Mangrove habitats provide refuge from climate change for reef-building corals

K. K. Yates[1], C. S. Rogers[2], J. J. Herlan[2,*], G. R. Brooks[3], N. A. Smiley[1], and R. A. Larson[3]

[1]U.S. Geological Survey, Coastal and Marine Science Center, St. Petersburg, Florida 33701, USA

[2]U.S. Geological Survey, Southeast Ecological Science Center, St. John, U.S. Virgin Islands, 00830, USA

[3]Eckerd College, Galbraith Marine Science Laboratory, St. Petersburg, Florida 33711, USA

*now at: Universidad Catolica del Norte, Larrondo 1281, Coquimbo, Chile

Correspondence to: K. K. Yates (kyates@usgs.gov)

Abstract

Risk analyses indicate that more than 90% of the world's reefs will be threatened by climate change and local anthropogenic impacts by the year 2030 under "business as usual" climate scenarios. Increasing temperatures and solar radiation cause coral bleaching that has resulted in extensive coral mortality. Increasing carbon dioxide reduces seawater pH, slows coral growth, and may cause loss of reef structure. Management strategies include establishment of marine protected areas with environmental conditions that promote reef resiliency. However, few resilient reefs have been identified, and resiliency factors are poorly defined.

Here we characterize the first natural, non-reef, coral refuge from thermal stress and ocean acidification and identify resiliency factors for mangrove-coral habitats. We measured diurnal and seasonal variations in temperature, salinity, photosynthetically active radiation (PAR), and seawater chemistry; characterized substrate parameters; and examined water circulation patterns in mangrove communities where scleractinian corals are growing attached to and under mangrove prop roots in Hurricane Hole, St. John, U.S. Virgin Islands. Additionally, we inventoried the coral species and quantified incidences of coral bleaching, mortality and recovery for two major reef-building corals, *Colpophyllia natans* and *Diploria labyrinthiformis*, growing in mangrove shaded and exposed (unshaded) areas.

At least 33 species of scleractinian corals were growing in association with mangroves. Corals were thriving in low-light (more than 70% attenuation of incident PAR) from mangrove shading and at higher temperatures than nearby reef tract corals. A higher percentage of *C. natans colonies* were living shaded by mangroves, and no shaded colonies bleached. Fewer *D. labyrinthiformis* colonies were shaded by mangroves, however more unshaded colonies bleached. A combination of substrate and habitat heterogeniety, proximity of different habitat types, hydrographic conditions, and biological influences on seawater chemistry generate chemical conditions that buffer against ocean acidification. This previously undocumented refuge for corals provides evidence for adaptation of coastal organisms and ecosystem transition due to recent climate change. Identifying and protecting other natural, non-reef coral refuges is critical for sustaining corals and other reef species into the future.

1 Introduction

Evidence that repeated coral bleaching events (Baker et al., 2008; Eakin et al., 2009; Fitt et al., 2001; Hoegh-Guldberg et al., 2007; Hoegh-Guldberg, 2011; Lesser, 2011) and ocean acidification (Fabricius et al., 2011; Kleypas and Yates, 2009; Kroeker et al., 2013, Silverman et al., 2009) will severely impede coral growth within the next few decades (Burke et al., 2011; Hooidonk et al., 2014) has prompted an urgent search for coral reef systems that provide natural refuges from climate threats and efforts to identify mechanisms that could help reef organisms acclimatize to changing climate. The complex interplay among climate, oceanographic, and biological factors that influences susceptibility and resilience of reefs has made identification and characterization of refuges challenging. Focus has been placed on identifying reefs with low exposure to or potential for adaptation to climate threats, and reduced local anthropogenic impacts (Keller et al., 2009; McClanahan et al., 2011; Mumby and Steneck, 2008; Salm et al., 2006; West and Salm, 2003). Recent studies have identified only a few reef systems in the Western Indian Ocean (McClanahan et al., 2011), on the Great Barrier Reef (Berkelmans, 2002), and in shallow bays of Palau (van Woesik et al., 2012) that show resistance to elevated temperatures and less coral bleaching. Only one reef, in the Florida Keys, has been identified as a potential refuge from ocean acidification (Manzello et al., 2012). To our knowledge, no alternative (non-reef) natural habitats have ever been identified as potential climate change refuges for corals.

Mangrove communities, while often near coral reef ecosystems, are not thought of as having suitable conditions for coral recruitment and growth due to high sedimentation rates, lack of suitable substrate, and inadequate water quality. Therefore, no prior focus has been placed on identifying mangrove-coral habitats, the scientific literature contains few references to scleractinian corals growing in mangroves (e.g. Macintyre et al., 2000; Rutzler et al., 2000), and no comprehensive surveys or multidisciplinary studies of these habitats have been performed.

In St. John, U.S. Virgin Islands, over 30 species of scleractinian corals are growing on and under mangrove prop roots in bays in Hurricane Hole within Virgin Islands Coral Reef National Monument (Table 1). Many are reef-building corals that survived a 2005 to 2006 bleaching and disease event that caused major losses of coral throughout the northeastern Caribbean (Miller et al., 2009). Qualitative surveys conducted in one bay in 1984 suggest that there has been an increase in the abundance and diversity of corals in mangrove communities since that time (Beets et al., 1986), possibly a response to climate change.

Keppel et al. (2012) define refugia as "habitats that components of biodiversity retreat to, persist in and can potentially expand from under changing environmental conditions." The presence of such a remarkable abundance and diversity of coral species in the mangroves of St. John, and their largely intact condition in contrast to severe declines of corals on nearby reefs following bleaching and a major disease outbreak support the concept of this habitat as a refuge. This ecosystem serves as an example of how some mangrove habitats could provide alternative refuges for corals from climate threats, particularly increasing seawater temperature, high levels of solar radiation, and decreasing pH. We identified and quantified physical, chemical, and biological resiliency factors in mangrove communities with corals in Hurricane Hole, St. John, U.S. Virgin Islands. We present a baseline list of resiliency factors to help guide identification of other alternative refuges for reef-building corals.

2 Methods

Physical, chemical, and biological attributes were characterized in three small, adjacent bays in Hurricane Hole including Water Creek, Otter Creek, and Princess Bay from November 2010 to July 2012 (Fig. 1). In each bay, we measured diurnal and seasonal variations in temperature, salinity, photosynthetically active radiation (PAR), and seawater chemistry [total alkalinity (A_T), dissolved inorganic carbon (C_T), pH_T (pH on the total H^+ scale), dissolved oxygen (DO), and nutrients]. We characterized substrate parameters and examined water circulation patterns associated with inner bay mangrove communities with no corals (MNC sites), nearby mid- to outer-bay mangrove communities with corals growing on and under prop roots (MC sites), and rock outcrops with un-shaded corals (ROC sites) in all three bays. Corals at these sites were growing near the coastline in shallow water ranging from 1.2 to 2.0 m water depth. Additionally, we inventoried coral species in all three bays, and quantified incidences of coral bleaching, mortality and recovery for two major reef-building corals, *Colpophyllia natans* and *Diploria labyrinthiformis*, growing in mangrove shaded and exposed (unshaded) areas in the bay with the highest coral diversity (Otter Creek). Logistics prevented concurrent collection of similar data from reefs around St. John. However, we collected limited data from 4 sites on a nearby reef in Long Bay (approximately 2 km from the nearest mangrove coral study site and 6.3 m water depth, Fig. 1) from July 16 to August 22, 2004. Latitude and longitude for ~~reefs~~ sites were site 1 = 18.337972, -64.675944; 2 = 18.337944, 64.676028; 3 = 18.337833, -64.675861; 4 = 18.337806, 64.675917. The reef site ~~was~~ characterized by scattered coral colonies of ~~*Orbicella annularis,*~~ *Orbicella annularis* *complex, Montastraea cavernosa~~,~~ Porites porites, Porites astreoides, Agaricia agaricites, Favia fragum, Diploria labyrinthiformis*, and the hydrocoral *Millepora alcicornis* growing among sea fans, other gorgonians, sponges, turf algae, macroalgae and coral rubble. All seawater chemistry data from Hurricane Hole and Long Bay reef sites were collected near the seafloor (less than 0.5 m from the bottom)~~, not from surface waters~~. Additionally, we collected vertical profile data of carbonate system parameters over a coral habitat at 6.5 m water depth near the mouth of Otter Creek (Fig. 1) at 7:00 am on July 19, 2011. Profile data were collected at 1.5 m, 3.0 m, 4.6 m, and 6.0 m depth.

2.1 Seawater chemistry

Seawater was collected for A_T, C_T, and pH_T analyses from each site every 4-hours (n = 7) throughout 24-hour periods in November 2010, July 2011, and July 2012. Measurements were made every 4-hours for 3 consecutive days (n=19) in Otter Creek during July 2012. No DO data were collected in Water Creek during July 2012 due to DO sensor failure. Twenty percent of pH ~~measurements~~ (47 of 225) were calculated from A_T and C_T. A peristaltic pump was used to pump seawater from approximately 1 m below the water surface through a 0.45 μm filter into 500 ml borosilicate glass bottles. Samples for A_T and C_T were preserved by adding 100 μL saturated $HgCL_2$ solution. Bottles were positive-pressure sealed with ground glass stoppers coated with Apiezon grease. Seawater samples for pH_T were collected from the same peristaltic pump and filtered into 30 mL glass optical cells, and were analyzed within 1 hour of collection. Samples were analyzed for A_T (±1 μmol kg^{-1}) using spectrophotometric methods of Yao and Byrne (1998) with an Ocean Optics USB2000 spectrometer and bromo-cresol purple indicator dye, for C_T (±3 μmol kg^{-1}) using a UIC carbon coulometer model CM5014 and CM5130 acidification module using methods of Dickson et al. (2007) and for pH_T (±0.005) via spectrophotometric methods of Zhang and Byrne (1996) with an Ocean Optics USB2000 spectrometer and thymol blue indicator dye. Dissolved oxygen (±0.1 mg l^{-1}), temperature (±0.01 ºC), and salinity (±0.01) were measured using a YSI multimeter calibrated daily. Certified reference materials (CRM) for A_T and C_T analyses were from the Marine Physical Laboratory of Scripps Institution of Oceanography (A. Dickson). Duplicate or triplicate analyses were performed on at least 10% of samples.

Seawater from Long Bay reef was also collected and analysed for A_T and C_T using the same methods as in Hurricane Hole. pH_T was calculated from A_T and C_T using the carbonate speciation program CO2sys (Pierrot et al., 2006). Dissolved oxygen (±0.1 mg l^{-1}), temperature (±0.01 ºC), and salinity (±0.01) were measured using a flow through analytical system and methods of Yates and Halley (2003). These data were collected at 7:00 am (n = 7) or 11:00 am (n = 3).

Vertical profile data were collected by attaching a weighted peristalic sampling tube (marked with depth increments) to the YSI multimeter and lowering the collection apparatus to depth along a guide line attached to a buoy at the surface and a weight at the seafloor. Samples and measurements for A_T, C_T, pH_T, DO, salinity, and temperature were collected and analyzed using the same methods as described for Hurricane Hole analyses. Carbonate system parameters for all study sites including aragonite mineral saturation state (Ω_A) and pCO_2 were calculated from A_T, pH_T (or A_T and C_T for Long Bay reef samples), temperature and salinity measurements using the carbonate speciation program CO2sys (Pierrot et al., 2006) with dissociation constants K1 and K2 from Merbach et al. (1973) refit by Dickson and Millero (1987), KSO_4 from Dickson (1990), and using the total pH scale (pH_T).

Seawater samples were collected for measurement of total nitrogen and phosphate in November 2010 and July 2011. In November 2010, nutrient samples were collected in transects spanning from the innermost reaches to the mouth of all three bays (58 samples). During July 2011, water samples were collected every 4-hours throughout 24-hour time periods at every sample site in all three bays. Water samples (20mL) were filtered through 0.22µm pore size Millepore Sterivex filters rinsed with 2 volumes of sample water. Samples were stored in 20mL acid-washed polypropylene scintillation vials at 0^oC until time of analysis. Nutrient samples were analyzed at the NOAA Atlantic Oceanographic and Meteorological Laboratory in Miami, FL.

2.2 Sediment samples

Bulk surface sediment samples (approximately 2 kg wet weight) were collected via grab-sampling from the seafloor (approximately 1.2 m water depth) at each study site in each bay (Fig. 1). Wet samples were dehydrated to remove water and salts within 6 hours of collection by rinsing with 70% isopropyl alcohol, allowing samples to settle, decanting the alcohol, and repeating this process two additional times. Dehydrated samples were then allowed to air dry prior to analysis for grain size and composition. Grain-size was measured via settling-tube for sand-sized fractions (Gibbs, 1974), and pipette for mud-sized fractions (Folk, 1965). Calcium carbonate content was determined by the acid leaching method (Milliman, 1974). Total organic matter (TOM) was measured by loss on ignition (LOI) at 550^oC for >2.5 hours

(Dean, 1974). Mineralogic composition was measured by XRD on a Bruker D-8 advanced system using cobalt radiation at the University of Georgia, Department of Geology.

2.3 Coral surveys

A list of coral species growing in Princess Bay, Otter Creek and Water Creek was compiled based on over 100 surveys conducted by snorkeling the perimeter of each bay and identifying all live coral colonies growing from the shoreline to a depth of approximately 6 m (Rogers and Herlan, 2012). Minor coral bleaching was observed in July 2010 with more severe bleaching in August through October 2010. From November 2010 to January 2011, a complete census of colonies of *Diploria labyrinthiformis* and *Colpolphyllia natans* (the most abundant framework-building corals in Hurricane Hole) was conducted in Otter Creek and Water Creek. The census included colonies growing up in the mangroves and on the nearby substrate that sloped to the sandy bottom in each of the bays. Coral depths ranged from near the surface to about 5 meters. Each coral was photographed and examined for condition (e.g., bleached or unbleached) and exposure (shaded or unshaded). A coral was considered shaded if it grew directly under mangroves or within a few meters of them where it received shading for at least a portion of each day. Subsets of these colonies in Otter Creek were re-examined in May 2011 to document recovery and mortality. Fisher's Exact tests performed in SAS 9.2 were used to compare the response of shaded and unshaded coral colonies.

2.4 Temperature and PAR measurements

Temperature measurements were collected every 2-hours during 2010 and 2011 using HOBO Pendant data loggers at 18 locations in Hurricane Hole (Table 2). Loggers were placed near mangrove and coral habitats at inner-, mid-, and outer-bay locations. Daily averages were generated from all loggers. Temperature data from long-term monitoring transects were collected every 2 hours from loggers at reef depth on the forereef slope area of 6 reefs around St. John during 2005 by Miller et al. (2009), and during 2010 by the National Park Service (2012). These data were used to calculate daily means at each site and averaged among sites to generate daily averages for the long-term reef transects. Photosynthetically Active Radiation (PAR) was measured every 15-minutes (15 minute averages) at study sites in Otter Creek and Water Creek approximately 20 cm above the seafloor using LiCor 4π sensors and approximately 3 m above sea level and the mangrove canopy using LiCor 2π sensors coupled with LiCor 1000 or LiCOR 1400 data loggers. PAR sensors were placed on the seafloor under the mangrove canopy and outside of the mangrove canopy at MNC and MC sites, on the seafloor at unshaded ROC sites, and above the mangrove canopy at MC and MNC sites.

3 Results and Discussion

3.1 Heterogeneity of the physical environment

Heterogeneity in the physical environment provides for semi-isolation of coastal water masses from open ocean water enabling local differentiation of physical, chemical, and biological attributes of coastal ecosystems. The potential for a refuge to sustain characteristics that promote climate change resiliency is, in part, ~~dependant~~ upon the ability of the system to remain out of equilibrium with open ocean chemical conditions.

The bays in Hurricane Hole range in area from 0.06 to 0.11 km^2, have small watersheds ranging in area from 0.11 km^2 to 0.43 km^2, are surrounded by steeply sloped, rocky hillsides, and have a narrow (up to approximately 10 m) fringe of red mangroves (*Rhizophora mangle*). Bedrock is exposed in cliffs and outcrops along the coast and consists of igneous and metamorphic rocks including Cretaceous basalt, andesite, keratophyre (Rankin, 1998). Carbonate sediments on St. John are *in situ* marine biogenic carbonates. There is no permanent source of freshwater inflow to any of the bays, nutrient concentrations are low, water clarity is generally high, and tidal range is low (<0.25m). The inner areas of the bays are very shallow, less than 2 m, and well protected from high winds and seas. The mangrove fringe is thickest in the inner bays. Prop roots support abundant communities of reef and mangrove organisms including crustose coralline algae, and are surrounded by communities of intermediate density seagrass (*Thalassia testudinum*), and calcareous algae including *Halimeda* spp. and *Penicillus* spp. Very few corals are growing near inner bay mangroves. Grain size analyses showed that sediments in the inner bays are primarily fine-grained ranging from 16 to 65% mud-sized fractions (Table 3).

Mid- to outer-bay areas are characterized by the narrowest mangrove fringe and shallow (<1 m) water depths immediately adjacent to the shoreline that slopes steeply to 5 to 10 m just beyond the mangrove canopy. The mangrove prop roots support sponges, crustose coralline algae, numerous scleractinian corals and other organisms (Fig. 2). The outer bays are infrequently exposed to storm waves that remove fine-grained sediments, and sediments consist primarily of 69 to 96% sand and gravel with occasional occurrences of large boulders (Table 3). Corals are growing attached directly to prop roots and to hard substrates under roots. Near the entrance to the bays, there are rock outcrops with few or no mangroves nearby. These sites have primarily hard bottom substrate with small pockets of coarse-grained sediments, corals growing directly on hard bottom, very sparse occurrences of calcareous algae, and little seagrass growing nearby.

3.2 Chemical heterogeneity

Heterogeneity in the physical environment and benthic community structure creates chemical micro-climates that can affect localized, adjacent habitats. Variations in chemical parameter trends were observed at sub-kilometer scale in each bay and in association with specific habitat types (Fig. 3). Inner bay sites where mangroves grow without corals (MNC sites) showed the lowest dissolved oxygen levels (with the exception of Otter Creek in November 2010), highest pCO_2, A_T, and C_T levels, and lowest pH_T and aragonite mineral saturation states (Ω_A). A_T and salinity showed the greatest range in variation during passage of Tropical Storm Tomás in November 2010 in Water Creek and Princess Bay, both of which have a larger watershed than Otter Creek and are more heavily influenced by terrestrial run-off during rain events. No consistent differences in chemical parameters were observed between mangrove-coral (MC) sites and rock outcrop coral (ROC) sites. MC and ROC sites showed higher DO, lower pCO_2, A_T, and C_T levels, and higher pH_T and aragonite saturation states than MNC sites indicating that seawater chemical characteristics of MC sites are more similar to ROC sites than to MNC sites. Diurnal variability in chemical parameters was also observed at each study site. Hurricane Hole data indicate that lowest carbonate mineral saturation states, pH_T, temperature and DO, and highest C_T, pCO_2, and TA generally occurred in the early morning and are reflected in our 7:00 am measurements (see http://doi.pangaea.de/10.1594/PANGAEA.825752) . Vertical profile data also showed water column heterogeneity with considerable differences in Ω_A (Δ 0.34), pH (Δ 0.04), pCO_2 (Δ 40 μatm), TA (Δ 45.3 μmol kg^{-1}) and C_T (Δ 20.9 μmol kg^{-1}) between surface and bottom water (Fig. 4, Table 3). Profile data demonstrate why one cannot assume that surface water measurements reflect bottom water conditions even in shallow water environments. Average total nitrate and phosphate values for all samples in November 2010 were 0.999 ± 2.626 and 0.072 ± 0.094, respectively. Average total nitrate and phosphate values for all samples collected in July 2011 were 0.238 ± 0.359 μmol l^{-1} and 0.066 ± 0.069 μmol l^{-1}, respectively.

The values of nutrient measurements distributed both temporally and spatially were near the range of analytical precision and accuracy for A_T measurements and, therefore, were not included in calculation of carbonate system parameters from A_T and pH_T measurements. Nutrient data are available at http://doi.pangaea.de/10.1594/PANGAEA.825752.

Calcification/dissolution thresholds are the levels of Ω_A below which (and pCO_2 levels above which) net dissolution of carbonate sediments exceeds calcification rates as determined by in situ, mesocosm, and modeling studies of coral reef ecosystems. Aragonite saturation states fell considerably lower than calcification/dissolution threshold ranges of 3.0 to 3.2 and/or pCO_2 exceeded thresholds of 504 to 584 µatm (Langdon et al., 2003; Silverman et al., 2009; Yamamoto et al., 2012; Yates and Halley, 2006) at all MNC study sites during both November and July, except in Otter Creek where thresholds were exceeded only during July 2011. Maximum pCO_2 values at MC sites and ROC sites exceeded the dissolution threshold during only 4 of 9 measurement periods and 2 of 9 measurement periods, respectively. Minimum aragonite saturation states at MC and ROC sites fell below dissolution thresholds during only 2 of 9 and 3 of 9 measurement periods, respectively. Maximum pCO_2 and minimum Ω_A observed at a coral site was 550 µatm (Water Creek MC site, July 2011) and 2.82 (Princess Bay ROC site, November 2010), respectively (Fig. 3g and h).

Reef data from Long Bay were collected only at 7:00 am and 11:00 am (Fig. 3, Table 4). Therefore, only the minimum Ω_A, pH, temperature and DO data, and maximum values for TA, C_T and pCO_2 are comparable to Hurricane Hole data. Median data for reef parameters may be biased toward lower or higher values because they do not reflect full diurnal cycle conditions; and comparison of reef data to Hurricane Hole excludes November 2010 data that reflect tropical storm conditions. Long Bay reef Ω_A showed a minimum value of 2.93 that was considerably lower than any other coral site in Hurricane Hole. This reef value is also lower than the reported range of dissolution thresholds. The lowest Ω_A of 3.18 at Hurricane Hole coral sites occurred in Otter Creek during July 2011, and this was the only coral site that showed a Ω_A that fell within the reported carbonate dissolution threshold ranges. All median and maximum values from Hurricane Hole coral sites in July 2011 and 2012 fell above dissolution threshold ranges, and maximum values reached 4.2. Minimum pH observed at the Long Bay reef was 7.894, and was lower than the lowest pH (7.95, also in Otter Creek during July 2011) recorded for any coral site in Hurricane Hole. Maximum pCO_2

values at Long Bay reef (626 μatm) were higher than any other coral site in Hurricane Hole (maximum = 550 μatm in Water Creek, July 2011) and fell above the reported dissolution threshold range. Our data indicate that maximum Ω_A at the seafloor where corals are growing was not consistently elevated in mangrove coral sites relative to the nearby reef. However, minimum values at mangrove coral sites were not as low as those at the reef site and in most locations remained above saturation state thresholds for carbonate dissolution unlike reef values.

X-ray diffraction analyses of surface sediment samples in Hurricane Hole indicate sediments at all three of the inner bay MNC sites have the lowest percentages of carbonate sediments (12 to 55%) and no high-magnesium calcite (high-Mg calcite, the most soluble phase of calcium carbonate) in two of the three bays (Princess Bay and Water Creek) (Tables 5 and 6) despite the presence of crustose coralline algae that produces high-Mg calcite. Percent total organic matter (TOM) is less than 12% throughout the bays, but higher at inner- and mid-bay sites than outer-bay sites. Low pH_T and high pCO_2 conditions generated by respiration and oxidation of organic matter in inner bays create a chemical environment that is conducive to dissolution of the fine-grained sediments produced by the calcareous green algae and coralline algae associated with these mangrove communities. Highest percentages of carbonate sediments (approximately 70 to 97%) are found in MC and ROC sites in the middle and outer bays, and high-Mg calcite is present at all locations. The only MNC site with high-Mg calcite in sediments was in Otter Creek. Highest pH_T of all MNC sites was in Otter Creek while the lowest was in Water Creek. The lowest pH_T observed at the MNC site in Otter Creek was 7.90, however no median pH_T dropped below 7.95. The lowest pH_T at the MNC site in Princess Bay (where no Mg-calcite was observed) was above 7.90; however median pH_T at this site fell to 7.93 during July 2011. The lowest median and minimum pH at a coral site was 7.97 and 7.93, respectively, and occurred at the MC site in Water Creek during July 2011. These findings suggest that dissolution of fine-grained carbonate sediments occurs in areas with frequent exposure to pH_T below 7.93 to 7.95, and coral growth is limited to areas with minimum pH_T above 7.93.

3.3 Process heterogeneity

Process heterogeneity resulting from spatial variations in community structure and hydrographic conditions is a key factor in maintaining disequilibrium between coastal and open ocean water masses. Correlation of salinity-normalized total alkalinity (nA_T) and dissolved inorganic carbon (nC_T) can be used to indicate the potential influence of calcification, carbonate sediment dissolution, photosynthesis, and respiration on seawater carbonate chemistry (Suzuki and Kawahata, 2003). A linear regression slope approaching 2 indicates calcification and dissolution are dominant processes, and the slope can be used to calculate the ratio of net ecosystem calcification (NEC) to net community production (NCP). Eighteen of 27 site measurements showed a correlation between nA_T and nC_T with a r^2 value of greater than 0.5 (Fig. 5). MNC sites showed the greatest range of nA_T and nC_T and the greatest potential/tendency toward carbonate sediment dissolution. This result is consistent with the low pH_T, high pCO_2, low mineral saturation state, and lower percentages of carbonate sediments characteristic of MNC sites. MC and ROC sites showed similar ranges and values of nA_T and nC_T. Ratios of NEC:NCP were calculated for the 18 site measurements with r^2 values greater than 0.5 (Table 7). NEC:NCP for all sites ranged from 0.14 to 12.1. Average values were lowest at MC sites (0.5 +/-0.6), highest at ROC sites (3.1 +/- 5.0), with intermediate values at MNC sites (0.9 +/-1.1). Standard deviations were large among study sites (Table 7). However, generally lower NEC:NCP ratios at MC sites and low TOM in sediments may help maintain higher pH_T at MC sites relative to MNC sites. Intermediate NEC:NCP ratios at MNC sites likely reflect the dominance of calcareous algae and seagrass, while highest NEC:NCP ratios at ROC sites reflect the dominance of corals and lack of seagrass and calcareous algae in close proximity.

Lagrangian drifter studies were conducted in Water Creek, Otter Creek, and Princess Bay during August 2011, and indicated that surface currents within the bays move primarily from inner to outer bay due to prevailing easterly winds (McKenzie, 2012). Additionally, estimated water mass residence times in each of these bays are long, on the time scale of days (McKenzie, 2012), which, combined with shallow water depths, can increase the impact of NEC and NCP on seawater chemistry (Anthony et al., 2011). Carbonate sediment dissolution (a process that consumes CO_2 and generates HCO_3^- and Ca^{2+}) at upstream, inner bay MNC sites may provide a source of alkalinity to downstream coral sites that helps to maintain mineral saturation states and support coral calcification. The collocation of corals with mangroves in areas of relatively high NCP, and low TOM in sediments also helps maintain pH_T and saturation states at MC sites that are similar to ROC sites. This combined effect of heterogeneity in community structure, hydrography, and biologically driven changes in seawater chemistry has been demonstrated as an effective means to buffer decreases in mineral saturation state and increase calcification in downstream communities in experimental coral/macroalgal assemblages (Anthony et al., 2011) and in seagrass/coralline algae and coral/seagrass assemblages on coral reefs in Tanzania and Moorea (Kleypas et al., 2011; Semesi et al., 2009a and b). This same combination of spatial and temporal variations in community structure and processes in mangrove/coral habitats may help buffer against ocean acidification.

3.4 Biological responses

The presence of decades-old coral colonies in these mangrove-lined bays suggests adaptation to higher water temperatures and more resistance to and rapid recovery from bleaching events such as the one that was followed by severe mortality from disease in 2005 on the island's coral reefs. Coral surveys indicate at least 33 species of scleractinian corals are growing in Hurricane Hole Bays (Table 1). Many coral colonies are growing directly on or close to mangrove prop roots, and others grow on rocks or hard substrate close to shore to a depth of approximately 6 m. Initial surveys of bleached and unbleached corals from November 2010 to January 2011 indicate that only 4.5% and 1.7% of *C. natans* colonies were bleached in Otter Creek and Water Creek, respectively, while 58.9% and 17.4% of *D. labyrinthiformis* colonies were bleached in Otter and Water Creeks, respectively. We chose these two coral species as the focus of our observations because they were the most abundant ~~major reef-building~~ species in Hurricane Hole, they are thriving in Hurricane Hole despite a decline in relative and absolute abundance of both species on St. John reefs during the 2005/2006 bleaching and disease event (Whelan et al. 2007, Miller et al. 2009), and both species typically occur in exposed (as opposed to cryptic) habitats on the reefs.

PAR measurements made above the sea surface and at the seafloor at MC sites and ROC sites of similar depth during November 2010 and July 2011 and 2012 indicate that PAR was attenuated during peak daylight hours of 10am to 2pm by 88.6 +/- 5.3%, 70.7 +/- 4.8%, and 72.0 +/- 1.7%, respectively (Fig. 6) where corals grow shaded by the mangroves at MC sites. In addition to shading by mangrove trees, colored dissolved organic matter (CDOM) in the water near mangroves, especially where there is frequent freshwater input, could also attenuate harmful visible and ultraviolet radiation and reduce the photo-oxidative stress on corals (Fitt and Warner, 1995, Shick et al., 1996, Zepp et al., 2008, Ayoub et al., 2012). We do not think that CDOM is likely to be playing a major role in providing additional shading, but it could be a contributing factor. The water clarity is generally very high particularly in shallow water near the mangrove prop roots at our study sites. PAR data in figure 6 shows that PAR at the rock outcrops which are in very close proximity to the mangroves is not considerably attenuated relative to PAR measured in air indicating that CDOM is likely not contributing much to attenuation of solar radiation.

Re-examination of a subset of Otter Creek colonies in spring 2011 showed general recovery from bleaching but some mortality. Different proportions of *C. natans* (72.5% shaded, 27.5% unshaded) and *D. labyrinthiformis* (18.2% shaded, 81.8% unshaded) were found in shaded versus un-shaded conditions (p<0.0001) and had different levels of initial bleaching (p<0.0001, *C. natans*: no shaded colonies bleached, 10.5% of unshaded colonies bleached; *D. labyrinthiformis*: 34.2% of shaded colonies bleached, 66.1% of unshaded colonies bleached). Different mortality outcomes were also observed combining partial and total mortality (p=0.0327) (Fig. 7, Table 8). There was no mortality of shaded *C. natans* colonies and 10.5% mortality in un-shaded colonies. *D. labyrinthiformis* showed 10.5% mortality in shaded and 12.3% mortality in un-shaded colonies, respectively. More *C. natans* colonies grew in the shade than *D. labyrinthiformis* colonies. The fact that *C. natans* (a non-cryptic coral) occurred statistically more often in the shade and that few of these colonies bleached supports the role of shading in providing refuge conditions. Although more un-shaded *D. labyrinthiformis* colonies bleached and bleaching of these was more severe~~,~~ shaded colonies were not more likely to recover normal pigmentation. For this species, shading affected the proportion of colonies that initially bleached (p<0.0001), but not the outcome (p=0.7582). Although more un-shaded colonies of *D. labyrinthiformis* bleached, the mortality outcome for shaded and un-shaded colonies was similar (p=0.7508). Overall, recovery from bleaching was high, with little mortality. Only two *C. natans* colonies bleached. Both had partial mortality and none of the initially unbleached corals showed any mortality (p<0.0001).

Comparison of temperature records in the shallow waters of Hurricane Hole to coral reefs around St. John (Miller et al., 2009; National Park Service, 2012) indicate that corals growing in Hurricane Hole are exposed to higher (0.5 +/- 0.5°C on average) and more variable temperatures than coral reefs around the island (Fig. 8). Low bleaching and mortality have been observed for corals growing on nearshore reefs of Palau that have constant exposure to high temperatures, more variable temperatures, and high vertical attenuation of light caused by suspended particulate matter (van Woesik et al., 2012). Similarly, the resilience of mangrove corals following elevated temperatures likely results from relief from solar radiation stress provided by shading of corals by mangroves.

4 Alternative refuges and resiliency factors

There is an urgent need to identify the characteristics of corals and other reef organisms that could enable them to adapt to the variety of stressors associated with climate change and ocean acidification. Research is needed on how these factors interact and how they will affect the overall biodiversity, function, and transition of these ecosystems. The high diversity of coral reefs (among species and within species) and variable response of organisms to climate change increases the likelihood that at least some reef species will be able to persist in locations with particular environmental conditions in the face of changing climate (Rogers, 2013). The presence and increase in abundance and diversity of corals in the mangrove habitats of St. John could be a recent phenomenon (within the past several decades). ~~Evidence of onshore migrations of coral in response to past changes in sea level rise is well documented in the geologic record (e.g. Hopley et al., 1983; Neumann and Macintyre, 1985). However, evidence for co-location of live corals and mangroves is not.~~ Mangrove-coral habitats provide evidence of ecosystem transition that may be a response to pressures from unprecedented rates of recent climate change. These habitats may serve as an example of a novel coastal ecosystem (Graham et al., 2014) resulting from differential species responses, and provide insights into future evolution of tropical coastal ecosystems with increasing sea level rise, thermal stress, and ocean acidification.

As reefs decline worldwide and sea level continues to rise, alternative (non-reef) shallow-water refuges like mangrove-coral habitats may be critical for insuring the survival of coral species. ~~More definitive research on reef refuges is needed.~~ Examining a hypothesis first proposed by Glynn (1996), Riegl and Piller (2003) evaluated the potential for reefs near cool, upwelled waters; reefs at moderate depth (10 to 20 m); and those associated with offshore banks and islands (far from detrimental human activities), to serve as refuges from elevated temperatures and irradiance. They found some evidence that upwelling areas reduce coral bleaching and increase recovery, and noted large areas (such as off the coast of South Africa) below 10 m, the depth above which (they note) most mortality occurs. However, they found that several of the most remote reefs they examined in the Caribbean had sustained significant loss of coral from bleaching and diseases. The potential for deep reefs (often defined as 30 m and deeper) to serve as refuges for corals and sources of replenishing larvae for shallower reef zones may be limited (Bongaerts et al., 2010). Deep (and moderately deep) reefs are not immune to major stressors including bleaching, disease (e.g. Riegl and Piller, 2003; Menza et al., 2007; Smith et al., 2010) and ocean acidification. Many coral species are not found over an entire range of depths, many do not broadcast (spawn) larvae, and deep corals may not, therefore, provide larvae that can settle and survive in shallow waters. Identification and protection of other natural, alternative, shallow-water refuges is essential as one of the few viable management strategies for sustaining coral and other reef species, and provides one of the only direct actions that can be taken locally to manage climate change impacts (Salm et al., 2006).

The unlikely association of corals with mangroves in many coastal ecosystems due to unsuitable growth conditions has dissuaded previous consideration of these habitats as potential coral refuges. Many mainland mangrove habitats especially those with large watersheds and high rates of freshwater run-off are not likely candidates for coral refuges. Despite the fact that St. John is chronically exposed to episodic storm events with high rainfall that can lower salinity (for example as shown in our November 2010 data), corals are thriving in the bays of Hurricane Hole and have been over decades. Study sites in Princess Bay showed lower coral diversity and abundance than in Otter and Water Creeks perhaps because it receives more freshwater runoff due to a larger watershed size. However, data are too few to quantify physical constraints on topographic boundaries that limit refuge potential for these coastal habitats. Numerous small tropical islands worldwide have physical characteristics similar to the U.S. Virgin Islands (for example where freshwater input is limited due to small watersheds and no permanent sources of freshwater inflow) and the potential for suitable mangrove-coral refuge conditions. Our findings identify the first naturally existing, alternative (non-reef) refuge from climate change for reef-building corals and provide baseline resiliency factors to assist in identifying and characterizing mangrove-coral and other alternative refuges around the world.

We consider the St. John mangrove habitat ~~that we have described~~ as a refuge because it provides relief from thermal and photo-oxidative stress through shading by mangroves and variability of seawater temperatures, and because biological and sedimentological processes buffer declines of pH and carbonate mineral saturation states that can impede growth of calcifying organisms. Exposure to warmer and more variable conditions in the mangroves may facilitate adaptation of these corals to higher temperatures and may enhance resiliency for future expansion under changing environmental conditions (van Woesik et al., 2012; Palumbi et al., 2014). Carbonate mineral saturation states and pH in the mangrove coral habitats are not elevated relative to the highest reported values on nearby Long Bay reef. However, they are not as low as those on the reef and generally remain outside of critical threshold ranges. We suggest that elevation of carbonate mineral saturation state relative to the highest reef environment values is not a refuge criterion requirement for ocean acidification. Rather, the ability of the refuge environment to buffer declines in pH and carbonate saturation state to keep them from surpassing critical thresholds relative to reef environments is the most important factor. Key resiliency factors for mangrove-coral habitats include: 1) high diversity and variable response of coral species to climate change stressors, 2) heterogeneity of benthic community composition, processes, and proximity of different habitat types, 3) hydrographic conditions that amplify biogeochemical effects on seawater chemistry and promote chemical characteristics that support coral growth, 4) exposure to variable water temperatures and physical shading of corals from solar radiation (Table 9). The appropriate combination of all of these factors for creating refuge conditions is not generally characteristic of most coral reef environments. Thus, only a few reef systems that protect against increased temperatures, solar radiation or ocean acidification have been identified, and none have been identified that protect from all three stressors like the mangrove-coral habitats of St. John.

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Table 1. Species list of corals living in mangroves.

Coral Species	Princess Bay	Otter Creek	Water Creek
Stephanocoenia intersepta	x	x	x
Acropora palmata			x
Agaricia agaricites	x	x	x
Agaricia spp		x	x
Siderastrea siderea	x	x	x
Siderastrea radians	x	x	x
Porites astreoides	x	x	x
Porites porites	x	x	x
Porites furcata	x	x	x
Porites divaricata	x		
Favia fragum	x	x	x
Diploria labyrinthiformis	x	x	x
Pseudodiploria clivosa		x	x
Pseudodiploria strigosa	x	x	x
Manicina areolata	x	x	x
Colpophyllia natans	x	x	x
Colpophyllia amaranthus		x	
Cladocora arbuscula	x		
Orbicella annularis	x	x	
Orbicella faveolata	x	x	x
Orbicella franksii		x	x
Montastraea cavernosa		x	x
Solenastrea bournoni		x	
Phyllangia americana		x	
Oculina diffusa	x	x	
Meandrina meandrites		x	x
Dichocoenia stokesi			x
Dendrogyra cylindrus		x	x
Scolylmia cubensis	x	x	x
Scolymia lacera		x	
Mycetophyllia spp.		x	x
Eusmilia fastigiata		x	x
Tubastrea aurea		x	x
Millepora spp.	x	x	x
Totals	19	30	26

Table 2. Location of HOBO temperature loggers in Hurricane Hole, St. John, USVI.

Logger ID	Location	Latitude (DD)	Longitude (DD)
1208639	Otter Creek mid-bay	18.34965	-64.69215
9712498	Princess Bay mid-bay	18.35562	-64.69455
9712499	Otter Creek mid-bay	18.35160	-64.69240
9712501	Water Creek mid-bay	18.34777	-64.69076
9712501	Water Creek mid-bay	18.34773	-64.69072
9712503	Water Creek inner-bay	18.34963	-64.68951
9712511	Otter Creek inner-bay	18.35119	-64.69111
9712522	Otter Creek outer-bay	18.34950	-64.69243
9712524	Otter Creek inner-bay	18.35008	-64.69069
9712525	Water Creek mid-bay	18.34850	-64.69146
9712534	Water Creek inner-bay	18.35066	-64.68871
9712537	Water Creek outer-bay	18.34596	-64.69165
9712538	Princess Bay outer-bay	18.35328	-64.69333
9712540	Otter Creek inner-bay	18.35107	-64.69013
9712541	Water Creek mid-bay	18.34890	-64.69048
9712545	Princess Bay inner-bay	18.35615	-64.69069
9712546	Water Creek mid-bay*	18.34755	-64.68956
9712547	Otter Creek inner-bay	18.35198	-64.69169

Table 3. Vertical Profile Data.

Depth (m)	Temp. (C^o)	Sal. (psu)	DO (mg L^{-1})	pH$_T$	TA (µmol kg^{-1})	C$_T$ (µmol kg^{-1})	pCO$_2$ (µatm)	Ω_A
1.5	28.9	36.1	5.97	8.043	2368	2018	404	3.98
3.0	28.9	36.1	5.96	8.025	2336	2001	419	3.80
4.6	28.9	36.1	5.95	8.012	2322	1997	433	3.69
6.0	28.9	36.1	5.92	8.004	2323	2003	443	3.64

Vertical profile data were collected between 7:00 am and 7:07 am on July 19, 2011 near the mouth of Otter Creek at study site number STJ17 (Fig. 1).

Table 4. Long Bay Reef Data.

Site	Date	Time	Temp. (C^{o})	Sal. (psu)	DO (mg L^{-1})	pH_T	TA (μmol kg^{-1})	C_T (μmol kg^{-1})	pCO_2 (μatm)	Ω_A
1	7/16/04	11:00	28.7	35.7	6.9	7.996	2267	1962	443	3.47
1	8/18/04	07:00	28.9	35.4	5.2	7.925	2283	2019	548	3.09
1	8/19/04	07:00	29.2	35.2	5.0	7.955	2309	2023	509	3.33
2	7/16/04	11:00	29.3	35.7	ND	8.031	2288	1954	404	3.80
2	7/17/04	07:00	28.3	35.7	4.6	7.943	2286	2014	520	3.14
2	8/18/04	07:00	28.6	35.4	5.3	7.937	2279	2010	528	3.12
2	8/19/04	07:00	29.1	35.2	4.5	7.894	2282	2033	595	2.93
3	7/20/04	11:00	28.8	35.7	7.2	8.006	2269	1956	431	3.55
3	8/22/04	07:00	29.0	34.9	4.7	7.950	2275	2000	510	3.22
4	8/22/04	07:00	29.0	34.9	4.9	7.936	2269	2002	529	3.13

Long Bay reef data were collected from four locations at 7:00 am or 11:00 am between July 16 and August 22, 2004. ND = no data.

Table 5. Grain size of surface sediments.

Sample Location	% Gravel	% Sand	% Silt	% Clay	% Mud	Mean Φ*	% Carbonate	% TOM[†]	% Insoluble Residue
STJ5	71.0	20.7	4.7	3.5	8.2	-0.4	93.9	2.2	3.9
STJ7	14.9	80.6	3.7	0.8	4.5	1.0	73.8	0.3	25.9
STJ8	58.2	25.8	11.6	4.4	16.0	0.4	69.7	7.1	23.2
STJ10	15.0	27.7	44.2	13.1	57.3	3.5	54.6	11.9	33.5
STJ11	2.7	81.7	13.6	2.0	15.6	1.9	20.0	1.0	79.0
STJ12	9.2	88.2	1.0	1.6	2.6	1.3	96.8	0.1	3.1
STJ13	24.2	52.4	17.6	5.9	23.5	2.0	82.8	1.4	15.8
STJ14	38.0	31.2	27.0	3.7	30.8	1.6	74.9	6.2	18.9
STJ15	0.5	35.0	61.8	2.6	64.5	4.3	11.7	2.9	85.4

*-$\log_2$ of the grain diameter in mm, [†]total organic matter from loss on ignition. See Fig. 1 for sample locations.

Table 6. Carbonate mineralogical composition of surface sediments.

Sample Location	Carbonate Mineralogy		
	% Aragonite	% Mg-Calcite	% Calcite
STJ5	53.3	8.8	37.9
STJ7	75.4	8.0	16.7
STJ8	60.2	21.1	18.8
STJ10	70.7	16.3	13.1
STJ11	65.8	0.0	34.2
STJ12	82.3	16.5	1.2
STJ13	58.9	34.6	6.4
STJ14	74.6	11.3	14.1
STJ15	78.9	0.0	21.1

Table 7. NEC:NEP ratios for study sites with nA_T vs. nC_T r^2 >0.5.

Date	Location	Site	NEC:NEP	LRE	r^2
November 2010	Otter Creek	MC	NA	0.17570x + 2063	0.12
		MNC	0.96	0.9795x + 376.87	0.86
		ROC	12.11	2.1779x – 2098.5	0.50
	Water Creek	MC	NA	-0.2660x + 3000.5	0.27
		MNC	0.33	0.5031x + 1354.2	0.83
		ROC	NA	-0.1158x + 2684.9	0.02
	Princess Bay	MC	0.32	0.4936x + 1343.3	0.57
		MNC	3.35	1.5414x – 823.71	0.93
		ROC	0.75	0.8602x + 600.04	0.91
July 2011	Otter Creek	MC	1.63	1.2413x – 181.92	0.87
		MNC	NA	0.3334x + 1616.5	0.17
		ROC	1.27	1.1153x + 66.438	0.70
	Water Creek	MC	0.44	0.6069x + 1075.7	0.68
		MNC	0.80	0.8863x + 516.13	0.84
		ROC	1.22	1.0582x + 192.54	0.58
	Princess Bay	MC	0.18	0.3060x + 1661.5	0.94
		MNC	0.44	0.6141x + 1069.5	0.72
		ROC	NA	0.0369x + 2179.8	0.01
July 2012	Otter Creek	MC	0.28	0.4376x + 1435.1	0.55
		MNC	NA	0.2189 + 1865.6	0.32
		ROC	NA	0.2080x + 1889.5	0.41
	Water Creek	MC	NA	0.1773x + 1950.7	0.45
		MNC	0.18	0.2965x + 1707.6	0.84
		ROC	NA	0.2915x + 1723.4	0.38
	Princess Bay	MC	0.25	0.4042x + 1507.2	0.89
		MNC	0.14	0.2513x + 1810.3	0.95
		ROC	0.31	0.4740x + 1366.3	0.85

Ratios of net ecosystem calcification to net community production (NEC:NCP) were calculated from the slopes of best-fit linear regression lines for 18 of 27 site measurements showing a correlation between nA_T and nC_T with r^2 >0.5. NEC:NCP was calculated using the equation 1/[(2/m)-1] where m = slope from the corresponding linear regression equation (LRE). MC = mangrove-coral sites, MNC = mangrove no coral sites, ROC = rock outcrop coral sites.

Table 8. Condition of colonies of *Diploria labyrinthiformis* and *Colpophyllia natans* during 2010-2011.

Colony condition	*D. labyrinthiformis* Shaded	*D. labyrinthiformis* Unshaded	*C. natans* Shaded	*C. natans* Unshaded
Total number of colonies	38	171	50	19
Bleached to dead	1	5	0	0
Bleached to partial mortality	1	10	0	2
Bleached to unbleached	11	98	0	0
Unbleached to dead	1	2	0	0
Unbleached to partial mortality	1	4	0	0
Unbleached to unbleached	23	52	50	17

Table 9. Resiliency factors for mangrove-coral refuges.

Resiliency factor	Local condition at mangrove-coral sites in St. John, USVI
Diversity and response of organisms	
·High diversity of coral species	·More than 30 coral species identified
·Variable response of organisms	·Preferential growth of *C. natans* in shaded areas, more bleaching of exposed than shaded *D. labyrinthiformis* colonies
Heterogeneity and habitat proximity	
·Community heterogeneity	·Collocation of corals and mangroves, upstream to downstream transition from mangrove/seagrass/algae to mangrove/coral habitat
·Available substrate for coral settlement	·Prop roots, hard bottom
·Low NEC:NCP ratios at upstream or coral locations and proximity to coral growth sites	·Average NEC:NEP of 0.5 to 0.9 at mangrove-coral (MC) sites and upstream mangrove, calcareous algae, seagrass communities (MNC), respectively
Hydrographic & chemical conditions	
·Limited or no influence from permanent freshwater inflow	·No permanent or frequent freshwater inflow
·Long water mass residence times	·Days (McKenzie, 2012)
·Hydrographic conditions that maintain substrate appropriate for coral settlement and growth	·Periodic influence from storm waves that prevents settlement of fine-grained sediments, low TOM (<12%), >69% sand and gravel
·Seawater chemistry conducive to coral growth	·Minimum pH 7.93, maximum pCO_2 550 μatm, minimum Ω_A 2.82
Exposure	
·Consistent exposure of corals to higher, more variable temperatures	·Average temperature 0.5 ± 0.5°C higher than reef tract temperatures (2010)
·Physical shading from solar radiation	·Mangrove canopy attenuates >70% of incident photosynthetically active radiation (PAR)

Figure 1. Study sites (STJ#s) in Hurricane Hole, St. John, USVI. MC = mangroves with corals growing on and near mangrove prop roots and shaded by the mangrove canopy, MNC = mangrove with no corals growing in association with them, ROC = rock outcrops with live corals and no shading from mangroves.

Figure 2. Corals growing under a mangrove canopy and attached to mangrove prop roots including a colony of *Colpophyllia natans* (center of photo).

Figure 3. Chemical and physical parameters. Median and range for chemical and physical parameters in Hurricane Hole bays during November 2010, and July 2011 and 2012 and for Long Bay reef during July and August 2004 (n = 10). Measurements were made every 4-hours throughout a diurnal cycle (n=7) at each study site during November 2010 and July 2011 and 2012, and for 3 consecutive days (n=19) in Otter Creek during July 2012. Measurements at Long Bay reef were made at 7am and 11am (n = 7 and 3, respectively). No DO data was collected in Water Creek during July 2012 due to DO sensor failure. Red shaded areas (3g and 3h) show reported ranges for pCO_2 and Ω_A thresholds for carbonate sediment calcification and dissolution. Data available at http://doi.pangaea.de/10.1594/PANGAEA.825752.

Figure 4. Vertical profile data of seawater chemical parameters collected at 7:00 a.m. on July 19, 2011 over coral habitat at 6.5 m water depth. Vertical axis = depth below sea surface.

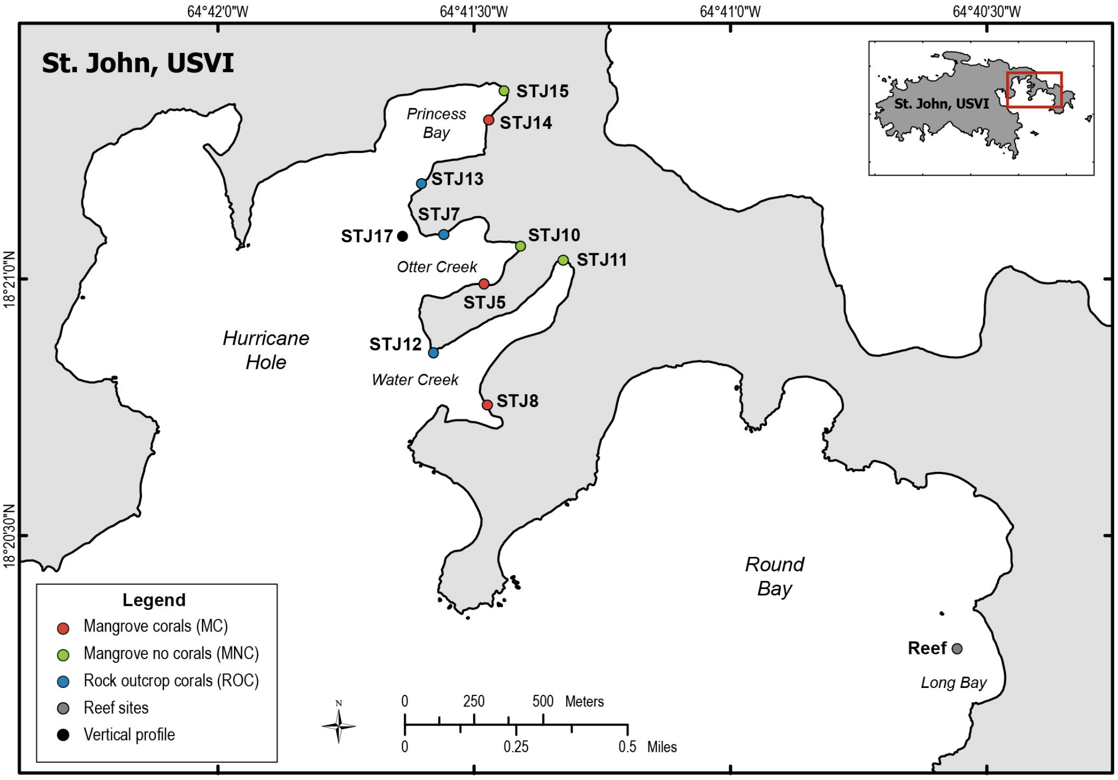
Figure 5. Salinity normalized total alkalinity (nA_T) and total carbon (nC_T) plots with best fit linear regressions (see Table ~~5~~ for equations and r^2 values) for November 2010, July 2011, and July 2012 in Otter Creek, Water Creek, and Princess Bay. Average nA_T and nC_T for each time period was calculated from all data collected from each site within each bay. Gray lines represent the theoretical impact of calcification (G), carbonate sediment dissolution (D), photosynthesis (P), respiration (R), CO_2 uptake (CU), and CO_2 release (CR) on A_T and C_T.

Figure 6. Photosynthetically active radiation (PAR) measurements at study sites in Otter Creek (a, b, and c) and Water Creek (d and e). Measurements represent 15-minute averages. STJ# = PAR sensor location as referenced in Fig. 1. Data available at http://doi.pangaea.de/10.1594/PANGAEA.825752.

Figure 7. Recovery results for shaded vs. un-shaded (a) *Diploria labyrinthiformis* (n=38 and n=171 shaded and un-shaded colonies, respectively) and (b) *Colpophylia natans* (n=50 and n=19 shaded and un-shaded colonies, respectively) from 2010 to 2011. Also refer to Table ~~6~~.

Figure 8. Temperature trends from mangrove-coral and reef tract habitats. Hurricane Hole temperature data was averaged from 18 data loggers distributed throughout Hurricane Hole bays (Table 2). Temperature measurements were recorded every 2-hours and daily averages were generated from all sites in Hurricane Hole, and from 6 reef sites around St. John. Data are available at http://doi.pangaea.de/10.1594/PANGAEA.825752.

782 Figure 1.



783
784

Figure 2.

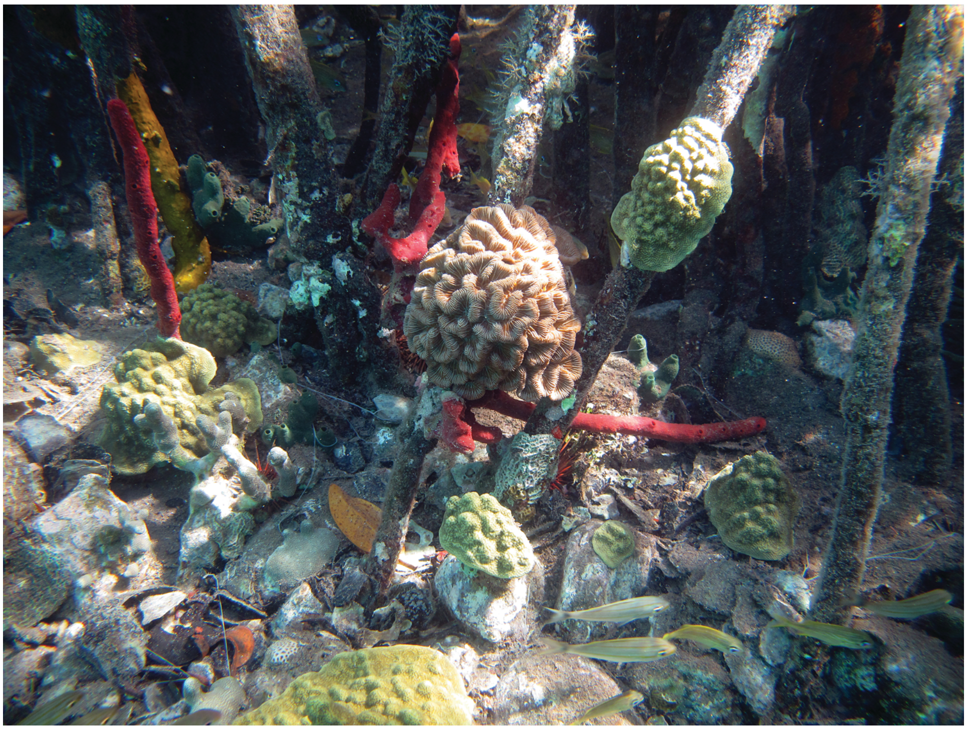
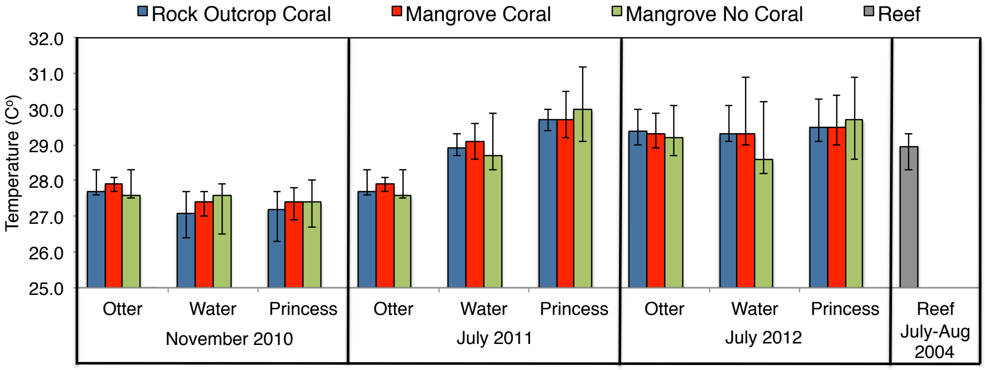


Figure 3a.



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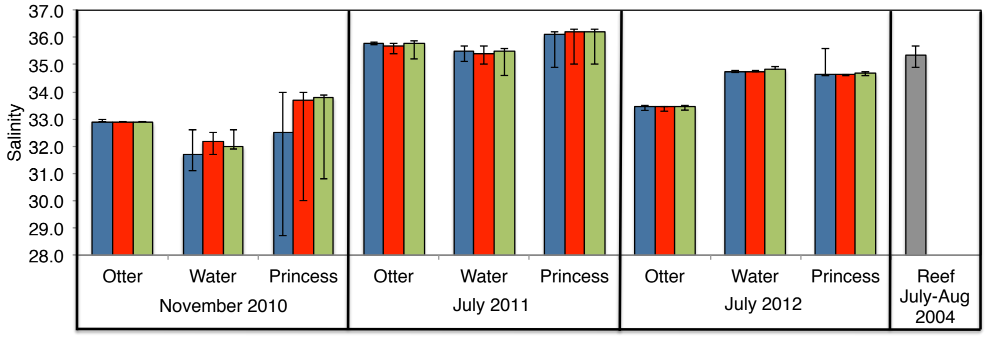

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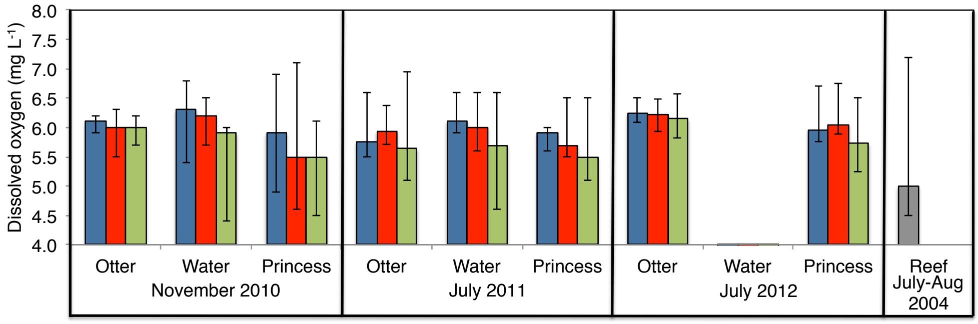

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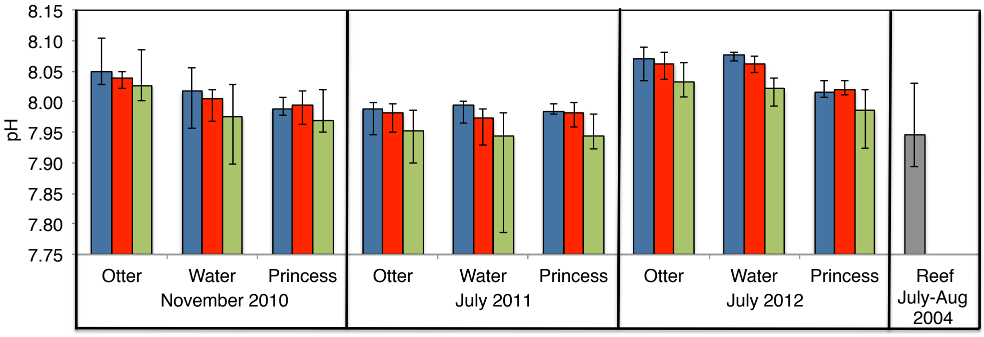

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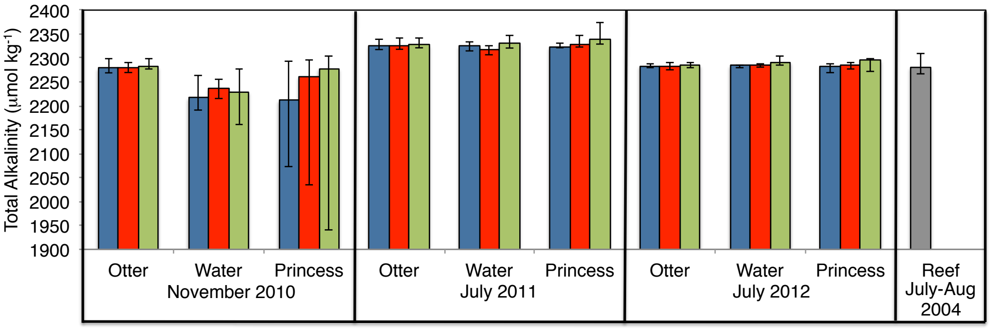
797 e.



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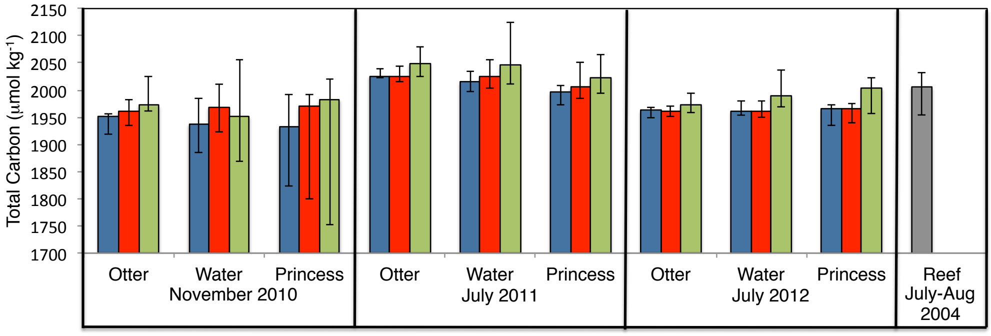

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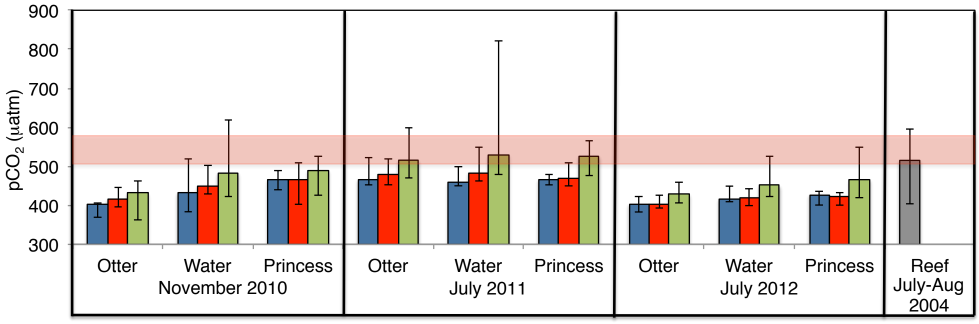
801 g.



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803 h.

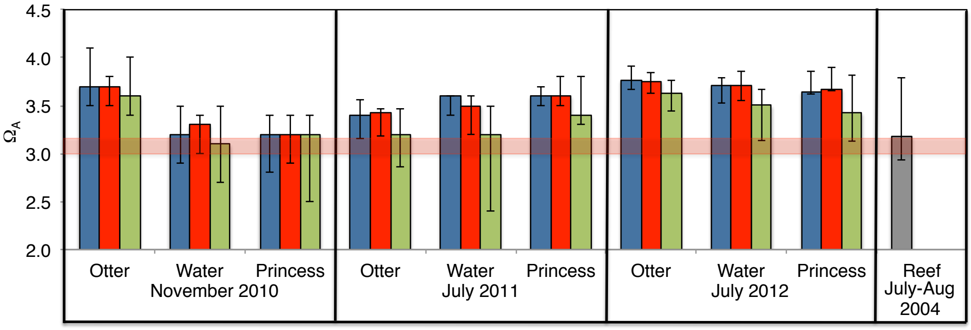

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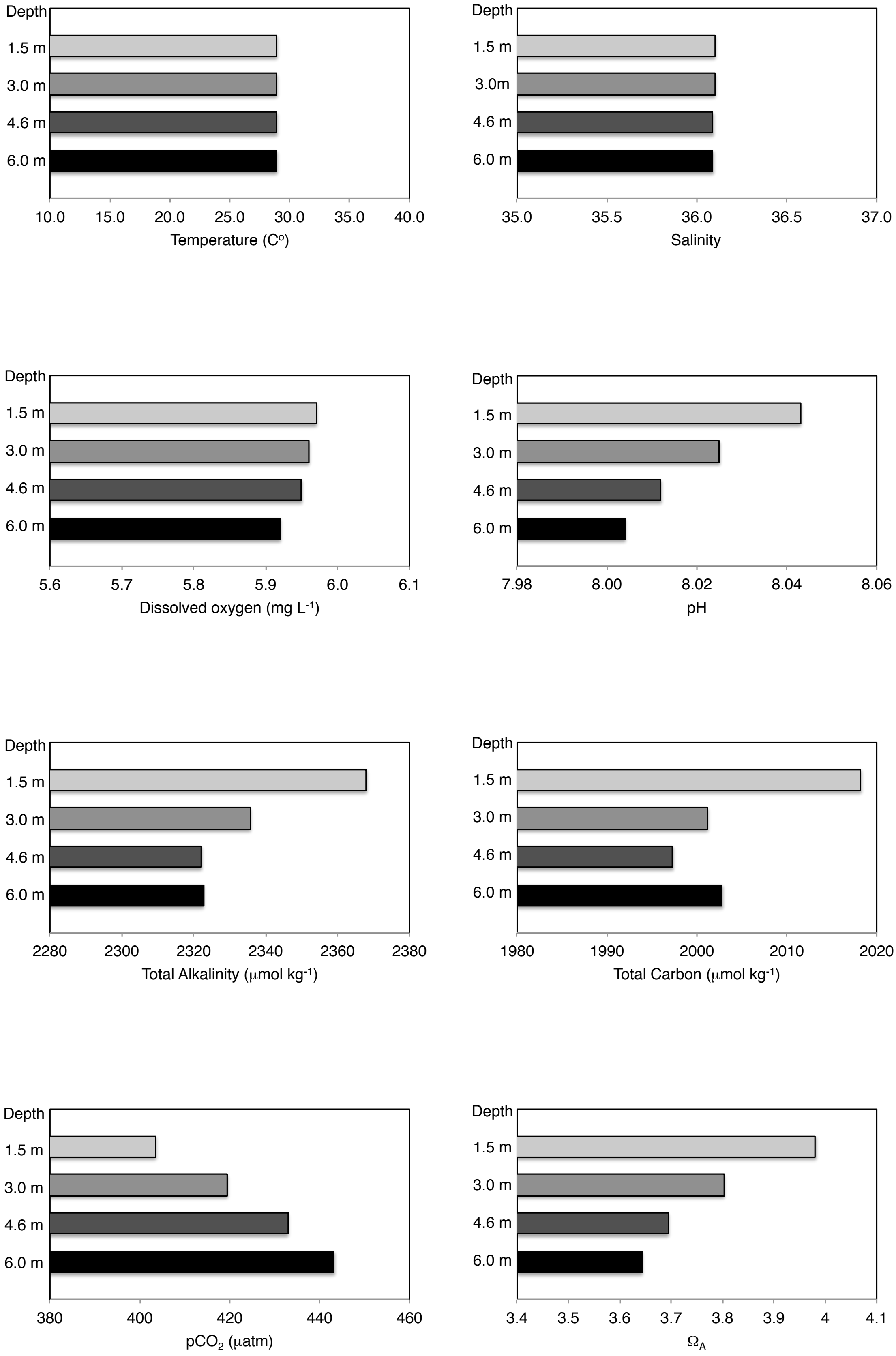
Figure 4.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3.0 m
4.6 m
6.0 m
10.0
15.0
20.0
25.0
30.0
35.0
40.0
Temperature (C°)
Depth
1.5 m
3.0m
4.6 m
6.0 m
35.0
35.5
36.0
36.5
37.0
Salinity
Depth
1.5 m
3.0 m
4.6 m
6.0 m
5.6
5.7
5.8
5.9
6.0
6.1
Dissolved oxygen (mg L-1)
Depth
1.5 m
3.0 m
4.6 m
6.0 m
7.98
8.00
8.02
8.04
8.06
pH
Depth
1.5 m
3.0 m
4.6 m
6.0 m
2280
2300
2320
2340
2360
2380
Total Alkalinity (μmol kg-1)
Depth
1.5 m
3.0 m
4.6 m
6.0 m
1980
1990
2000
2010
2020
Total Carbon (μmol kg-1)
Depth
1.5 m
3.0 m
4.6 m
6.0 m
380
400
420
440
460
pCO2 (μatm)
Depth
1.5 m
3.0 m
4.6 m
6.0 m
3.4
3.5
3.6
3.7
3.8
3.9
4
4.1
ΩA

Figure 5.

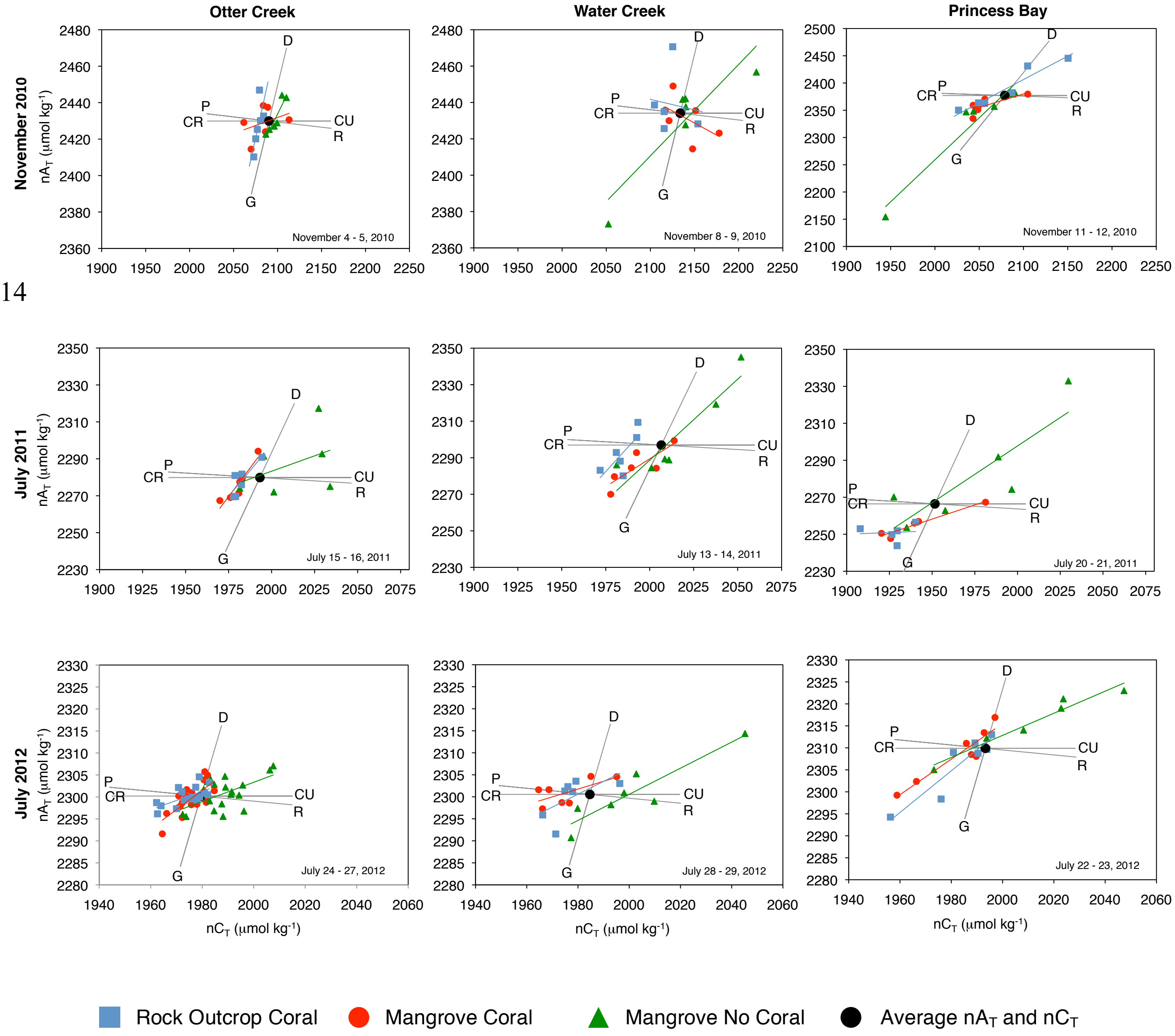
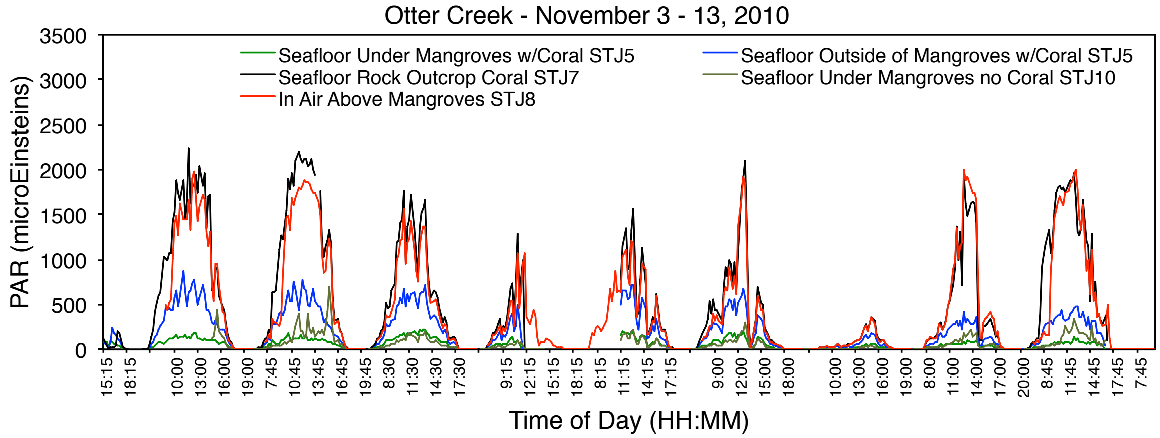

Otter Creek
Water Creek
Princess Bay
November 2010
July 2011
July 2012
nA$_T$ (µmol kg^{-1})
nC$_T$ (µmol kg^{-1})
November 4 - 5, 2010
November 8 - 9, 2010
November 11 - 12, 2010
July 15 - 16, 2011
July 13 - 14, 2011
July 20 - 21, 2011
July 24 - 27, 2012
July 28 - 29, 2012
July 22 - 23, 2012
D
P
CR
CU
R
G
2480
2460
2440
2420
2400
2380
2360
2500
2450
2400
2350
2300
2250
2200
2150
2100
1900
1950
2000
2050
2100
2150
2200
2250
2350
2330
2310
2290
2270
2250
2230
1925
1975
2025
2075
2330
2325
2320
2315
2310
2305
2300
2295
2290
2285
2280
1940
1960
1980
2000
2020
2040
2060
Rock Outcrop Coral
Mangrove Coral
Mangrove No Coral
Average nA$_T$ and nC$_T$

Figure 6

a.


Otter Creek - November 3 - 13, 2010
Seafloor Under Mangroves w/Coral STJ5
Seafloor Outside of Mangroves w/Coral STJ5
Seafloor Rock Outcrop Coral STJ7
Seafloor Under Mangroves no Coral STJ10
In Air Above Mangroves STJ8
PAR (microEinsteins)
3500
3000
2500
2000
1500
1000
500
0
15:15
18:15
10:00
13:00
16:00
19:00
7:45
10:45
13:45
16:45
19:45
8:30
11:30
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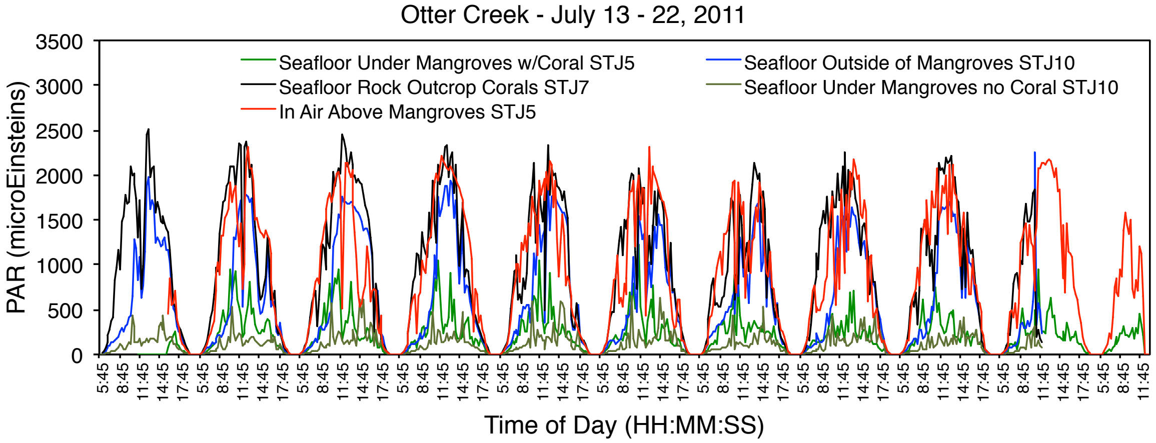
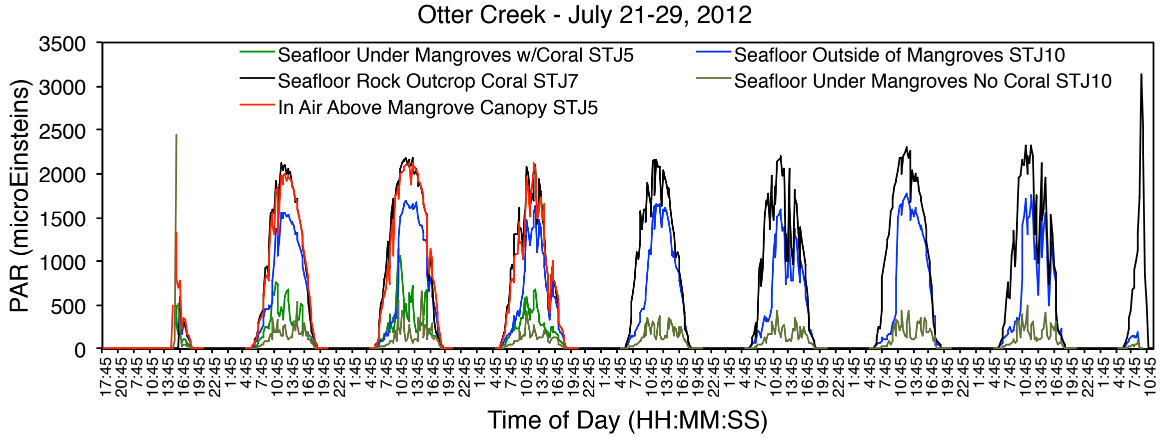
9:00
12:00
15:00
18:00
10:00
13:00
16:00
19:00
8:00
11:00
14:00
17:00
20:00
8:45
11:45
14:45
17:45
7:45
Time of Day (HH:MM)

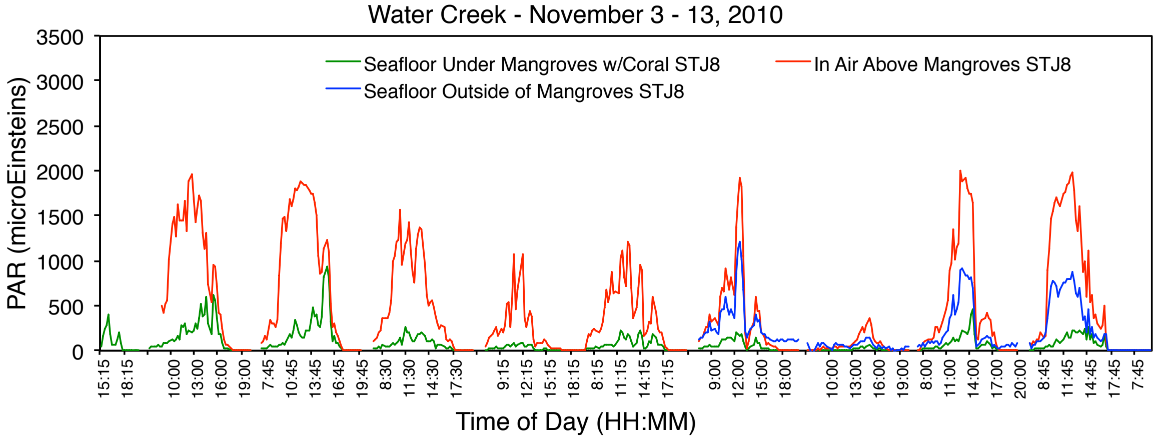
b.


Otter Creek - July 13 - 22, 2011
Seafloor Under Mangroves w/Coral STJ5
Seafloor Outside of Mangroves STJ10
Seafloor Rock Outcrop Corals STJ7
Seafloor Under Mangroves no Coral STJ10
In Air Above Mangroves STJ5
PAR (microEinsteins)
3500
3000
2500
2000
1500
1000
500
0
5:45
8:45
11:45
14:45
17:45
Time of Day (HH:MM:SS)

c.


Otter Creek - July 21-29, 2012
Seafloor Under Mangroves w/Coral STJ5
Seafloor Outside of Mangroves STJ10
Seafloor Rock Outcrop Coral STJ7
Seafloor Under Mangroves No Coral STJ10
In Air Above Mangrove Canopy STJ5
PAR (microEinsteins)
3500
3000
2500
2000
1500
1000
500
0
17:45
20:45
7:45
10:45
13:45
16:45
19:45
22:45
1:45
4:45
Time of Day (HH:MM:SS)

d.


Water Creek - November 3 - 13, 2010
Seafloor Under Mangroves w/Coral STJ8
In Air Above Mangroves STJ8
Seafloor Outside of Mangroves STJ8
PAR (microEinsteins)
3500
3000
2500
2000
1500
1000
500
0
15:15
18:15
10:00
13:00
16:00
19:00
7:45
10:45
13:45
16:45
19:45
8:30
11:30
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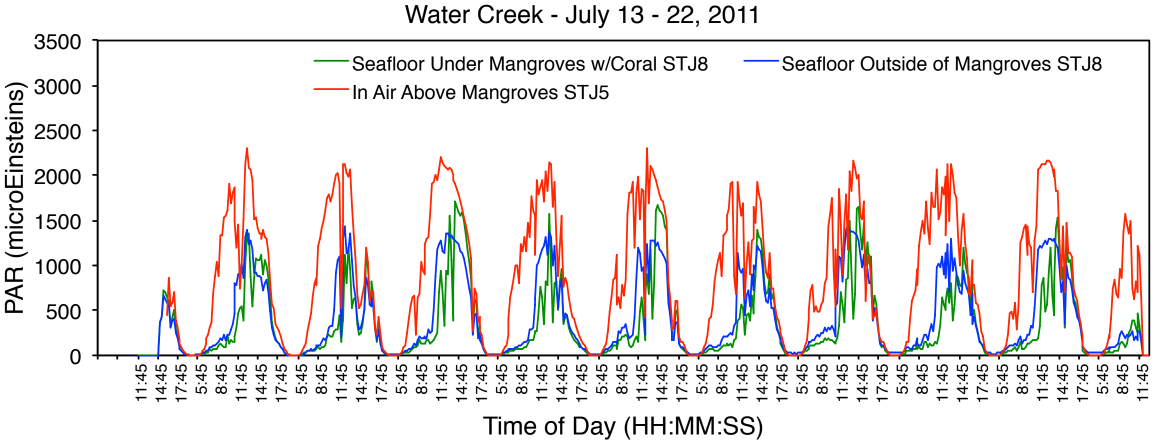
8:00
11:00
14:00
17:00
20:00
8:45
11:45
14:45
17:45
7:45
Time of Day (HH:MM)

e.


Water Creek - July 13 - 22, 2011
Seafloor Under Mangroves w/Coral STJ8
Seafloor Outside of Mangroves STJ8
In Air Above Mangroves STJ5
PAR (microEinsteins)
3500
3000
2500
2000
1500
1000
500
0
11:45
14:45
17:45
5:45
8:45
11:45
14:45
17:45
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5:45
8:45
11:45
Time of Day (HH:MM:SS)

Figure 7.

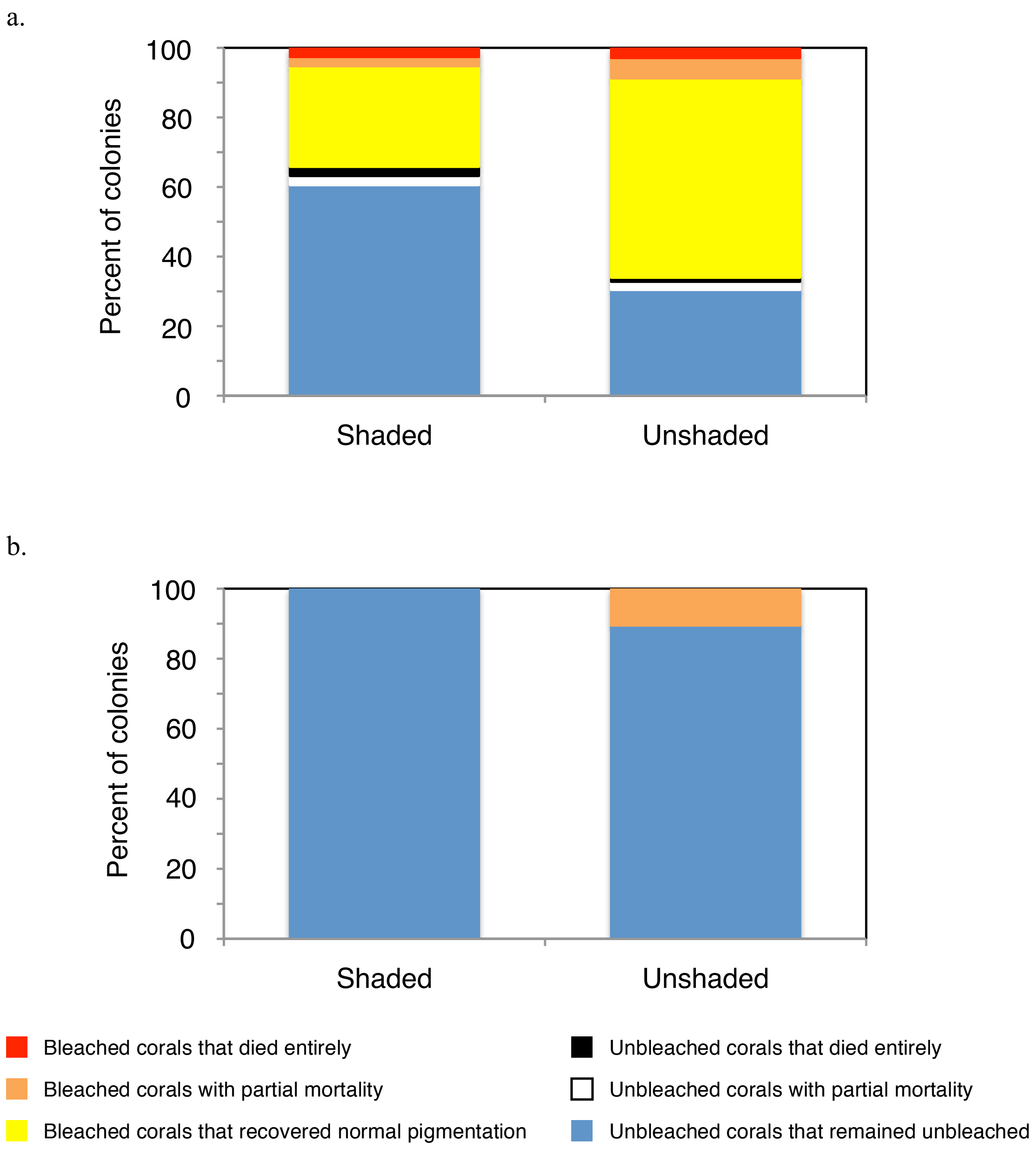
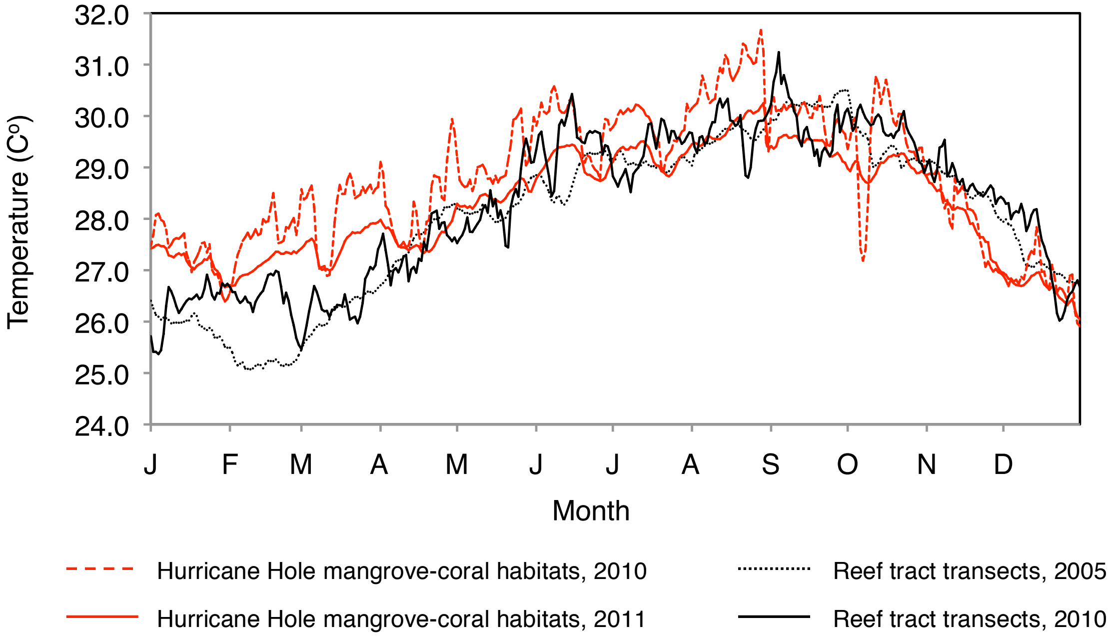

a.
Percent of colonies
100
80
60
40
20
0
Shaded
Unshaded
b.
Percent of colonies
100
80
60
40
20
0
Shaded
Unshaded
🟥 Bleached corals that died entirely
🟧 Bleached corals with partial mortality
🟨 Bleached corals that recovered normal pigmentation
■ Unbleached corals that died entirely
☐ Unbleached corals with partial mortality
🟦 Unbleached corals that remained unbleached

Figure 8.



Temperature (C°)
32.0
31.0
30.0
29.0
28.0
27.0
26.0
25.0
24.0
J
F
M
A
M
J
J
A
S
O
N
D
Month
Hurricane Hole mangrove-coral habitats, 2010
Hurricane Hole mangrove-coral habitats, 2011
Reef tract transects, 2005
Reef tract transects, 2010