Phenotypic plasticity across differing reef habitats in two species of Hawaiian corals

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ABSTRACT

With sea-surface temperatures predicted to rise due to global climate change, research investigating coral thermotolerance and phenotypic plasticity may provide important insights into coral adaptability. In Puako Bay, Hawaii, *Porites lobata* was common in both the thermally variable back reef and the thermally stable fore reef. In contrast, *Pocillopora meandrina* was rare in the back reef but common on the fore reef. Using PAM fluorometry, we tested whether there were physiological differences between corals of the same species living in differing reef habitats, as well as corals of different species living in the same reef habitat. We also tested whether such differences would become more pronounced under desiccation stress. We found no differences in yield between species in the fore reef, but *P. lobata* had a higher yield that *P. meandrina* in the back reef, suggesting that *P. lobata* is better adapted to the back reef. There were no differences between the same species living in different reef habitats, most likely due to local adaptation. Unexpectedly, we found that short-term desiccation did not initiate a stress response, but rather increased photosynthetic yields, most likely due to reduced CO_2 resistance in air. In addition, the yields of fore reef corals increased more than those of the back reef corals, suggesting fore reef corals may be able to out compete back reef corals under elevated CO_2.

INTRODUCTION

Coral reefs are both economically and ecologically vital, yet they have been deteriorating at an alarming rate over the last several decades (Hughes et al. 2003). One of the most common causes of coral reef deterioration is bleaching, or the expulsion of symbiotic algae from the coral host (Hughes et al. 2003). Although bleaching can be caused by numerous stressors, including UV radiation, changes in salinity, and sedimentation, the majority of bleaching events have been linked to increases in sea-surface temperatures (Downs et al. 2000, Fitt et al 2001, Lesser and Farrell 2004). Under current global climate change models, sea-surface temperatures are predicted to increase, as are the number and severity of coral bleaching events (Donner and Potere 2007). Research investigating coral thermotolerance and phenotypic plasticity may provide important insight into the physiological mechanisms of acclimatization necessary for corals to persist.

Predictions for how corals and their symbionts will respond to climate change are under much debate and study (Buddemeier and Smith 1999, Gates and Edmunds 1999, Toller et al. 2001). Where as it was once assumed that the symbionts played a passive role in coral adaptation, numerous studies have suggested that much of the phenotypic plasticity that allows corals to live in varying environments is in part due to which clade of the dinoflagellate species symbiodinium the coral houses (Baker 2003, Fabricius et al 2004, Rowan 2006). For instance, Fabricius et al. (2004) found that corals living in warmer environments house a higher proportion of clade D, suggesting its importance as a stress tolerant strain. Therefore, investigating the physiology of such stress-tolerant strains, as well as the interactions between these strains and their host, may provide valuable insights into how coral reefs will adapt to environmental change.

Information regarding how corals will respond to elevated temperatures is also dependent on history of thermal exposure. That is, corals that have been exposed frequently to fluctuations in sea-surface temperatures or to elevated temperatures may be better able to withstand temperature extremes (Brown et al. 2002, Castillo and Helmuth 2005). Understanding how physiological responses to temperature are related to thermal history is critical to understanding acclimatization. The goal of the present study was to investigate thermotolerance and phenotypic plasticity in *Porites lobata* and *Pocillopora meandrina*, two species of Hawaiian corals living in two distinct reef environments. We were interested in the following questions:

1) Are there differences in thermal regime between the reef environments?
2) If so, do these differences affect coral physiological performance?
3) Are there differences between two common Hawaiian corals, *Porites lobata* and *Pocillopora meandrina*, found across these reef environments?
4) If the species differ, do they become more pronounced under stress?

MATERIALS AND METHODS

Study system and study site—We studied corals in the waters in Puako Bay, on the North Kahalo Coast of the Big Island of Hawaii. Puako Beach has an extensive network of coral reefs consisting of a wave-protected back reef and wave-exposed fore reef. The

back reef is located approximately 25-50 m from shore and is composed of small networks of shallow coral heads extending approximately 1-2 m from the ocean floor. The fore reef begins 100-125 m from shore and is composed of continuous reef extending up approximately 5 m from the ocean floor.

Porites lobata and *Pocillopora meandrina* are common corals in Hawaiian reef systems that are found in both back and fore reefs (Gosliner et al. 1996). *P. lobata* is the most common coral species in Hawaii, dominating the reef landscape. The branches form large lobes and the colony itself can be very large, extending several meters in length and height (Fig. 1). *P. meandrina* forms small, upright bushes with dichotomous branches that extend from the initial growth point (Fig. 1). Our observations suggest that *P. lobata* is common on both the fore and back reef, while *P. meandrina* was more abundant on the fore reef, with very few colonies persisting closer to shore. For this reason, coupled with the observation that water temperature increased from the fore reef to the back reef (see Results), it was hypothesized that *P. lobata* is the more temperature tolerant of these two coral species.

FIGURE 1: *Porites lobata* (left) and *Pocillopora meandrina* (right) are two common coral species found on Hawaiian reefs. *P. lobata* was ubiquitous throughout both the fore and back reef habitats, while P. *meandrina* was more abundant in the fore reef.

Data collection—To determine if sea-surface temperatures differed between the fore and back reef, we fastened temperature-data loggers (Onset Computer Corporation, Pocasset, Massachusetts, USA) to coral or rock projections using zipties. The loggers were programmed to record temperature at one-minute intervals and were deployed for five days (Jan 8 – Jan 12, 2007). We placed two loggers each on the fore and back reefs approximately 35 meters apart.

We collected three coral fragments of both *P. lobata* and *P. meandrina* from the fore and back reef and took initial physiological measurements to assess whether coral species or reef location would yield differences in performance. The colonies were collected at approximately 1 m depth using a hammer and chisel. To determine if there were initial differences in photosynthetic parameters between species, as well as between reefs, the fragments were first dark-adapted in a light-proof plastic bin filled with seawater for 30 minutes. Using an underwater pulse amplitude modulation (PAM) fluorometer, we measured quantum yield induction curves for each of the coral fragments. These curves measure the increase in photosynthetic efficiency from a dark-adapted state to the saturation of the photosystem. Induction curves provide an index of the photosynthetic efficiency of the coral endosymbionts.

To test the hypothesis that differences between species and/or habitats might become more pronounced under stress, we collected three fragments each of *P. lobata* and *P. meandrina* from the fore and back reefs and subjected the colonies to desiccation. To compare the corals to an intertidal organism that regularly experiences desiccation we also collected three zoanthid colonies from back reef tide pools. All the samples were dark adapted and measured using a PAM fluorometer. Colonies were left in the dark to desiccate for ~1/2 hr after which they were re-measured with the PAM. Because these measurements were taken out of water, we also compared measurements both in air and in water to determine whether the surrounding medium had an effect upon the photosynthetic parameters. We found no difference between measurements taken either in or out of water (data not shown) therefore we are confident that any differences between our desiccation measurements were due to the treatment and not the medium in which the measurement was taken.

Statistical analyses—Temperature data: To test whether temperature differed between the fore and back reefs, we used repeated measures ANOVA with our data loggers as the repeated measure. Because we hypothesized that night and day temperature differences between the fore and back reef may differ, we divided our data into two parts. Temperatures were classified as either 'day' (between 08:00 and 20:00) or 'night' (between 20:00 and 08:00). To simplify our data, we first took the mean temperature of the minute recordings for each hour and used these hourly means in the analyses.

PAM data: To compare yields between the fore and back reef corals we used repeated measures ANOVA with reef type, coral species and their interaction as the independent variables. Yield measurements of the induction curve on an individual coral were considered repeated. For the desiccation experiment, we first tested whether individuals differed in maximum yield before and after the treatment using a paired *t*-test. To determine the effects of species, reef type and treatment we used repeated measures ANOVA on the yield induction curves. The difference between the before and after yields was the dependent variable and species, reef type, their interaction and the coral (or zoanthid) individual within the species were independent variables. All analyses were done using SAS version 9.1.

RESULTS

Fore and back reef comparisons—The mean sea-surface temperature of the back reef was significantly warmer than the fore reef during the day ($P < 0.0001$), but significantly cooler than the fore reef during the night ($P < 0.0001$). Temperatures on the back reef were also more variable than temperatures on the fore reef during both the day and night (Fig. 2). The mean hourly back reef temperatures ranged from 23.72 to 28.43°C while temperatures on the fore reef ranged from 24.84 to 26.35°C.

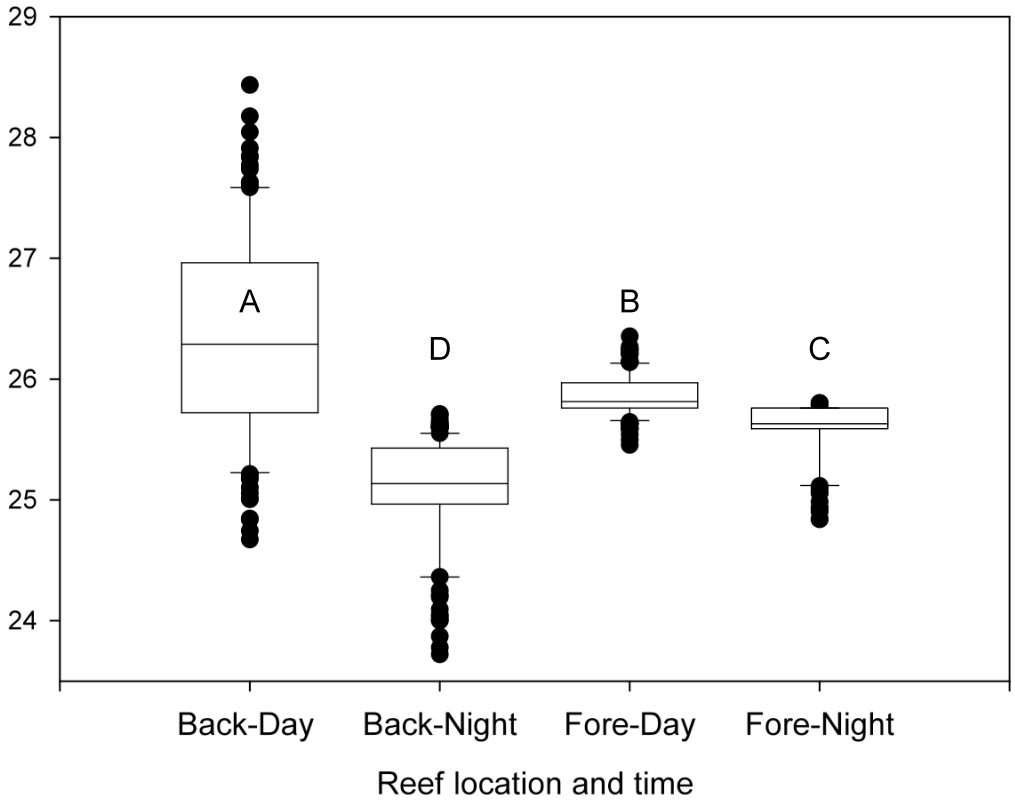

FIGURE 2. Mean (± SE) day and night sea-surface temperatures for the fore and reef habitats at Puako Bay, Hawaii from January 8 to January 12, 2007. Temperatures between 08:00-20:00 were considered 'day' and those between 20:00-08:00 were considered 'night'. Means with different letters are significantly different from one another.

Comparison of fore and back reef corals—There were no differences in yields between the species in the fore reef but the *P. lobata* had higher yields than *P. meandrina* in the back reef ($F_{1,160} = 6.01$, $P = 0.01$).

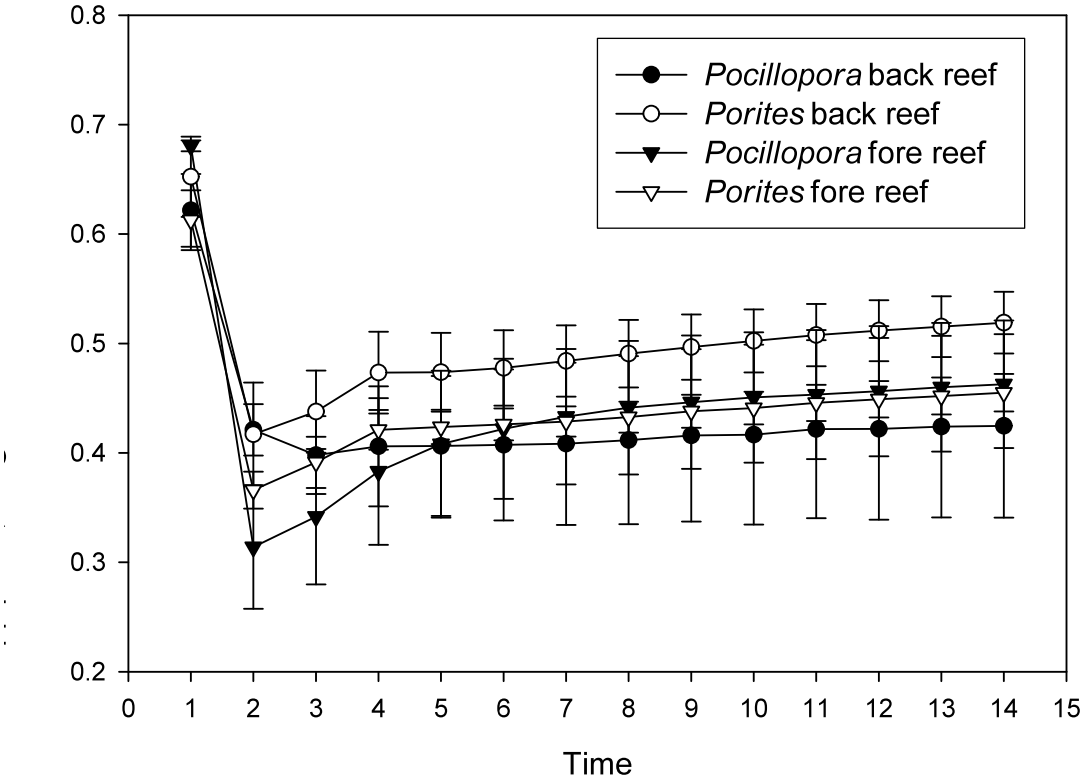

FIGURE 3. Initial measurements of fore and back reef *P. lobata* and *P. meandrina.* Time refers to point measurements from a PAM fluorometer that increase in light intensity. At the beginning of the curve, colonies were dark adapted. This allowed us to compare how quickly each colony became saturated with light and was performing to maximum photosynthetic efficiency.

Desiccation experiment—Corals and zoanthids overall had higher maximum yields after desiccation (t_{14}= 3.89, P = 0.0019). Their was a significant interaction between species and reef position ($F_{1,185}$ = 16.27, P < 0.0001). *P. lobata* had a smaller difference in yield due to desiccation than *P. meandrina* in the back reef but a greater difference in the fore reef. In general, back reef corals showed less of a change than fore reef corals ($F_{1,185}$ = 88.76, P < 0.0001). Although it was not significant, *P. meandrina* appeared to show less variation in response to desiccation than *P. lobata* ($F_{2,185}$ = 1.19, P = 0.37). Zoanthids exhibited a response to desiccation that fell between that of corals from the two reefs (Fig. 4).

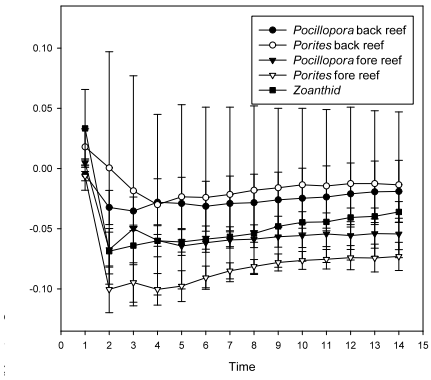

FIGURE 4. Comparisons of the difference in quantum yield before and after 30 minutes of desiccation in *Porites lobata*, *Pocillopora meandrina* and Zoanthid colonies. *P. lobata and P. meandrina* were collected from back and fore reefs at Puako Bay, Hawaii. Zoanthids are only found in the back reef and were collected mainly from tide pools. Time refers to point measurements from a PAM fluorometer that increase in light intensity. At the beginning of the curve, colonies were dark adapted. This allowed us to compare how quickly each colony became saturated with light and was performing to maximum photosynthetic efficiency.

DISCUSSION

We found significant differences in both average day and night sea-surface temperatures between the fore and back reef at Puako Bay (Fig. 2). Back reef environments are characteristically shallow (Heyman and Kjerfve 1999) and have restricted water circulation (Thattai et al. 2003), thereby augmenting solar heating during the day and radiative cooling during the night. In contrast fore reefs are continually receiving inputs of colder, deeper water from currents and waves. These small-scale oceanographic

differences explain why temperatures were warmer in the back reef during the day and cooler during the night and more variable overall. Because temperature fluxuations can be stressful to organisms and corals in particular (Coles and Jokiel 1977), our results suggest that the back reef environment may be more stressful than the fore reef.

Most interestingly, we found that the two Hawaiian corals we studied differed in their ability to both colonize a potentially stressful environment and to tolerate stress. *Porites lobata* had a broader range in the back reef than *P. meandrina* at Puako Bay and the back reef was more variable in its temperature extremes than the fore reef (Fig. 2). Additionally, *P. lobata* had higher overall yields than *P. meandrina* in the back reef (Fig. 3), suggesting that it was better adapted to the back reef environment. However, when the corals were stressed with desiccation, back reef *P. meandrina* was able to utilize more of the available CO_2 and had higher yields than back reef *P. lobata*. It may be that corals in highly variable environments have been selected to maintain a constant photosynthetic capacity in spite of changing conditions as suggested but the general trend that the back reef corals showed less change in photosynthesis after desiccation than fore reef corals (Fig. 4). Therefore, the ability of back reef *P. lobata* to maintain photosynthetic capacity may contribute to its success and prevalence in the back reef.

Our yield measurements suggest that corals were locally adapted to their environment. Although back reef *P. lobata* had the highest yields, the two species did not differ in the fore reef and *P. meandrina* showed no difference regardless of reef habitat. Both *P. lobata* and *P. meandrina* are broadcast spawners, releasing thousands of gametes into the water column. Because the spatial scale separating the fore and back reefs is relatively small, it is likely that gametes from both habitats combine, limiting the possibility of genetic differentiation between back and fore reef populations. Additionally, fore reef coral fragments may be transported to the back reef during storm events. Therefore, local adaptation is most likely the result of phenotypic plasticity and not population subdivision. It is also possible that the two reefs are not different enough to elicit differences in performance however the differences shown in the desiccation experiment suggest that these corals differed in photosynthetic performance.

After a 30-minute emersion period, yields of both coral species increased, regardless of habitat (Fig. 4). When exposed to air, corals prevent water loss via polyp retraction and mucus secretion and the ability of the Hawaiian corals to photosynthesize after desiccation in our experiments suggests that the corals were likely offsetting desiccation via these means. Romaine et al. (1997) showed similar results for *Stylophora pistillata*, which was able to preserve photosynthetic capacity after 4 hours of emersion. They found a steady increase in net photosynthesis during the first 180 minutes following exposure. Numerous intertidal macroalgal and seagrass species exposed to air during low tide increase their photosynthetic yield (Johnson et al. 1974, Dring and Brown 1982, Gao et al. 1999, Seddon and Cheshire 2001). The ability to increase yield when in air is most likely due to decreased resistance to CO_2 diffusion in air versus water (Seddon and Cheshire 2001). Our results support this conclusion and show that *P. lobata* and *P. meandrina* are able to persist and thrive in air for at least 30 minutes.

Interestingly, yields of both *P. lobata and P. meandrina* collected from the fore reef increased more so than their back reef counterparts following desiccation (Fig. 4). Initially we predicted that emersion would cause coral stress and that back reef corals, exposed to a more fluctuating environment, would outperform fore reef corals under such

conditions. However, air exposure actually increased photosynthetic yield, and it is possible that living in a more stable environment actually enabled the fore reef corals to out compete their back reef counterparts when CO_2 resistance was decreased. An important next step would be to test whether back reef corals are able to last longer before photosynthesis decreases and eventually shuts down under desiccation.

There is a great deal of uncertainty surrounding how corals will adapt to global climate change. Investigating the physiology of corals that experience stressful or fluctuating conditions may provide clues as to how thermal history shapes coral susceptibility to bleaching and other temperature-related stressors. Our results suggest back reef corals are exposed to highly fluctuating temperatures, where as fore reef corals live in a more thermally-stable environment. Corals seem to be locally adapted to their respective reef habitats. However, *P. lobata* had a higher yield than *P. meandrina* in the back reef, suggesting *P. lobata* might be better adapted to fluctuating environments. Short-term emersion increases photosynthetic yield for all corals, but especially those collected from the fore reef, suggesting fore reef corals may be able to out-compete back reef corals under elevated CO_2.

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APPENDIX 1—Coral responses to algal exudates.

Coral decline has been associated with increases in algal growth; however, algae may also have indirect effects on corals. Smith et al. (2006) found that algae can cause coral mortality in experimental chambers by enhancing microbial activity on the coral surface via the release of dissolved organic compounds. It is unclear, however, whether these effects could occur in natural ecosystems. Our original design was to subject naturally occurring tide pool corals to increased algal exudates to determine if we would see a similar decrease in quantum yield in the wild as was shown by Smith et al. (2006) in experimental chambers. However, we were unable to execute this experiment for two main reasons. First, at Puako Beach, there were few corals present in the tide pools, making replication difficult. Additionally, algae were uncommon at the site, at least in January. Second, after characterizing the tide pools, we discovered that the lava bedrock of these pools was extremely porous. Therefore there was high turnover of water in the tide pools which would have potentially flushed out any exudates released by the algae. Although algae may have long term effects on coral communities in these lava tide pools and tidal waters, we decided that it would be unfruitful to run a short term experiment in these tide pools. Consequently, we decided to test whether these Hawaiian tidal corals would be affected by algae in experimental containers.

MATERIALS AND METHODS

Set up—To test whether corals responded to algal exudates, we set up 12 Glad 1500 ml containers containing one fragment of *Pocilloptera meandrina* and one of *Porites lobata*. We collected three colonies of each species from the subtidal fore reef at Puako Beach. Each colony was broken into four fragments and these were randomly distributed among the treatment containers. Three control containers contained two colonies, one of each of the species, and were filled with sea water collected at Puako. Approximately 10 grams of algae (a roughly equal mix of *Sargassum* sp. and *Ahnfeltia* sp.) was added to each of the treatment containers. The algae were contained within a mesh bag to reduce direct contact between the corals and algae.

Measurements—We measured photosynthetic efficiency of our coral colonies using pulse amplitude modulation (PAM) fluorometry. We measured induction curves for the corals in one control container and three of the treatment containers. These curves measure the increase in photosynthetic efficiency from a dark-adapted state to the saturation of the photosystem. Because induction curves are time consuming we made point measurements of yield and non-photochemical quenching for the remaining colonies. For these measurements, we measured dark adapted corals then measured them again after light adapting the corals under full spectrum florescent bulbs for 10 minutes. All corals were measured initially at the beginning of the treatment (after allowing for a brief acclimatization to their environment) and then after approximately 12 hours in the containers. Containers were aerated once after about 6 hrs to bring up dissolved oxygen levels to approximately 8 mg/L.

Analyses—We used paired *t*-tests to determine whether the yield differed before and after 12 hrs in the treatments. To determine whether the change in yield (initial – 12hrs later) varied with our independent variables of treatment (control or algae added), coral species, their interaction or container we used ANOVA. For corals without point measurements, we used the first and last measurements of the induction curves to determine the dark and light adapted yields, respectively. Because we saw no differences for the full data set of point measurements (see Results), we did not analyse the yield curves for the containers with these data. Analyses were done using SAS version 9.1.

RESULTS AND DISCUSSION

All corals had lowered dark-adapted ($t_{23} = 5.53$, $P < 0.0001$) and maximal ($t_{23} = 7.53$, $P < 0.0001$) yields after 12 hrs in the containers. However, we found no differences between treatments ($P >> 0.05$). This suggests that all corals were stressed by the treatments (with or without algae) but the addition of algae did not alter the stress (Fig. 1). Although not significant, it does appear that there is a trend toward *P. lobata* out performing *P. meandrina* under stress (Fig. 1). Likely the lack of aeration was the biggest problem with this design.

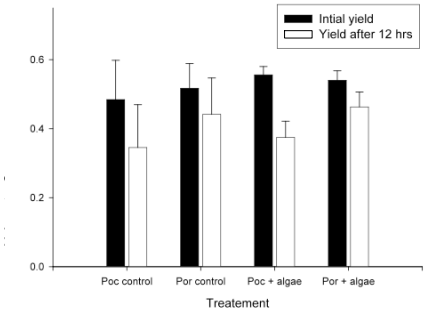

FIGURE 1. Comparisons of maximal light adapted photosynthetic yields (± 1 SE) in corals exposed algae for ~12 hours. Poc = *Pocillopora meandrina*, Por = *Porites lobata*. Control treatments just contained corals while algae treatments contained corals and a mix of *Sargassum* sp. and *Ahnfeltia* sp.

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APPENDIX 2—Zoanthid responses to an environmental gradient.

The original purpose of our project was to examine the thermotolerance and phenotypic plasticity of tide pool corals in relation to their subtidal counterparts via a reciprocal transplant experiment. We were only able to find a few corals in tide pools at Puako Beach however, and decided to perform a transplant using zooanthids, which were abundant in both tidepools and subtidal areas. Zoanthids are colonial marine invertebrates within the phylum cnidaria. They most closely resemble sea anemones, but tend to be smaller and may incorporate debris into their cell walls for protection. Although zoanthids are notoriously difficult to identify, our study organism is most likely in the genus *Zoanthus*, members of this genus being common in Hawiian tide pools and on reef flats. Like other members of cnidaria, zoanthids house symbiotic zooxanthellae, the photosynthetic efficiency of which can be used to gauge organism health.

MATERIALS AND METHODS

Three tidepools of varying sizes were selected for experimental manipulation based on zoanthid presence and isolation from the open ocean at low tide. Temperature loggers were attached to a rock in each tide pool and were programmed to record temperature at minute intervals. The colonial nature of zoanthids allowed for clonal replication, thereby eliminating the possibility that the resulting differences in yield were due to individual variation and not treatment effect. In each tidepool, as well as 3 adjacent subtidal locations, loose rocks with zoanthids were collected. (Tidepool 1: $N = 8$, Tidepool 2: $N = 3$, Tidepool 3: $N = 5$, subtidal areas: $N = 5$). The location of the rocks was marked with flagging so that the transplant controls could be returned to their original destination. The zoanthids were dark adapted in a large light-proof plastic bin containing seawater for 30 minutes. Using an underwater PAM fluorometer, induction curves were created for each zoanthid rock. The colonies were then broken in half, with one of the fragments returning to its collection location, and the other fragment being transplanted to the reciprocal location. Z-spar marine epoxy was used to anchor the zoanthid rocks to the substratum, as well as to mark the fragments. The following day, we returned to Puako Bay to take temperature and dissolved oxygen measurements of the tidepools and adjacent subtidal areas. Tidepool dimensions were also measured and percent algal cover and invertebrate presence was used to characterize the pools (Table 1).

RESULTS AND DISCUSSION

Strikingly similar temperature and dissolved oxygen measurements for tidepool and subtidal habitats lead us to believe that our habitats were not as distinct as we originally perceived. As previously mentioned, this is most likely the result of the porous nature of the lava, allowing exchange of water and oxygen into and out of the tidepools, even during low tide. Because the two habitats were so similar, we did not expect a sufficient change in photosynthetic efficiency of the zoanthid zooxanthellae, and therefore decided to pursue another project.

TABLE 1: Characterization of three tide pools at Puako Beach, Hawaii. Physical measurements and organism surveys were conducted on January 6, 2007 during a low tide at approximately 1:30pm.

	Pool 1	Pool 2	Pool 3
Physical characteristics:			
Size (m)	12.5 x 9.5	1.8 x 1.0	4.3 x 2.4
Depth at deepest point (m)	0.44	0.07	0.24
Temperature (ºC)	29.3	29	29
Dissolved oxygen (mg/L)	9.6	12.0	10.6
Organisms:			
Fish	yes	yes, few	yes
Algae (% cover)	25% *Pollysiphonia* sp 20% brown crust 5% *Cladophora* sp 5% *Gelidium* sp 10% unknown	50% brown crust 10% crustose coralline algae 5% *Gelidium* sp 25% bare rock 5% sand	50% *Pollysiphonia* sp 25% *Cladophora* sp 25% brown crust 10% unknown 5% *Gelidium* sp 5% crustose coralline algae 10% bare rock
Invertebrates (presence)	urchins gastropods limpits brittle star oysters anemone worms sea stars	urchins gastropods limpits oysters worms snails	urchins gastropods oysters worms crabs snails

APPENDIX 3—Coral transplants between reef types.

We transplanted corals from the fore reef into the back reef to determine whether they would respond to the temperature differences. We also transplanted back reef corals back into the back reef as a control for the transplant.

MATERIALS AND METHODS

Data collection—To test whether corals from the fore reef were less stress tolerant than the back reef corals we transplanted both fore and back reef coral fragments into the back reef. The difficulty and danger of transplanting rocks to the wave-exposed fore reef prevented the reciprocal transplant. We fixed the coral heads to flat lava rocks collected from the beach (~30 x 20 cm). On each rock, the six coral fragments of the same species were attached using Z-spar Marine Epoxy. Three fragments were collected from the fore reef and three from the back reef, with colored zipties designating location. The lava rocks were then placed on the back reef by wedging the rock into the reef and collected after five days. Two *P. lobata* fragments were missing, one collected from the back reef and the other collected from the fore reef. Each colony was measured using PAM prior to the transplant and then again after the five day transplant.

Statistical Analyses—Because the patterns from graphing the data were difficult to interpret, we did not follow up these results.

RESULTS AND DISCUSSION

Following transplantation, yields changed in an unpredictable pattern for the corals from the fore and back reefs. *Porites lobata* from the fore reef and *P. meandrina* from the back reef exhibited a decrease in yield while *P. lobata* from the back reef and *P. meandrina* from the fore reef decreased in yield (Fig. 1). There are many possible explanations for this result. First, it is possible that the different colonies responded differently to the experimental manipulation itself. Some corals may be differentially affected by separation from the colony and placed in epoxy, regardless of species or original location. It is also possible that *P. lobata* from the fore reef were able to quickly adapt to their new surroundings and *P. meandrina* was unable to similarly adapt. However, based on the transplant time of 5 days, this seems highly unlikely. In fact, transplant times for other coral experiments range from weeks to months (Gleason 1993; West et al. 1993; Baker 2001). Given more time, changes in physiology representative of temperature stress may have become apparent. Additionally, it is possible that photosynthetic yield alone does not accurately reflect coral health. Castillo and Helmuth (2005) measured both photosynthesis and respiration in the Caribbean coral *Montastraea annularis*, finding that both increased with increasing water temperature. Expressing the results as photosynthesis to respiration (P/R) ratios, estimating the degree to which production (photosynthesis rate) by the zooxanthellae exceeds maintenance (respiration rate) requirements of both the zooxanthellae and the coral host (Coles and Jokiel 1977), showed a more rapid increase in respiration to production (Castillo and Helmuth 2005). These results suggest a diminishing autotrophic capacity on the part of the zooxanthellae,

possibly signalling stress at elevated temperatures (Castillo and Helmuth 2005). In the current study, it is possible that although photosynthetic yield did not change after transplantation, respiration increased, resulting in a lower P/R ratio and reduced autotrophic capacity.

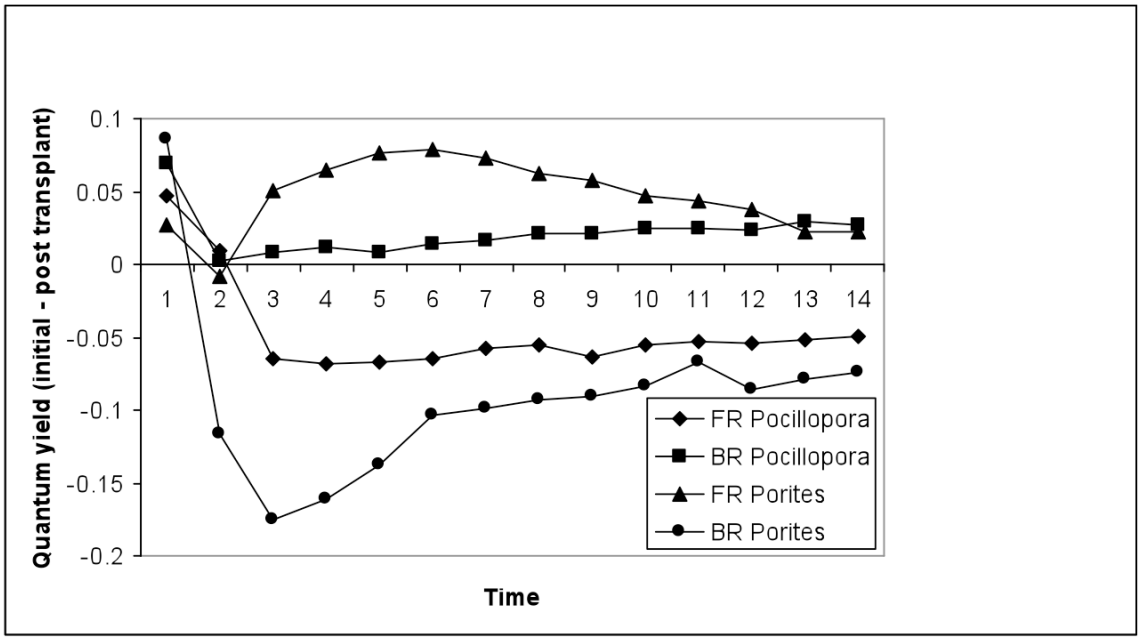

FIGURE 1. Comparisons of *Porites lobata* and *Pocillopora meandrina* fore (FR) and back reef (BR) corals transplanted back into the back reef of Puako Bay. Time refers to point measurements from a PAM fluorometer that increase in light intensity.

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