ocean temperatures coupled with local extremes lead to extensive bleaching, where the coral-algal symbiosis breaks down and corals may die, compromising the structure and function of reefs. Although the symbiotic nature of the coral colony has historically been a focus of research on coral resilience, the host itself is a foundational component in the response to thermal stress. Fixed effects in the coral host set trait baselines through evolutionary processes, acting on many loci of small effect to create mosaics of thermal tolerance across latitudes and individual coral reefs. These genomic differences can be strongly heritable, producing wide variation among clones of different genotypes or families of a specific larval cross. Phenotypic plasticity is overlaid on these baselines and a growing body of knowledge demonstrates the potential for acclimatization of reefbuilding corals through a variety of mechanisms that promote resilience and stress tolerance. The longterm persistence of coral reefs will require many of these mechanisms to adjust to warmer temperatures within a generation, bridging the gap to reproductive events that allow recombination of standing diversity and adaptive change. Business-as-usual climate scenarios will probably lead to the loss of some coral populations or species in the future, so the interaction between intragenerational effects and evolutionary pressure is critical for the survival of reefs.

Edmunds, P. J. (2020). Vital rates of small reef corals are associated with variation in climate. *Limnology* and Oceanography. <u>https://doi.org/10.1002/lno.11650</u>

With coral cover declining on most tropical reefs, efforts are intensifying to understand the mechanisms by which environmental stressors are driving populations into demographic deficit. Here, the population dynamics of sexual cohorts of small corals (<= 4 cm diameter) in St. John, US Virgin Islands were used to test the hypothesis that the association of vital rates with environmental conditions has changed over 22 yr. The annual fate of 3999 corals at six sites and 7-9 m depth were used to populate Leslie Matrices and calculate assemblage growth rates (lambda, without recruitment), mortality of the smallest corals, and graduation from the largest size class. Vital rates were tested for associations with temperature, the number of days with seawater warmer than 29.4 degrees C (i.e., hot days), and rainfall. Transition probabilities varied among years, and usually more corals remained in their original size class than moved among size classes. Corals in the smallest size class had the highest mortality rate (42% yr(-1)), lambda had a grand mean of 0.688, and there were trends for lambda to vary with the number of hot days and rainfall through quadratic relationships. The linear dependence of lambda on rainfall over consecutive 3-yr periods declined over two decades, suggesting that this colony size-defined coral assemblage has undergone phenotypic change in their responsiveness to varying environmental conditions.

Fox, M. D., Carter, A. L., Edwards, C. B., Takeshita, Y., Johnson, M. D., Petrovic, V., . . . Smith, J. E. (2019). Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. *Coral Reefs*, 38(4), 701-712. <u>https://doi.org/10.1007/s00338-019-01796-7</u>

During 2015-2016, an El Nino and associated warm water event caused widespread coral bleaching across the equatorial Pacific. Here, we combine 8 yr of benthic monitoring data from permanent photoguadrats with remotely sensed and in situ temperature measurements to assess the impact of the warming event on benthic communities at Palmyra Atoll. We quantified bleaching prevalence across two distinct reef habitats using the best available data. On the fore reef (similar to 10 m depth), we quantified bleaching severity within 100-200 m(2) large-area plots using the custom visualization and analysis software, Viscore. On the reef terrace (similar to 5 m depth), we used 95 focal colonies across three species that have been monitored annually since 2014. The 2015-2016 warm water event was the most extreme such event recorded on Palmyra in the past several decades with a maximum cumulative heat stress (degree heating weeks) of 11.9 degrees C-weeks. On the fore reef, 90% of live coral cover exhibited some degree of bleaching (32% severe bleaching). On the shallow reef terrace, bleaching was observed in 93% of the focal colonies across all species. Overall, coral cover declined 9% on the fore reef from 2014 to 2017, whereas coral cover did not change on the terrace. These contrasting results may be associated with typical daily temperature ranges on the terrace that are three times greater than on the fore reef. Permanent photoquadrats showed that turf algae initially colonized skeletons of recently dead corals but transitioned to crustose coralline algae within a year. Collectively, our study emphasizes that comprehensive monitoring of benthic communities over time combined with in situ temperature data can provide taxonomically precise trajectories of community change during and following thermal stress.

Guan, Y., Hohn, S., Wild, C., & Merico, A. (2020). Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication. *Global Change Biology*, 26(10), 5646-5660. https://doi.org/10.1111/gcb.15293

Coral reefs are threatened by global and local stressors. Yet, reefs appear to respond differently to different environmental stressors. Using a global dataset of coral reef occurrence as a proxy for the long-term adaptation of corals to environmental conditions in combination with global environmental data, we show here how global (warming: sea surface temperature; acidification: aragonite saturation state, omega(arag)) and local (eutrophication: nitrate concentration, and phosphate concentration) stressors influence coral reef habitat suitability. We analyse the relative distance of coral communities to their regional environmental optima. In addition, we calculate the expected change of coral reef habitat suitability across the tropics in relation to an increase of 0.1 degrees C in temperature, an increase of 0.02 mu mol/L in nitrate, an increase of 0.01 mu mol/L in phosphate and a decrease of 0.04 in omega(arag). Our findings reveal that only 6% of the reefs worldwide will be unaffected by local and global stressors and can thus act as temporary refugia. Local stressors, driven by nutrient increase, will affect 22% of the reefs worldwide, whereas global stressors will affect 11% of these reefs. The remaining 61% of the reefs will be simultaneously affected by local and global stressors. Appropriate wastewater treatments can mitigate local eutrophication and could increase areas of temporary refugia to 28%, allowing us to 'buy time', while international agreements are found to abate global stressors.

 Hedouin, L., Rouze, H., Berthe, C., Perez-Rosales, G., Martinez, E., Chancerelle, Y., . . . Planes, S. (2020). Contrasting patterns of mortality in Polynesian coral reefs following the third global coral bleaching event in 2016. *Coral Reefs*, 39(4), 939-952. <u>https://doi.org/10.1007/s00338-020-01914-w</u>

In 2016, many tropical corals worldwide were exposed to anomalously high temperatures due to one of the strongest El Nino events ever recorded. Bleaching impacts were reported on 23 islands within three archipelagos of French Polynesia (Tuamotu, Society and Marquesas archipelagos). A detailed study on the effects of elevated temperatures on corals was performed on five islands (Mo'orea, Makemo, Hikueru, Marutea and Katiu) and revealed contrasting patterns of coral bleaching responses between Mo'orea (Society Archipelago) and the four islands of the Tuamotu Archipelago. While some reefs from the Tuamotu lost more than half of their coral cover, in Mo'orea, less than 1% mortality was recorded 6 months after bleaching. During the 2016 bleaching event, certain reefs at 12 m depth in the outer reef habitats were not exposed to sufficiently long high-temperature periods (heat stress not exceeding 1.1 degrees C weeks in Mo'orea) to cause large-scale bleaching-related coral mortality. In contrast, other reefs in the Tuamotu Archipelago had DHW reaching up to 9.2 degrees C weeks and experienced severe mortality (up to 71%). Our study showed how differential heat stress exposure across reefs of French Polynesia led to different impacts on corals. Until now, Mo'orea reefs have been spared abnormally high temperatures leading to mortality and should be considered an important source of larvae to help maintain reefs on the surrounding islands.

Howells, E. J., Vaughan, G. O., Work, T. M., Burt, J. A., & Abrego, D. (2020). Annual outbreaks of coral disease coincide with extreme seasonal warming. *Coral Reefs*, 39(3), 771-781. <u>https://doi.org/10.1007/s00338-020-01946-2</u>

Reef-building corals living in extreme environments can provide insight into the negative effects of future climate scenarios. In hot environments, coral communities experience disproportionate thermal stress as they live very near or at their upper thermal limits. This results in a high frequency of bleaching episodes, but it is unknown whether temperature-driven outbreaks of coral disease follow a similar trajectory. Here we tracked outbreaks of a white-syndrome (WS) disease over three years in the hottest region inhabited by reef-building corals, the southern Persian Gulf. From 2014 to 2016, WS affected 10 of the 16 scleractinian genera recorded at inshore and offshore sites. Intra- and inter-specific transmission of lesions was frequently observed, indicative of a single contagious disease infecting multiple coral taxa. Colonies of Acropora were the most susceptible to WS disease and were more than twice as likely to experience lesions than any other genera. Prevalence reached 42% of Acropora colonies and lesions progressed at an average rate of 1 mm day-1. Platygyra colonies were the second most susceptible to WS disease, where prevalence reached 33% and lesions progressed at 0.3 mm day-1. Affected colonies of both of these genera suffered considerable partial mortality that was not recovered between years, promoting the fragmentation of larger colonies into smaller size classes. Across the 3 years of our study, the onset of WS outbreaks occurred early in summer and prevalence increased exponentially with cumulative heat exposure (coral community $r^2 = 0.55$, Acropora $r^2 = 0.72$, Platygyra r2 = 0.75). Peak levels of community-wide prevalence occurred in August (10% of all coral colonies) to September (14%) when preceding 4-week and 8-week average temperatures exceeded 34.5 °C and 34 °C, respectively. Outbreaks ceased following the return of cooler temperatures with prevalence remaining below 0.5% between December and June. Levels of bleaching remained relatively low (< 5% prevalence), despite exposure to daily temperatures ≥ 35 °C each summer. These findings demonstrate that thermal stress on coral reefs does not always manifest as coral bleaching and diseases can present as a primary sign of thermal stress. Consequently, temperature-driven outbreaks of coral disease are expected to become more widespread as climate warming pushes corals to be living increasingly closer to their upper thermal limits.

Hughes, T. P., Kerry, J. T., Baird, A. H., Connolly, S. R., Dietzel, A., Eakin, C. M., . . . Torda, G. (2018). Global warming transforms coral reef assemblages. *Nature*, 556(7702), 492-+. https://doi.org/10.1038/s41586-018-0041-2

Global warming is rapidly emerging as a universal threat to ecological integrity and function, highlighting the urgent need for a better understanding of the impact of heat exposure on the resilience of ecosystems and the people who depend on them(1). Here we show that in the aftermath of the record-breaking marine heatwave on the Great Barrier Reef in 2016(2), corals began to die immediately on reefs where the accumulated heat exposure exceeded a critical threshold of degree heating weeks, which was 3-4 degrees C-weeks. After eight months, an exposure of 6 degrees C-weeks or more drove an unprecedented, regional-scale shift in the composition of coral assemblages, reflecting markedly divergent responses to heat stress by different taxa. Fast-growing staghorn and tabular corals suffered a catastrophic die-off, transforming the three-dimensionality and ecological functioning of 29% of the 3,863 reefs comprising the world's largest coral reef system. Our study bridges the gap between the theory and practice of assessing the risk of ecosystem collapse, under the emerging framework for the International Union for Conservation of Nature (IUCN) Red List of Ecosystems(3), by rigorously defining

both the initial and collapsed states, identifying the major driver of change, and establishing quantitative collapse thresholds. The increasing prevalence of post-bleaching mass mortality of corals represents a radical shift in the disturbance regimes of tropical reefs, both adding to and far exceeding the influence of recurrent cyclones and other local pulse events, presenting a fundamental challenge to the long-term future of these iconic ecosystems.

Johnston, M. A., Hickerson, E. L., Nuttall, M. F., Blakeway, R. D., Sterne, T. K., Eckert, R. J., & Schmahl, G.
P. (2019). Coral bleaching and recovery from 2016 to 2017 at East and West Flower Garden
Banks, Gulf of Mexico. *Coral Reefs*, 38(4), 787-799. <u>https://doi.org/10.1007/s00338-019-01788-7</u>

East Flower Garden Bank (EFGB) and West Flower Garden Bank (WFGB), part of Flower Garden Banks National Marine Sanctuary (FGBNMS) in the northwestern Gulf of Mexico, support tropical coral reefs that exhibit over 50% living coral cover. These reefs have been monitored annually since 1989, and in 2016 were exposed to higher than normal seawater temperatures leading to a severe bleaching event. Corals at EFGB and WFGB showed no signs of bleaching until September 2016, occurring later in the year compared to other reefs in the Caribbean region. Coral bleaching and subsequent recovery at each bank were documented through a time series of repetitive photographs within previously established longterm monitoring stations. Preceding the event, mean live coral cover within monitoring stations was collectively 64 +/- 2%. Prior to signs of bleaching from July to September 2016, seawater temperatures on the reef were above 30 degrees C for a total of 36 d at EFGB and 21 d at WFGB. By October 2016, 67 +/- 5% of the coral cover within EFGB monitoring stations and 25 +/- 3% within WFGB monitoring stations exhibited signs of bleaching or paling stress, with dissimilarities in the amount of bleaching most likely due to significant differences in thermal profiles between banks. Significantly increasing long-term trends for daily mean seawater temperature indicate that temperatures on the banks have become warmer over time, and calculated bleaching threshold curves suggest that more than 50 d above 29.5 degrees C would initiate a bleaching year at EFGB and WFGB. Even though recovery within monitoring stations at both banks was documented with no significant declines in mean coral cover from 2016 to 2017 (64% and 62%, respectively), it is likely FGBNMS will be subject to additional and more frequent bleaching events in the future as ocean temperatures continue to rise.

Jury, C. P., & Toonen, R. J. (2019). Adaptive responses and local stressor mitigation drive coral resilience in warmer, more acidic oceans. *Proceedings of the Royal Society B-Biological Sciences*, 286(1902). <u>https://doi.org/10.1098/rspb.2019.0614</u>

Coral reefs have great biological and socioeconomic value, but are threatened by ocean acidification, climate change and local human impacts. The capacity for corals to adapt or acclimatize to novel environmental conditions is unknown but fundamental to projected reef futures. The coral reefs of Kane'ohe Bay, Hawai'i were devastated by anthropogenic insults from the 1930s to 1970s. These reefs experience naturally reduced pH and elevated temperature relative to many other Hawaiian reefs whiCh are not expected to face similar conditions for decades. Despite catastrophic loss in coral cover owing to human disturbance, these reefs recovered under low pH and high temperature within 20 years after sewage input was diverted. We compare the pH and temperature tolerances of three dominant Hawaiian coral species from within Kaneohe Bay to conspecifics from a nearby control site and show that corals from Kane'ohe are far more resistant to acidification and warming. These results show that

corals can have different pH and temperature tolerances among habitats and understanding the mechanisms by which coral cover rebounded within two decades under projected future ocean conditions will be critical to management. Together these results indicate that reducing human stressors offers hope for reef resilience and effective conservation over coming decades.

Levas, S., Schoepf, V., Warner, M. E., Aschaffenburg, M., Baumann, J., & Grottoli, A. G. (2018). Long-term recovery of Caribbean corals from bleaching. *Journal of Experimental Marine Biology and Ecology*, 506, 124-134. https://doi.org/10.1016/j.jembe.2018.06.003

Mass coral bleaching events are increasing in frequency and intensity and are predicted to occur annually in the coming decades. However, it remains poorly understood how quickly Caribbean corals can recover from bleaching. To explore the responses to heat stress and subsequent recovery in Caribbean corals, three species (Porites divaricata, Porites astreoides, and Orbicella faveolata) were experimentally bleached in outdoor flow through tanks for 15 days then allowed to recover on the reef for 1.5 and 11 months. At each interval on the reef, endosymbiont concentrations, energy reserves (i.e., total soluble lipid, soluble animal carbohydrate, soluble animal protein), calcification, and stable carbon and nitrogen isotope values of the animal host (delta C-13(h), delta N-15(h)) and endosymbiotic algal fractions (delta C-13(e), delta Ne-15) were measured in treatment and control fragments of each species. Despite variations in bleaching recovery strategies among the coral species, all corals recovered within one year. Specifically, bleached P. divaricata catabolized lipids and decreased calcification in response to lower endosymbiont concentrations. In contrast, both P. astreoides and O. faveolata maintained energy reserves despite lower endosymbiont concentrations, yet both decreased calcification rates after bleaching. Overall, these findings indicate that these corals are capable of surviving and recovering from a mild bleaching event within one year. Though these finding indicate that P. astreoides and O. faveolata may be resilient through single isolated bleaching events under annual bleaching, many Caribbean coral reefs may still experience a decline over the coming decades.

Magel, J. M. T., Burns, J. H. R., Gates, R. D., & Baum, J. K. (2019). Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. *Scientific Reports*, 9. <u>https://doi.org/10.1038/s41598-018-37713-1</u>

Structural complexity underpins the ecological functioning of coral reefs. However, rising ocean temperatures and associated coral bleaching threaten the structural integrity of these important ecosystems. Despite the increased frequency of coral bleaching events, few studies to date have examined changes in three-dimensional (3D) reef structural complexity following severe bleaching. The influence of local stressors on reef complexity also remains poorly understood. In the wake of the 2015-2016 El Nino-induced mass coral bleaching event, we quantified the effects of severe heat stress on 3D reef structural complexity across a gradient of local human disturbance. Using Structure-from-Motion photogrammetry we created 3D reconstructions of permanent reef plots and observed substantial declines in reef structural complexity, measured as surface rugosity and terrain ruggedness, and a detectable loss of habitat volume one year after the bleaching event. 3D reef complexity also declined with increasing levels of human disturbance, and with decreasing densities of branching and massive corals. These findings improve our understanding of the effects of local and global stressors on the structural foundation of coral reef ecosystems. In the face of accelerating climate change, mitigating

local stressors may increase reef structural complexity, thereby heightening reef resilience to future bleaching events.

Manzello, D. P., Enochs, I. C., Kolodziej, G., Carlton, R., & Valentino, L. (2018). Resilience in carbonate production despite three coral bleaching events in 5 years on an inshore patch reef in the Florida Keys. *Marine Biology*, 165(6), 99. <u>https://doi.org/10.1007/s00227-018-3354-7</u>

The persistence of coral reef frameworks requires that calcium carbonate (CaCO(3)) production by corals and other calcifiers outpaces CaCO(3) loss via physical, chemical, and biological erosion. Coral bleaching causes declines in CaCO(3) production, but this varies with bleaching severity and the species impacted. We conducted census-based CaCO(3) budget surveys using the established ReefBudget approach at Cheeca Rocks, an inshore patch reef in the Florida Keys, annually from 2012 to 2016. This site experienced warm-water bleaching in 2011, 2014, and 2015. In 2017, we obtained cores of the dominant calcifying coral at this site, Orbicella faveolata, to understand how calcification rates were impacted by bleaching and how they affected the reef-wide CaCO(3) budget. Bleaching depressed O. faveolata growth and the decline of this one species led to an overestimation of mean (± std. error) reefwide CaCO(3) production by $+ 0.68 (\pm 0.167)$ to $+ 1.11 (\pm 0.236)$ kg m(-2) year(-1) when using the static ReefBudget coral growth inputs. During non-bleaching years, the ReefBudget inputs slightly underestimated gross production by $-0.10 (\pm 0.022)$ to $-0.43 (\pm 0.100)$ kg m(-2) year(-1). Carbonate production declined after the first year of back-to-back bleaching in 2014, but then increased after 2015 to values greater than the initial surveys in 2012. Cheeca Rocks is an outlier in the Caribbean and Florida Keys in terms of coral cover, carbonate production, and abundance of O. faveolata, which is threatened under the Endangered Species Act. Given the resilience of this site to repeated bleaching events, it may deserve special management attention.

Maynard, J., Gove, J., Tracey, D., Johnson, J., Lecky, J., Conklin, E., . . . Kramer, L. (2019). Coral Reefs: Vulnerability to Climate Change in West Hawai'i. <u>https://doi.org/10.25923/5d9q-pv87</u>

The vulnerability of a coral reef to changes in climate depends on the frequency and severity of climate disturbances, such as coral bleaching. Vulnerability also depends on the sensitivity of coral reefs to these disturbances. Sensitivity is a combination of coral reef resilience — their capacity to resist and recover from disturbance — and whether resilience is compromised by human impacts. Our team has generated information on climate change, resilience, and human impacts, and then combined these inputs to assess coral reef ecosystem vulnerability. The results indicate that vulnerability to climate change varies greatly among the coral reefs of West Hawai'i. Coral reef vulnerability is relatively low near Kīholo, Kealakekua Bay, Hōnaunau, and Miloli'i, and relatively high near Puakō, Keāhole Point, and Kailua-Kona. Reef fish productivity is likely to be lower where coral reef vulnerability is high and productivity is likely to be higher where coral reef vulnerability is high and productivity is likely to be higher where coral reef vulnerability is near value and productivity is likely to be higher where coral reef vulnerability is high and productivity is likely to be higher where coral reef vulnerability is high and productivity is likely to be higher where coral reef vulnerability is low.

McClanahan, T. R., Darling, E. S., Maina, J. M., Muthiga, N. A., D'Agata, S., Jupiter, S. D., . . . Leblond, J. (2019). Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Nino. Nature Climate Change, 9(11), 845-+. <u>https://doi.org/10.1038/s41558-019-0576-8</u>

Under extreme heat stress, corals expel their symbiotic algae and colour (that is, 'bleaching'), which often leads to widespread mortality. Predicting the large-scale environmental conditions that reinforce or mitigate coral bleaching remains unresolved and limits strategic conservation actions(1,2). Here we assessed coral bleaching at 226 sites and 26 environmental variables that represent different mechanisms of stress responses from East Africa to Fiji through a coordinated effort to evaluate the coral response to the 2014-2016 El Nino/Southern Oscillation thermal anomaly. We applied common time-series methods to study the temporal patterning of acute thermal stress and evaluated the effectiveness of conventional and new sea surface temperature metrics and mechanisms in predicting bleaching severity. The best models indicated the importance of peak hot temperatures, the duration of cool temperatures and temperature bimodality, which explained similar to 50% of the variance, compared to the common degree-heating week temperature index that explained only 9%. Our findings suggest that the threshold concept as a mechanism to explain bleaching alone was not as powerful as the multidimensional interactions of stresses, which include the duration and temporal patterning of hot and cold temperature extremes relative to average local conditions.

McClanahan, T. R., Darling, E. S., Maina, J. M., Muthiga, N. A., D'Agata, S., Leblond, J., . . . Grimsditch, G. (2020). Highly variable taxa-specific coral bleaching responses to thermal stresses. *Marine Ecology Progress Series*, 648, 135-151. <u>https://doi.org/10.3354/meps13402</u>

Complex histories of chronic and acute sea surface temperature (SST) stresses are expected to trigger taxon- and location-specific responses that will ultimately lead to novel coral communities. The 2016 El Nino-Southern Oscillation provided an opportunity to examine largescale and recent environmental histories on emerging patterns in 226 coral communities distributed across 12 countries from East Africa to Fiji. Six main coral communities were identified that largely varied across a gradient of Acropora to massive Porites dominance. Bleaching intensity was taxon-specific and was associated with complex interactions among the 20 environmental variables that we examined. Coral community structure was better aligned with the historical temperature patterns between 1985 and 2015 than the 2016 extreme temperature event. Additionally, bleaching responses observed during 2016 differed from historical reports during past warm years. Consequently, coral communities present in 2016 are likely to have been reorganized by both long-term community change and acclimation mechanisms. For example, less disturbed sites with cooler baseline temperatures, higher mean historical SST background variability, and infrequent extreme warm temperature stresses were associated with Acropora-dominated communities, while more disturbed sites with lower historical SST background variability and frequent acute warm stress were dominated by stress-resistant massive Porites corals. Overall, the combination of taxon-specific responses, community-level reorganization over time, geographic variation, and multiple environmental stressors suggest complex responses and a diversity of future coral communities that can help contextualize management priorities and activities.

McClanahan, T. R., Maina, J. M., Darling, E. S., Guillaume, M. M. M., Muthiga, N. A., D'Agata, S., . . . Grimsditch, G. (2020). Large geographic variability in the resistance of corals to thermal stress. *Global Ecology and Biogeography*, 29(12), 2229-2247. <u>https://doi.org/10.1111/geb.13191</u>

Aim Predictions for the future of coral reefs are largely based on thermal exposure and poorly account for potential geographic variation in biological sensitivity to thermal stress. Without accounting for complex sensitivity responses, simple climate exposure models and associated predictions may lead to poor estimates of future coral survival and lead to policies that fail to identify and implement the most appropriate interventions. To begin filling this gap, we evaluated a number of attributes of coral taxa and communities that are predicted to influence coral resistance to thermal stress over a large geographic range. Location Western Indo-Pacific and Central Indo-Pacific Ocean Realms. Major taxa studied Zooxanthellate Scleractinia - hard corals. Methods We evaluated the geographic variability of coral resistance to thermal stress as the ratio of thermal exposure and sensitivity in 12 countries during the 2016 global-bleaching event. Thermal exposure was estimated by two metrics: (a) historical excess summer heat (cumulative thermal anomaly, CTA), and (b) a multivariate index of sea-surface temperature (SST), light, and water flow (climate exposure, CE). Sensitivity was estimated for 226 sites using coordinated bleaching observations and underwater surveys of coral communities. We then evaluated coral resistance to thermal stress using 48 generalized linear mixed models (GLMMs) to compare the potential influences of geography, historical SST variation, coral cover and coral richness. Results Geographic faunal provinces and ecoregions were the strongest predictors of coral resistance to thermal stress, with sites in the Australian, Indonesian and Fiji-Caroline Islands coral provinces having higher resistance to thermal stress than Africa-India and Japan-Vietnam provinces. Ecoregions also showed strong gradients in resistance with highest resistance to thermal stress in the western Pacific and Coral Triangle and lower resistance in the surrounding ecoregions. A more detailed evaluation of Coral Triangle and non-Coral Triangle sites found higher resistance to thermal stress within the Coral Triangle, associated withc. 2.5 times more recent historical thermal anomalies and more centralized, warmer, and cool-water skew SST distributions, than in non-Coral Triangle sites. Our findings identify the importance of environmental history and geographic context in future predictions of bleaching, and identify some potential drivers of coral resistance to thermal stress. Main conclusions Simple threshold models of heat stress and coral acclimation are commonly used to predict the future of coral reefs. Here and elsewhere we show that large-scale responses of coral communities to heat stress are geographically variable and associated with differential environmental stresses and histories.

Mollica, N. R., Cohen, A. L., Alpert, A. E., Barkley, H. C., Brainard, R. E., Carilli, J. E., . . . Young, C. W. (2019). Skeletal records of bleaching reveal different thermal thresholds of Pacific coral reef assemblages. *Coral Reefs*, 38(4), 743-757. <u>https://doi.org/10.1007/s00338-019-01803-x</u>

Ocean warming is negatively impacting coral reef ecosystems and considerable effort is currently invested in projecting coral reef futures under 21st century climate change. A limiting factor in these projections is lack of quantitative data on the thermal thresholds of different reef communities, due in large part to spatial and temporal gaps in bleaching observations. Here we apply a coral bleaching proxy, skeletal stress bands, to reconstruct the history of bleaching on eight coral reefs in the central equatorial Pacific (CEP) and use this information to constrain the thermal thresholds of their coral communities. First, three genera of massive corals collected on both Pacific and Caribbean reefs are used to derive a calibration between the proportion of corals that form stress bands during a bleaching event, and the total observed bleaching incidence in the community of mixed coral taxa. The correlation is highly

significant, indicating that stress bands in massive corals reflect community-level bleaching severity (R-2 = 0.945, p < 0.001). We applied the calibration to stress band records from eight Pacific reefs, reconstructing their bleaching histories over the period 1982 to 2015. A percentile-based method of estimating thermal stress (Degree Heating Weeks) for CEP reefs was developed and applied. Comparing the level of thermal stress experienced by each coral community during each event with the reconstructed bleaching response, we characterized the thermal sensitivities of each reef community and quantified the thermal threshold (b(1/2)) at which 50% of the coral community bleached. Our analysis reveals a unique non-linear thermal response curve for each reef. The most thermally tolerant reefs in the study (Jarvis and Kanton Islands) experienced 50% bleaching at seven to nine times more thermal stress than did the least resistant reef in the study (Maiana Island). An exploration of the potential drivers of thermal tolerance revealed a strong correlation between b(1/2) and the history of thermal stress events in each reef system. Thermal tolerance was also correlated with concentrations of dissolved inorganic nitrate in the water column and with estimates of coral energetic reserve.

Muñiz-Castillo, A. I., & Arias-González, J. E. (2021). Drivers of coral bleaching in a Marine Protected Area of the Southern Gulf of Mexico during the 2015 event. *Marine Pollution Bulletin*, 166, 112256. <u>https://doi.org/10.1016/j.marpolbul.2021.112256</u>

Here we report the bleached coral cover and its drivers observed at Alacranes Reef in 2015. Our results show that 2015 was an unprecedented heat stress event. However, we observed low coral bleaching, with the most substantial impact on sites with a 10–20% of coral cover with bleaching. Depth was the most relevant variable related to coral bleaching and the bleaching severity index, with deeper reefs being most affected. Further, our results show that reefs with higher structural complexity based on species composition were among the most affected. We identified that accumulated heat stress and thermal variation in the last 28 days were relevant drivers of coral bleaching. This work highlights the importance of multidimensional frameworks in assessing the spatial variation of coral bleaching, demonstrating the importance of structural habitat variables such as depth in high heat stress events and at a reef scale.

 Nielsen, J. J. V., Kenkel, C. D., Bourne, D. G., Despringhere, L., Mocellin, V. J. L., & Bay, L. K. (2020).
Physiological effects of heat and cold exposure in the common reef coral Acropora millepora. *Coral Reefs*, 39(2), 259-269. <u>https://doi.org/10.1007/s00338-019-01881-x</u>

Reef-forming corals are under threat globally from climate change, leading to changes in sea temperatures with both hot and cold events recorded and projected to increase in frequency and severity in the future. Tolerance to heat and cold exposure has been found to be mutually exclusive in other marine invertebrates, but it is currently unclear whether a trade-off exists between hot and cold thermal tolerance in tropical corals. This study quantified the changes in physiology in Acropora millepora from the central Great Barrier Reef subjected to three temperature treatments; sub-lethal cold, ambient and sub-lethal heat (23.0 °C, 27.0 °C and 29.5 °C, respectively). After 10 weeks, pigment content and Symbiodiniaceae density increased in cold-treated corals but decreased in heat-treated corals relative to corals at ambient conditions. Heat-treated corals gained less mass relative to both ambient and cold-treated corals. These results indicate that the physiological condition of A. millepora corals examined here improved in response to mild cold exposure compared to ambient exposure and

decreased under mild heat exposure despite both these temperatures occurring in situ around 15% of the year. The energetic condition of corals in the hotter treatment was reduced compared to both ambient and cooler groups, indicating that corals may be more resilient to mild cold exposure relative to mild heat exposure. The results indicate that the corals shifted their resource allocation in response to temperature treatment, investing more energy into skeletal extension rather than maintenance. No evidence of thermal tolerance trade-offs was found, and cold thermal tolerance was not lost in more heat-tolerant individuals. An enhanced understanding of physiological responses of corals at both ends of the thermal spectrum is important for predicting the resilience of corals under projected climate change conditions.

Olguin-Lopez, N., Hernandez-Elizarraga, V. H., Hernandez-Matehuala, R., Cruz-Hernandez, A., Guevara-Gonzalez, R., Caballero-Perez, J., . . . Rojas-Molina, A. (2019). Impact of El Nino-Southern Oscillation 2015-2016 on the soluble proteomic profile and cytolytic activity of Millepora alcicornis ("fire coral") from the Mexican Caribbean. *Peerj*, 7. <u>https://doi.org/10.7717/peerj.6593</u>

Reef-forming cnidarians are extremely susceptible to the "bleaching" phenomenon caused by global warming. The effect of elevated seawater temperature has been extensively studied on Anthozoans; however, to date the impact of thermal stress on the expression of genes and proteins in Hydrozoan species has not been investigated. The present study aimed to determine the differential proteomic profile of Millepora alcicornis, which inhabits the Mexican Caribbean, in response to the El Nirio-Southern Oscillation 2015-2016. Additionally, the cytolytic activity of the soluble proteomes obtained from normal and bleached M. alcicornis was assessed. Bleached specimens showed decreased symbiont's density and chlorophyll a and c2 levels. After bleaching, we observed a differential expression of 17 key proteins, tentatively identified as related to exocytosis, calcium homeostasis, cytoskeletal organization, and potential toxins, including a metalloprotease, a phospholipase A2 (PLA2), and an actitoxin. Although, some of the differentially expressed proteins included potential toxins, the hemolytic, PLA2, and proteolytic activities elicited by the soluble proteomes from bleached and normal specimens were not significantly different. The present study provides heretofore-unknown evidence that thermal stress produces a differential expression of proteins involved in essential cellular processes of Hydrozoan species. Even though our results showed an over-expression of some potential toxinrelated proteins, the cytolytic effect (as assessed by hemolytic, PLA2, and caseinolytic activities) was not increased in bleached M. alcicornis, which suggests that the cytolysis is mainly produced by toxins whose expression was not affected by temperature stress. These findings allow hypothesizing that this hydrocoral is able to prey heterotrophically when suffering from moderate bleaching, giving it a better chance to withstand the effects of high temperature.

Pisapia, C., Hochberg, E. J., & Carpenter, R. (2019). Multi-Decadal Change in Reef-Scale Production and Calcification Associated With Recent Disturbances on a Lizard Island Reef Flat. *Frontiers in Marine Science*. <u>https://doi.org/10.3389/fmars.2019.00575</u>

Climate change is threatening the persistence of coral reef ecosystems resulting in both chronic and acute impacts which include higher frequency and severity of cyclones, warming sea surface temperatures, and ocean acidification. This study measured net ecosystem primary production (NEP)

and net ecosystem calcification (NEC) on a reef flat after the most severe El Nino-driven mass bleaching event on Australia's Great Barrier Reef (GBR) in 2016 and again in 2018 after another consecutive bleaching event in 2017. Our results indicate that reef metabolism is altered as result of both the continuing press disturbance of ocean acidification and severe pulse disturbances (cyclones and bleaching events). In 2016, NEP was within the range of values reported in past studies, however it declined in 2018. NEC over a 12-h period was lower in 2016 than 2018; but when compared with past studies there was a severe decline in daytime net calcification from 2008-2009, to 2016 followed by an increase in 2018 (but still NEC remained lower than values reported in 2008-2009). Conversely, nighttime net calcification was similar to that reported in 2009 indicating nighttime dissolution did not increase over the past decade. Overall coral cover remained stable following recent disturbances, however algal turf was the dominant benthic component on the reef flat, while calcifiers (corals and calcified algae) were minor components (< 20% of total benthic cover). This study documented changes in community function following major pulse disturbances (bleaching events and cyclones) within the context of ongoing OA at the same location over the last decade. Repeated pulse disturbances could jeopardize the persistence of the reef flat as a net calcifying entity, with the potential for cascading effects on other ecosystem services.

Quintanilla, E., Madurell, T., Wilke, T., & Sanchez, J. A. (2019). Dynamic Interplay of ENSO Events and Local Hydrodynamic Parameters Drives Demography and Health Status of Gorgonian Sea Fan Populations on a Remote Tropical Eastern Pacific Island. *Frontiers in Marine Science*, 6. <u>https://doi.org/10.3389/fmars.2019.00694</u>

Gorgonian corals occurring in shallow waters are vulnerable to changing environmental conditions and human-related pressures such as pollution, overfishing, and diseases. However, anthropogenic effects on coral systems are difficult to quantify due to the lack of base-line data of unaffected populations. In order to assess the impact of global and local environmental parameters on gorgonian populations removed from direct anthropogenic impact, we evaluated demographic parameters and the health status of Pacifigorgia cairnsi (Gorgoniidae: Octocorallia) populations in Malpelo Island, a remote and pristine marine area in the Tropical Eastern Pacific of Colombia. Specifically, we studied P. cairnsi densities and population size structures under different habitat and local environmental conditions. We also studied whether ENSO events and local hydrodynamic features including locality, water depth, and upwelling conditions drive P. cairnsi growth rates. Finally, we evaluated the prevalence of the necrotic patch disease and rates of disease recovery. Major findings were that local hydrodynamic parameters shaped P. cairnsi size structures, that growth rates were affected by thermal anomalies associated to ENSO events and partly by water depth, that overall disease prevalence was low (6%) and that it did not correlate with the environmental parameters studied, and that most diseased colonies (57%) recovered via tissue breakage. The fact that P. cairnsi, a keystone species within the regional benthic food web, is affected by thermal anomalies remains of concern because these global events are predicted to increase in frequencies and severity in the future. Nonetheless, the low level of disease prevalence found indicates that the island's pristine conditions might facilitate disease resistance. Moreover, the findings suggest an interesting trade-off between growth rates and colony recovery in shallow waters related to tissue breakage. This study provides crucial base-line data for future investigations aiming at understanding coral responses to anthropogenic pressures and the impact of global climate change on coral communities.

Ritson-Williams, R., & Gates, R. D. (2020). Coral community resilience to successive years of bleaching in Kāne'ohe Bay, Hawai'i. *Coral Reefs*, 39(3), 757-769. <u>https://doi.org/10.1007/s00338-020-01944-4</u>

The Hawaiian Islands are at the northern edge of coral reef distributions, and corals found there are exposed to large seasonal temperature changes. Historically, coral bleaching in the Hawaiian Islands was extremely rare and had only occurred in 1996. However, in the summers of both 2014 and 2015, successive bleaching events occurred in Kāne'ohe Bay, O'ahu. Seawater temperatures were above 28 °C for approximately 1 month in 2014 and 3 months in 2015 and peaked above 30 °C in both years. Patterns of bleaching did not vary among the three sites within Kāne'ohe Bay. Severe bleaching and paling covered 77 and 55% of reefs in 2014 and 2015, respectively. Different species showed a range of susceptibility with 80–100% of Pocillopora spp. bleaching in both years, but less than 50% bleaching of Porites compressa and Montipora capitata in Kāne'ohe Bay. Less than 1% of the encrusting coral Leptastrea purpurea colonies bleached in both years. Sixty individual colonies of P. compressa and M. capitata and 28 colonies of Pocillopora damicornis were tagged and monitored for rates of bleaching, recovery and mortality throughout the two-year period. Most of the colonies that bleached recovered their symbionts within 3–4 months, though P. compressa visually recovered more rapidly than M. capitata and P. damicornis. Cumulatively, 19% of P. damicornis, 10% of M. capitata and no P. compressa died by May 2016. Partial mortality within a colony did not occur in 2014, but impacted 13% of the colonies in 2015, with P. damicornis and M. capitata having higher rates of partial mortality than P. compressa. Relatively, low susceptibility in the dominant species and low rates of mortality combined with rapid rates of recovery show coral resilience to anomalously high temperatures in Kane'ohe Bay, Oʻahu.

Robinson, J. P. W., Williams, I. D., Yeager, L. A., McPherson, J. M., Clark, J., Oliver, T. A., & Baum, J. K. (2018). Environmental conditions and herbivore biomass determine coral reef benthic community composition: implications for quantitative baselines. *Coral Reefs*, 37(4), 1157-1168. https://doi.org/10.1007/s00338-018-01737-w

Our ability to understand natural constraints on coral reef benthic communities requires quantitative assessment of the relative strengths of abiotic and biotic processes across large spatial scales. Here, we combine underwater images, visual censuses and remote sensing data for 1566 sites across 34 islands spanning the central-western Pacific Ocean, to empirically assess the relative roles of abiotic and grazing processes in determining the prevalence of calcifying organisms and fleshy algae on coral reefs. We used regression trees to identify the major predictors of benthic composition and to test whether anthropogenic stress at inhabited islands decouples natural relationships. We show that sea surface temperature, wave energy, oceanic productivity and aragonite saturation strongly influence benthic community composition; overlooking these factors may bias expectations of calcified reef states. Maintenance of grazing biomass above a relatively low threshold ($\sim 10-20$ kg ha-1) may also prevent transitions to algal-dominated states, providing a tangible management target for rebuilding overexploited herbivore populations. Biophysical relationships did not decouple at inhabited islands, indicating that abiotic influences remain important macroscale processes, even at chronically disturbed reefs. However, spatial autocorrelation among inhabited reefs was substantial and exceeded abiotic and grazing influences, suggesting that natural constraints on reef benthos were superseded by unmeasured anthropogenic impacts. Evidence of strong abiotic influences on reef benthic communities underscores

their importance in specifying quantitative targets for coral reef management and restoration that are realistic within the context of local conditions.

Sakai, K., Singh, T., & Iguchi, A. (2019). Bleaching and post-bleaching mortality of Acropora corals on a heat-susceptible reef in 2016. *Peerj*, 7. <u>https://doi.org/10.7717/peerj.8138</u>

In 2016, global temperatures were the highest on record, and mass coral bleaching occurred worldwide. However, around Sesoko Island, Okinawa, southwestern Japan, the heat stress assessed by degree heating week (DHW) based on local temperature measurements was moderate in 2016; in 1998, DHW was three times higher than in 2016 (10.6 vs. 3.3 in September in respective years). On a reef flat of Sesoko Island where the effect of severe coral bleaching on coral assemblage was monitored in 1998, significant coral bleaching occurred in 2016. Bleaching of the heat stress sensitive Acropora corals began in July 2016 on the reef flat as seawater temperature rose. We observed the bleaching and postbleaching mortality status of individual colonies of Acropora spp. in 2016 in fixed plots on the reef flat. In total, 123 Acropora colonies were followed for six months after seawater temperature became normal by multiple surveys. At the beginning of September 2016, 99.2% of colonies, were either completely (92.7%) or partially (6.5%) bleached. Of those, the dominant species or species groups were A. gemmifera (Ag), A. digitifera (Ad), and tabular Acropora (tA). For all Acropora colonies, the overall whole and partial mortality was 41.5% and 11.4%, respectively. Whole mortality rate differed significantly among species; 72.5%, 17.9%, and 27.8% in Ag, Ad, and tA, respectively. Mortality rates at the end of the surveys were similar in smaller (<= 10 cm in diameter) and larger Ag, but the former suffered mortality earlier than the latter. Higher survival of smaller colonies was observed only in tA (100%), which may be associated with large morphological differences between smaller and larger colonies. Some of the dominant Acropora colonies had survived without partial mortality including 15.0% survival of the most vulnerable Ag at the end of the surveys. These results suggest that moderate heat stress may have a potential for selecting heat-tolerant genotypes. A longer period of mortality lasting for six months, was observed in Ag in addition to immediate whole mortality after bleaching, due to the continuous loss of living tissue by partial mortality. This highlights the need for multiple surveys at least during several months to accurately assess the impact of thermal stress event to corals. In contrast to DHW based on local measurements, DHW obtained from satellite data were similar between 1998 and 2016. Although satellite-based measurement of sea surface temperature is very useful to reveal variations in heat stress at a large spatial scale, temperature should be measured on site when variations at smaller spatial scales are of interest.

Schoepf, V., D'Olivo, J. P., Rigal, C., Jung, E. M. U., & McCulloch, M. T. (2021). Heat stress differentially impacts key calcification mechanisms in reef-building corals. *Coral Reefs*. <u>https://doi.org/10.1007/s00338-020-02038-x</u>

Coral reefs are increasingly threatened by climate change, mass bleaching events and ocean acidification (OA). Coral calcification, a process that is critical to build and maintain the structure of tropical coral reefs, is highly sensitive to both warming and acidifying oceans. However, in contrast to the impacts of OA on coral calcification, significant knowledge gaps remain regarding how coral biomineralization mechanisms are impacted by heat stress and bleaching. Using a combined physiological and geochemical approach, we investigated how a marine heatwave impacted coral symbiotic status

(chlorophyll a, algal symbiont density), the carbonate chemistry of the coral calcifying fluid (via delta B-11 and B/Ca) and skeletal trace element composition in the branching coral Acropora aspera. Importantly, we recorded in situ temperature throughout the bleaching event and recovery as well as coral symbiotic status during peak bleaching and after 7 months of recovery. We show that heatstressed Acropora corals continued to upregulate the pH of their calcifying fluid (cf); however, dissolved inorganic carbon upregulation inside the cf was significantly disrupted by heat stress. Similarly, we observed suppression of the typical seasonality in the trace element (TE) temperature proxies Sr/Ca, Mg/Ca, Li/Ca and Li/Mg, indicating disruption of important calcification mechanisms, Rayleigh fractionation and reduced growth rates. Anomalies in TE/Ca ratios were still observed 7 months after peak bleaching, even though algal symbiont densities and chlorophyll a concentrations were fully restored at this point. Interestingly, the biomineralization response to heat stress did not differ between thermally distinct reef habitats harbouring coral populations with different heat tolerance, nor between heat-stressed colonies with different severity of bleaching. Our findings suggest that coral biomineralization mechanisms in Acropora are highly sensitive to heat stress, showing similar patterns of biogeochemical stress response as other coral taxa.

Schramek, T. A., Colin, P. L., Merrifield, M. A., & Terrill, E. J. (2018). Depth-Dependent Thermal Stress Around Corals in the Tropical Pacific Ocean. *Geophysical Research Letters*, 45(18), 9739-9747. <u>https://doi.org/10.1029/2018gl078782</u>

Thermally driven bleaching events are a growing concern for reef ecosystems across the tropics. To assess and predict thermal stress impacts on reefs, remotely observed sea surface temperature (SST) commonly is used; however, reef communities typically extend to depths where SST alone may not be an accurate measure of in situ variability. Here nearly two decades of temperature observations (2- to 90-m depth) at three stations around Palau are used to develop an empirical model of temperature variability versus depth based on SST and sea level anomaly (SLA). The technique yields depth-averaged R-2 values >0.88, with SLA predicting fore reef temperatures near the thermocline and SST capturing upper mixed layer temperatures. SLA complements SST by providing a proxy for vertical isotherm displacements driven by local and remote winds on intraseasonal to interannual time scales. Utilizing this concept, thermal stress on corals can be predicted from the surface through the mesophotic zone. Plain Language Summary Coral reefs are often bleached, leading to their death, due to exceedingly warm ocean temperatures. The temperature of the ocean's surface, measured globally by satellites, is often used as an indicator of the temperature and stress that corals experience, but it can only tell us what is happening near the surface. We present nearly two decades of temperature records from the reefs of Palau, an island nation in the tropical Pacific. This array of instruments was maintained by skilled divers routinely going deeper than 90 m. The observations allow us to show that the height of the ocean surface is a strong indicator of how ocean temperatures are changing tens of meters below. This can be coupled with observed sea surface temperature to predict the temperatures experienced by coral reefs living near the surface as well as those living deeper, down through the mesophotic zone, an area between 30 and 150 m deep. The research suggests that significant improvements can be made to how temperature stress on corals is assessed. We also find that thermal stress events can penetrate into the realm of deep mesophotic coral reefs, meaning that this zone might not be refugia for corals living in a warming ocean.

Slattery, M., Pankey, M. S., & Lesser, M. P. (2019). Annual Thermal Stress Increases a Soft Coral's Susceptibility to Bleaching. *Scientific Reports*, 9. <u>https://doi.org/10.1038/s41598-019-44566-9</u>

Like scleractinian corals, soft corals contain photosymbionts (Family Symbiodiniaceae) that provide energy for the host. Recent thermal events have resulted in soft coral bleaching in four of five years on Guam, where they dominated back-reef communities. Soft coral bleaching was examined in Sinularia maxima, S. polydactyla, and their hybrid S. maxima x polydactyla. Results from annual field surveys indicated that S. maxima and the hybrid were more susceptible to bleaching than S. polydactyla, and this was related to differences in their Symbiodiniaceae communities in 2016 and 2017. The photosymbionts of S. polydactyla were apparently more stress tolerant and maintained higher photosynthetic potential through three years of bleaching, in contrast to the other species that exhibited a decline in photosynthetic potential after the first year of bleaching. Nonetheless, by the 2017 bleaching event all soft coral populations exhibited significant bleaching-mediated declines and loss of photosynthetic efficiency suggesting a declining resiliency to annual thermal stress events. While S. polydactyla initially looked to succeed the other species as the dominant space occupying soft coral on Guam back-reefs, cumulative bleaching events ultimately turned this "winner" into a "loser", suggesting the trajectory for coral reefs is towards continued loss of structure and function.

Steneck, R., Arnold, S., Boenish, R., León, R. d., Mumby, P., Rasher, D., & Wilson, M. (2019). Managing Recovery Resilience in Coral Reefs Against Climate-Induced Bleaching and Hurricanes: A 15 Year Case Study From Bonaire, Dutch Caribbean. *Frontiers in Marine Science*. <u>https://doi.org/10.3389/fmars.2019.00265</u>

Coral reefs are among the world's most endangered ecosystems. Coral mortality can result from ocean warming or other climate-related events such as coral bleaching and intense hurricanes. While resilient coral reefs can recover from these impacts as has been documented in coral reefs throughout the tropical Indo-Pacific, no similar reef-wide recovery has ever been reported for the Caribbean. Climate change-related coral mortality is unavoidable, but local management actions can improve conditions for regrowth and for the establishment of juvenile corals thereby enhancing the recovery resilience of these ecosystems. Previous research has determined that coral reefs with sufficient herbivory limit macroalgae and improve conditions for coral recruitment and regrowth. Management that reduces algal abundance increases the recovery potential for both juvenile and adult corals on reefs. Every other year on the island of Bonaire, Dutch Caribbean, we quantified patterns of distribution and abundance of reef fish, coral, algae, and juvenile corals along replicate fixed transects at 10 m depth at multiple sites from 2003 to 2017. Beginning with our first exploratory study in 2002 until 2007 coral was abundant (45% cover) and macroalgae were rare (6% cover). Consecutive disturbances, beginning with Hurricane Omar in October 2008 and a coral bleaching event in October 2010, resulted in a 22% decline in coral cover and a sharp threefold increase in macroalgal cover to 18%. Juvenile coral densities declined to about half of their previous abundance. Herbivorous parrotfishes had been declining in abundance but stabilized around 2010, the year fish traps were phased out and fishing for parrotfish was banned. The average parrotfish biomass from 2010 to 2017 was more than twice that reported for coral reefs of the Eastern Caribbean. During this same period, macroalgae declined and both juvenile coral density and total adult coral cover returned to pre-hurricane and bleaching levels. To our knowledge, this is the first example of a resilient Caribbean coral reef ecosystem that fully recovered from severe climate-related mortality events.

Stuhr, M., Meyer, A., Reymond, C. E., Narayan, G. R., Rieder, V., Rahnenfuhrer, J., . . . Hallock, P. (2018). Variable thermal stress tolerance of the reef-associated symbiont-bearing foraminifera Amphistegina linked to differences in symbiont type. *Coral Reefs*, 37(3), 811-824. https://doi.org/10.1007/s00338-018-1707-9

Adaptation, acclimatization and symbiont diversity are known to regulate thermal tolerance in corals, but the role of these mechanisms remains poorly constrained in other photosymbioses, such as large benthic foraminifera (LBFs), which are known to bleach at temperatures that are likely to be exceeded in the near future. LBFs inhabit a broad range of shallow-water settings. Within species, differences in thermal tolerance have been found among populations from different habitats, but it is not clear whether such differences occur among LBFs inhabiting similar habitats, but differing in other aspects, such as symbiont type. To this end, we compared responses to thermal stress in specimens from a population of Amphistegina lessonii, an abundant Indo-Pacific species, to specimens of Amphistegina gibbosa, its Atlantic counter-part, from a similar environment but two different water depths (5 and 18 m). Test groups of each species were exposed in a common experiment to three thermal stress scenarios over a four-week period. Growth, respiration, mortality and motility were measured to characterize the holobiont response. Coloration, photosynthesis and chlorophyll a content were measured to determine the response of the endosymbiotic diatoms. The photosymbionts were characterized by genetic fingerprinting. Our results show that, although groups of A. gibbosa were collected from different habitats, their responses were similar, indicating only marginally higher tolerance to thermal peaks in specimens from the shallower site. In contrast, species-specific differences were stronger, with A. lessonii showing higher tolerance to episodic stress and less pronounced impacts of chronic stress on motility, growth and photosymbiont performance. These interspecies variations are consistent with the presence of different and more diverse symbiont assemblages in A. lessonii compared with A. gibbosa. This study demonstrates the importance of considering symbiont diversity in the assessment of infra- and interspecific variations in stress responses in LBFs.

Wright, R. M., Strader, M. E., Genuise, H. M., & Matz, M. (2019). Effects of thermal stress on amount, composition, and antibacterial properties of coral mucus. *Peerj*, 7. https://doi.org/10.7717/peerj.6849

The surface mucus layer of reef-building corals supports feeding, sediment clearing, and protection from pathogenic invaders. As much as half of the fixed carbon supplied by the corals' photosynthetic symbionts is incorporated into expelled mucus. It is therefore reasonable to expect that coral bleaching (disruption of the coral-algal symbiosis) would affect mucus production. Since coral mucus serves as an important nutrient source for the entire reef community, this could have substantial ecosystem-wide consequences. In this study, we examined the effects of heat stress-induced coral bleaching on the composition and antibacterial properties of coral mucus. In a controlled laboratory thermal challenge, stressed corals produced mucus with higher protein (beta = 2.1, p < 0.001) and lipid content (beta = 15.7, p = 0.02) and increased antibacterial activity (likelihood ratio = 100, p < 0.001) relative to clonal controls. These results are likely explained by the expelled symbionts in the mucus of bleached individuals. Our study suggests that coral bleaching could immediately impact the nutrient flux in the coral reef ecosystem via its effect on coral mucus.

Zhang, Z. H., Jones, A., & Crabbe, M. J. C. (2018). Impacts of stratospheric aerosol geoengineering strategy on Caribbean coral reefs. *International Journal of Climate Change Strategies and Management*, 10(4), 523-532. <u>https://doi.org/10.1108/ijccsm-05-2017-0104</u>

Currently, negotiation on global carbon emissions reduction is very difficult owing to lack of international willingness. In response, geoengineering (climate engineering) strategies are proposed to artificially cool the planet. Meanwhile, as the harbor around one-third of all described marine species, coral reefs are the most sensitive ecosystem on the planet to climate change. However, until now, there is no quantitative assessment on the impacts of geoengineering on coral reefs. This study aims to model the impacts of stratospheric aerosol geoengineering on coral reefs. The HadGEM2-ES climate model is used to model and evaluate the impacts of stratospheric aerosol geoengineering could significantly mitigate future coral bleaching throughout the Caribbean Sea; (2) Changes in downward solar irradiation, sea level rise and sea surface temperature caused by geoengineering implementation should have very little impacts on coral reefs; (3) Although geoengineering would prolong the return period of future hurricanes, this may still be too short to ensure coral recruitment and survival after hurricane damage. This is the first time internationally to quantitatively assess the impacts of geoengineering on coral reefs.

Section 6: Ocean Acidification

Allemand, D., & Osborn, D. (2019). Ocean acidification impacts on coral reefs: From sciences to solutions. *Regional Studies in Marine Science*, 28, 100558. https://doi.org/10.1016/j.rsma.2019.100558

Coral reefs distinctly illustrate the close relationship between biodiversity and ecosystem services. They are rich marine ecosystems, hosting extensive biological diversity, and yet that diversity and the ecosystem services provided are among the most endangered because of global changes. By reducing and altering coral reef biodiversity, global changes are endangering the lives of hundreds of millions of people. It was therefore appropriate that the ongoing workshop series "Bridging the gap between Ocean Acidification and Economic Valuation" dedicated, during the International Year of Coral Reefs, its 4thedition in search of solutions inspired by the most recent data of the Natural, Economic and Social Sciences. This article summarizes the ecological and human importance of coral reefs, the reasons for their sensitivity to global changes, and presents the major conclusions of the workshop as well as policy options

Bahr, K. D., Tran, T., Jury, C. P., & Toonen, R. J. (2020). Abundance, size, and survival of recruits of the reef coral Pocillopora acuta under ocean warming and acidification. *PLOS ONE*, 15(2), e0228168. https://doi.org/10.1371/journal.pone.0228168

Ocean warming and acidification are among the greatest threats to coral reefs. Massive coral bleaching events are becoming increasingly common and are predicted to be more severe and frequent in the near future, putting corals reefs in danger of ecological collapse. This study quantified the abundance, size, and survival of the coral Pocillopora acuta under future projections of ocean warming and acidification. Flow-through mesocosms were exposed to current and future projections of ocean warming or acidification, nor their combination, influenced the size or abundance of P. acuta recruits, but heating impacted subsequent health and survival of the recruits. During annual maximum temperatures, coral recruits in heated tanks experienced higher levels of bleaching and subsequent mortality. Results of this study indicate that P. acuta is able to recruit under projected levels of ocean warming and acidification but are susceptible to bleaching and mortality during the warmest months.

 Bove, C. B., Ries, J. B., Davies, S. W., Westfield, I. T., Umbanhowar, J., & Castillo, K. D. (2019). Common Caribbean corals exhibit highly variable responses to future acidification and warming. *Proceedings of the Royal Society B-Biological Sciences*, 286(1900), 20182840. <u>https://doi.org/10.1098/rspb.2018.2840</u>

We conducted a 93-day experiment investigating the independent and combined effects of acidification (280-3300 µatm pCO(2)) and warming (28°C and 31°C) on calcification and linear extension rates of four key Caribbean coral species (Siderastrea siderea, Pseudodiploria strigosa, Porites astreoides, Undaria tenuifolia) from inshore and offshore reefs on the Belize Mesoamerican Barrier Reef System. All species exhibited nonlinear declines in calcification rate with increasing pCO(2). Warming only reduced calcification in Ps. strigosa. Of the species tested, only S. siderea maintained positive calcification in the

aragonite-undersaturated treatment . Temperature and pCO(2) had no effect on the linear extension of S. siderea and Po. astreoides, and natal reef environment did not impact any parameter examined. Results suggest that S. siderea is the most resilient of these corals to warming and acidification owing to its ability to maintain positive calcification in all treatments, Ps. strigosa and U. tenuifolia are the least resilient, and Po. astreoides falls in the middle. These results highlight the diversity of calcification responses of Caribbean corals to projected global change.

Eyre, B. D., Cyronak, T., Drupp, P., De Carlo, E. H., Sachs, J. P., & Andersson, A. J. (2018). Coral reefs will transition to net dissolving before end of century. *Science*, 359(6378), 908. <u>https://doi.org/10.1126/science.aao1118</u>

The uptake of anthropogenic carbon dioxide from the atmosphere is reducing the pH of the oceans. Ocean acidification means that calcium carbonate—the material with which coral reefs are built—will be more difficult for organisms to generate and will dissolve more quickly. Eyre et al. report that some reefs are already experiencing net sediment dissolution. Worryingly, the rates of loss will increase as ocean acidification intensifies.Science, this issue p. 908Ocean acidification refers to the lowering of the ocean's pH due to the uptake of anthropogenic CO2 from the atmosphere. Coral reef calcification is expected to decrease as the oceans become more acidic. Dissolving calcium carbonate (CaCO3) sands could greatly exacerbate reef loss associated with reduced calcification but is presently poorly constrained. Here we show that CaCO3 dissolution in reef sediments across five globally distributed sites is negatively correlated with the aragonite saturation state (Ω ar) of overlying seawater and that CaCO3 sediment dissolution is 10-fold more sensitive to ocean acidification than coral calcification. Consequently, reef sediments globally will transition from net precipitation to net dissolution when seawater Ω ar reaches 2.92 ± 0.16 (expected circa 2050 CE). Notably, some reefs are already experiencing net sediment dissolution.

Guan, Y., Hohn, S., Wild, C., & Merico, A. (2020). Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication. *Global Change Biology*, 26(10), 5646-5660. <u>https://doi.org/10.1111/gcb.15293</u>

Coral reefs are threatened by global and local stressors. Yet, reefs appear to respond differently to different environmental stressors. Using a global dataset of coral reef occurrence as a proxy for the long-term adaptation of corals to environmental conditions in combination with global environmental data, we show here how global (warming: sea surface temperature; acidification: aragonite saturation state, omega(arag)) and local (eutrophication: nitrate concentration, and phosphate concentration) stressors influence coral reef habitat suitability. We analyse the relative distance of coral communities to their regional environmental optima. In addition, we calculate the expected change of coral reef habitat suitability across the tropics in relation to an increase of 0.1 degrees C in temperature, an increase of 0.02 mu mol/L in nitrate, an increase of 0.01 mu mol/L in phosphate and a decrease of 0.04 in omega(arag). Our findings reveal that only 6% of the reefs worldwide will be unaffected by local and global stressors and can thus act as temporary refugia. Local stressors, driven by nutrient increase, will affect 22% of the reefs worldwide, whereas global stressors will affect 11% of these reefs. The remaining 61% of the reefs will be simultaneously affected by local and global stressors. Appropriate wastewater

treatments can mitigate local eutrophication and could increase areas of temporary refugia to 28%, allowing us to 'buy time', while international agreements are found to abate global stressors.

 Hennige, S. J., Wolfram, U., Wickes, L., Murray, F., Roberts, J. M., Kamenos, N. A., . . . Etnoyer, P. J. (2020). Crumbling Reefs and Cold-Water Coral Habitat Loss in a Future Ocean: Evidence of "Coralporosis" as an Indicator of Habitat Integrity. *Frontiers in Marine Science*, 7(668). https://doi.org/10.3389/fmars.2020.00668

Ocean acidification is a threat to the net growth of tropical and deep-sea coral reefs, due to gradual changes in the balance between reef growth and loss processes. Here we go beyond identification of coral dissolution induced by ocean acidification and identify a mechanism that will lead to a loss of habitat in cold-water coral reef habitats on an ecosystem-scale. To quantify this, we present in situ and year-long laboratory evidence detailing the type of habitat shift that can be expected (in situ evidence), the mechanisms underlying this (in situ and laboratory evidence), and the timescale within which the process begins (laboratory evidence). Through application of engineering principals, we detail how increased porosity in structurally critical sections of coral framework will lead to crumbling of loadbearing material, and a potential collapse and loss of complexity of the larger habitat. Importantly, in situ evidence highlights that cold-water corals can survive beneath the aragonite saturation horizon, but in a fundamentally different way to what is currently considered a biogenic cold-water coral reef, with a loss of the majority of reef habitat. The shift from a habitat with high 3-dimensional complexity provided by both live and dead coral framework, to a habitat restricted primarily to live coral colonies with lower 3-dimensional complexity represents the main threat to cold-water coral reefs of the future and the biodiversity they support. Ocean acidification can cause ecosystem-scale habitat loss for the majority of cold-water coral reefs.

Jury, C. P., & Toonen, R. J. (2019). Adaptive responses and local stressor mitigation drive coral resilience in warmer, more acidic oceans. *Proceedings of the Royal Society B-Biological Sciences*, 286(1902). <u>https://doi.org/10.1098/rspb.2019.0614</u>

Coral reefs have great biological and socioeconomic value, but are threatened by ocean acidification, climate change and local human impacts. The capacity for corals to adapt or acclimatize to novel environmental conditions is unknown but fundamental to projected reef futures. The coral reefs of Kane'ohe Bay, Hawai'i were devastated by anthropogenic insults from the 1930s to 1970s. These reefs experience naturally reduced pH and elevated temperature relative to many other Hawaiian reefs whiCh are not expected to face similar conditions for decades. Despite catastrophic loss in coral cover owing to human disturbance, these reefs recovered under low pH and high temperature within 20 years after sewage input was diverted. We compare the pH and temperature tolerances of three dominant Hawaiian coral species from within Kaneohe Bay to conspecifics from a nearby control site and show that corals from Kane'ohe are far more resistant to acidification and warming. These results show that corals can have different pH and temperature tolerances among habitats and understanding the mechanisms by which coral cover rebounded within two decades under projected future ocean conditions will be critical to management. Together these results indicate that reducing human stressors offers hope for reef resilience and effective conservation over coming decades.

Kealoha, A. K., Doyle, S. M., Shamberger, K. E. F., Sylvan, J. B., Hetland, R. D., & DiMarco, S. F. (2020).
Localized hypoxia may have caused coral reef mortality at the Flower Garden Banks. *Coral Reefs*, 39(1), 119-132. <u>https://doi.org/10.1007/s00338-019-01883-9</u>

On July 25, 2016, turbid water and dead corals, sponges and other invertebrates were discovered at the East Bank (EB) of the Flower Garden Banks (FGB) National Marine Sanctuary. Mortality was spread over 0.06 km2, with up to 80% coral mortality reported in some areas. Within days, response efforts were underway to investigate the potential mechanisms leading to the mortality event. Hydrographic surveys, moored buoy data, and a regional hydrodynamic model were used to characterize water chemistry, hydrography, and microbial communities within the FGB. Low salinity (~ 31–33), total alkalinity (~ 2284– 2330 µmol kg-1), and dissolved inorganic carbon (DIC, ~ 1968–2011 µmol kg-1) were detected in surface waters over the EB and eastern stations, revealing the presence of river-derived water. The Mississippi/Atchafalaya rivers were the primary sources of freshwater during the event, although Texas rivers, all of which had unusually high discharge during 2016, contributed approximately one-fifth to the total freshwater mass. At 75 m depth, high density, salinity, DIC, ammonium, and abundance of microbial taxa associated with deep waters were coincident with low temperature and aragonite saturation state at the northern and eastern stations, indicating a deeper source water at these stations. Cross-slope density gradients were also consistent with an upwelling circulation pattern. Using these observations and data, we hypothesize that the mortality event was most likely caused by the combination of two processes. The turbid freshwater layer inhibited photosynthesis, leading to net respiration of coral reef organic matter. Additionally, deep, dense waters upwelled onto the bank and formed a stratified bottom layer, which prevented re-oxygenation from the overlying water column and led to localized areas of hypoxia within pockets on the reef. Hypoxia likely formed rapidly, within two days. Moving forward, high-frequency temporal measurements of oxygen and carbonate chemistry are critical for monitoring risks (e.g., hypoxia and acidification) associated with freshwater discharge and upwelling, since these processes may adversely affect coral reef health.

Lebrec, M., Stefanski, S., Gates, R., Acar, S., Golbuu, Y., Claudel-Rusin, A., . . . Swarzenski, P. W. (2019). Ocean acidification impacts in select Pacific Basin coral reef ecosystems. *Regional Studies in Marine Science*, 28. <u>https://doi.org/10.1016/j.rsma.2019.100584</u>

In the vast tropical Pacific Basin islands, corals reef ecosystems are one of the defining marine habitats, critical for maintaining biodiversity and supporting highly productive fisheries. These reefs are also vital for tourism and armoring exposed shorelines against erosion and other storm-related effects. Since the 1980's, there has been growing evidence that these Pacific Basin coral reef ecosystems are highly vulnerable to the combined effects of both climatic and non-climatic stressors. Observations of widespread bleaching in the region has been linked to acute temperature stress, and the heightened recurrence intervals and intensity of storms has been correlated to recent climate-change induced impacts. Ocean acidification is another ubiquitous stressor with dramatic consequences to biological systems. In this paper we describe what sets this region apart from other coral reef regions around the world, and highlight some examples of the diverse response to ocean acidification threats and associated socio-economic impacts.

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. *Frontiers in Marine Science*. <u>https://doi.org/10.3389/fmars.2019.00038</u>

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 Ω arag. 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 Ω arag. 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 Ω arag are important drivers affecting coral growth rates in the Southwestern Caribbean. Therefore, we suggest upcoming variations of AMO and future trajectories of Ω arag in the Anthropocene could have a substantial influence on future disturbances, ecological process and responses of the Caribbean reefs.

Martinez, A., Crook, E. D., Barshis, D. J., Potts, D. C., Rebolledo-Vieyra, M., Hernandez, L., & Paytan, A. (2019). Species-specific calcification response of Caribbean corals after 2-year transplantation to a low aragonite saturation submarine spring. *Proceedings of the Royal Society B-Biological Sciences*, 286(1905), 20190572. <u>https://doi.org/10.1098/rspb.2019.0572</u>

Coral calcification is expected to decline as atmospheric carbon dioxide concentration increases. We assessed the potential of Porites astreoides, Siderastrea siderea and Porites porites to survive and calcify under acidified conditions in a 2-year field transplant experiment around low pH, low aragonite saturation (Ω (arag)) submarine springs. Slow-growing S. siderea had the highest post-transplantation survival and showed increases in concentrations of Symbiodiniaceae, chlorophyll a and protein at the low Ω (arag) site. Nubbins of P. astreoides had 20% lower survival and higher chlorophyll a concentration at the low Ω (arag) site. Only 33% of P. porites nubbins survived at low Ω (arag) and their linear extension and calcification rates were reduced. The density of skeletons deposited after transplantation at the low Ω (arag) spring was 15-30% lower for all species. These results suggest that corals with slow calcification rates and high Symbiodiniaceae, chlorophyll a and protein concentrations may be less susceptible to ocean acidification, albeit with reduced skeletal density. We postulate that corals in the springs are

responding to greater energy demands for overcoming larger differences in carbonate chemistry between the calcifying medium and the external environment. The differential mortality, growth rates and physiological changes may impact future coral species assemblages and the reef framework robustness.

Ocaña, F. A., Pech, D., Simões, N., & Hernández-Ávila, I. (2019). Spatial assessment of the vulnerability of benthic communities to multiple stressors in the Yucatan Continental Shelf, Gulf of Mexico.
Ocean & Coastal Management, 181, 104900.
https://doi.org/10.1016/j.ocecoaman.2019.104900

Here, we show a spatially explicit assessment of the vulnerability of benthic communities from the Yucatan Continental Shelf (YCS) to multiple pressures: fishing activities, shipping traffic, storms and hurricanes, and marine acidification. The vulnerability index was obtained by combining benthic biological traits with exposure and sensitivity and recovery capacity; this was then represented in a spatially explicit model. Moreover, we estimated a cumulative vulnerability index using three different scenarios that were based on 1) equal weight for each vulnerability layer to each stressor, 2) results of expert consultation and 3) a linear reduction in the weight of the pressures. By comparing scenarios, the synergistic and antagonistic effects of the multiple stressors were determined. The main results showed that, independent of the considered scenario, approximately 90% of the YCS presented moderate to high vulnerability to cumulative pressures, while areas with high recovery and high potential impact on a particular stressor showed low or moderate vulnerability to the pressures. Meanwhile, areas classified as having medium impact levels and low recovery capacities of benthic fauna showed moderate to high vulnerability to the same threats. Our findings also showed that ship traffic and marine acidification were the threats that contributed to the greatest vulnerability. The paired comparison of scenarios allows for the identification of areas with higher probabilities of synergistic effects. No antagonistic effects were detected. Overall, our results constitute the first effort to understand the ecological status of the benthic communities of the YCS and their potential vulnerability to the multiple pressures they face.

Pisapia, C., Hochberg, E. J., & Carpenter, R. (2019). Multi-Decadal Change in Reef-Scale Production and Calcification Associated With Recent Disturbances on a Lizard Island Reef Flat. *Frontiers in Marine Science*. <u>https://doi.org/10.3389/fmars.2019.00575</u>

Climate change is threatening the persistence of coral reef ecosystems resulting in both chronic and acute impacts which include higher frequency and severity of cyclones, warming sea surface temperatures, and ocean acidification. This study measured net ecosystem primary production (NEP) and net ecosystem calcification (NEC) on a reef flat after the most severe El Nino-driven mass bleaching event on Australia's Great Barrier Reef (GBR) in 2016 and again in 2018 after another consecutive bleaching event in 2017. Our results indicate that reef metabolism is altered as result of both the continuing press disturbance of ocean acidification and severe pulse disturbances (cyclones and bleaching events). In 2016, NEP was within the range of values reported in past studies, however it declined in 2018. NEC over a 12-h period was lower in 2016 than 2018; but when compared with past studies there was a severe decline in daytime net calcification from 2008-2009, to 2016 followed by an increase in 2018 (but still NEC remained lower than values reported in 2008-2009). Conversely,

nighttime net calcification was similar to that reported in 2009 indicating nighttime dissolution did not increase over the past decade. Overall coral cover remained stable following recent disturbances, however algal turf was the dominant benthic component on the reef flat, while calcifiers (corals and calcified algae) were minor components (< 20% of total benthic cover). This study documented changes in community function following major pulse disturbances (bleaching events and cyclones) within the context of ongoing OA at the same location over the last decade. Repeated pulse disturbances could jeopardize the persistence of the reef flat as a net calcifying entity, with the potential for cascading effects on other ecosystem services.

 Robinson, J. P. W., Williams, I. D., Yeager, L. A., McPherson, J. M., Clark, J., Oliver, T. A., & Baum, J. K. (2018). Environmental conditions and herbivore biomass determine coral reef benthic community composition: implications for quantitative baselines. *Coral Reefs*, 37(4), 1157-1168. https://doi.org/10.1007/s00338-018-01737-w

Our ability to understand natural constraints on coral reef benthic communities requires quantitative assessment of the relative strengths of abiotic and biotic processes across large spatial scales. Here, we combine underwater images, visual censuses and remote sensing data for 1566 sites across 34 islands spanning the central-western Pacific Ocean, to empirically assess the relative roles of abiotic and grazing processes in determining the prevalence of calcifying organisms and fleshy algae on coral reefs. We used regression trees to identify the major predictors of benthic composition and to test whether anthropogenic stress at inhabited islands decouples natural relationships. We show that sea surface temperature, wave energy, oceanic productivity and aragonite saturation strongly influence benthic community composition; overlooking these factors may bias expectations of calcified reef states. Maintenance of grazing biomass above a relatively low threshold ($\sim 10-20$ kg ha-1) may also prevent transitions to algal-dominated states, providing a tangible management target for rebuilding overexploited herbivore populations. Biophysical relationships did not decouple at inhabited islands, indicating that abiotic influences remain important macroscale processes, even at chronically disturbed reefs. However, spatial autocorrelation among inhabited reefs was substantial and exceeded abiotic and grazing influences, suggesting that natural constraints on reef benthos were superseded by unmeasured anthropogenic impacts. Evidence of strong abiotic influences on reef benthic communities underscores their importance in specifying quantitative targets for coral reef management and restoration that are realistic within the context of local conditions.

Section 7: Nutrient Enrichment

Carreon-Palau, L., Parrish, C. C., Perez-Espana, H., & Aguiniga-Garcia, S. (2018). Elemental ratios and lipid classes in a coral reef food web under river influence. *Progress in Oceanography*, 164, 1-11. https://doi.org/10.1016/j.pocean.2018.03.009

Coral reefs in the Caribbean and Gulf of Mexico are increasingly suffering from anthropogenic nutrient inputs principally from fertilizers as identified by their delta N-15 signatures. To determine if primary producers are passively affected by anthropogenic nitrogen enrichment in a coral reef community, carbon: nitrogen ratios (C:N mol mol(-1)) were measured. The C:N ratio was used as a proxy for nitrogen enrichment in primary producers when the ratio decreases, and for lipid plus carbohydrate in terms of C, and protein in terms of N in primary producers and consumers. Lipid classes and the triacylglycerol to sterol (TAG:ST) ratio were used to evaluate energy storage as an indication of nutritional quality in the six most abundant primary producers, and of nutritional condition in ten ubiquitous consumers in a coral reef in the Gulf of Mexico under river influence. A low C:N ratio revealed nitrogen enrichment in primary producers. Among the lipids, high TAG proportions were detected in phytoplankton and zooxanthellae suggesting that they have a higher nutritional quality in terms of energy, followed by sea grass, mangrove, and macroalgae. During the rainy season TAG:ST increased in primary consumers such as echinoderms, and top predators such as the perciform fish Bodianus rufus, Ocyurus chrysurus and Caranx hippos, suggesting an increase in energy storage. In contrast, TAG:ST decreased in the principal habitat providing coral Montastrea cavernosa, along with a decrease in the phospholipid proportion suggesting a poor nutritional condition. There were three species with no change in their TAG:ST ratio: the sponge Aplysina sp., the masked goby Coryphopterus personates and the surgeon fish Achanturus chirurgus. The lower value of TAG, TAG:ST ratio and phospholipid proportion in the coral M. cavernosa suggests that the reported abundance of zooplankton does not satisfy the energy demand of M. cavernosa during the rainy season.

Guan, Y., Hohn, S., Wild, C., & Merico, A. (2020). Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication. *Global Change Biology*, 26(10), 5646-5660. https://doi.org/10.1111/gcb.15293

Coral reefs are threatened by global and local stressors. Yet, reefs appear to respond differently to different environmental stressors. Using a global dataset of coral reef occurrence as a proxy for the long-term adaptation of corals to environmental conditions in combination with global environmental data, we show here how global (warming: sea surface temperature; acidification: aragonite saturation state, omega(arag)) and local (eutrophication: nitrate concentration, and phosphate concentration) stressors influence coral reef habitat suitability. We analyse the relative distance of coral communities to their regional environmental optima. In addition, we calculate the expected change of coral reef habitat suitability across the tropics in relation to an increase of 0.1 degrees C in temperature, an increase of 0.02 mu mol/L in nitrate, an increase of 0.01 mu mol/L in phosphate and a decrease of 0.04 in omega(arag). Our findings reveal that only 6% of the reefs worldwide will be unaffected by local and global stressors and can thus act as temporary refugia. Local stressors, driven by nutrient increase, will affect 22% of the reefs worldwide, whereas global stressors will affect 11% of these reefs. The remaining 61% of the reefs will be simultaneously affected by local and global stressors. Appropriate wastewater treatments can mitigate local eutrophication and could increase areas of temporary refugia to 28%, allowing us to 'buy time', while international agreements are found to abate global stressors.

Horta-Puga, G., Tello-Musi, J. L., Córdova, A., Gutiérrez-Carrillo, A., Gutiérrez-Martínez, J., & Morales-Aranda, A. A. (2020). Spatio-temporal variability of benthic macroalgae in a coral reef system highly influenced by fluvial discharge: Veracruz, Gulf of Mexico. *Marine Ecology*, 41(4), e12596. https://doi.org/10.1111/maec.12596

The Veracruz Reef System, in the southern Gulf of Mexico, is a suitable area for the study of the temporal and spatial variability of macroalgae abundance, at reef settings influenced by the fluvial discharge of the Jamapa River, and by human activities in the city and port of Veracruz. With this purpose, the bottom cover of each morpho-functional group of benthic macroalgae (frondoses, turf, and crustose corallines), and hermatypic corals, was determined at ten selected coral reefs, on a seasonal basis (rainy and dry seasons), for the 2009?2015 period. The average cover of benthic macroalgae was high (53.1%), with turf as the dominant morpho-functional group (31.9%), as in several reef ecosystems in the tropical Atlantic, followed by crustose corallines (15.2%), and frondoses (6.1%). Although turf macroalgae is dominant, due to their high temporal and spatial variability, the Veracruz Reef System could not be considered to be in a stable state, but just in an intermediate unstable equilibrium state, which is highly influenced by a high sediment load. As expected, nearshore reefs presented higher macroalgae covers, and unexpectedly, the outer-shelf reefs presented the highest cover of frondoses. Despite fluvial discharge influence, no differences in cover were found between the rainy and dry seasons. There was a negative and significantly correlation between the cover of frondoses and turf, which suggests that the driver/s of the abundance of these macroalgae, act in opposite ways for each group. Three clusters of reefs, defined by community structure and conservation degree, were determined: nearshore or degraded, offshore or moderately conserved, and conserved; and the entire Veracruz Reef System is considered to be in a moderately state of conservation.

Lapointe, B. E., Brewton, R. A., Herren, L. W., Porter, J. W., & Hu, C. (2019). Nitrogen enrichment, altered stoichiometry, and coral reef decline at Looe Key, Florida Keys, USA: a 3-decade study. *Marine Biology*, 166(8), 108. <u>https://doi.org/10.1007/s00227-019-3538-9</u>

Increased loadings of nitrogen (N) from fertilizers, top soil, sewage, and atmospheric deposition are important drivers of eutrophication in coastal waters globally. Monitoring seawater and macroalgae can reveal long-term changes in N and phosphorus (P) availability and N:P stoichiometry that are critical to understanding the global crisis of coral reef decline. Analysis of a unique 3-decade data set for Looe Key reef, located offshore the lower Florida Keys, showed increased dissolved inorganic nitrogen (DIN), chlorophyll a, DIN:soluble reactive phosphorus (SRP) ratios, as well as higher tissue C:P and N:P ratios in macroalgae during the early 1990s. These data, combined with remote sensing and nutrient monitoring between the Everglades and Looe Key, indicated that the significant DIN enrichment between 1991 and 1995 at Looe Key coincided with increased Everglades runoff, which drains agricultural and urban areas extending north to Orlando, Florida. This resulted in increased P limitation of reef primary producers that can cause metabolic stress in stony corals. Outbreaks of stony coral disease, bleaching, and mortality between 1995 and 2000 followed DIN enrichment, algal blooms, and increased DIN:SRP ratios, suggesting that eutrophication interacted with other factors causing coral reef decline at Looe Key. Although water temperatures at Looe Key exceeded the 30.5 °C bleaching threshold repeatedly over the 3-decade study, the three mass bleaching events occurred only when DIN:SRP ratios increased following heavy rainfall and increased Everglades runoff. These results suggest that Everglades discharges, in conjunction with local nutrient sources, contributed to DIN enrichment, eutrophication, and increased N:P ratios at Looe Key, exacerbating P limitation, coral stress and decline. Improved management of

water quality at the local and regional levels could moderate N inputs and maintain more balanced N:P stoichiometry, thereby reducing the risk of coral bleaching, disease, and mortality under the current level of temperature stress.

McCauley, M., & Goulet, T. L. (2019). Caribbean gorgonian octocorals cope with nutrient enrichment. *Marine Pollution Bulletin*, 141, 621-628. <u>https://doi.org/10.1016/j.marpolbul.2019.02.067</u>

Corals inhabit oligotrophic waters, thriving amidst limited nutrients such as nitrogen and phosphorous. When nutrient levels increase, usually due to human activity, the symbiosis of dinoflagellates (family Symbiodiniaceae) with scleractinian corals can break down. Although gorgonian corals dominate many Caribbean reefs, the impact of enrichment on them and their algae is understudied. We exposed two gorgonian species, Pseudoplexaura porosa and Eunicea tourneforti, to elevated concentrations of either ammonium (10 μ M or 50 μ M) or phosphate (4 μ M). Enrichment with 10 μ M ammonium increased chlorophyll content and algal density in both species, whereas the host biochemical composition was unaffected. Exposure to 50 μ M ammonium only reduced the quantum yield in P. porosa and mitotic indices in both species. Conversely, algal carbon and nitrogen content within E. tourneforti increased with 4 μ M phosphate exposure. These gorgonian species coped with short-term nutrient enrichment, furthering our understanding of the success of Caribbean gorgonians.

Murray, J., Prouty, N. G., Peek, S., & Paytan, A. (2019). Coral Skeleton δ15N as a Tracer of Historic Nutrient Loading to a Coral Reef in Maui, Hawaii. *Scientific Reports*, 9(1), 5579. https://doi.org/10.1038/s41598-019-42013-3

Excess nutrient loading to nearshore environments has been linked to declining water quality and ecosystem health. Macro-algal blooms, eutrophication, and reduction in coral cover have been observed in West Maui, Hawaii, and linked to nutrient inputs from coastal submarine groundwater seeps. Here, we present a forty-year record of nitrogen isotopes (δ 15N) of intra-crystalline coral skeletal organic matter in three coral cores collected at this site and evaluate the record in terms of changes in nitrogen sources. Our results show a dramatic increase in coral δ 15N values after 1995, corresponding with the implementation of biological nutrient removal at the nearby Lahaina Wastewater Reclamation Facility (LWRF). High δ 15N values are known to be strongly indicative of denitrification and sewage effluent, corroborating a previously suggested link between local wastewater injection and degradation of the reef environment. This record demonstrates the power of coral skeletal δ 15N as a tool for evaluating nutrient dynamics within coral reef environments.

Rey-Villiers, N., Sánchez, A., & González-Díaz, P. (2021). Stable nitrogen isotopes in octocorals as an indicator of water quality decline from the northwestern region of Cuba. *Environmental Science* and Pollution Research, 28(15), 18457-18470. <u>https://doi.org/10.1007/s11356-020-09956-x</u>

Eutrophication is one of the causes of the degradation of reefs worldwide. The aim of this research is to determine if sewage discharge reaches the fore reefs at northwest of Cuba using δ 15N in tissues of the octocorals Eunicea flexuosa and Plexaura kuekenthali and the concentration of microbiological and

physical-chemical variables. Thirteen reefs at 10-m depth were selected near river basins and far from the urban and industrial development of Havana City. Branch tips of both species were collected, the concentrations of nutrient and microorganisms in water samples were quantified, and horizontal visibility in the water (Vis) was determined. Overall, δ 15N of E. flexuosa ranged from 1.5 to 6.3‰ and P. kuekenthali from 1.7 to 6.7‰. The tissue of both species was significantly enriched in 15N in reefs near polluted watersheds compared with reefs far from pollution by anthropogenic activities. The δ 15N of both species showed a positive and significant correlation with the concentration of fecal and total coliform bacteria, heterotrophic bacteria, and NH4+ and a negative and significant correlation with the Vis. The δ 15N of the two species and microbiological and physical-chemical variables evidenced water quality decline by sewage discharge that reached reefs near polluted watersheds.

Silbiger, N. J., Nelson, C. E., Remple, K., Sevilla, J. K., Quinlan, Z. A., Putnam, H. M., . . . Donahue, M. J. (2018). Nutrient pollution disrupts key ecosystem functions on coral reefs. *Proceedings of the Royal Society B-Biological Sciences*, 285(1880). <u>https://doi.org/10.1098/rspb.2017.2718</u>

There is a long history of examining the impacts of nutrient pollution and pH on coral reefs. However, little is known about how these two stressors interact and influence coral reef ecosystem functioning. Using a six-week nutrient addition experiment, we measured the impact of elevated nitrate (NO(-)(3)) and phosphate (PO(3-)(4)) on net community calcification (NCC) and net community production (NCP) rates of individual taxa and combined reef communities. Our study had four major outcomes: (i) NCC rates declined in response to nutrient addition in all substrate types, (ii) the mixed community switched from net calcification to net dissolution under medium and high nutrient conditions, (iii) nutrients augmented pH variability through modified photosynthesis and respiration rates, and (iv) nutrients disrupted the relationship between NCC and aragonite saturation state documented in ambient conditions. These results indicate that the negative effect of NO(-)(3) and PO(3-)(4) addition on reef calcification is likely both a direct physiological response to nutrients and also an indirect response to a shifting pH environment from altered NCP rates. Here, we show that nutrient pollution could make reefs more vulnerable to global changes associated with ocean acidification and accelerate the predicted shift from net accretion to net erosion.

Section 8: Water clarity

Abaya, L. M., Wiegner, T. N., Beets, J. P., Colbert, S. L., Carlson, K. a. M., & Kramer, K. L. (2018). Spatial distribution of sewage pollution on a Hawaiian coral reef. *Marine Pollution Bulletin*, 130, 335-347. <u>https://doi.org/10.1016/j.marpolbul.2018.03.028</u>

While sewage pollution is contributing to the global decline of coral reefs, its offshore extent and direct reef impacts from water column mixing and benthic seeps are poorly documented. We addressed this knowledge gap on a Hawaiian coral reef using sewage indicator and benthic cover measurements, macroalgal bioassays, and a pollution scoring tool. Fecal indicator bacteria (FIB) and nutrient concentrations were spatially variable in surface and benthic waters, with shoreline values being highest. Shoreline macroalgae δ 15N and %N indicated high nitrogen loads containing sewage, while offshore surface and benthic values suggested lower nitrogen loads from environmental sources. Coral cover was negatively correlated with FIB, macroalgal δ 15N, and nutrient concentrations. Benthic salinity and temperature measurements detected daily tidal groundwater pulses which may explain these associations. While pollution scores revealed that sewage was largely concentrated along the shoreline, results showed some reached the reef and may be contributing to its declining condition.

Aguiar, D. K. (2020). *Detection and Impact of Sewage Pollution on South Kohala's Coral Reefs.* (Master of Science), University of Hawaii, Hilo, HI. Retrieved from <u>http://hdl.handle.net/10790/5297</u> Retrieved from <u>http://hdl.handle.net/10790/5297</u>

Sewage pollution is a land-based stressor impacting coral reefs worldwide. In the Hawaiian Islands, Onsite sewage disposal systems (OSDS) and wastewater injection wells have been associated with the pollution of inshore waters. Further offshore, OSDS and wastewater injection may be contributing to the chronic degradation of coral reefs in South Kohala, Hawai'i. Conducting benthic sampling and employing a multi-indicator approach, this study sought to determine the presence and impact of sewage on South Kohala's reefs. Our results suggest water motion and groundwater are diluting sewage found on South Kohala's reefs. South Kohala's reefs are dominated by turf algae, while sewage pollution may also be facilitating growth anomalies and algal overgrowth on South Kohala's reefs. With natural processes facilitating connectivity between land and sea, this study illustrates the need for improved sewage treatment and disposal near coastlines.

Tisthammer, K. H., Timmins-Schiffman, E., Seneca, F. O., Nunn, B. L., & Richmond, R. H. (2021). Physiological and molecular responses of lobe coral indicate nearshore adaptations to anthropogenic stressors. *Scientific Reports*, 11(1), 3423. <u>https://doi.org/10.1038/s41598-021-82569-7</u>

Corals in nearshore marine environments are increasingly exposed to reduced water quality, which is the primary local threat to Hawaiian coral reefs. It is unclear if corals surviving in such conditions have adapted to withstand sedimentation, pollutants, and other environmental stressors. Lobe coral populations from Maunalua Bay, Hawaii showed clear genetic differentiation between the 'polluted, high-stress' nearshore site and the 'less polluted, lower-stress' offshore site. To understand the driving force of the observed genetic partitioning, reciprocal transplant and common-garden experiments were conducted to assess phenotypic differences between these two populations. Physiological responses differed significantly between the populations, revealing more stress-resilient traits in the nearshore corals. Changes in protein profiles highlighted the inherent differences in the cellular metabolic processes and activities between the two; nearshore corals did not significantly alter their proteome between the sites, while offshore corals responded to nearshore transplantation with increased abundances of proteins associated with detoxification, antioxidant defense, and regulation of cellular metabolic processes. The response differences across multiple phenotypes between the populations suggest local adaptation of nearshore corals to reduced water quality. Our results provide insight into coral's adaptive potential and its underlying processes, and reveal potential protein biomarkers that could be used to predict resiliency.

Section 9: Contaminants

Abaya, L. M., Wiegner, T. N., Beets, J. P., Colbert, S. L., Carlson, K. a. M., & Kramer, K. L. (2018). Spatial distribution of sewage pollution on a Hawaiian coral reef. *Marine Pollution Bulletin*, 130, 335-347. <u>https://doi.org/10.1016/j.marpolbul.2018.03.028</u>

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Besson, M., Metian, M., Bustamante, P., & Hedouin, L. (2020). Metal(loid)s in superficial sediments from coral reefs of French Polynesia. *Marine Pollution Bulletin*, 155. <u>https://doi.org/10.1016/j.marpolbul.2020.111175</u>

French Polynesia exhibits a wide diversity of islands and coral-reef habitats, from urbanized high islands to remote atolls. Here, we present a geographically extensive baseline survey that examine the concentrations of nine metals (Ag, Cd, Co, Cu, Fe, Mn, Ni, Pb and Zn) and one metalloid (As) in superficial sediments from 28 sites spread over three islands of French Polynesia. We used Principal Component Analysis, Pearson's correlation, hierarchical cluster analysis and generalized linear mixed-effect models on Pollution Load Index to investigate site contamination and metal(loid) associations. At most sites, metal(loid) concentrations were below commonly applied sediment quality guidelines. However, a few

sites located near farming activities, river discharges and urbanized areas showed concentrations above these guidelines. This study provides critical baseline values for metal(loid) contaminants in this region and in coral-reef areas in general, and spur decreased discharge of metal (loid) contaminants in the anthropogenised areas of French Polynesia.

Celis-Hernandez, O., Rosales-Hoz, L., Cundy, A. B., Carranza-Edwards, A., Croudace, I. W., & Hernandez-Hernandez, H. (2018). Historical trace element accumulation in marine sediments from the Tamaulipas shelf, Gulf of Mexico: An assessment of natural vs anthropogenic inputs. *Science of The Total Environment*, 622-623, 325-336. <u>https://doi.org/10.1016/j.scitotenv.2017.11.228</u>

The Gulf of Mexico is considered one of the world's major marine ecosystems, supporting important fisheries and habitats such as barrier islands, mangrove forests, seagrass beds, coral reefs etc. It also hosts a range of complex offshore petroleum exploration, extraction, and refining industries, which may have chronic or acute impacts on ecosystem functioning. Previous work on the marine effects of this activity is geographically incomplete, and has tended to focus on direct hydrocarbon impacts, while impacts from other related contaminants (e.g. heavy metals, salt-rich drilling muds) which may be discharged from oil facilities have not been widely assessed. Here, we examine historical trace element accumulation in marine sediments collected from four sites in the Tamaulipas shelf, Gulf of Mexico, in the area of the Arenque oil field. Dated sediment cores were used to examine the sources, and historical and contemporary inputs, of trace metals (including those typically present in oil industry discharges) and their potential biological impact in the Tamaulipas aquatic environment over the last 100years. CaO (i.e. biogenic component) normalized data showed increasing V, Cr, Zn, Cu, Pb, Zr and Ba towards the sediment surface in three of the four cores, with Ba and V (based on an adverse effect index) possibly associated with adverse effects on organisms. Dated Ba/CaO profiles show an increase of 30-137% after opening of oil installations in the study area, and can be broadly correlated with increasing oil industry activities across the wider Gulf of Mexico. Data do not record however a clear enhancement of Ba concentration in sediment cores collected near to oil platforms over more distal cores, indicating that any Ba released from drilling platforms is incorporated quickly into the sediments around the drilling sites, and once this element has been deposited its rate of resuspension and mobility is low. Capsule abstract Sediment core data from the Tamaulipas shelf show the influence of oil industry activities on selected trace element concentrations, with Ba/CaO broadly correlating with increasing oil industry activities across the wider Gulf of Mexico.

Corinaldesi, C., Marcellini, F., Nepote, E., Damiani, E., & Danovaro, R. (2018). Impact of inorganic UV filters contained in sunscreen products on tropical stony corals (Acropora spp.). *Science of The Total Environment*, 637-638, 1279-1285. <u>https://doi.org/10.1016/j.scitotenv.2018.05.108</u>

Most coral reefs worldwide are threatened by natural and anthropogenic impacts. Among them, the release in seawater of sunscreen products commonly used by tourists to protect their skin against the harmful effects of UV radiations, can affect tropical corals causing extensive and rapid bleaching. The use of inorganic (mineral) filters, such as zinc and titanium dioxide (ZnO and TiO2) is increasing due to their broad UV protection spectrum and their limited penetration into the skin. In the present study, we evaluated through laboratory experiments, the impact on the corals Acropora spp. of uncoated ZnO nanoparticles and two modified forms of TiO2 (Eusolex(R)T2000 and Optisol), largely utilized in

commercial sunscreens together with organic filters. Our results demonstrate that uncoated ZnO induces a severe and fast coral bleaching due to the alteration of the symbiosis between coral and zooxanthellae. ZnO also directly affects symbiotic dinoflagellates and stimulates microbial enrichment in the seawater surrounding the corals. Conversely, Eusolex(R) T2000 and Optisol caused minimal alterations in the symbiotic interactions and did not cause bleaching, resulting more eco-compatible than ZnO. Due to the vulnerability of coral reefs to anthropogenic impacts and global change, our findings underline the need to accurately evaluate the effect of commercial filters on stony corals to minimize or avoid this additional source of impact to the life and resilience ability of coral reefs.

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). *Marine Biodiversity*, 50(3). <u>https://doi.org/10.1007/s12526-020-01057-9</u>

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 longterm 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 (similar to 9.3 10(6) L) of crude oil were released from a refinery in Bahia Las Minas (Caribbean Panama) contaminating an area of about 40 km(2) 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.

 He, T., Tsui, M. M. P., Tan, C. J., Ma, C. Y., Yiu, S. K. F., Wang, L. H., . . . Murphy, M. B. (2019). Toxicological effects of two organic ultraviolet filters and a related commercial sunscreen product in adult corals. *Environmental Pollution*, 245, 462-471. https://doi.org/10.1016/j.envpol.2018.11.029

Corals are exposed to organic ultraviolet (UV) filters and other personal care product (PCP) ingredients in the environment, but the toxicities of organic UV filters and their related PCP to corals are not well understood. In this study, 7-day exposures were conducted to evaluate the toxicities and

bioaccumulation of two organic UV filters, ethylhexylmethoxy-cinnamate (EHMC; octinoxate) and octocrylene (OC) (single- and combined-chemical tests), and diluted sunscreen wash-off water containing both active ingredients to the adult life stage of two hard coral species, Seriatopora caliendrum and Pocillopora damicornis. In the single-chemical tests, death (33.3%) and bleaching (83.3%) were only observed in the 1000mug/L EHMC treatment of S. caliendrum. In the sunscreen product exposures, 5% sunscreen water (containing 422.34+/-37.34mug/L of EHMC and 33.50+/-7.60mug/L of OC at Day 0) caused high mortality in S. caliendrum (66.7-83.3%) and P. damicornis (33.3-50%), and tissue concentrations were up to 10 times greater than in the single-chemical exposures; co-exposure to EHMC and OC at similar levels to those in the sunscreen product resulted in bioaccumulation similar to the single-chemical tests. These results confirm the bioaccumulation potential of EHMC and OC and show that other ingredients in sunscreen products may increase the bioavailability of active ingredients to corals and exacerbate the toxicity of sunscreen products. Future studies on the toxicities of PCPs to aquatic organisms should not only focus on the toxicities of active ingredients.

 He, T., Tsui, M. M. P., Tan, C. J., Ng, K. Y., Guo, F. W., Wang, L. H., . . . Murphy, M. B. (2019). Comparative toxicities of four benzophenone ultraviolet filters to two life stages of two coral species. *Science of The Total Environment*, 651(Pt 2), 2391-2399. https://doi.org/10.1016/j.scitotenv.2018.10.148

The benzophenone (BP) organic ultraviolet (UV) filters have been measured in seawater at ng/L to mug/L levels, but more data on their effects in non-target marine organisms are needed. Corals can be exposed to BPs due to wastewater discharges and coastal recreational activities. In this study, toxicities and bioaccumulation of BP-1 (2,4-dihydroxybenzophenone), BP-3 (oxybenzone), BP-4 (sulisobenzone) and BP-8 (dioxybenzone) to larvae and adults of two coral species, Pocillopora damicornis and Seriatopora caliendrum, were assessed at concentrations ranging from 0.1-1000mug/L. BP-1 and BP-8 exposure caused significant settlement failure, bleaching and mortality of S. caliendrum larvae [lowest observed effect concentration (LOEC): >/=10mug/L] compared to the other BPs, while none of the tested compounds and concentrations affected P. damicornis larvae. Nubbins were more sensitive to BP-3, BP-1 and BP-8 than larvae. Overall, BP-1 and BP-8 were more toxic to the two tested species than BP-3 and BP-4, which matches the relative bioaccumulation potential of the four BPs (BP-8>BP-1 approximately BP-3>BP-4). A conservative risk assessment using the effect concentrations derived from this study showed that BP-3, BP-1 and BP-8 pose high or medium risk to the health of corals in popular recreational areas of Taiwan and Hong Kong. Our study suggests that future ecotoxicological studies of corals should take their sensitivities, life stages and metabolic capacities into consideration.

Martins, C. C., Castellanos-Iglesias, S., Cabral, A. C., de Souza, A. C., Ferraz, M. A., & Alves, T. P. (2018). Hydrocarbon and sewage contamination near fringing reefs along the west coast of Havana, Cuba: A multiple sedimentary molecular marker approach. *Marine Pollution Bulletin*, 136, 38-49. https://doi.org/10.1016/j.marpolbul.2018.08.031

Organic contamination is a major environmental concern in coastal regions, and it can be evaluated by the determination of aliphatic hydrocarbons (AHs), polycyclic aromatic hydrocarbons (PAHs), faecal sterols and linear alkylbenzenes (LABs). The concentrations of these organic markers were obtained

from nine surface sediment samples to evaluate a possible contamination near a fringing reef on the west coast of Havana, Cuba. The AH levels ranged from 1.24 to 135.6 μ g g-1, the PAH levels were up to 2133 ng g-1, the faecal sterol levels ranged from 0.03 to 1.54 μ g g-1, and the total LAB levels were up to 22.7 ng g-1. The highest concentrations were obtained at sites close to Havana Bay and at the sources of untreated sewage input. A decreasing concentration gradient was observed from Havana Bay to the outer sites. Although only two sites presented high levels of contamination, untreated sewage discharged close to the fringing reef may affect its environment.

Mitchelmore, C. L., Burns, E. E., Conway, A., Heyes, A., & Davies, I. A. (2021). A Critical Review of Organic Ultraviolet Filter Exposure, Hazard, and Risk to Corals. *Environmental Toxicology and Chemistry*, 40(4), 967-988. <u>https://doi.org/10.1002/etc.4948</u>

There has been a rapid increase in public, political, and scientific interest regarding the impact of organic ultraviolet (UV) filters to coral reefs. Such filters are found in sunscreens and other consumer products and enter the aquatic environment via direct (i.e., recreational activities, effluents) or indirect (i.e., land runoff) pathways. This review summarizes the current state of the science regarding the concentration of organic UV filters in seawater and sediment near coral reef ecosystems and in coral tissues, toxicological data from early and adult life stages of coral species, and preliminary environmental risk characterizations. Up to 14 different organic UV filters in seawater near coral reefs have been reported across 12 studies, with the majority of concentrations in the nanograms per liter range. Nine papers report toxicological findings from no response to a variety of biological effects occurring in the micrograms per liter to milligrams per liter range, in part given the wide variations in experimental design and coral species and/or life stage used. This review presents key findings; scientific data gaps; flaws in assumptions, practice, and inference; and a number of recommendations for future studies to assess the environmental risk of organic UV filters to coral reef ecosystems.

Mitchelmore, C. L., He, K., Gonsior, M., Hain, E., Heyes, A., Clark, C., . . . Blaney, L. (2019). Occurrence and distribution of UV-filters and other anthropogenic contaminants in coastal surface water, sediment, and coral tissue from Hawaii. *Science of The Total Environment*, 670, 398-410. <u>https://doi.org/10.1016/j.scitotenv.2019.03.034</u>

The occurrence of UV-filters in the environment has raised concerns over potentially adverse impacts on corals. In this study, the concentrations of 13 UV-filters and 11 hormones were measured in surface seawater, sediment, and coral tissue from 19 sites in Oahu, Hawaii. At least eight UV-filters were detected in seawater, sediment, and coral tissue and total mass concentrations of all UV-filters were <750 ng L-1, <70 ng g-1 dry weight (dw), and <995 ng g-1 dw, respectively. Four UV-filters were detected in water, sediment, and coral tissue at detection frequencies of 63–100%, 56–91%, and 82–100%, respectively. These UV-filter concentrations generally varied as follows: water, homosalate (HMS) > octisalate (OS) > benzophenone-3 (BP-3, also known as oxybenzone) > octocrylene (OC); sediment, HMS > OS > OC > BP-3; coral, OS \approx HMS > OC \approx BP-3. BP-3 concentrations in surface seawater were <10 ng L-1 at 12 of 19 sites and highest at Waikiki beach (e.g., 10.9–136 ng L-1). While BP-3 levels were minimal in sediment (e.g., <1 ng g-1 dw at 18 of 19 sites), and ranged from 6.6 to 241 ng g-1 dw in coral tissue. No quantifiable levels of 2-ethylhexyl 4-methoxycinnamate (also known as octinoxate) were recorded in surface seawater or coral tissues, but 5–12.7 ng g-1 dw was measured for sediment at 5 of

19 sites. No hormones were detected in seawater or sediment, but 17α -ethinylestradiol was present in three corals from Kaneohe Bay. Surfactant degradation products were present in seawater, especially at Waikiki beach. These results demonstrate ubiquitous parts-per-trillion concentrations of UV-filters in surface seawater and is the first report of UV-filters in coral tissue from U.S.A. coastal waters. These data inform the range of environmentally-relevant concentrations for future risk assessments on the potential impacts of UV-filters on coral reefs in Oahu, Hawaii.

Nordborg, F. M., Jones, R. J., Oelgemöller, M., & Negri, A. P. (2020). The effects of ultraviolet radiation and climate on oil toxicity to coral reef organisms – A review. *Science of The Total Environment*, 720, 137486. <u>https://doi.org/10.1016/j.scitotenv.2020.137486</u>

Oil pollution remains a significant local threat to shallow tropical coral reef environments, but the environmental conditions typical of coral reefs are rarely considered in oil toxicity testing and risk assessments. Here we review the effects of three environmental co-factors on petroleum oil toxicity towards coral reef organisms, and show that the impacts of oil pollution on coral reef taxa can be exacerbated by environmental conditions commonly encountered in tropical reef environments. Shallow reefs are routinely exposed to high levels of ultraviolet radiation (UVR), which can substantially increase the toxicity of some oil components through phototoxicity. Exposure to UVR represents the most likely and harmful environmental co-factor reviewed here, leading to an average toxicity increase of 7.2-fold across all tests reviewed. The clear relevance of UVR co-exposure and its strong influence on tropical reef oil toxicity highlights the need to account for UVR as a standard practice in future oil toxicity studies. Indeed, quantifying the influence of UVR on toxic thresholds of oil to coral reef species is essential to develop credible oil spill risk models required for oil extraction developments, shipping management and spill responses in the tropics. The few studies available indicate that co-exposure to elevated temperature and low pH, both within the range of current daily and seasonal fluctuations and/or projected under continued climate change, can increase oil toxicity on average by 3.0- and 1.3fold, respectively. While all three of the reviewed environmental co-factors have the potential to substantially increase the impacts of oil pollution in shallow reef environments, their simultaneous effects have not been investigated. Assessments of the combined effects of oil pollution, UVR, temperature and low pH will become increasingly important to identify realistic hazard thresholds suitable for future risk assessments over the coming century.

Nunes, B. Z., Zanardi-Lamardo, E., Choueri, R. B., & Castro, Í. B. (2021). Marine protected areas in Latin America and Caribbean threatened by polycyclic aromatic hydrocarbons. *Environmental Pollution*, 269, 116194. <u>https://doi.org/10.1016/j.envpol.2020.116194</u>

The present study is a literature-based analysis investigating occurrence and the possible consequences of polycyclic aromatic hydrocarbons (PAH) in marine protected areas (MPAs) of Latin America and Caribbean. The approach using overlapping of georeferenced MPA polygons with data compiled from peer-reviewed literature, published during the last 15 years, showed 341 records of PAH in 9 countries. PAH was reported to occur within the boundaries of 36 MPAs located in Argentina, Brazil, Colombia, Mexico, Nicaragua and Uruguay. According to quality guidelines, low to moderate impacts are expected in MPAs categorized in different management classes. Considering sediment samples, 13% of the records presented concentrations enough to cause occasional toxicity. Such level of risk was also seen in

Ramsar sites and in Amazonian MPAs. In addition, based on concentrations reported in biota, occasional deleterious effects on organisms from Biosphere Reserves might occur. Diagnostic ratios pointed out petrogenic and pyrolytic processes as PAH predominant sources, and were mainly attributed to the proximity to ports, industries and urban areas. MPAs located in the vicinity of impact-generating areas may be under threat and require government attention and action, mainly through implementation of contamination monitoring programs.

Sweet, M., Stelfox, M., & Lamb, J. (2019). *Plastics and shallow water coral reefs: Synthesis of the science for policy-makers*. United Nations Environment Programme Retrieved from http://hdl.handle.net/20.500.11822/27646

The overall purpose of this brief is to provide policy and management recommendations for addressing and reducing the impacts of plastics on shallow water coral reefs, based on current scienti c knowledge. In doing so, the brief will contribute to achieving the related global, national and regional goals and targets, including the Sustainable Development Goals (SDGs). The brief promotes integrated planning and management, awareness-raising, and other efforts to improve and standardise the monitoring of plastics on reefs. It is primarily aimed at national and state policy-makers. The supporting scienti c evidence provides rationale for recommendations and more detailed information for government of cials with technical roles, as well as regional environmental organisations and conservation organizations.

Wood, E. (2019). *Impacts of sunscreens on coral reefs*. International Coral Reef Initiative Retrieved from https://www.icriforum.org/wp-content/uploads/2019/12/ICRI_Sunscreen.pdf

There is intense concern about the future health and ecological integrity of coral reefs in the face of global climate change. This is considered to be one of the greatest threats to reefs worldwide and is causing coral bleaching and ecosystem change at unprecedented levels. Coral reefs are also under considerable stress from overfishing, destructive fishing, coastal development and pollution. There is universal agreement that coral reefs face an unpredictable future and that action needs to be taken at all levels if their integrity and values are to be maintained.

In recent years, a number of studies have shown that sunscreens and other cosmetic products contain chemical substances that are adding to the pollution burden faced by coral reefs. Exposure to ultraviolet (UV) solar radiation poses a threat to public health, including the risk of sunburn, photo-aging and skin cancer (Pathak, 1987), and growing concern about these harmful effects has led to an increase in use of sunscreens. The world's coastal population and coastal tourism are expected to grow during this century and it is anticipated that the use of sunscreens and cosmetics containing UV-filters will rise further. Given the status of reefs, it is essential that the impact of sunscreens on corals is assessed and addressed. Xiang, N., Jiang, C., Huang, W., Nordhaus, I., Zhou, H., Drews, M., & Diao, X. (2019). The impact of acute benzo(a)pyrene on antioxidant enzyme and stress-related genes in tropical stony corals (Acropora spp.). *Science of The Total Environment*, 694, 133474. https://doi.org/10.1016/j.scitotenv.2019.07.280

Coral reefs have extremely high ecological value in tropical and subtropical waters worldwide. However, they have been subjected to the most extensive and prolonged damage in recent decades. Polycyclic aromatic hydrocarbons (PAHs) are ubiquitous hazardous pollutants and are highly resistant to degradation in marine environments. Among these compounds, benzo(a)pyrene (BaP) has exerted pressure on corals due to water discharges, oil spills and coastal tourism. In the present study, the physiological response, oxidative stress and stress-related genetic expressions of two Acropora spp. (Acropora formosa and Acropora nasuta) were analysed. These two coral species were exposed to 10 and 40 μ g·L-1 BaP for 24 hand 72 h, respectively. The results show that (1) BaP affects the health of the zooxanthellae in coral symbiosis after BaP exposure for 72 h due to a significant decline in chlorophyll a concentrations in Acropora spp. during this period. (2) An exposure of 10 μ g·L-1 BaP for 24 h induced serious oxidative damage to Acropora spp., with a significant decline and increase in superoxide dismutase (SOD) activities in A. formosa and A. nasuta. (3) The P-gp gene is more sensitive in A. formosa, while the Hsp70 gene is more sensitive in A. nasuta. (4) A. formosa showed a lower ability to resist organic pollutants in coral reefs. Overall, further ecotoxicological studies are needed to investigate the impact of chemical pollutants on corals and to compare their different response mechanisms.

Section 10: Symbiotic Species

 Abesamis, R. A., Langlois, T., Birt, M., Thillainath, E., Bucol, A. A., Arceo, H. O., & Russ, G. R. (2018). Benthic habitat and fish assemblage structure from shallow to mesophotic depths in a stormimpacted marine protected area. *Coral Reefs*, 37(1), 81-97. <u>https://doi.org/10.1007/s00338-017-1635-0</u>

Baseline ecological studies of mesophotic coral ecosystems are lacking in the equatorial Indo-West Pacific region where coral reefs are highly threatened by anthropogenic and climate-induced disturbances. Here, we used baited remote underwater video to describe benthic habitat and fish assemblage structure from 10 to 80 m depth at Apo Island, a well-managed marine protected area in the Philippines. We conducted surveys 2 yr after two storms (in 2011 and 2012) caused severe damage to shallow coral communities within the no-take marine reserve (NTMR) of Apo Island, which led to declines in fish populations that had built up over three decades. We found that hard coral cover was restricted to < 40 m deep in the storm-impacted NTMR and a nearby fished area not impacted by storms. Benthic cover at mesophotic depths (> 30 m) was dominated by sand/rubble and rock (dead coral) with low cover of soft corals, sponges and macroalgae. Storm damage appeared to have reached the deepest limit of the fringing reef (40 m) and reduced variability in benthic structure within the NTMR. Species richness and/or abundance of most trophic groups of fish declined with increasing depth regardless of storm damage. There were differences in taxonomic and trophic structure and degree of targeting by fisheries between shallow and mesophotic fish assemblages. Threatened shark species and a fish species previously unreported in the Philippines were recorded at mesophotic depths. Our findings provide a first glimpse of the benthic and fish assemblage structure of Philippine coral reef ecosystems across a wide depth gradient. This work also underscores how a combination of limited coral reef development at mesophotic depths close to shallow reefs and severe habitat loss caused by storms would result in minimal depth refuge for reef fish populations.

Álvarez-Hernández, S., Lozano-Ramírez, C., & Rodríguez-Palacio, M. C. (2019). Influence of the Habitat on Marine Macroalgae Toxicity. *Annual Research & Review in Biology*, 1-9. <u>https://doi.org/10.9734/arrb/2019/v33i130113</u>

Macroalgae synthesize molecules that may be toxic to other organisms. These molecules are synthesized as a defense strategy against herbivores. It has been proven that the synthesis process is directed by several physiological, chemical and even spatial-temporal variables. The purpose of this study was to determine whether the complexity of the habitat influences on the expression of marine macroalgae toxicity. Algae of 31 species (39 samples) were collected in localities with different habitat morphology: a coral reef in the Mexican Caribbean, three myxohaline localities in the Yucatán peninsula and six rocky intertidal localities, four of these in the Mexican Pacific and two in the Gulf of Mexico. Results identified 19 strongly toxic species from the reef, followed by algae collected in the rocky intertidal area, and the least number of toxic species in the myxohaline environments. The results support the hypothesis established by several researchers worldwide regarding the complexity of coral reefs, which promotes the synthesis of toxic substances as a defense against herbivores. These substances have been employed as molecules that are useful in the fight against diseases or as synthesis matrices of other compounds with pharmacological potential.

Polinski, J. M., & Voss, J. D. (2018). Evidence of photoacclimatization at mesophotic depths in the coral-Symbiodinium symbiosis at Flower Garden Banks National Marine Sanctuary and McGrail Bank. *Coral Reefs*, 37(3), 779-789. <u>https://doi.org/10.1007/s00338-018-1701-2</u>

Similar to shallower conspecifics, mesophotic scleractinian corals found at ~ 30–150 m depths maintain important symbioses with photosynthetic microalgae in the genus Symbiodinium. Despite the importance of coral-algal symbioses in corals' ability to thrive in multiple dynamic environments and potential role in connectivity, few studies have focused on mesophotic Symbiodinium assemblages. This study examines these assemblages in Montastraea cavernosa found at shallow (20–25 m) and mesophotic (45–50 m) depths at Flower Garden Banks National Marine Sanctuary and McGrail Bank, in the northwest Gulf of Mexico. Mesophotic corals contained significantly more Symbiodinium cells, more chlorophyll a per Symbiodinium cell, and more chlorophyll a and c2 per unit area coral tissue than shallow corals. However, both mesophotic and shallow M. cavernosa contained similar chlorophyll c2 per Symbiodinium cell. Next-generation sequencing of the internal transcribed spacer region (ITS2) of the ribosomal DNA indicated similar Symbiodinium assemblage diversity at all banks and between depths. All assemblages were dominated by sequences most closely related to S. goreaui, type C1, with three additional low-abundance sequences, identified as 2 C types and 1 A type, also consistently observed among colonies. Both the dominant C1 sequence and the background sequences persisted over two sampling years. These results suggest that algal symbiont assemblages will not limit connectivity potential in M. cavernosa in the northwest Gulf of Mexico. Furthermore, we hypothesize that increased Symbiodinium abundance may represent an effective light-harvesting strategy on lightlimited mesophotic coral reefs.

Williams, I., Kindinger, T. L., Couch, C., Walsh, W., Minton, D., & Oliver, T. A. A. (2019). Can Herbivore Management Increase the Persistence of Indo-Pacific Coral Reefs? *Frontiers in Marine Science*, 6. <u>https://doi.org/10.3389/fmars.2019.00557</u>

Due to climate change, coral reefs have experienced mass bleaching, and mortality events in recent years. Although coral reefs are unlikely to persist in their current form unless climate change can be addressed, local management can have a role to play by extending the time frame over which there are functional reef systems capable of recovery. Here we consider the potential application of one form of local management – management of herbivorous fishes. The premise behind this approach is that increased herbivory could shift reef algal assemblages to states that are benign or beneficial for corals, thereby increasing corals' ability to recover from destructive events such as bleaching and to thrive in periods between events. With a focus on Indo-Pacific coral reefs, we review what is known about the underlying processes of herbivory and coral-algal competition that ultimately affect the ability of corals to grow, persist, and replenish themselves. We then critically assess evidence of effectiveness or otherwise of herbivore management within marine protected areas (MPAs) to better understand why many MPAs have not improved outcomes for corals, and more importantly to identify the circumstances in which that form of management would be most likely to be effective. Herbivore management is not a panacea, but has the potential to enhance coral reef persistence in the right circumstances. Those include that: (i) absent management, there is an "algal problem" – i.e., insufficient herbivory to maintain algae in states that are benign or beneficial for corals; and (ii) management actions are able to increase net herbivory. As increased corallivory is a potentially widespread negative consequence of management, we consider some of the circumstances in which that is most likely to be a problem as

well as potential solutions. Because the negative effects of certain algae are greatest for coral settlement and early survivorship, it may be that maintaining sufficient herbivory is particularly important in promoting recovery from destructive events such as mass bleaching. Thus, herbivore management can have a role to play as part of a wider strategy to manage and reduce the threats that currently imperil coral reefs.

Section 11: Disease

Caldwell, J. M., Aeby, G., Heron, S. F., & Donahue, M. J. (2020). Case-control design identifies ecological drivers of endemic coral diseases. *Scientific Reports*, 10(1), 2831. https://doi.org/10.1038/s41598-020-59688-8

Endemic disease transmission is an important ecological process that is challenging to study because of low occurrence rates. Here, we investigate the ecological drivers of two coral diseases–growth anomalies and tissue loss–affecting five coral species. We first show that a statistical framework called the case-control study design, commonly used in epidemiology but rarely applied to ecology, provided high predictive accuracy (67–82%) and disease detection rates (60–83%) compared with a traditional statistical approach that yielded high accuracy (98–100%) but low disease detection rates (0–17%). Using this framework, we found evidence that 1) larger corals have higher disease risk; 2) shallow reefs with low herbivorous fish abundance, limited water motion, and located adjacent to watersheds with high fertilizer and pesticide runoff promote low levels of growth anomalies, a chronic coral disease; and 3) wave exposure, stream exposure, depth, and low thermal stress are associated with tissue loss disease risk during interepidemic periods. Variation in risk factors across host-disease pairs suggests that either different pathogens cause the same gross lesions in different species or that the same disease may arise in different species under different ecological conditions.

Durán-Riveroll, L. M., Cembella, A., & Okolodkov, Y. (2019). A Review on the Biodiversity and Biogeography of Toxigenic Benthic Marine Dinoflagellates of the Coasts of Latin America. *Frontiers in Marine Science*, 6. <u>https://doi.org/10.3389/fmars.2019.00148</u>

Many benthic dinoflagellates are known or suspected producers of lipophilic polyether phycotoxins, particularly in tropical and subtropical coastal zones. These toxins are responsible for diverse intoxication events of marine fauna and human consumers of seafood, but most notably in humans, they cause toxin syndromes known as diarrhetic shellfish poisoning (DSP) and ciguatera fish poisoning (CFP). This has led to enhanced, but still insufficient, efforts to describe benthic dinoflagellate taxa using morphological and molecular approaches. For example, recently published information on epibenthic dinoflagellates from Mexican coastal waters includes about 45 species from 15 genera, but many have only been tentatively identified to the species level, with fewer still confirmed by molecular criteria. This review on the biodiversity and biogeography of known or putatively toxigenic benthic species in Latin America, restricts the geographical scope to the neritic zones of the North and South American continents, including adjacent islands and coral reefs. The focus is on species from subtropical and tropical waters, primarily within the genera Prorocentrum, Gambierdiscus/Fukuyoa, Coolia, Ostreopsis and Amphidinium. The state of knowledge on reported taxa in these waters is inadequate and timeseries data are generally lacking for the prediction of regime shift and global change effects. Details of their respective toxigenicity and toxin composition have only recently been explored in a few locations. Nevertheless, by describing the specific ecosystem habitats for toxigenic benthic dinoflagellates, and by comparing those among the three key regions - the Gulf of Mexico, Caribbean Sea and the subtropical and tropical Pacific coast, insights for further risk assessment of the global spreading of toxic benthic species is generated for the management of their effects in Latin America.

Estrada-Saldívar, N., Quiroga-García, B. A., Pérez-Cervantes, E., Rivera-Garibay, O. O., & Alvarez-Filip, L. (2021). Effects of the Stony Coral Tissue Loss Disease Outbreak on Coral Communities and the Benthic Composition of Cozumel Reefs. *Frontiers in Marine Science*. https://doi.org/10.3389/fmars.2021.632777

In the Caribbean, disease outbreaks have emerged as significant drivers of coral mortality. Stony Coral Tissue Loss Disease (SCTLD) is a novel white plague-type disease that was first reported off the Florida coast in 2014. This disease affects > 20 coral species and is spreading rapidly throughout the Caribbean. In December 2018, SCTLD reached southwestern (SW) Cozumel, one of the healthiest reef systems in the Caribbean. In this study, we integrate data from multiple survey protocols conducted between July 2018 and April 2020 to track the progression of the outbreak in SW Cozumel and to quantify the impacts of SCTLD on coral communities and the benthic composition of reefs. Given that the SCTLD outbreak coincided with a period of prolonged thermal stress that concluded in widespread coral bleaching in autumn 2019, we also investigated whether this event further exacerbated coral mortality. Our findings show that SCTLD spread throughout SW Cozumel in only two months and reached a peak after only five months. By the summer of 2019, most of the afflicted corals were already dead. Species of the families Meandrinidae, Faviinae, and Montastraeidae showed 33–95% mortality. The widespread coral die-off caused an overall loss of 46% in coral cover followed by a rapid increase of algae cover across all surveyed reefs that persisted until at least April 2020. In November 2019, more than 15% of surveyed coral colonies were bleached. However, we did not find that bleaching further increased coral mortality at either the colony or the community level, which suggests that the coral communities were able to recover from this event despite still being affected by the disease. In conclusion, SCTLD is radically changing the ecology of coral reefs by decimating the populations of several key reef-builders and reconfiguring the benthic assemblages. The actions needed to restore coral populations have to be accompanied by stringent controls related to the effects of climate change, coastal development, and wastewater treatment to improve coral conditions and ecosystem resilience.

Howells, E. J., Vaughan, G. O., Work, T. M., Burt, J. A., & Abrego, D. (2020). Annual outbreaks of coral disease coincide with extreme seasonal warming. *Coral Reefs*, 39(3), 771-781. <u>https://doi.org/10.1007/s00338-020-01946-2</u>

Reef-building corals living in extreme environments can provide insight into the negative effects of future climate scenarios. In hot environments, coral communities experience disproportionate thermal stress as they live very near or at their upper thermal limits. This results in a high frequency of bleaching episodes, but it is unknown whether temperature-driven outbreaks of coral disease follow a similar trajectory. Here we tracked outbreaks of a white-syndrome (WS) disease over three years in the hottest region inhabited by reef-building corals, the southern Persian Gulf. From 2014 to 2016, WS affected 10 of the 16 scleractinian genera recorded at inshore and offshore sites. Intra- and inter-specific transmission of lesions was frequently observed, indicative of a single contagious disease infecting multiple coral taxa. Colonies of Acropora were the most susceptible to WS disease and were more than twice as likely to experience lesions than any other genera. Prevalence reached 42% of Acropora colonies and lesions progressed at an average rate of 1 mm day–1. Platygyra colonies were the second most susceptible to WS disease, where prevalence reached 33% and lesions progressed at 0.3 mm day–1. Affected colonies of both of these genera suffered considerable partial mortality that was not recovered between years, promoting the fragmentation of larger colonies into smaller size classes. Across the 3 years of our study, the onset of WS outbreaks occurred early in summer and prevalence

increased exponentially with cumulative heat exposure (coral community r2 = 0.55, Acropora r2 = 0.72, Platygyra r2 = 0.75). Peak levels of community-wide prevalence occurred in August (10% of all coral colonies) to September (14%) when preceding 4-week and 8-week average temperatures exceeded 34.5 °C and 34 °C, respectively. Outbreaks ceased following the return of cooler temperatures with prevalence remaining below 0.5% between December and June. Levels of bleaching remained relatively low (< 5% prevalence), despite exposure to daily temperatures ≥ 35 °C each summer. These findings demonstrate that thermal stress on coral reefs does not always manifest as coral bleaching and diseases can present as a primary sign of thermal stress. Consequently, temperature-driven outbreaks of coral disease are expected to become more widespread as climate warming pushes corals to be living increasingly closer to their upper thermal limits.

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. <u>https://doi.org/10.1371/journal.pone.0199462</u>

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 spacelimited 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.

Noonan, K. R., & Childress, M. J. (2020). Association of butterflyfishes and stony coral tissue loss disease in the Florida Keys. *Coral Reefs*, 39(6), 1581-1590. <u>https://doi.org/10.1007/s00338-020-01986-8</u>

Since 2014, stony coral tissue loss disease (SCTLD) has rapidly spread throughout the Florida reef tract infecting and killing dozens of coral species. Previous studies have found that corallivorous fishes, such as butterflyfishes, are positively correlated with coral disease prevalence at both local and regional scales. This study investigates the association of SCTLD infection and butterflyfish abundance and behaviors on ten reefs in the middle Florida Keys. Divers conducted video surveys of reef fish abundance and disease prevalence in June 2017, 2018, and 2019; before, during, and after the outbreak of SCTLD infections. SCTLD prevalence increased from 3.2% in 2017 to 36.9% in 2018 and back to 2.7% in 2019. Butterflyfish abundances also showed a similar pattern with a twofold increase in abundance in 2018

over abundances in 2017 and 2019. To better understand the association of individual species of butterflyfishes and diseased corals, 60 coral colonies (20 healthy, 20 diseased, 20 recently dead) were tagged and monitored for butterflyfish activity using both diver-based AGGRA fish counts and 1-h time-lapse videophotography collected in the summers of 2018 and 2019. All reef fishes were more abundant on corals with larger surface areas of live tissue, but only the foureye butterflyfish preferred corals with larger surface areas of diseased tissues. Estimates of association indicate that foureye butterflyfish were found significantly more on diseased corals than either healthy or recently dead corals when compared with the other species of butterflyfishes. Foureye butterflyfish were observed to feed directly on the SCTLD line of infection, while other butterflyfish were not. Furthermore, association of foureye butterflyfish with particular diseased corals decreased from 2018 to 2019 as the SCTLD infections disappeared. Our findings suggest that foureye butterflyfish recruit to and feed on SCTLD-infected corals which may influence the progression and/or transmission of this insidious coral disease.

Shore-Maggio, A., Aeby, G. S., & Callahan, S. M. (2018). Influence of salinity and sedimentation on Vibrio infection of the Hawaiian coral Montipora capitata. *Diseases of Aquatic Organisms*, 128(1), 63-71. <u>https://doi.org/10.3354/dao03213</u>

Environmental cofactors alter host-pathogen interactions and influence disease dynamics by impairing host resistance and/or increasing pathogen virulence. Terrestrial runoff is recognized as a major threat to coral reef health. However, the direct links between runoff and coral disease are not clear. Montipora white syndrome (MWS) is a coral disease that occurs in the Hawaiian archipelago, can be caused by various bacterial pathogens, including Vibrio species, and is linked to conditions associated with heavy rainfall and runoff. The objective of this study was to determine whether a short-term hyposalinity stress (20 ppt for 24 h) or sedimentation stress (1000 g m-2 d-1) would influence bacterial infection of the coral Montipora capitata. Hyposalinity increased M. capitata susceptibility to infection by 2 MWS pathogens, Vibrio coralliilyticus strain OCN008 and Vibrio owensii strain OCN002. Specifically, hyposalinity allowed OCN008 to infect at lower doses (106 CFU ml-1 compared with 108 CFU ml-1) and reduced the amount of time before onset of OCN002 infection at high doses (108 CFU ml-1). In contrast, short-term sedimentation stress did not affect M. capitata infection by either of these 2 pathogens. Although several studies have found a correlation between runoff and increased coral disease prevalence in field studies, this is the first study to show that one aspect of runoff (reduced salinity) enhances bacterial infection of coral using manipulative experiments.

Weil, E. (2019). Disease Problems. In *Mesophotic Coral Ecosystems.* Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.), (Vol. 12, pp. 779-800) <u>https://doi.org/10.1007/978-3-319-92735-0_41</u>

Worldwide ecological deterioration of coral reefs is mostly caused by disease-induced mass mortalities linked to thermal anomalies, and aided by local anthropogenic stressors. Mesophotic coral ecosystems (MCEs; 30-150 m) are found deeper where temperatures are cooler, in low light, and mostly offshore. These characteristics are proposed to protect MCEs ("deep reef refugia" hypothesis) from shallow-water threats (e.g., thermal stress and pollution). The most commonly reported mesophotic health problem is thermal-induced bleaching, which is now more widespread due to global climate change (GCC). The oldest deep bleaching report (90 m) is from 1989, in the Caribbean, but recent reports indicate bleached corals below 120 m in Grand Cayman. Cold-water intrusions and turbidity can also cause mesophotic

coral bleaching. Not much is known about biotic diseases and potential drivers in MCEs. "White syndromes" (WS) seem to be the most common in Puerto Rico and the US Virgin Islands. Overall, 9 of the 28 common MCE scleractinian species have been observed with disease signs similar to shallow WS and white plague disease. A new disease termed "intercostal mortality syndrome" affected 19% of the colonies of Orbicella, Siderastrea, and Agaricia spp. in Hind Bank. MCE surveys showed coral community disease prevalence in Puerto Rico varied between 0% and 15%, with a mean of 6%. This chapter presents a summary of what is known about disease threats to MCEs and the disruptive potential of GCC-induced changes in seawater thermal dynamics on species susceptibility, and how this could affect the protection these deeper environments may provide.

Section 12: Ocean Deoxygenation

Hebbeln, D., Wienberg, C., Dullo, W.-C., Freiwald, A., Mienis, F., Orejas, C., & Titschack, J. (2020). Coldwater coral reefs thriving under hypoxia. *Coral Reefs*, 39(4), 853-859. <u>https://doi.org/10.1007/s00338-020-01934-6</u>

Reefs formed by scleractinian cold-water corals represent unique biodiversity hot spots in the deep sea, preferring aphotic water depths of 200–1000 m. The distribution of the most prominent reef-building species Lophelia pertusa is controlled by various environmental factors including dissolved oxygen concentrations and temperature. Consequently, the expected ocean deoxygenation and warming triggered by human-induced global change are considered as a serious threat to cold-water coral reefs. Here, we present results on recently discovered reefs in the SE Atlantic, where L. pertusa thrives in hypoxic and rather warm waters. This sheds new light on its capability to adapt to extreme conditions, which is facilitated by high surface ocean productivity, resulting in extensive food supply. Putting our data in an Atlantic-wide perspective clearly demonstrates L. pertusa's ability to develop population-specific adaptations, which are up to now hardly considered in assessing its present and future distributions.

Hughes, D. J., Alderdice, R., Cooney, C., Kühl, M., Pernice, M., Voolstra, C. R., & Suggett, D. J. (2020).
Coral reef survival under accelerating ocean deoxygenation. *Nature Climate Change*, 10(4), 296-307. https://doi.org/10.1038/s41558-020-0737-9

Global warming and local eutrophication simultaneously lower oxygen (O2) saturation and increase biological O2 demands to cause deoxygenation. Tropical shallow waters, and their coral reefs, are particularly vulnerable to extreme low O2 (hypoxia) events. These events can drive mass mortality of reef biota; however, they currently remain unaccounted for when considering coral reef persistence under local environmental alterations and global climatic change. In this Perspective, we integrate existing biological, ecological and geochemical evidence to consider how O2 availability and hypoxia affect reef biota, with particular focus on the ecosystem architects, reef-building corals, that operate as both O2 consumers and producers. We pinpoint fundamental knowledge gaps and highlight the need to understand sub-lethal hypoxia effects that are likely already in play.

Kealoha, A. K., Doyle, S. M., Shamberger, K. E. F., Sylvan, J. B., Hetland, R. D., & DiMarco, S. F. (2020).
Localized hypoxia may have caused coral reef mortality at the Flower Garden Banks. *Coral Reefs*, 39(1), 119-132. <u>https://doi.org/10.1007/s00338-019-01883-9</u>

On July 25, 2016, turbid water and dead corals, sponges and other invertebrates were discovered at the East Bank (EB) of the Flower Garden Banks (FGB) National Marine Sanctuary. Mortality was spread over 0.06 km2, with up to 80% coral mortality reported in some areas. Within days, response efforts were underway to investigate the potential mechanisms leading to the mortality event. Hydrographic surveys, moored buoy data, and a regional hydrodynamic model were used to characterize water chemistry, hydrography, and microbial communities within the FGB. Low salinity (~ 31–33), total alkalinity (~ 2284–2330 μ mol kg–1), and dissolved inorganic carbon (DIC, ~ 1968–2011 μ mol kg–1) were detected in surface waters over the EB and eastern stations, revealing the presence of river-derived water. The

Mississippi/Atchafalaya rivers were the primary sources of freshwater during the event, although Texas rivers, all of which had unusually high discharge during 2016, contributed approximately one-fifth to the total freshwater mass. At 75 m depth, high density, salinity, DIC, ammonium, and abundance of microbial taxa associated with deep waters were coincident with low temperature and aragonite saturation state at the northern and eastern stations, indicating a deeper source water at these stations. Cross-slope density gradients were also consistent with an upwelling circulation pattern. Using these observations and data, we hypothesize that the mortality event was most likely caused by the combination of two processes. The turbid freshwater layer inhibited photosynthesis, leading to net respiration of coral reef organic matter. Additionally, deep, dense waters upwelled onto the bank and formed a stratified bottom layer, which prevented re-oxygenation from the overlying water column and led to localized areas of hypoxia within pockets on the reef. Hypoxia likely formed rapidly, within two days. Moving forward, high-frequency temporal measurements of oxygen and carbonate chemistry are critical for monitoring risks (e.g., hypoxia and acidification) associated with freshwater discharge and upwelling, since these processes may adversely affect coral reef health.

Nelson, H. R., & Altieri, A. H. (2019). Oxygen: the universal currency on coral reefs. *Coral Reefs*, 38(2), 177-198. <u>https://doi.org/10.1007/s00338-019-01765-0</u>

Coral reefs are suffering unprecedented declines worldwide. Most studies focus on stressors such as rising temperatures, nutrient pollution, overfishing, and ocean acidification as drivers of this degradation. However, recent mass mortality events associated with low oxygen on coral reefs indicate that oxygen is a critical factor that can be limiting in reef environments. Here, we present evidence that integrates across disciplines and perspectives to reveal how natural and anthropogenic factors drive variation in oxygen at multiple scales on coral reefs. This variation, in turn, limits essential processes such as productivity, respiration, and calcification on reefs and often plays a role in the outcome of interactions between corals and their competitors, pathogens, and mutualists. Moreover, the apparent effects of temperature, eutrophication, acidification, and other stressors on corals are commonly mediated by oxygen. As a consequence, the imprint of oxygen variation is evident in many patterns including reef biodiversity, coral bleaching, colony morphology, and fish behavior. We suggest that the structure and dynamics of coral reefs can be fully understood only by considering the ubiquitous role of oxygen, and we identify critical areas of future oxygen research to guide the study and management of coral reefs in a changing world.

Section 13: General Habitat Information

Birkeland, C. (2019). Chapter 2 - Global Status of Coral Reefs: In Combination, Disturbances and Stressors Become Ratchets. In World Seas: an Environmental Evaluation (Second Edition). C. Sheppard (Ed.), (pp. 35-56): Academic Press <u>https://doi.org/10.1016/B978-0-12-805052-1.00002-4</u>

Although there are still many local coral-reef communities that display remarkably rapid recovery, numerous surveys have indicated that the average living coral cover is decreasing circumtropically. This is partly because disturbance is nearly always faster than recovery, damaged or stressed corals tend to produce fewer larvae, reef community recovery times become longer when fast-growing branching corals are more vulnerable to stresses and disturbances and are replaced by more tolerant slow-growing corals, disturbances become more frequent and do not allow sufficient time for recovery, combinations of local and global disturbances and stresses result in positive feedbacks that accelerate reef degradation, and degraded reefs decrease the proportion of habitat acceptable to recruiting larvae. In the recent past, many reefs had time to largely recover before the next disturbance; otherwise, the reefs at the sites would not have developed as well as they had. As more reefs are disturbed and become less favorable for survival of recruits, connectivity is reduced by fewer larvae produced, more areas become unattractive to larvae for settlement, distances between fewer favorable sites become longer, and larval pelagic duration sometimes becomes shorter with increasing temperature. The processes listed above determine that prevention is more efficient and effective than repair. Marine reserves and fixing local problems are important to continue, but they are not buying time. The time has arrived and we have to act directly on the reduction of CO2 emissions.

Carlson, R. R., Foo, S. A., & Asner, G. P. (2019). Land Use Impacts on Coral Reef Health: A Ridge-to-Reef Perspective. *Frontiers in Marine Science*, 6. <u>https://doi.org/10.3389/fmars.2019.00562</u>

Over 60% of the world's reefs experience damage from local activities such as overfishing, coastal development, and watershed pollution. Land-based sources of pollution are a critical threat to coral reefs, and understanding "ridge-to-reef" changes is urgently needed to improve management and coral survival in the Anthropocene. We review existing literature on spatial-ecological connections between land use and coral health, specifically examining vegetative, agricultural, urban, and other land-use types. In general, forested land use is positively related to metrics of coral condition, while anthropogenic land uses like urban development and agriculture drive a decline in coral cover, diversity, colony size, and structural complexity. However, land-use and land-cover impacts vary across time and space, and small portions of the landscape (e.g., discrete segments of unpaved roads, grazed and scalded hillsides) may have an outsized effect on reef pollution, presenting opportunities for targeted conservation. Some coral species show resilience under land-use and land-cover change, and the impact of land use on coral recovery from bleaching remains an active area of research. Finally, a spatial bibliography of existing literature reveals that most ridge-to-reef studies focus on a handful of regional hotspots, surface water, and watershed-scale dynamics; more research is needed to address groundwater connectivity and to compare land-use impacts across multiple regions and scales. Approaches from landscape ecology that assess spatial patterns of, and synergies between, interlocking land cover may assist conservation managers in designing more resilient reefscapes.

Donovan, C., Towle, E. K., Kelsey, H., Allen, M., Barkley, H., Besemer, N., . . . Viehman, S. (2020). Coral reef condition: A status report for U.S. coral reefs. https://doi.org/10.25923/wbbj-t585

Reef-building corals provide the foundational architecture for coral reefs. These colorful reefs provide vital habitat for a variety of commercially and ecologically important marine fishes and invertebrates. The abundance of reef marine resources as well as their beauty sustain local economies by supporting industries such as ecotourism and both recreational and commercial fishing. Reef capacity to absorb intense wave energy, especially during severe storms, also make coral reefs critical to disaster preparedness. Despite their importance, coral reefs are subject to local degradation via pollution and overfishing, as well as global degradation due to warming water and ocean acidification. Human production of excess greenhouse gases makes coral reefs vulnerable to continued degradation.

Duran, A., Shantz, A. A., Burkepile, D. E., Collado-Vides, L., Ferrer, V. M., Palma, L., . . . Gonzalez-Diaz, P. (2018). Fishing, pollution, climate change, and the long-term decline of coral reefs off Havana, Cuba. *Bulletin of Marine Science*, 94(2), 213-228. <u>https://doi.org/10.5343/bms.2017.1061</u>

Understanding temporal and spatial variation of coral reef communities allows us to analyze the relative effects of local stressors, such as fishing and eutrophication, and global stressors, such as ocean warming. To test for spatial and temporal changes in coral reef communities, we combined recent benthic and fish surveys from 2016 with long-term data, dating back to the late 1990s, from four zones located at different distances from Central Havana, Cuba's largest population center. These changes may indicate the shifting importance of local vs global stressors affecting reef communities. Regardless of the distance from Havana, we found that coral cover was uniformly low (approximately 10%), whereas macroalgal abundance was often high (approximately 65%). Similarly, fish biomass was low across zones, particularly for herbivorous fishes (approximately 12 g m -2) that are critical ecological drivers of reef structure and coral resilience. Analyses of longer-term trends revealed that coral cover near Havana has been below about 10% since at least 1995, potentially because of local stressors. In contrast, reefs farther from Havana maintained relatively high coral cover (approximately 30%) until the early 2000s, but declined more recently to approximately 15%, putting them near the Caribbean-wide average. These distinct spatial and temporal trajectories of reef communities may be the result of the expansion of local stressors away from Havana as the human population increased, or as fishers ventured farther away to exploit new resources. Alternatively, the more recent decline of reefs farther from population centers may have resulted from increasingly frequent global stressors, such as bleaching events and hurricanes.

Field, M. E., Storlazzi, C. D., Gibbs, A. E., D'Antonio, N. L., & Cochran, S. A. (2019). The major coral reefs of Maui Nui, Hawai'i—distribution, physical characteristics, oceanographic controls, and environmental threats. U. S. G. SurveyReston, VA. <u>https://doi.org/10.3133/ofr20191019</u>

Coral reefs are widely recognized as critical to Hawai'i's economy, food resources, and protection from damaging storm waves. Yet overfishing, land-based pollution, and climate change are threatening the health and sustainability of those reefs, and accordingly, both the Federal and State governments have called for protection and effective management. In 2000, the U.S. Coral Reef Task Force stated that 20 percent of coral reefs should be protected by 2010. In 2016, the Governor of Hawai'i committed to

effective management of 30 percent of Hawaiian coastal habitats by 2030 to protect coral reefs. At present, the amount of coral protected in the main Hawaiian Islands is less than 1 percent.

Most of the large, highly diverse coral reef tracts in the main Hawaiian Islands surround the four islands of Maui, Moloka'i, Lāna'i, and Kaho'olawe, collectively known as Maui Nui. This report provides fundamental information on the location, extent, coral cover, threats, and connectivity of these major coral reef tracts in Maui Nui essential for identifying areas for management and protection.

By combining high-resolution bathymetric data with available maps, publications, and satellite and underwater images, nine major coral reef tracts are identified in the coastal waters of Maui Nui. Three very large reef tracts lie along the south side of Moloka'i, two on the east side of Lāna'i, and four off Maui. The factors that make these Maui Nui coral reef tracts a major and important resource for Hawai'i include their vast size and high coral cover (nearly 16,000 acres of reef, most of which has more than 50 percent live coral cover); diversity of shape, size, and location; and separation between reefs while retaining connectivity via currents. The decline in the health of these coral reefs over the past several decades has been slow but persistent. Punctuation of the decline by large-scale disturbance events, such as the thermal bleaching that occurred in 2015, is accelerating the loss of viable reef areas by an order of magnitude.

The economic, cultural, and recreational value of these coral reef tracts highlights the importance of their long-term survival to the local communities and all of Hawai'i. There is scientific consensus that increasing pressures from climate change, overfishing, and land-based pollution will virtually assure the continued, and perhaps accelerating, decline of Hawai'i's coral reefs unless action is taken. Information presented in this report, coupled with the results of numerous scientific studies, provides scientific underpinning to help establish a network of large-scale, connected Marine Protected Areas to meet the Federal and State governments' call for effective management and protection of coral reefs in Maui Nui.

Furman, B. T., Peterson, B. J., & Heck, K. L., Jr. (2020). Will the Florida Big Bend Area Become the Next Gulf of Mexico Reef Tract? *Frontiers in Marine Science*. https://doi.org/10.3389/fmars.2020.00334

It now seems reasonable to expect that the extensive hard bottom habitats in the Big Bend region of Florida will come to support the development of coral reefs in the near future. We make this assertion for a number of reasons: (1) abundant substrate is available in the form of the largest carbonate platform in the region (Morey et al., 2017), (2) low-relief outcroppings are particularly abundant in the 10–20 m isobath (Phillips et al., 1990) where light and temperature will likely be conducive for reef accretion, (3) areas of the WFS influenced by the warm Loop Current waters currently support hermatypic reefs, and (4) extant reef systems offer a supply of potential recruits. Seasonal wind patterns (Morey et al., 2003, 2017; Todd et al., 2014) and simulated drifter experiments (Johnson et al., 2017) suggest periodic connectivity to the Florida Middle Grounds, FKNMS and to a lesser extent the Flower Garden Banks, a luxuriant reef system in the northwestern GoM (Figure 1A). Thus, reefs should be seeded by a supply of coral larvae spawned by the massive and plating corals (genera: Orbicella, Agaricia, and Leptoseris) and the branching species (Acropora spp.). The extent to which these species are presently delivering ill-fated propagules to the Big Bend Area is unknown, representing a critical knowledge gap in our understanding of potential range expansion in the region.

Gil-Agudelo, D. L., Cintra-Buenrostro, C. E., Brenner, J., González-Díaz, P., Kiene, W., Lustic, C., & Pérez-España, H. (2020). Coral Reefs in the Gulf of Mexico Large Marine Ecosystem: Conservation Status, Challenges, and Opportunities. *Frontiers in Marine Science*. https://doi.org/10.3389/fmars.2019.00807

The importance of coral reefs (CR) within marine ecosystems has become widely recognized. Although shallow CR are not as abundant in the Gulf of Mexico (GoM) as in other areas such as the Caribbean, their uniqueness, singularity, isolation and conservation status make their conservation highly important. Corals and CR, both shallow and deep, are more widely distributed throughout the GoM than previously thought, providing new venues of research but also new challenges for their sustainable management. They are widely present in the three countries circumscribing the GoM (Cuba, Mexico and the United States). Corals are also distributed throughout different depths, from the keys of corals of Florida and Cuba, to the mesophotic reefs in Flower Garden Banks, Pulley Ridge and submerged banks in the southern GoM; additional coral presence occurs even beyond mesophotic depths (~30-150 m). Like reefs around the world, they are subject to an increased threat from anthropogenic causes, including overfishing, pollution and climate change. But there is also hope. Some reefs in the area, such as those in Flower Garden Banks National Marine Sanctuary are probably the best-preserved reefs in the region, with coral cover greater than 50%, which is unusual in the Wider Caribbean. Others are experiencing new protections through the work of government and local communities. The objectives of this manuscript are to summarize the overall status of corals and CR in the GoM, analyze some of the current and future threats, and explore opportunities for their conservation in the region. Aside from the above mentioned anthropogenic threats bleaching, coral diseases and hurricanes have been identified as main contributors for CR declines not only in the GoM but abroad; some nowadays present but likely to increase threats are invasion by alien species or by Sargassum spp. Among some of the opportunities identified are to capitalize on existing and emerging multilateral agreements and initiatives (e.g., GoM Large Marine Ecosystem, trinational sanctuaries agreement); increase financial support for conservation through international initiatives and the private sector; and a need to comprehend the inherent interconnection among corals, CR and deeper bank ecosystems as they do not function in isolation.

Gonzalez-Barrios, F. J., Cabral-Tena, R. A., & Alvarez-Filip, L. (2021). Recovery disparity between coral cover and the physical functionality of reefs with impaired coral assemblages. *Global Change Biology*, 27(3), 640-651. <u>https://doi.org/10.1111/gcb.15431</u>

The ecology and structure of many tropical coral reefs have been markedly altered over the past few decades. Although long-term recovery has been observed in terms of coral cover, it is not clear how novel species configurations shape reef functionality in impaired reefs. The identities and life-history strategies of the corals species that recover are essential for understanding reef functional dynamics. We used a species identity approach to quantify the physical functionality outcomes over a 13 year period across 56 sites in the Mexican Caribbean. This region was affected by multiple stressors that converged and drastically damaged reefs in the early 2000s. Since then, the reefs have shown evidence of a modest recovery of coral cover. We used Bayesian linear models and annual rates of change to estimate temporal changes in physical functionality and coral cover. Moreover, a functional diversity framework was used to explore changes in coral composition and the traits of those assemblages. Between 2005 and 2018, physical functionality increased at a markedly lower rate compared to that of

coral cover. The disparity between recovery rates depended on the identity of the species that increased (mainly non-framework and foliose-digitate corals). No changes in species dominance or functional trait composition were observed, whereas non-framework building corals consistently dominated most reefs. Although the observed recovery of coral cover and functional potential may provide some ecological benefits, the long-term effects on reef frameworks remain unclear, as changes in the cover of key reefbuilding species were not observed. Our findings are likely to be representative of many reefs across the wider Caribbean basin, as declines in coral cover and rapid increases in the relative abundance of weedy corals have been reported regionally. A coral identity approach to assess species turnover is needed to understand and quantify changes in the functionality of coral reefs.

Harris, P. T. (2020). Chapter 3 - Anthropogenic threats to benthic habitats. In *Seafloor Geomorphology as Benthic Habitat (Second Edition).* P. T. Harris & E. Baker (Eds.), (pp. 35-61): Elsevier <u>https://doi.org/10.1016/B978-0-12-814960-7.00003-8</u>

Anthropogenic threats to benthic habitats do not pose an equal risk, nor are they uniformly distributed over the broad depth range of marine habitats. Deep-sea benthic environments have, by and large, not been heavily exploited and most are in relatively good condition. In contrast, shelf and coastal habitats, and deep ocean pelagic fisheries, have been exploited extensively and human impacts here are locally severe. A critical point is that anthropogenic threats do not act in isolation; rather, they are cumulative and the impacts are compounded for every affected habitat. In general, the impacts of humans on benthic habitats are poorly understood. Habitat mapping provides condition assessments and establishes baselines against which changes can be measured. GeoHab scientists ranked the impacts on benthic habitats from fishing as the greatest threat, followed by pollution and litter, aggregate mining, oil and gas, coastal development, tourism, cables, shipping, invasive species, climate change, and construction of wind farms. The majority of authors (84%) reported that monitoring changes in habitat condition over time was a planned or likely outcome of the work carried out. In this chapter the main anthropogenic threats to benthic habitats are reviewed in relation to their potential impacts on benthic environments.

Lager, C. V. A., Hagedorn, M., S. Rodgers, K., & Jokiel, P. L. (2020). The impact of short-term exposure to near shore stressors on the early life stages of the reef building coral Montipora capitata. *Peerj*, 8, e9415. <u>https://doi.org/10.7717/peerj.9415</u>

Successful reproduction and survival are crucial to the continuation and resilience of corals globally. As reef waters warm due to climate change, episodic largescale tropical storms are becoming more frequent, drastically altering the near shore water quality for short periods of time. Therefore, it is critical that we understand the effects warming waters, fresh water input, and run-off have on sexual reproduction of coral. To better understand the effects of these near shore stressors on Hawaiian coral, laboratory experiments were conducted at the Institute of Marine Biology to determine the independent effects of suspended sediment concentrations (100 mg l–1 and 200 mg l–1), lowered salinity (28‰), and elevated temperature (31 °C) on the successful fertilization, larval survival, and settlement of the scleractinian coral Montipora capitata. In the present study, early developmental stages of coral were exposed to one of three near shore stressors for a period of 24 h and the immediate (fertilization) and latent effects (larval survival and settlement) were observed and

measured. Fertilization success and settlement were not affected by any of the treatments; however, larval survival was negatively affected by all of the treatments by 50% or greater (p > 0.05). These data show that early life stages of M. capitata may be impacted by near shore stressors associated with warming and more frequent storm events.

McFarland, B. J. (2018). The Context of Coral Reef Degradation and Loss. In *Conservation of Tropical Coral Reefs*. (pp. 5-62) <u>https://doi.org/10.1007/978-3-030-57012-5_2</u>

The author begins chapter 2 with the general locations of warm water coral reefs (Australia and South Pacific; Southeast Asia; East Africa, and Indian Ocean; and in/around the Caribbean Sea) and outlines the specific countries that host warm water coral reefs. The author then provides an historical and current context of tropical coral reef degradation and loss. The author presents a more detailed discussion about the global factors contributing to degradation and loss (global climate change and ocean acidification), along with regional factors (natural disasters, pollution runoff, plastics, and overfishing) and local factors (noise pollution, disease, invasive species, and high-human traffic). The author then concludes with an explanation of why coral reefs are valuable, such as due to their provisioning, regulating, habitat or supporting, and cultural services.

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. *Environmental Monitoring and Assessment*, 190(4), 213. https://doi.org/10.1007/s10661-018-6562-1

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.

Ortiz-Lozano, L., Gutierrez-Velazquez, A., Aja-Arteaga, A., Arguelles-Jimenez, J., & Castillo, V. R. (2021). Distribution, threats, and management of submerged reefs in the north of the reef corridor of the Southwest Gulf of Mexico. *Ocean & Coastal Management*, 201. <u>https://doi.org/10.1016/j.ocecoaman.2020.105428</u>

It is important to know the presence and distribution of benthic habitats on the continental shelves, and the relationship they have with the different human activities that take place in the marine environment. Platform reefs are relevant in regions such as the Southwest Gulf of Mexico, where reefs, emerged and submerged, form an ecological corridor. The main challenge for the management of this corridor is the lack of knowledge about the presence and distribution of submerged reef habitats. Here, we update the information on previously discovered submerged reefs in the northern zone of the reef corridor of the Southwest GoM, and we report four new reef structures (three submerged and one fringing reef) unknown until now to science. In this region, there are 9 submerged reefs, whose surface is so far greater than the emerged ones. These reefs are used only for fishing activities. However, there is strong oil activity in the area and significant maritime traffic. Here we analyze each of the activities that take place in the area and contrast them with the management tools that the Mexican government has for the conservation of this ecosystems.

Rocha, L. A., Pinheiro, H. T., Shepherd, B., Papastamatiou, Y. P., Luiz, O. J., Pyle, R. L., & Bongaerts, P. (2018). Mesophotic coral ecosystems are threatened and ecologically distinct from shallow water reefs. *Science*, 361(6399), 281. <u>https://doi.org/10.1126/science.aaq1614</u>

Coral reefs are under intense pressure from anthropogenically induced climate warming and habitat destruction. It has been suggested that coral reefs in deeper waters may provide a refuge less affected by human development and climate change. Rocha et al., however, show that shallow and deep reefs are biologically different. Furthermore, deep (or mesophotic) reefs are also suffering from human impacts. Thus, deep reefs do not represent a potential refuge for other reef ecosystems. Indeed, they too are threatened and need protection.Science, this issue p. 281The rapid degradation of coral reefs is one of the most serious biodiversity problems facing our generation. Mesophotic coral reefs (at depths of 30 to 150 meters) have been widely hypothesized to provide refuge from natural and anthropogenic impacts, a promise for the survival of shallow reefs. The potential role of mesophotic reefs as universal refuges is often highlighted in reef conservation research. This hypothesis rests on two assumptions: (i) that there is considerable overlap in species composition and connectivity between shallow and deep populations and (ii) that deep reefs are less susceptible to anthropogenic and natural impacts than their shallower counterparts. Here we present evidence contradicting these assumptions and argue that mesophotic reefs are distinct, impacted, and in as much need of protection as shallow coral reefs.

Sanchez, J. A., Gomez-Corrales, M., Gutierrez-Cala, L., Vergara, D. C., Roa, P., Gonzalez-Zapata, F. L., . . . Sarmiento, A. (2019). Steady Decline of Corals and Other Benthic Organisms in the SeaFlower Biosphere Reserve (Southwestern Caribbean). *Frontiers in Marine Science*, 6. <u>https://doi.org/10.3389/fmars.2019.00073</u>

Coral reef decline persists as a global issue with ties to climate change and human footprint. The SeaFlower Biosphere reserve includes some of the most isolated oceanic coral reefs in the Southwestern Caribbean, which provide natural experiments to test global and/or basin-wide factors affecting coral reefs. In this study, we compared coral and other substrate cover (algae, cyanobacteria, and octocorals), along population densities of keystone urchin species from two atolls (Serrana and Roncador Banks), during 1995, 2003, and 2015/2016. We also surveyed benthic foraminifera as a water quality proxy for coral growth in the last period. A steady reduction in coral cover was clearly observed at Roncador's lagoon, but not at Serrana's reefs, with significant differences between 1995 and 2015/2016. Percent cover of fleshy algae decreased significantly also at Roncador between 1995 and 2003 but did not change notably from 1995 to 2016 at Serrana. However, both Banks exhibited a loss in crustose coralline algae from 2003 to 2015/2016. Likewise, a reduction in bottom complexity, measured as bottom rugosity, was evident between 1995 and 2003. Roncador Bank had unprecedented high octocoral densities, which increased almost threefold from 2003 to 2015. In contrast, urchin densities were low in Roncador; only Diadema antillarum increased from 2003 to 2016 in Serrana Bank. The Foraminifera in Reef Assessment and Monitoring (FORAM) Index (FI) in the two Banks was below the range expected for healthy coral reefs. Although both Banks follow a reduction in CCA and CA cover, Roncador Bank also faces an alarming decline in coral cover, urchins and bottom complexity (rugosity) in contrast to increases in octocoral densities and potential loss of resilience and eutrophication suggested by the FI index. These unexpected findings led us to consider and discuss potential outcomes, where these reefs deteriorate (i.e., erode and drown) providing ideal conditions for octocoral growth. Hence, it is of utmost urgency to start monitoring reef budgets, octocorals and nutrient sources.

Schulz, M., Los, A., Skowronek, P., & Strachecka, A. (2019). Influence of environmental and anthropogenic agents on the occurrence of coral reef bleaching syndrome and coral diseases. *Medycyna Weterynaryjna-Veterinary Medicine-Science and Practice*, 75(4), 221-231. https://doi.org/10.21521/mw.6139

Coral reefs are the most productive ecosystems on Earth. They ensure the conservation of biodiversity and are a live habitat for 25% of all marine organisms. The main relationship on the coral reef is the symbiosis between corals and algae from the genus Symbiodinium (commonly called zooxanthellae). The authors of this publication have characterized and described the factors limiting the occurrence of coral reefs, including: water temperature, salinity, access to sunlight, contamination, physicochemical and hydromechanical parameters of water. Moreover anthropogenic threats to coral reefs have been specified, including diving tourism, ecological disasters (e.g. oil spills) and the development of marine aquaristics. Rapid changes in the basic living conditions are dangerous for corals and their symbionts and may cause the unsuitability of the new environment resulting in diseases such as coral bleaching. Corals bleaching is a disease associated with the break of the coral and algae relationship which results in a coral reef death on a global scale. Awareness of these negative factors, often related to human activity, may allow us to better understand the ecological processes that are the basis of reef functioning and might enable us to prevent and oppose to the changes and ecological recessions of coral reefs.

Slattery, M., & Lesser, M. P. (2019). The Bahamas and Cayman Islands. In *Mesophotic Coral Ecosystems*. Y. Loya, K. A. Puglise, & T. C. L. Bridge (Eds.), (Vol. 12, pp. 47-56) <u>https://doi.org/10.1007/978-3-319-92735-0_3</u>

As shallow coral reefs worldwide are increasingly degraded by natural and anthropogenic stressors, mesophotic coral ecosystems (MCEs; similar to 30-150 m) represent a potential refugia that may act as

seed banks for coral reef resilience. This is particularly true in the Caribbean Basin where phase shifts from coral dominance to either algal or sponge dominance have been reported with increasing frequency. However, coral reefs of the Bahamas and Cayman Islands are less impacted than other Caribbean reefs, and they offer an opportunity to assess the ecology of MCEs and the connectivity between shallow and mesophotic coral reefs. The MCEs of the Bahamas and Cayman Islands are composed of a shallow sloped upper zone (similar to 30-60 m) and a vertical lower zone (60-100+ m). The upper MCE zone has similar biodiversity and percent cover to nearby shallow reefs, but the lower MCE zone is dominated by sponges, and it includes many species not found on shallow reefs. The ecological importance of the mesophotic sponges is unequivocal; they provide habitat for a variety of species and play a significant role in benthic-pelagic coupling via filtration of bacterioplankton, and their symbiotic microbes are sources of nitrogen cycling. Moreover, our data indicate that sponge diversity on MCEs in the Bahamas and the Cayman Islands is more similar to one another than the sponge diversity among shallow and mesophotic reefs in each region. Threats to shallow reefs (e.g., climate change and invasive species) may also impact MCEs; conservation will require mitigation of these stressors.

Stimson, J. (2018). Recovery of coral cover in records spanning 44 yr for reefs in Kāne'ohe Bay, Oa'hu, Hawai'i. *Coral Reefs*, 37(1), 55-69. <u>https://doi.org/10.1007/s00338-017-1633-2</u>

Published and unpublished long-term studies are assembled to examine trends in coral cover and the dependence of change in coral cover on the initial coral cover in Kane'ohe Bay over the last 44 yr. Each study showed there had been periods of increase in coral cover in the bay and showed that the rate of change in cover has been inversely dependent on the initial cover at a site. When coral cover is high on upper reef slopes, the fragile structure of reefs in this sheltered bay often collapses, resulting in a decrease in coral cover. The rate of change in coral cover was also inversely dependent on cover in one of the two studies that included analysis of reef-flat corals; the cause of decrease in cover in this habitat is thought to be attributable to particularly low sea levels in Hawai'i in the late 1990s and 2009–2010. The inverse relationship between initial coral cover and change in cover, and the intersections of the regression lines of these variables with the x-axis at intermediate values of coral cover, is indicative of resilience in this ecosystem over the last 44 yr. In the 1970s, the invasive macroscopic green alga Dictyosphaeria cavernosa covered a high percentage of coral habitat and commonly displaced corals from the reef slope and outer reef flats; the change was cited as an example of a phase shift on a reef. This alga has virtually disappeared from the bay, thus increasing the space available to corals; its disappearance is coincident with the increase in coral cover. Other species of macroalgae, including alien species, have not replaced D. cavernosa as major space competitors. The increase in coral cover and virtual disappearance of D. cavernosa constitute an example of a phase-shift reversal.

Turner, R. E., & Rabalais, N. N. (2019). Chapter 18 - The Gulf of Mexico. In World Seas: an Environmental Evaluation (Second Edition). C. Sheppard (Ed.), (pp. 445-464): Academic Press <u>https://doi.org/10.1016/B978-0-12-805068-2.00022-X</u>

The Gulf of Mexico (GOM) is a mesotidal marginal sea of the western Atlantic Ocean bordered by the United States, Mexico, and Cuba. The two largest rivers are the Mississippi (north) and Grijalva-Usumacinta (south). The 18,261km2 wetlands in the GOM and 9743km2 of seagrass habitat are quasiprotected by a mixture of local, state, national, and international agreements, but will be

compromised by an accelerating sea-level rise anticipated this century. There are many estuarinedependent and offshore fish stocks that are overfished, or close to their maximum yield, a large humancaused hypoxic zone near the Mississippi River, and smaller ones in local estuaries. The Deepwater Horizon oil spill (2010) affected most deep- and shallow-water ecosystems that have rich species diversity. Restoration seems possible in some instances, but prevention is more prudent in the long run. Improvements to regional science-based data gathering, adaptive management attitudes, and ecosystem models will advance the achievement of water quality improvement goals, stabilize or even improve fish stocks, and build community health and well-being.

van Heuven, S., Webb, A. E., de Bakker, D. M., Meesters, E., van Duyl, F. C., Reichart, G. J., & de Nooijer,
L. J. (2018). In-situ incubation of a coral patch for community-scale assessment of metabolic and chemical processes on a reef slope. *Peerj*, 6, e5966. <u>https://doi.org/10.7717/peerj.5966</u>

Anthropogenic pressures threaten the health of coral reefs globally. Some of these pressures directly affect coral functioning, while others are indirect, for example by promoting the capacity of bioeroders to dissolve coral aragonite. To assess the coral reef status, it is necessary to validate community-scale measurements of metabolic and geochemical processes in the field, by determining fluxes from enclosed coral reef patches. Here, we investigate diurnal trends of carbonate chemistry, dissolved organic carbon, oxygen, and nutrients on a 20 m deep coral reef patch offshore from the island of Saba, Dutch Caribbean by means of tent incubations. The obtained trends are related to benthic carbon fluxes by quantifying net community calcification (NCC) and net community production (NCP). The relatively strong currents and swell-induced near-bottom surge at this location caused minor seawater exchange between the incubated reef and ambient water. Employing a compensating interpretive model, the exchange is used to our advantage as it maintains reasonably ventilated conditions, which conceivably prevents metabolic arrest during incubation periods of multiple hours. No diurnal trends in carbonate chemistry were detected and all net diurnal rates of production were strongly skewed towards respiration suggesting net heterotrophy in all incubations. The NCC inferred from our incubations ranges from -0.2 to 1.4 mmol CaCO(3) m(-2) h(-1) (-0.2 to 1.2 kg CaCO(3) m(-2) year(-1)) and NCP varies from -9 to -21.7 mmol m(-2) h(-1) (net respiration). When comparing to the consensus-based ReefBudget approach, the estimated NCC rate for the incubated full planar area (0.36 kg CaCO(3) m(-2) year(-1)) was lower, but still within range of the different NCC inferred from our incubations. Field trials indicate that the tent-based incubation as presented here, coupled with an appropriate interpretive model, is an effective tool to investigate, in situ, the state of coral reef patches even when located in a relatively hydrodynamic environment.