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Please refer to the corresponding final paper in BG if available.

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

K. K. Yates¹, C. S. Rogers², J. J. Herlan^{2,*}, G. R. Brooks³, N. A. Smiley¹, and R. A. Larson³

¹US Geological Survey, Coastal and Marine Science Center, St. Petersburg, Florida 33701, USA

²US Geological Survey, Southeast Ecological Science Center, St. John, US Virgin Islands, 00830, USA

³Eckerd College, Galbraith Marine Science Laboratory, St. Petersburg, Florida 33711, USA
* now at: Universidad Catolica del Norte, Larrondo 1281, Coquimbo, Chile

Received: 20 February 2014 – Accepted: 12 March 2014 – Published: 31 March 2014

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

Published by Copernicus Publications on behalf of the European Geosciences Union.

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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, US 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 was 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 heterogeneity, 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

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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 Woosik 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

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contains few references to scleractinian corals growing in mangroves (e.g. Macintyre et al., 2000; Rützler et al., 2000), and no comprehensive surveys or multidisciplinary studies of these habitats have been performed.

In St. John, US 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. This ecosystem is 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, US 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

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with unshaded corals (ROC sites) in all three bays. 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).

2.1 Seawater chemistry

Seawater was collected for A_T , C_T , and pH_T analyses from each site every 4 h ($n = 7$) throughout 24 h periods in November 2010, July 2011, and July 2012. Measurements were made every 4 h for 3 consecutive days ($n = 19$) in Otter Creek during July 2012. No DO data was 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 $0.45 \mu\text{m}$ 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 h of collection. Samples were analyzed for A_T ($\pm 1 \mu\text{mol kg}^{-1}$) using spectrophotometric methods of Yao and Byrne (1998) with an Ocean Optics USB2000 spectrometer and bromo-cresol purple indicator dye, for C_T ($\pm 3 \mu\text{mol kg}^{-1}$) 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 ($\pm 0.1 \text{ mg L}^{-1}$), temperature ($\pm 0.01 \text{ }^\circ\text{C}$), 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 samples were also collected for measurement of total nitrogen and phosphate in

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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 h throughout 24 h time periods at every sample site in all three bays. Water samples (20 mL) were filtered through 0.22 μm pore size Millepore Sterivex filters rinsed with 2 volumes of sample water. Samples were stored in 20 mL acid-washed polypropylene scintillation vials at 0 °C until time of analysis. Nutrient samples were analyzed at the NOAA Atlantic Oceanographic and Meteorological Laboratory in Miami, FL. Carbonate system parameters including aragonite mineral saturation state (Ω_A) and $p\text{CO}_2$ were calculated from A_T , pH_T , 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).

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 h 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 °C for > 2.5 h (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 *Colpophyllia 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 6 m. 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 h 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 h 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 min

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(15 min averages) at study sites in Otter Creek and Water Creek approximately 20 cm above the seafloor using LI-COR 4π sensors and approximately 3 m above sea level and the mangrove canopy using LI-COR 2π sensors coupled with LI-COR 1000 or LI-COR 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 km², have small watersheds ranging in area from 0.11 km² to 0.43 km², are surrounded by steeply sloped, rocky hillsides, and have a narrow (up to approximately 10 m) fringe of red mangroves (*Rhizophora mangle*). 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 (< 0.25 m). 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 near 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).

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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 $p\text{CO}_2$, 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 $p\text{CO}_2$, 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.

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 $0.238 \pm 0.359 \mu\text{molL}^{-1}$ and $0.066 \pm 0.069 \mu\text{molL}^{-1}$, 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>.

X-ray diffraction analyses of surface sediment samples 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 3 and 4). 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 generate 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.

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Calcification/dissolution thresholds are the levels of aragonite saturation state below which (and $p\text{CO}_2$ 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 $p\text{CO}_2$ 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 $p\text{CO}_2$ 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 $p\text{CO}_2$ 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).

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. 4). 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 $p\text{CO}_2$, low mineral saturation state, and lower percentages of carbonate sediments characteristic of MNC

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 in 2005 that was followed by severe mortality from disease 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.

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 10 a.m. to 2 p.m. by $88.6 \pm 5.3\%$, $70.7 \pm 4.8\%$, and $72.0 \pm 1.7\%$, respectively (Fig. 5) where corals grow shaded by the mangroves at MC sites. 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 vs. unshaded 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. 6, Table 6). There was no mortality of shaded *C. natans* colonies and 10.5% mortality in unshaded colonies. *D. labyrinthiformis* showed 10.5% mortality in shaded and 12.3% mortality in unshaded colonies, respectively. More *C. natans* colonies grew in the shade than *D. labyrinthiformis* colonies. Although more unshaded *D. labyrinthiformis* colonies

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and diversity of corals in the mangrove habitats of St. John could be a recent phenomenon (within the past several decades). Evidence of shoreward 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 are critical for ensuring the survival of coral species. 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. However, numerous small tropical islands worldwide have physical characteristics similar to the US Virgin Islands 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 mangrove–coral and other alternative refuges around the world. Key resiliency factors for mangrove–coral habitats include: (1) high diversity and variable responses 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 7).

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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

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Table 4. 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

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Table 5. NEC : NEP ratios for study sites with nA_T vs. nC_T $r^2 > 0.5$.

Date	Location	Site	NEC : NEP	LRE	r^2
Nov 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
Jul 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
Jul 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.

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[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)**Table 6.** Condition of colonies of *Diploria labyrinthiformis* and *Colpophyllia natans* during 2010–2011.

Colony condition	<i>D. labyrinthiformis</i> Shaded	<i>D. labyrinthiformis</i> Unshaded	<i>C. natans</i> Shaded	<i>C. natans</i> 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

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Table 7. Resiliency factors for mangrove–coral refuges.

Resiliency factor	Local condition at mangrove–coral sites in St. John, USVI
Diversity and response of organisms	
<ul style="list-style-type: none"> High diversity of coral species Variable response of organisms 	<ul style="list-style-type: none"> More than 30 coral species identified Preferential growth of <i>C. natans</i> in shaded areas, more bleaching of exposed than shaded <i>D. labyrinthiformis</i> colonies
Heterogeneity and habitat proximity	
<ul style="list-style-type: none"> Community heterogeneity Available substrate for coral settlement Low NEC : NCP ratios at upstream or coral locations and proximity to coral growth sites 	<ul style="list-style-type: none"> Collocation of corals and mangroves, upstream to downstream transition from mangrove/seagrass/algae to mangrove/coral habitat Prop roots, hard bottom Average NEC : NEP of 0.5 to 0.9 at mangrove–coral (MC) sites and upstream mangrove, calcareous algae, seagrass communities (MNC), respectively
Hydrographic and chemical conditions	
<ul style="list-style-type: none"> Limited or no influence from permanent freshwater inflow Long water mass residence times Hydrographic conditions that maintain substrate appropriate for coral settlement and growth Seawater chemistry conducive to coral growth 	<ul style="list-style-type: none"> No permanent or frequent freshwater inflow Days (McKenzie, 2012) Periodic influence from storm waves that prevents settlement of fine-grained sediments, low TOM (< 12%), > 69% sand and gravel Minimum pH 7.93, maximum $p\text{CO}_2$ 550 μatm, minimum Ω_A 2.82
Exposure	
<ul style="list-style-type: none"> Consistent exposure of corals to higher, more variable temperatures Physical shading from solar radiation 	<ul style="list-style-type: none"> Average temperature $0.5 \pm 0.5^\circ\text{C}$ higher than reef tract temperatures (2010) Mangrove canopy attenuates > 70% of incident photosynthetically active radiation (PAR)

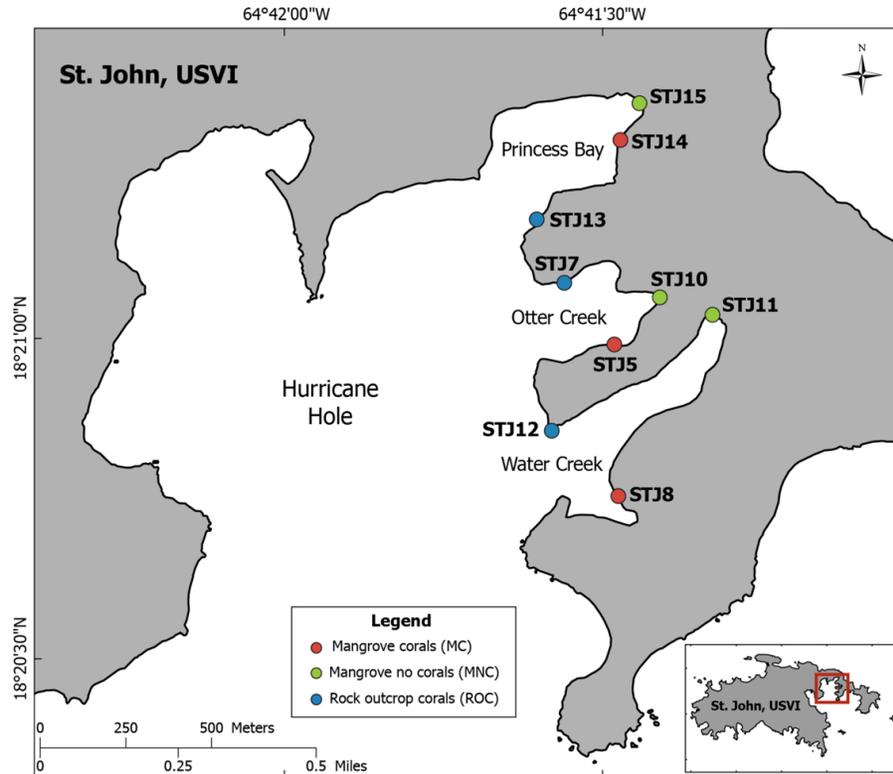


Fig. 1. Study sites (STJ#s) in Hurricane Hole, St. John, USVI. MC = mangroves with corals growing on and near mangrove prop roots and shaded by the mangrove canopy, MNC = mangrove with no corals growing in association with them, ROC = rock outcrops with live corals and no shading from mangroves.

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

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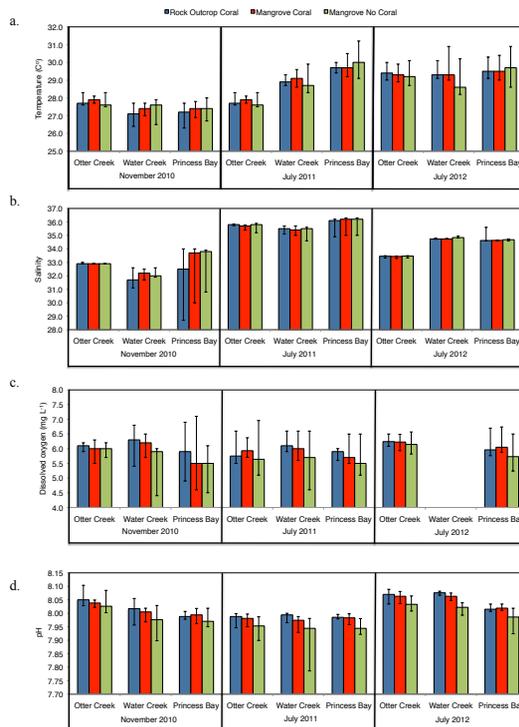


Fig. 3. Chemical and physical parameters. Median and range for chemical and physical parameters in Hurricane Hole bays during November 2010, and July 2011 and 2012. Measurements were made every 4 h throughout a diurnal cycle ($n = 7$) at each study site during November 2010 and July 2011 and 2012, and for 3 consecutive days ($n = 19$) in Otter Creek during July 2012. 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 $p\text{CO}_2$ and Ω_A thresholds for carbonate sediment calcification and dissolution. Data available at <http://doi.pangaea.de/10.1594/PANGAEA.825752>.

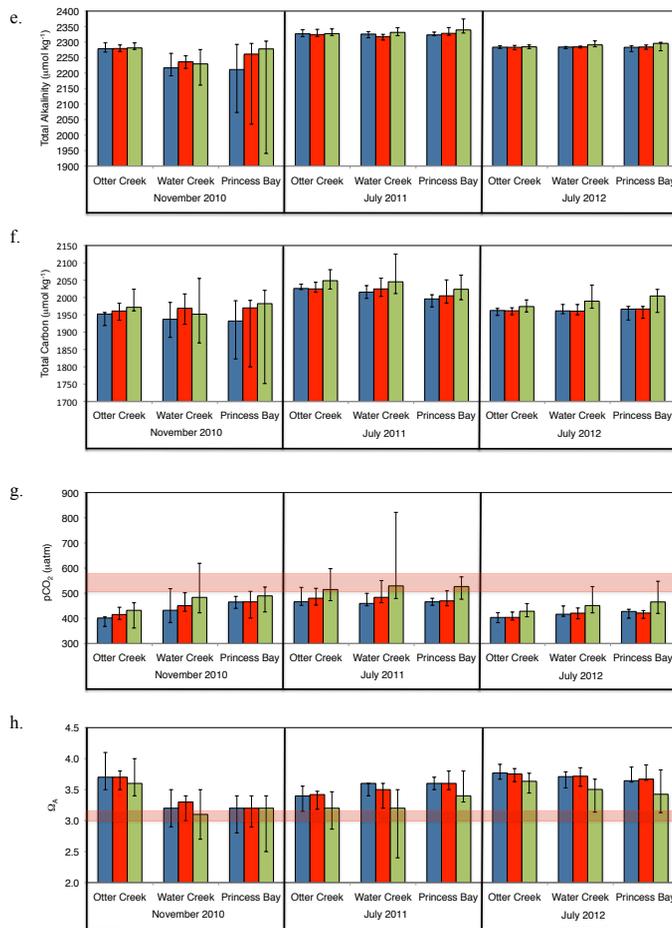


Fig. 3. Continued.

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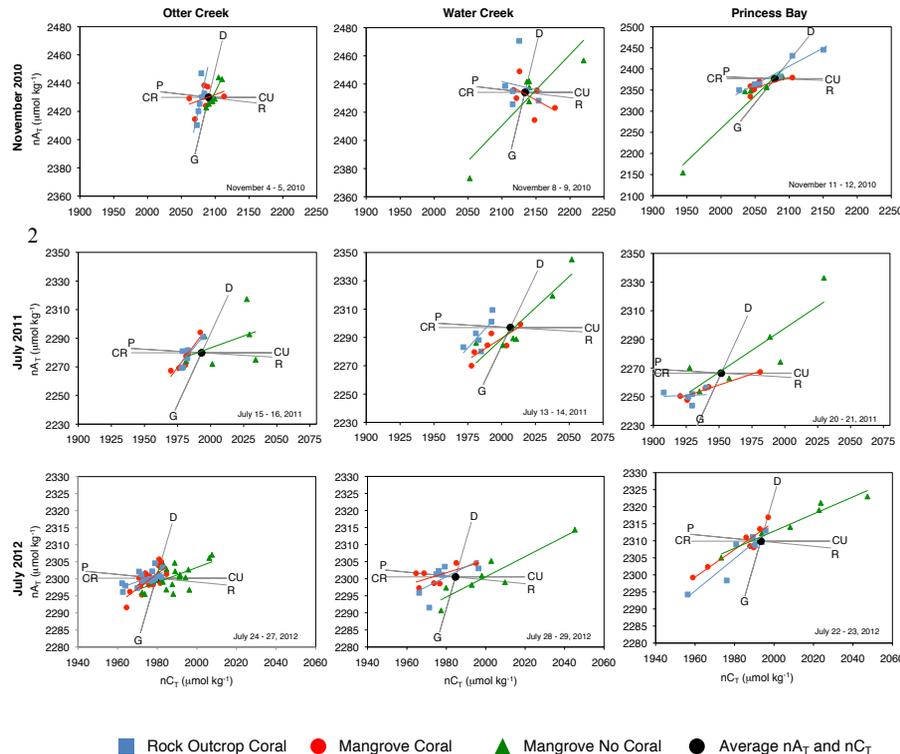


Fig. 4. Salinity normalized total alkalinity (nA_T) and total carbon (nC_T) plots with best fit linear regressions (see Table 5 for equations and r^2 values) for November 2010, July 2011, and July 2012 in Otter Creek, Water Creek, and Princess Bay. Average nA_T and nC_T for each time period was calculated 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 .

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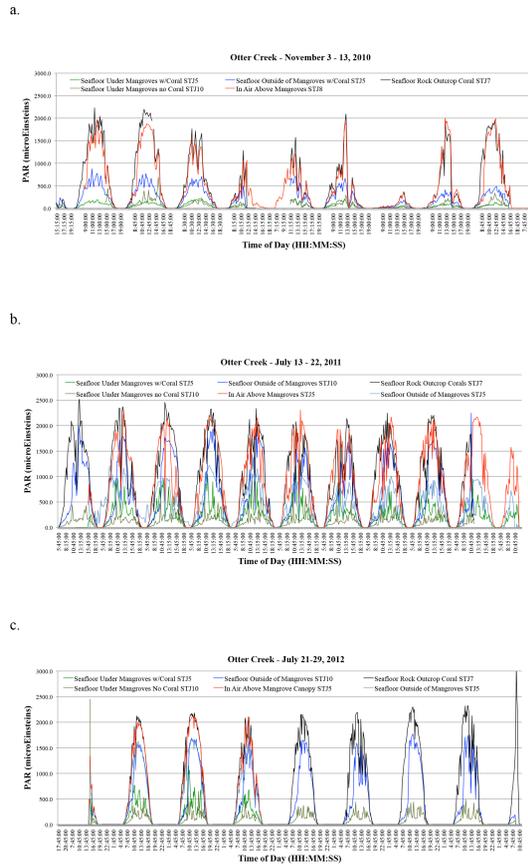


Fig. 5. Photosynthetically active radiation (PAR) measurements at study sites in Otter Creek (**a**, **b** and **c**) and Water Creek (**d** and **e**). Measurements represent 15 min averages. STJ# = PAR sensor location as referenced in Fig. 1. Data available at <http://doi.pangaea.de/10.1594/PANGAEA.825752>.

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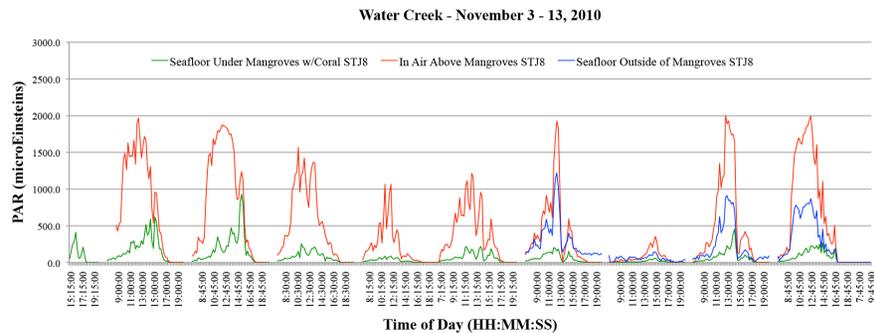
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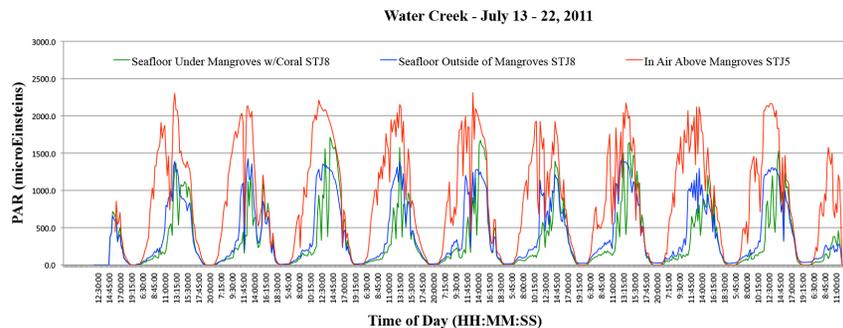


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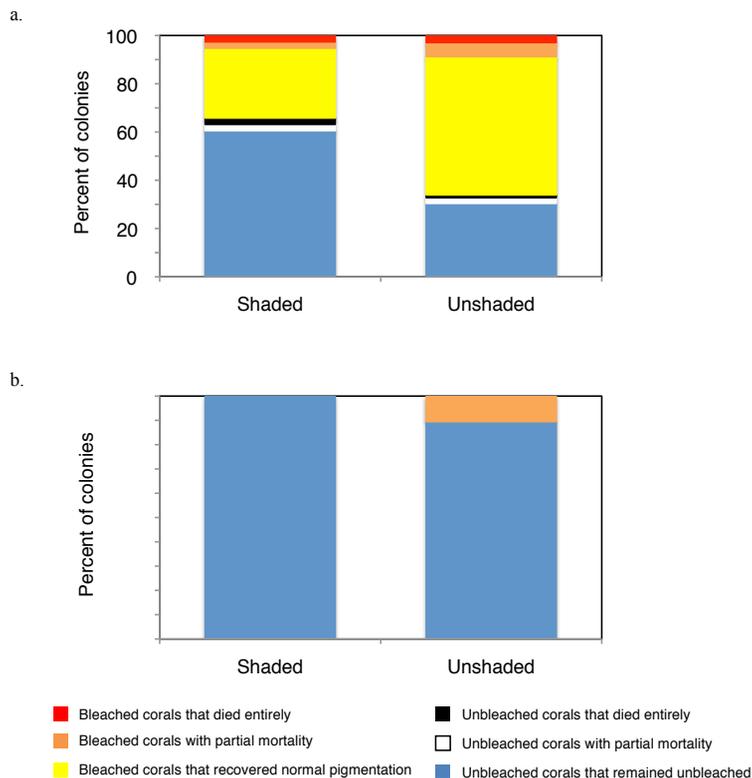


Fig. 6. Recovery results for shaded vs. unshaded **(a)** *Diploria labyrinthiformis* ($n = 38$ and $n = 171$ shaded and unshaded colonies, respectively) and **(b)** *Colpophylia natans* ($n = 50$ and $n = 19$ shaded and unshaded colonies, respectively) from 2010 to 2011. Also refer to Table 6.

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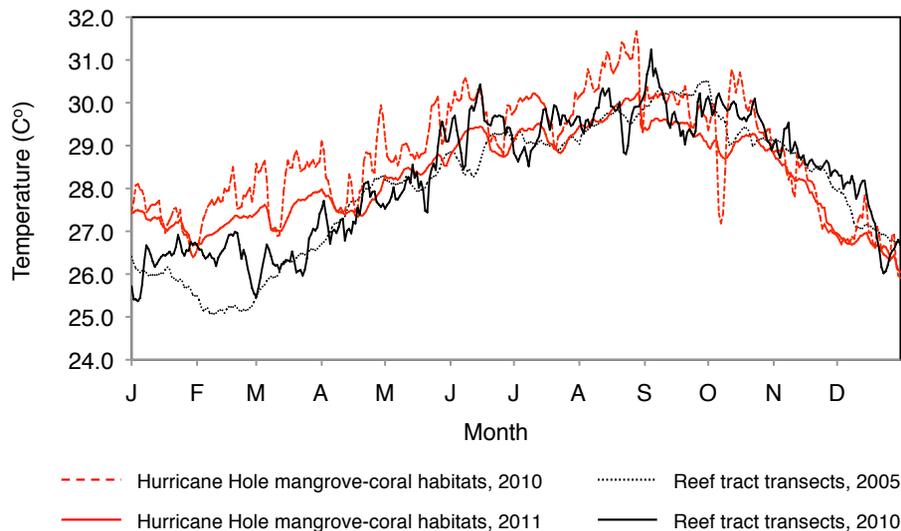


Fig. 7. Temperature trends from mangrove–coral and reef tract habitats. Hurricane Hole temperature data was averaged from 18 data loggers distributed throughout Hurricane Hole bays (Table 2). Temperature measurements were recorded every 2 h and daily averages were generated from all sites in Hurricane Hole, and from 6 reef sites around St. John. Data are available at <http://doi.pangaea.de/10.1594/PANGAEA.825752>.

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