A Comparison of Orbicellid Responses to Thermal Stress:
Orbicella faveolata and Orbicella franksi

Elin Chan[1], Leanna Cherrette[1], Zhixian Sun[1]

[1] Boston University, Boston, MA

Abstract

As the global climate changes, two reef-building coral, *Orbicella franksi* and *O. faveolata*, from Flower Garden Banks National Marine Sanctuary (FGBNMS) in the Gulf of Mexico are under threat. Although heat stress leading to coral bleaching is relatively well known, there is limited understanding on how these two species will respond to different types of thermal changes. The aim of this study is to better understand their physiological responses to both hot and cold thermal stress. We distributed three replicates of five genets of each species across three temperature treatments: hot-ramp, cold-ramp, and control. Over the 11-day experiment, we measured photosynthetic efficiency and chlorophyll density. Our results found that *O. franksi* had higher chlorophyll density when averaging across treatments and days compared to *O. faveolata* but had insignificant differences in photosynthetic efficiencies. Additionally, we found that while all corals displayed a decline in health as the thermal stress increased, the decline was more dramatic in the heat treatment. Our study's findings implicates that *O. franksi* may be more resilient to climate change than *O. faveolata* as they were more successful in maintaining their symbiotic relationship while subjected to thermal stress. The trend of a decline in symbiont density and thus photosynthetic efficiency in corals exposed to heat stress compared to cold stress indicates that this reef will become more vulnerable as ocean temperatures continue to increase. This study suggests that as the effects of climate change accumulates, both species will be negatively impacted. However, it is indicated that *O. franksi* may continue to dominate FGBNMS as they are potentially more tolerant to thermal stress. Therefore conservation efforts should be focused on *O. franksi* in preserving coral reefs in FGBNMS.

Introduction

Climate change is the result of anthropogenic activities, which has led to increasing global temperatures and more frequent drastic weather events (Rummukainen, 2012). According to the ICUN's 2013 IPCC report, the ocean absorbs 93% of the energy trapped by the enhanced greenhouse effect (IUCN, 2017). Coral reefs are one of many habitats being negatively impacted by climate change (Hoegh-Guldberg, *et al*., 2007; Eddy, *et al*., 2021). These reefs are some of the most biodiverse marine ecosystems and provide an estimated ecosystem service value of $1 trillion USD annually (Costanza, *et al*., 2014; ICUN, 2017). As a result of global warming, corals are reaching the upper limit of their thermal threshold and these conditions combined with anthropogenic activities have resulted in an estimated 50% loss of coral coverage globally since 1950 (Eddy, *et al*., 2021). A significant amount of coral mortality happens as a result of coral bleaching. Coral bleaching is the loss of *Symbiodininaceae* dinoflagellate symbionts within the coral's tissues when exposed to environmental stresses (such as thermal, photo, pathogenic, and nutrient stress) which leaves behind the white calcium carbonate skeleton of the coral (Desalvo, *et al*., 2008; Downs, *et al*., 2013; Carballo-Bolaños, *et al*., 2020). Without their symbionts, corals lose their source of food and eventually die of starvation (Voolstra, 2020). In addition to rapidly warming ocean temperatures, short periods of cold water events, which can be the result of storms, also cause severe damage to these reefs. For example, a cold snap in the winter of 1977 in Florida Bay and northern Bahamas resulted in a 91% mortality rate on a shallow reef (Roberts, *et al*., 1982). A storm in 2010 in the Florida Keys resulted in seawater temperatures dropping to 18-11ºC which resulted in a sharp decrease in coral cover where some species did not recover even after three years (Kemp, *et al*., 2016).

Since the 1970s, coral reefs in the western Atlantic have declined in live coral cover by approximately 80% (Contreras-Silva, *et al*., 2020). In contrast, reefs in the Flower Garden Banks National Marine Sanctuary (FGBNMS) have retained more than 50% of their coral cover since 1989 (Johnston et al. 2021). The resilience of FGBNMS reefs in the face of climate change stressors is not the only thing that makes Flower Garden Banks interesting. They also harbor healthy populations of Orbicellid corals, important reef-builders whose populations are threatened globally (Egan, *et al*., 2021). *Orbicella franksi*, a colonial stony coral, is one of the most frequently observed species in Flower Garden banks, yet it is considered a vulnerable species by the IUCN (Aronsen, *et al*., 2008; Hernandez, 2021). Another Orbicellid that is abundant in the FGB, *O. faveolata*, is considered an endangered species (Aronsen, *et al*., 2008; Manzello, *et al*., 2021). Due to their abundance within the Flower Garden Banks, and their threatened status globally, these two species present interesting objects of study. Additionally, their differing threatened status is interesting because they are such similar corals: they are both Orbicellids and they share the same life-history patterns (Levitan, *et al*., 2004). Prior research has even found that *O. faveolata* and *O. franksi*

collected from FGBNMS have the same symbiont composition when collected from the same bank (Green, *et al*., 2014). For these reasons, many studies lump these two species together when predicting future population ranges, but this may not be sufficient to predict their individual responses to climate change (Egan, *et al*., 2021). In exploring their response to thermal stress, we may help to illuminate their responses to future warming or extreme weather events.

Temperature is one of the best predictors of the distribution of *O. faveolata* and *O. franksi* (Egan, *et al*., 2021). While it is well known that heat stress often causes bleaching and coral mortality, fewer studies have been conducted examining the effects of cold stress, despite the fact that it can also cause mass mortality for reef-building corals (Kemp, *et al*., 2016). With increasing extreme weather events due to climate change, future cold anomalies could be a threat to the health of coral reefs (Wang and Lee 2010). In comparing their responses to thermal stress, we can fill the gap in the knowledge of how these individual species are affected by temperature changes to help predict future distributions. This information will become increasingly important as the climate change continues to accelerate and people search for solutions to help protect these threatened corals.

This study aims to compare how the two species of *Orbicella* from the east bank of the FGB respond to hot and cold stress by quantifying the photosynthetic efficiency and bleaching status (symbiont or chlorophyll density) of the corals across a range of thermal conditions. We hypothesize that when sea water temperatures deviate further from 26ºC, both *O. faveolata* and *O. franksi* will exhibit decreased photosynthetic efficiency and symbiont density, and *O. franksi* will exhibit a stronger acclimation response with respect to photosynthetic efficiency and bleaching status when compared to *O. faveolata* given that *O. faveolata* appears to be more endangered that *O. franksi.* Taken together, this study will help to predict the individual distributions of these two species and provide insight into future reef conditions.

Methods

Sample Collection. Fragments of five different *O. faveolata* (< 20cm*10cm with only one larger <35cm*10cm) and five *O. franksi* colonies (<20cm*10cm) were collected from the east FGBNMS (ca. 27°58′28.63″ N, 93°37′46.67″W) on August 2–3, 2018 (Fig. 1). All colonies were returned to Boston University and subsequently fragmented into equally sized nubbins, affixed to cement dishes with genotype labels and were maintained long term in the Marine Invertebrate Research Facility seawater tanks at 26ºC. Five genotypes from both species were carefully selected, each genotype having three healthy nubbins that were all comparable in size with each other. Before starting the experiment, all nubbins were placed in a flatworm wash for 5 minutes (flatworm RX) to eliminate cryptic coral-associated organisms hidden inside

the nubbins. The cement dishes were scrubbed and trimmed to remove algal growth. All nubbins were then acclimated under 26ºC with salinity maintained at approximately 35 ppt for one day before experimentation. Light levels in the experiment were kept at 60 photosynthetically active radiation (PAR), which were the same levels experienced in their original tanks.

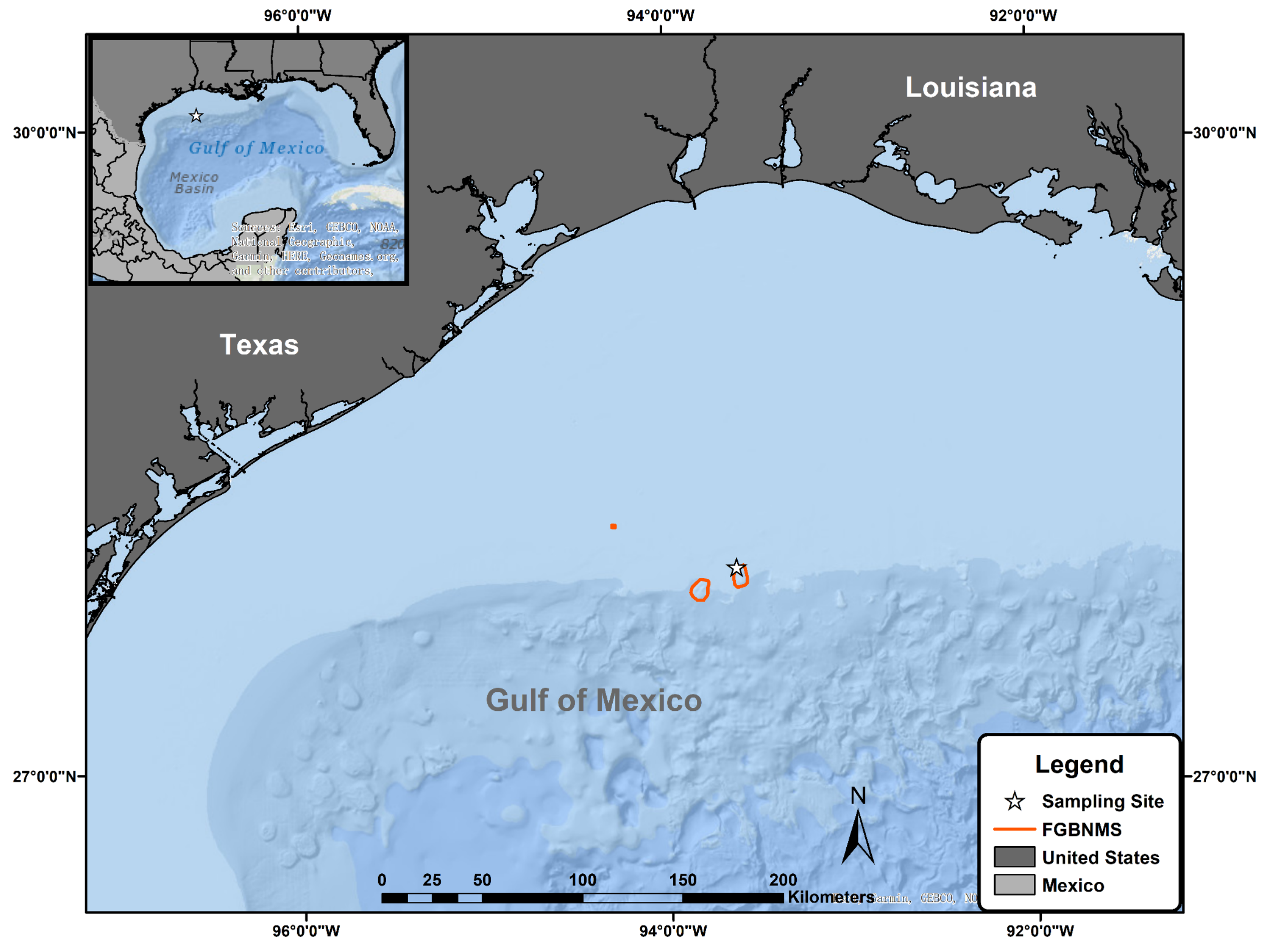


Figure 1. The sampling site of *Orbicella* spp. at the east bank of the Flower Garden Banks National Marine Sanctuary (FGBNMS).

Experimental Design. The distribution of nubbins in the tanks was carefully designed. Each treatment had three identical tanks, which were connected to a shared sump system. One nubbin from each genotype was placed in each treatment condition to account for genetic variation in thermal tolerances (Fig. 2a, Table 1). In order to reduce the potential for differential interactions between different genets, the combinations of nubins across tanks were kept the same across all treatments. In addition, nubbins were rotated daily following a counterclockwise direction (Fig. 2b) in order to control for differing light levels in the tank, and they were fed freshly hatched brine shrimp every other day. The current pumps were placed in the same

position in each tank to keep water flow the same. All treatments were started at control conditions (26ºC ±0.2ºC), and salinity in each treatment was maintained between 32 and 35 ppt.

Manipulation and maintenance of tank conditions. Throughout the experiment, temperature and salinity were monitored using a YSI Pro 30 probe three times daily. A HOBO Pendant MX Temp was placed in each treatment for continuous temperature tracking (Fig. 2c). Nitrates were tested both at the beginning and the end of the experiment using a Nitrate Pro reef test kit. Temperatures in the thermal stress treatments were manipulated to deviate up or down from the 26ºC starting temperature by approximately 1ºC every 24 hours while the control was maintained at 26ºC (Fig. 2c). Temperatures were controlled using APEX. Salinity was manipulated with inputs of either RO or seawater to the sumps as water evaporated to maintain 32-35 ppt. The tanks were lit using AquaIllumination AI Hydra 32 HD LED which were set on a 12 hour light cycle with a light intensity of 60 PAR.

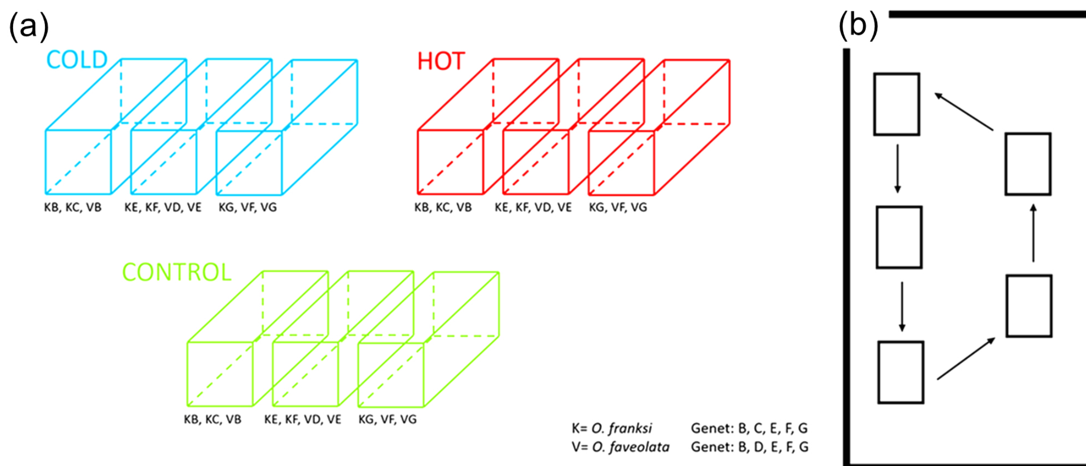
Monitoring photosynthetic efficiency. Photochemical efficiency of photosystem II was approximated using Fv/Fm values, which were measured five times during the experiment using a Junior pulse amplitude modulator (PAM) (Genty, *et al*., 1989). PAM data were assessed after 10 hours (PAM should be finished before lights on) of dark acclimation. Two Fv/Fm values (within 0.05 of each other and between 0.2 and 0.75) were noted for each coral nubbin and then averaged for that day.

Color Analysis. Photos were taken of coral nubbins three times over the course of the experiment using an Olympus Tough TG 6 camera: on day 1, day 5, and day 11. The camera settings, tripod height, and both spotlight positionings were kept the same across days. These pictures were then whitebalanced in Photoshop CC 2017 before they were analyzed for red color intensity in Matlab R2021b AnalyzeIntensity package following Winters, *et al*. (2009). We used red color intensity as a proxy for chlorophyll density as prior studies have found that these values are highly correlated (Winters, *et al*., 2009).

Statistical Analysis. The effect of treatment, species, and day on PAM Fv/Fm values were analyzed in R using ANOVA tests. We also conducted ANOVAs in R using the Matlab colour analysis data to analyze the effects of treatment, species, and day on chlorophyll density. The color intensity values were inverted to make graphs more intuitive.

Table 1. Distribution of coral nubbins in the three treatment tanks

Species	Genotype	Sample ID	Treatment	Species	Genotype	Sample ID	Treatment
		VB12	Hot			KB17	Hot
	B	VB14	Control		B	KB18	Control
		VB6	Cold			KB2	Cold
		VD3	Hot			KC2	Hot
	D	VD13	Control		C	KC3	Control
		VD1	Cold			KC1	Cold
		VE21	Hot			KE3	Hot
Orbicella faveolata	E	VE25	Control	*Orbicella franksi*	E	KE15	Control
		VE7	Cold			KE4	Cold
		VF29	Hot			KF4	Hot
	F	VF41	Control		F	KF6	Control
		VF24	Cold			KF21	Cold
		VG23	Hot			KG25	Hot
	G	VG24	Control		G	KG34	Control
		VG13	Cold			KG13	Cold



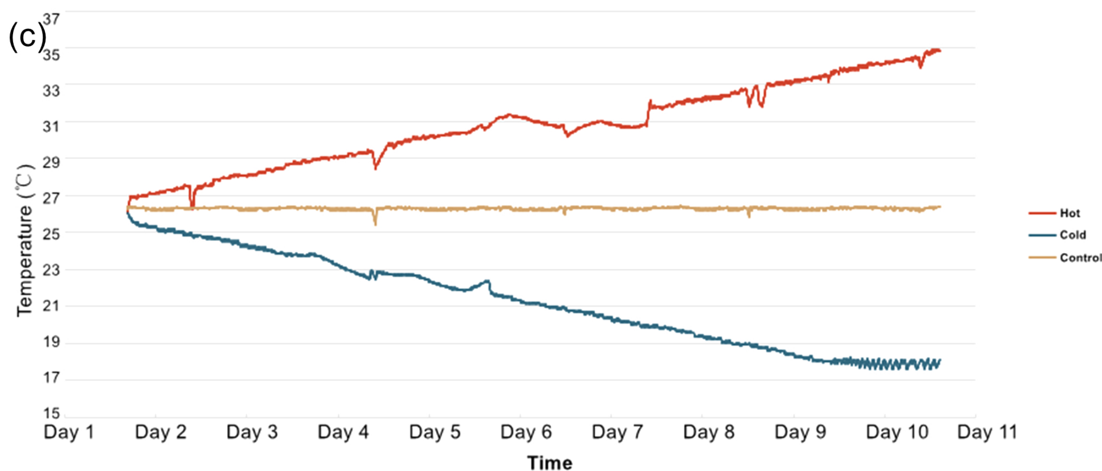
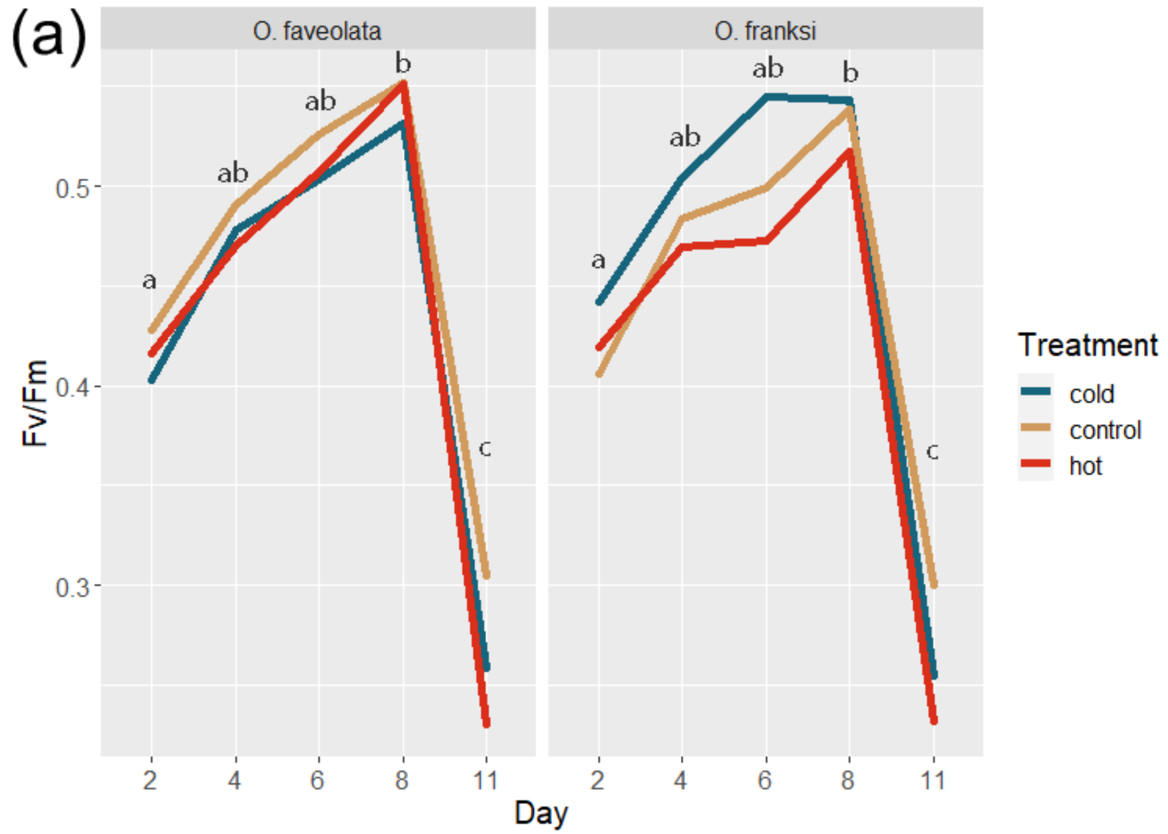


Figure 2. (a) Distribution of genets across tanks; **(b)** nubbins rotation following counterclockwise direction; **(c)** ex-situ HOBO Temperature Pendant tracking the change in temperature (ºC) for the cold, hot and control treatments.

Results

Photosynthetic Efficiency. Time significantly affected photosynthetic efficiency of photosystem II (Fv/Fm) for both *O. franksi* (ANOVA p=2.53e-12) and *O. faveolata* (ANOVA p=4.53e-10). For both species, the Fv/Fm values for day 11 were significantly lower than all other days, and day 8 had significantly higher Fv/Fm values than day 2 (Fig. 3a TukeyHSD). Photosynthetic efficiency did not differ significantly across species or thermal stress treatment (ANOVA p≥0.05). When looking at the final day of the experiment, we see that the photosynthetic efficiency of *O. faveolata* corals is significantly lower in the heat treatment than the control treatment, but the cold did not differ significantly from either the control or heat treatments (Fig. 3b TukeyHSD p=0.0131). There were no significant differences between the *O. franksi* corals in different treatments on the final day (ANOVA p≥0.05).


(a)
O. faveolata
O. franksi
a
ab
ab
b
c
a
ab
ab
b
c
0.5
0.4
0.3
Fv/Fm
2
4
6
8
11
Day
Treatment
cold
control
hot

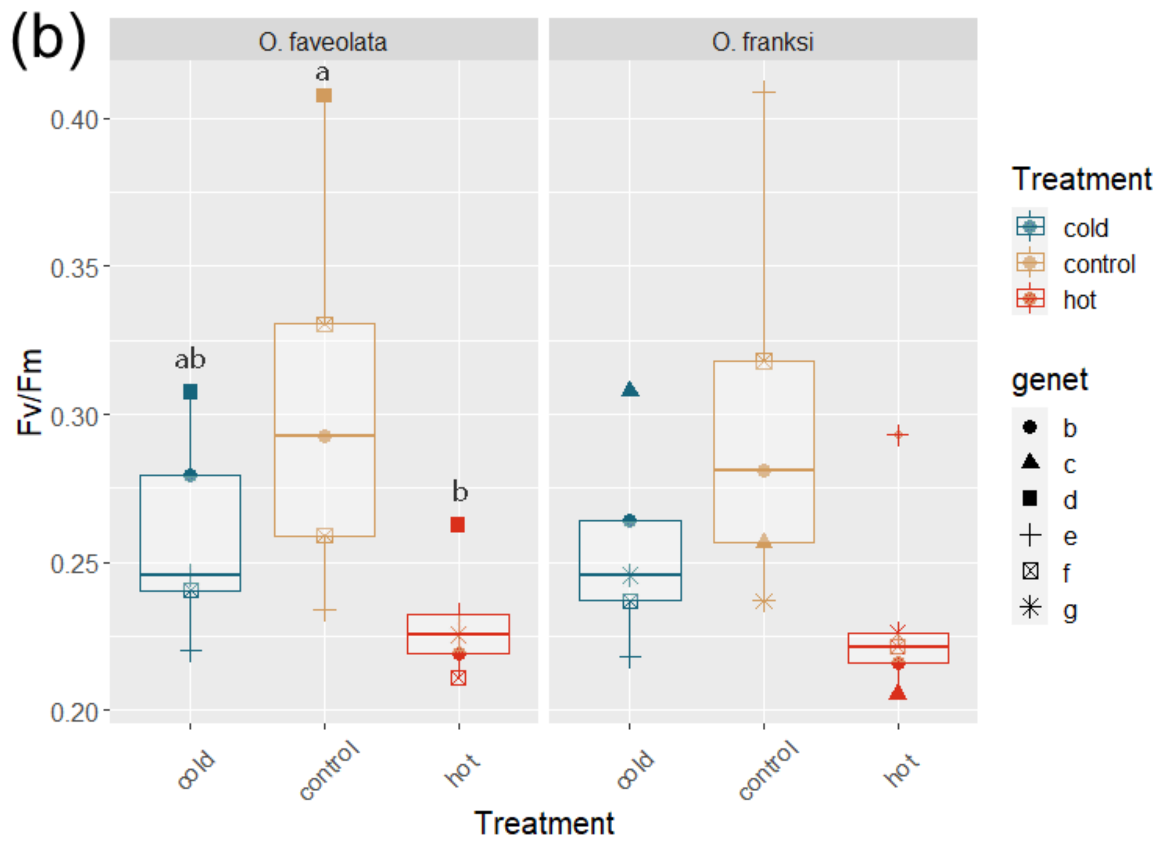

(b)
O. faveolata
O. franksi
a
ab
b
0.40
0.35
0.30
0.25
0.20
Fv/Fm
cold
control
hot
Treatment
Treatment
cold
control
hot
genet
b
c
d
e
f
g

Figure 3. (a) Fv/Fm measured using a JuniorPAM on *Orbicella faveolata* and *Orbicella franksi* across cold, hot, and control treatments on day 2, 4, 6, 8, and 11. These data showcase a significant difference (p=4.53e-10, p=2.53e-12) in Fv/Fm between days (indicated by different letters) for *O. faveolata* and *O. franksi* respectively. **(b)** Photosynthetic efficiency (Fv/Fm) of *O. faveolata* and *O. franksi* on day 11 across cold, hot, and control treatments, with point shape differentiating genets. These data showcase a significant difference (p=0.0161) between treatments (indicated by different letters; TukeyHSD p<0.05) for *O. faveolata*.

Chlorophyll density. Using red channel intensity as a proxy for chlorophyll density, we found that *O. franksi* corals had significantly higher chlorophyll density than *O. faveolata* corals overall (Fig. 4c ANOVA p=0.030). Treatment did not have a significant difference for red channel intensity in either species (Fig. 4a, ANOVA p≥0.05). In *O. faveolata* corals, chlorophyll density was significantly higher in day 5 compared to day 1 and day 11 (Fig. 4a ANOVA p=0.0471). *O. franksi* corals showed a similar trend, but it was marginally insignificant (ANOVA p=0.0549). Looking at the final day, there was no significant difference in chlorophyll density between species, although there was a trend towards higher red channel intensity values for *O. franksi* corals compared to *O. faveolata* (Fig. 4b ANOVA p=0.0635). Additionally, there was a trend towards significant differences between treatment on day 11, but it was marginally insignificant for both corals overall (Fig. 4b ANOVA p=0.0426, TukeyHSD p=0.997; 0.066, 0.077).

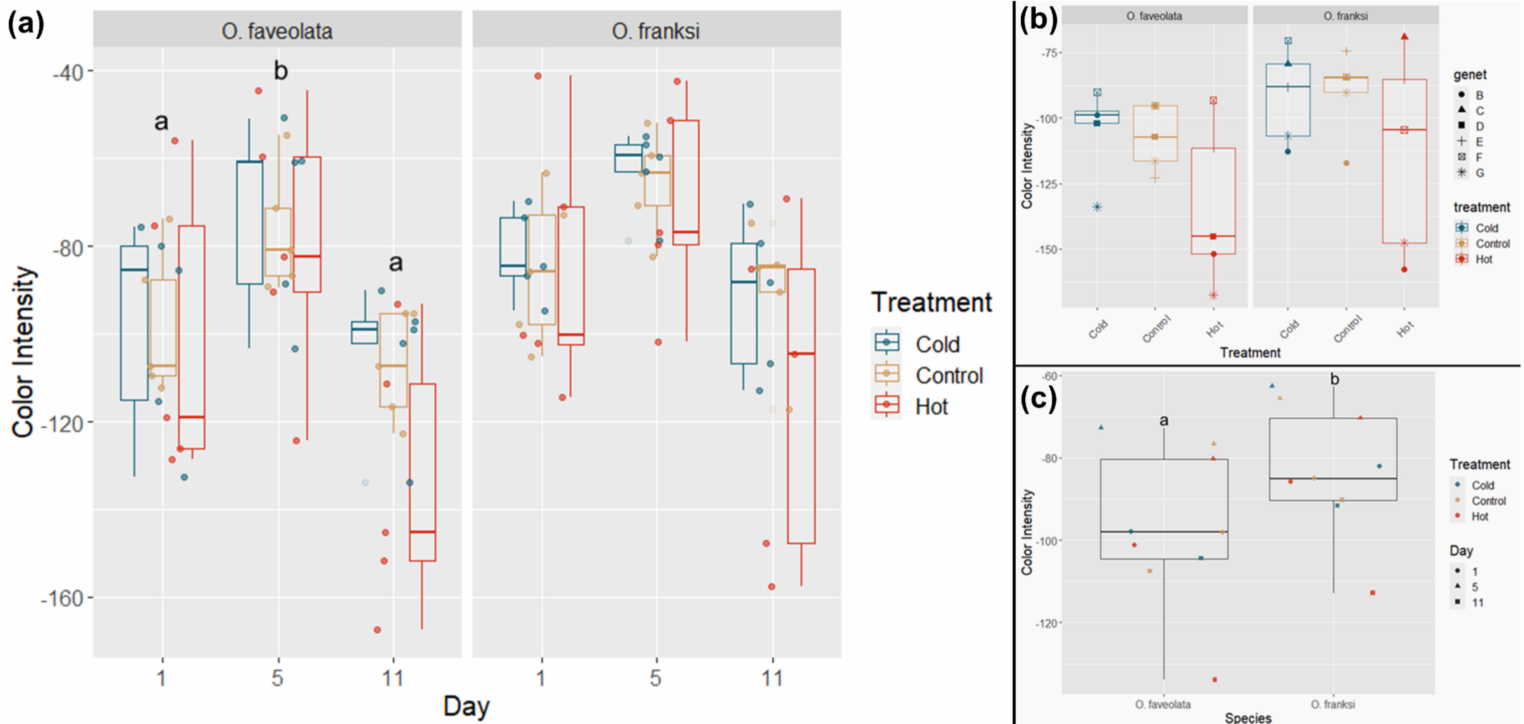


Figure 4. (a) Red colour intensity (proxy for symbiont loss) measured from photographs of *Orbicella faveolata* and *Orbicella franksi* across cold, hot, and control treatments on day 1, 5, and 11. These data showcase a significant difference (p=0.0471) in colour intensity of *O. faveolata* corals across days (indicated by different letters; TukeyHSD p<0.05) between the three days. **(b)** Red colour intensity of *O. faveolata* and *O. franksi* on day 11 across cold, hot, and control treatments with point shapes showing the distinct genets. These data showcase a marginally insignificant difference between treatments. **(c)** Overall red color intensity of *O. faveolata* and *O. franksi*. These data showcase a significant difference (p=0.030) in color intensity between two species.

Discussion

Our study aims to understand the responses of two species of Orbicellids to thermal stress in order to better understand the ways that they might respond to climate change. We hypothesized that both coral species would exhibit decreased photosynthetic efficiency and chlorophyll density in response to thermal stress, but *O. franksi* would be more resilient to the changes than *O. faveolata.* We instead found that all corals had a decreased photosynthetic efficiency by the end of the experiment regardless of species or treatment. However, when looking at the final day *O. faveolata* had significantly lower photosynthetic efficiency in the hot treatment than in the other treatments, while *O. franksi* did not have any significant differences. Additionally, *O. franksi* corals had higher overall chlorophyll density than *O. faveolata* corals.

Photosynthetic efficiency. The photosynthetic efficiency curve (Fig. 3a) showed an interesting peak in both species on day 8 which then sharply dropped by day 11. The annual average seawater temperature in FGBNMS ranged from 18 to 30 ºC (Schmahl, Hickerson, & Precht, 2008), and both cold and hot treatment temperature reached outside this range. A previous study on *O. faveolata* found that visible paling happened 3 days after exposure to 32.2ºC of thermal stress (Desalvo, *et al*., 2008), and may explain why photosynthetic efficiency decreased after day 8. However, the hot water treatment reached 33 ºC (Fig. 2c) on day 8 and which should be over the thermal threshold of *O. faveolata*. The symbiont algae density might have already dropped to a very low level when the final PAM measurements were taken on day 11. In fact, several corals had low readings (Fv/Fm<0.20) during the final measurement and were indeed visibly bleached (Fig. 5b). The drop in photosynthetic efficiency in *O. franksi* may also be attributed to its thermal threshold. Both species' photosynthetic efficiencies also dropped significantly after day 8 in the cold treatment as. It could be interpreted as both species reaching their lower temperature thresholds at some point between 19 and 17 ºC (Fig. 2c). Moreover, this significant drop in photosynthetic efficiency was also found in the control group which is difficult to explain as temperatures were kept at 26 ± 0.2ºC. One reason suggested from a previous study might be that nutrient levels, low light conditions, or confounding factors attributed to the photosynthetic efficiency decrease (Desalvo, *et al*., 2008). Here, there is little possibility that low light conditions impact the corals as we kept the light levels the same as their original tank light levels. Another potential reason might be the "batch effect". For the final measurement, corals in all

treatments might be affected by the same factor such as hand touching when doing PAM and photographing. Though the cryptic factor is hard to figure out, it is still comparable within the final day data. The photosynthetic efficiency difference between thermal stress groups and the control group still showed that both species have the lowest photosynthetic efficiencies in the hot treatment and also a lower photosynthetic efficiency in the cold treatment. The photosynthetic efficiency under different thermal stress of *O. faveolata* and *O. franksi* showed a similar trend according to the final day measurement. Although the differences were not statistically significant (ANOVA $p \geq 0.05$) across treatments in *O. franksi*, we can still see a trend that the photosynthetic efficiency is much lower in the hot treatment compared to the cold and control treatments. This pattern implies that *O. franksi* potentially has more thermal resilience than *O. faveolata*, but further studies are required.

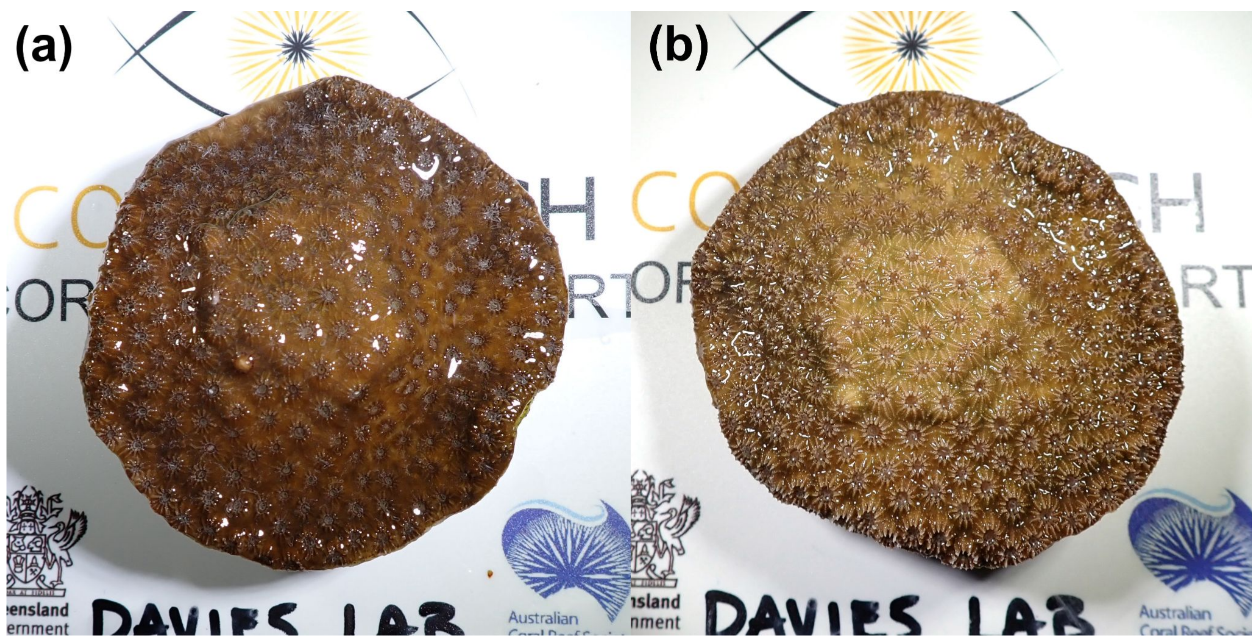


Figure 5. Comparison of *Orbicella faveolata* bleaching status using nubbin VB12 from the hot treatment. Images were white balance calibrated in Photoshop CC 2017 **(a)** Photographed on day 1; **(b)** photographed on day 11.

Chlorophyll density. The decrease in red colour intensity (used as a proxy for chlorophyll density) between day 5 and day 11 (Fig. 4a) suggests that as the thermal range deviates from 22-29ºC, the symbionts are no longer functioning optimally and thus are ejected from the coral's tissues. This is congruent with our PAM results showing a decrease in photosynthetic efficiency past day 8 (Fig. 3a) and is consistent with a prior study finding 18-30ºC as their natural average range (Schmahl, Hickerson, & Precht, 2008). A potential explanation for the increase in red colour intensity between day 1 and day 5 may be the presence of fluorescent proteins corals produce when exposed to ambient stress to protect against photo-damage associated with oxidative stress in anticipation of the ejection of symbiont (Alieva, *et al*., 2008; Voolstra, 2020). One of the most common fluorescent proteins produced by corals is phenotypically green (Alieva,

et al, 2008) which may be mistaken in colour analyses and PAM as photosynthetic pigments. However the upregulation of fluorescent proteins is found to be a response to symbionts loss (Bollati, *et al*., 2020), and thus may not be the response our data is demonstrating. Overall, there was a lack of significant differences in chlorophyll density both across treatments from day 1 to day 11 compared to the control (Fig. 4a) and between species on the day 11 (Fig. 4b). This may be a result of confounding factors as Desalvo, *et al*. (2008) also experienced slight bleaching in control fragments which was attributed to nutrient levels, light intensity, handling stress, and more. Although the lack of significant change in chlorophyll density may be in part due to the short nature of the experiment, it may also be because of the lack of variance from the natural thermal range that these corals experience which can also affect their thermal tolerances (Coles and Brown, 2003). Data collected from NOAA stations show that between 1990 and 2019, the corals experienced a maximum of 32.3ºC and a minimum of 17.4ºC (Fig. 6). This is also reflected in a trend towards a greater difference in chlorophyll density found hot stress versus control compared to cold versus control stress (Fig. 4b) as our experiment deviated further from their natural heat range compared to their cold range (Fig. 2c). However this trend of greater loss in chlorophyll density for both species in response to heat stress has dangerous implications as ocean warming continues. Despite having no significant differences in day 11, *O. franksi* maintained a greater density of chlorophyll during thermal stress compared to *O. faveolata* when averaged over all days and treatments (Fig. 4c). Host thermal tolerances can be influenced by symbiont communities (Carballo-Bolaños, *et al.*, 2020), however, both *O. faveolata* and *O. franksi* contain similar symbiont communities within their tissues (Green, *et al*., 2014), eliminating this as a factor. This implies that *O. franksi* could be more tolerant to thermal stress. This is reflected in the reef as it is the more dominant species (Hernandez, 2021) and indicates that *O. franksi* will continue to be the more dominant species or even may outcompete *O. faveolata* in FGBNMS.

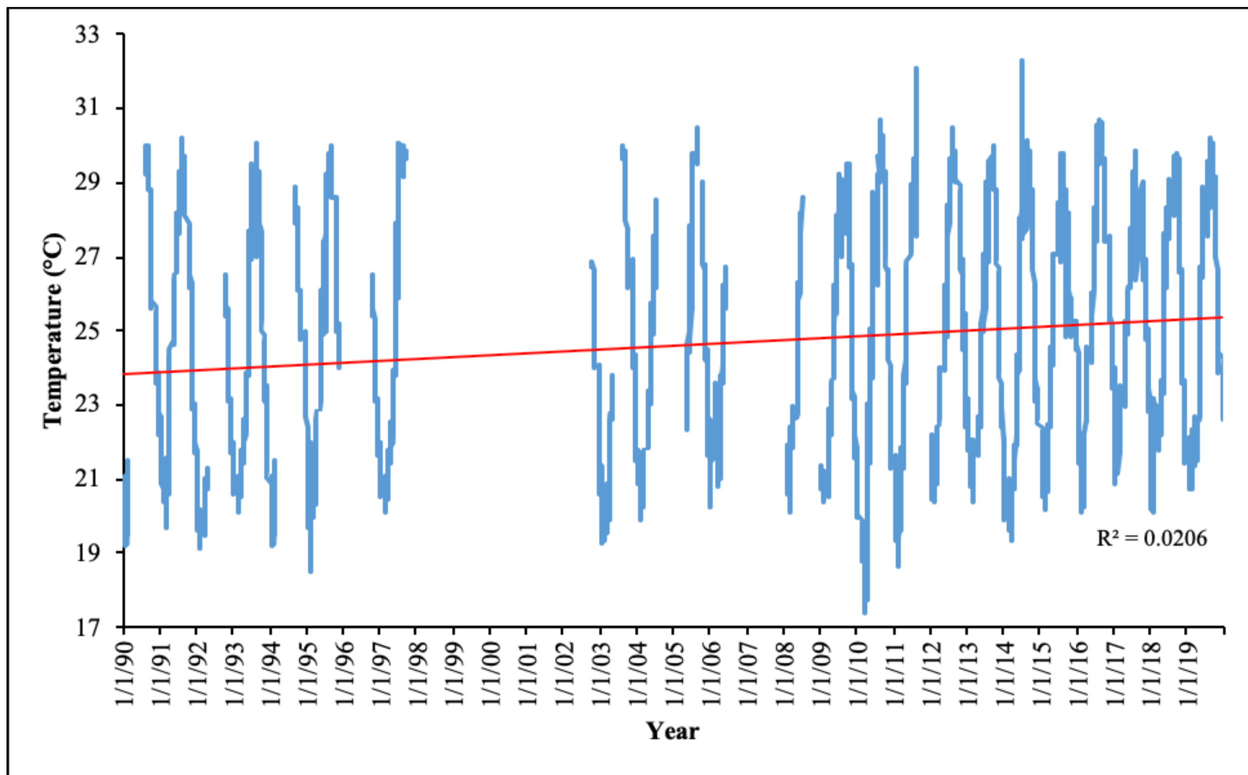


Figure 6: Daily mean seawater temperature (ºC) from 1990 to 2019 in East Flower Garden Bank taken from NOAA monitoring stations. Showing a historical maximum temperature of 32.3ºC and historical minimum of 17.4ºC and a 2018 maximum temperature of 29.8ºC and a minimum of 20.1ºC.

Experimental Limitations. While our experiment does show evidence of differing resilience between *Orbicella franksi* and *Orbicella faveolata*, there were limitations that should be addressed in future studies. First, due to limited time, our experiment was very short. This presents a problem because the temperature changes at a rate much faster than the corals would normally experience, and consequently our results are potentially less representative of how corals might react in nature. Additionally, because we only gave the corals one day to acclimate after being moved to experimental tanks, it is possible that their photosynthetic efficiency was lower at the beginning of the experiment than it might otherwise have been. Future studies should consider extending their experiment in order to account for these problems and give opportunity for corals to exhibit acclimation responses to stress treatments.

Additionally, there was an unexplained decline in the photosynthetic efficiency and chlorophyll density of the corals in the control treatment. While we cannot say exactly what caused this response, there is potential that non-ideal tank conditions played a role. For example, we did not measure pH at all during the experiment, and if conditions were too acidic or basic, the corals would have shown a decline in health (Desalvo, *et al*., 2008). Varying initial health of the corals selected for the experiment may have also factored into this response.

Lastly, we must also consider the batch effect. Due to the fact that there were multiple different people collecting data, it is probable that there were systematic differences in the way that these data were collected that are unrelated to actual biological differences (Lazar, *et al*., 2013). This is especially a concern with the photosynthetic efficiency data, which was collected over multiple different days by rotating groups of people.

Bibliography

Alieva, N.O, Konzen, K.A, Field, S.F, Meleshkevitch, E.A, *et al*. "Diversity and evolution of coral fluorescent proteins." *PLoS ONE* 3(2008): e2680.

Aronson, R., Bruckner, A., Moore, J., Precht, B. & E. Weil. 2008. Montastraea faveolata. The IUCN Red List of Threatened Species 2008: e.T133373A3712432. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T133373A3712432.en.

Aronson, R., Bruckner, A., Moore, J., Precht, B. & E. Weil. 2008. Montastraea franksi. The IUCN Red List of Threatened Species 2008: e.T133012A3542659. https://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T133012A3542659.en.

Carballo-Bolaños, Rodrigo, Soto, Derek, Chen, Chaolun Allen. "Thermal stress and resilience of corals in a climate-changing world." *Marine Science and Engineering* 8(2020)

Coles S.L, Brown B.E. "Coral Bleaching - Capacity for acclimatization and adaptation." *Advanced Marine Biology* 46(2003): 183-223.

Costanza, Robert, et al. "Changes in the Global Value of Ecosystem Services." Global Environmental Change, vol. 26, May 2014, pp. 152–158, www.sciencedirect.com/science/article/pii/S0959378014000685, 10.1016/j.gloenvcha.2014.04.002.

Contreras-Silva, Ameris I., et al. "A meta-analysis to assess long-term spatiotemporal changes of benthic coral and macroalgae cover in the Mexican Caribbean." *Scientific reports* 10.1 (2020): 1-12.

Desalvo MK, Voolstra CR, Sunagawa S, Schwarz JA, et al. "Differential gene expression during thermal stress and bleaching in the Caribbean coral *Monstastraea faveolata*." *Molecular Ecology*, 17(2008):3953-3971.

Downs, CA, McDougall, Kathleen E., Woodley, Cheryl M., Fauth, John E., *et al*. "Heat-stress and light-stress induce different cellular pathologies in the symbiotic dinoflagellate during coral

bleaching." *PLOS One* 8(2013);12:e77173.
Eddy, Tyler D, Lam, Vicky W.Y, Reygondeau, Gabriel, Bruno, John F, *et al*. "Global decline in capacity of coral reefs to provide ecosystem services." *One Earth* 4(2021): 1278-1285.
Egan, Katharine E., et al. "Predicting the distribution of threatened orbicellid corals in shallow and mesophotic reef ecosystems." *Marine Ecology Progress Series* 667 (2021): 61-81.
Genty, Bernard, Jean-Marie Briantais, and Neil R. Baker. "The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence." *Biochimica et Biophysica Acta (BBA)-General Subjects* 990.1 (1989): 87-92.
Green, Elizabeth A., et al. "Quantifying cryptic Symbiodinium diversity within Orbicella faveolata and Orbicella franksi at the Flower Garden Banks, Gulf of Mexico." *PeerJ* 2 (2014): e386.
Hernandez, Rebekah Alicia. *Assessing Long-Term Coral Coverage at East and West Flower Garden Banks*. Diss. The University of Texas Rio Grande Valley, 2021.
Hoegh-Guldberg, O, Mumby, P.J, Hooten, A.J, Steneck, R.S, et al. "Coral reefs under rapid climate change and ocean acidification." *Science* 318.5857 (2007): 1737-1742.
IUCN. "Coral Reefs and Climate Change." IUCN, 6 Nov. 2017 www.iucn.org/resources/issues-briefs/coral-reefs-and-climate-change.
Johnston, M.A., K. O'Connell, R.D. Blakeway, J. MacMillan, M.F. Nuttall, X. Hu, J.A. Embesi, E.L. Hickerson, and G.P. Schmahl. "Long-Term Monitoring at East and West Flower Garden Banks: 2019 Annual Report." *National Marine Sanctuaries Conservation Series ONMS-21-02*. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Flower Garden Banks National Marine Sanctuary, Galveston, TX. 88 pp. 2021.
Kemp, Dustin W., Colella, Michael A, Bartlett, Lucy A, Ruzicka, Rob R, et al. "Life after cold death: reef coral and coral reef responses to the 2010 cold water anomaly in the Florida Keys." *Ecosphere* 7.6 (2016): e01373.
Lazar, Cosmin, et al. "GENESHIFT: a nonparametric approach for integrating microarray gene expression data based on the inner product as a distance measure between the distributions of genes." *IEEE/ACM transactions on computational biology and bioinformatics* 10.2 (2013): 383-392.
Levitan, Don R., et al. "Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the Montastraea annularis species complex." *Evolution* 58.2 (2004): 308-323.
Manzello, Derek P., et al. "Increasing coral calcification in Orbicella faveolata and Pseudodiploria strigosa at Flower Garden Banks, Gulf of Mexico." *Coral Reefs* (2021): 1-15.
Roberts, H. H., Rouse, L. J., Walker, N. D, Hudson, J. H. "Cold-Water Stress in Florida Bay and Northern Bahamas: A Product of Winter Cold-Air Outbreaks." *SEPM Journal of Sedimentary*

Research, Vol. 52, 1982, pubs.geoscienceworld.org/sepm/jsedres/article/52/1/145/97453/Cold-water-stress-in-Florida-Bay-and-northern, 10.1306/212f7efa-2b24-11d7-8648000102c1865d. Accessed 6 Dec. 2021.

Rummukainen, Markku. “Changes in climate and weather extremes in the 21st century.” *WIREs Climate Change* 3(2012): 115-129. doi:10.1002/wcc.160

Schmahl, G.P., Hickerson E.L., and Precht W.F. “Biology and ecology of coral reefs and coral communities in the Flower Garden Banks Region, Northwestern Gulf of Mexico.Coral Reefs of the USA.” Dordrecht: *Springer* (2008), 221–262.

Voolstra, CR. “Coral Bleaching: A Colourful Struggle for Survival.” *Current Biology* 30(2020): 768-770.

Wang, Chunzai, Liu, Hailong , and Lee, Sang Ki. "The record breaking cold temperatures during the winter of 2009/2010 in the Northern Hemisphere." *Atmospheric Science Letters* 11.3 (2010): 161-168.

Winters, G., et al. "Photographic assessment of coral chlorophyll contents: implications for ecophysiological studies and coral monitoring." Journal of Experimental Marine Biology and Ecology 380.1-2 (2009): 25-35.