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### Extreme reef environments as natural laboratories

*Mechanisms underlying coral acclimatization to future ocean conditions*

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# Chapter 6

## Synthesis

The aim of this thesis was to assess the mechanisms underlying coral tolerance to extreme environmental conditions, which provides critical insights into coral adaptive capacity to future ocean conditions. To this end, I used inland bays as natural laboratories to investigate the functional traits and holobiont dynamics of corals that naturally persist under conditions considered stressful for most reef-building corals. I combined both laboratory- and field- based experiments to increase our understanding of how corals respond to complex, novel environmental regimes. I investigated coral acclimatization capacity to both more extreme, highly variable environmental conditions or to more benign, stable conditions, and examined the effects of acclimatization on heat tolerance. This synthesis will explore the key findings from the thesis, provide guidance on how corals from inland bay habitats may be useful for proactive restoration initiatives, and discuss the utility of the inland bays as natural laboratories to investigate coral adaptive capacity under intensifying climate change and local stressors.

### **Utility of Curaçao's inland bays to investigate adaptive capacity to future ocean conditions**

Habitats where corals survive and/or thrive under naturally extreme conditions provide valuable insights into the mechanisms that may allow corals to survive under future climate change and intensifying local stressors (Perry and Larcombe 2003; Camp et al. 2018; Schoepf et al. 2023). These natural laboratories harbor populations of corals that have already adapted or acclimatized to abiotic conditions considered stressful for most

reef-building corals (Camp et al. 2018; Burt et al. 2020). While the current rate of environmental change on coral reefs may be too fast for corals to rapidly adapt (e.g., Bay et al. 2017), these naturally extreme habitats for corals nonetheless can provide crucial information on the diversity of abiotic conditions under which corals can persist and on environmental tipping points beyond which coral populations can no longer survive (Camp et al. 2018). The inland bays of Curaçao are an example of one such habitat, characterized by environmental conditions considered extreme for most reef-building corals (de Jong et al. 2025; Schoepf et al. 2023). These sub-optimal conditions make the inland bays useful natural laboratories where the functional traits of naturally stress-tolerant corals can be investigated to advance our knowledge on the adaptive capacity of corals.

In this thesis, we provide characterization of the physicochemical conditions of two inland bays and two adjacent fringing reef sites, which demonstrated that the bays are consistently more variable and more extreme, in terms of their abiotic characteristics, compared to reef sites (Chapters 2 and 4). We captured the diel and seasonal variability of seawater temperatures, pH, dissolved oxygen concentrations, light levels (photosynthetically active radiation; PAR), and salinity across several years. Average daily temperature was  $\sim 0.5$ - $1^\circ\text{C}$  warmer in the bays compared to the reefs, however, these temperature differences tended to be most distinct between bays and reefs during the cooler, dry seasons. Maximum temperatures in the bays surpassed the maximum monthly mean ( $29^\circ\text{C}$ ; NOAA Coral Reef Watch 2025), even during the cool, dry season. Daily temperature ranges in the bays were consistently  $0.3$ - $0.6^\circ\text{C}$  higher than on the reefs, with maximum daily ranges of up to  $2.4^\circ\text{C}$  in the bays compared to  $1.8^\circ\text{C}$  on the reef (Chapter 2). PAR levels were similar at both reef and bay sites, despite bay sites being about 2-3m shallower, which is explained by the high turbidity in the bays (de Kock and de Wilde 1964; de Jong et al. 2025). Daily ranges of pH and dissolved oxygen concentrations were also much higher in the bays compared to reefs, regardless of season, with maximum daily ranges of up to 0.35 pH units and  $6.0\text{ mg L}^{-1}$  of  $\text{O}_2$  in the bay while these daily ranges were only 0.17 pH units and  $3.14\text{ mg L}^{-1}$  of  $\text{O}_2$  on the reefs. During two different wet seasons, dissolved oxygen concentrations in the bay temporarily reached hypoxic levels as low as  $1.94\text{ mg L}^{-1}$ , co-occurring with seasonally high seawater temperatures. Average salinity was consistently 5-8% higher in the bays compared to the reefs.

Further, we assessed average concentrations of inorganic nutrient concentrations (nitrate, ammonium, phosphate concentrations) in both habitat types across seasons and years, which revealed contrasting patterns across years. Namely, we found that during certain years, nutrient concentrations were highest during the warm, wet seasons (Chapter 2), while in other years it tended to be higher near the end of the cooler, dry season (Chapter 4). These findings agree with the dynamic seasonal patterns observed in the bays in Sanchez Baranco et al. (2025), where variability in nutrients was associated with season-dependent bay-ocean exchange rates. Given that inorganic nutrient input likely occurs in pulses following heavy rainfall (Den Haan et al. 2016) and our sampling was limited to opportunistically collected discrete water samples, our data only provide limited insights. Thus, higher resolution measurements of inorganic nutrients are needed to establish seasonal patterns of inorganic eutrophication in the inland bays.

No natural laboratories are perfect analogues for future reefs (Camp et al. 2018), and the inland bays of Curaçao are no exception. Environmental extremeness for corals within the bays is primarily due to the higher diel and seasonal variability of temperature, pH, and dissolved oxygen, higher turbidity, and higher toxic chemical pollution compared to nearby reefs (de Jong et al. 2025). However, investigating coral communities under diverse combinations of extreme conditions provides valuable insights into possible mechanisms of resilience (e.g., Camp et al. 2018, Schoepf et al. 2023). The inland bays are especially useful for investigating adaptive capacity to future ocean conditions given that corals in these habitats experience multiple, co-occurring abiotic stressors. Average pH and dissolved oxygen concentrations in the bays generally fall within the range of present-day conditions, however, the high variability of temperature, pH, and dissolved oxygen regularly, but temporarily exposes corals to levels expected to occur in the open ocean under moderate-to-severe climate scenarios (IPCC 2021; de Jong et al. 2025). Therefore, while the bays included in this thesis lack a few key characteristics expected under climate change, including chronically lower average pH and dissolved oxygen concentrations, corals in the bays experience pulses of co-occurring high seawater temperatures and low pH and dissolved oxygen concentrations. This stands in contrast to other extreme natural laboratories that are characterized by chronically higher average temperatures and lower pH and dissolved oxygen concentrations, such as

the semi-enclosed lagoons of Bouraké, New Caledonia (Maggioni et al. 2021). The inland bays are also only 0.5-1°C warmer on average compared to the reefs, making them much less thermally extreme than many other natural laboratories (e.g., Oliver and Palumbi 2011; Schoepf et al. 2015; Howells et al. 2016). The thermal extremeness of the inland bays is similar to other mangrove lagoons (Camp et al. 2016, 2019; Maggioni et al. 2021), but slightly more thermally extreme than nearshore reefs (Kenkel et al. 2015; Barott et al. 2021; Baumann et al. 2021).

The inland bays are more extreme for corals than some of these other natural laboratories in terms of local stressors, as the bays have high sedimentation rates, high (in)organic nutrient concentrations, and chemical pollution (de Jong et al. 2025; Sanchez Baranco et al. 2025). Other systems, such as the semi-enclosed lagoons of Bouraké (Maggioni et al. 2021) and Nikko Bay of Palau (e.g., Barkley et al. 2015, Kurihara et al. 2021) are also characterized by higher (in)organic nutrients, which also offer insights into the effects of more extreme temperatures, pH, and dissolved oxygen concentrations combined with local impacts (Camp et al. 2018; Schoepf et al. 2023). These local impacts may not necessarily represent future expected conditions on a global scale, however, as human population densities near coral reefs increase, local stressors will increasingly impact nearshore ecosystems (França et al. 2020; Sing Wong et al. 2022). Given that most research to-date has focused on adaptive capacity to one or few stressors (Pendleton et al. 2016), our work contributes to a growing body of knowledge on complex interactions of multiple co-occurring global and local stressors on coral populations (Camp et al. 2018; Harborne et al. 2017; Ellis et al. 2019). Thus, the inland bays should continue to be used as natural laboratories to investigate adaptive capacity of naïve corals, and potential for directions for future work is discussed throughout this synthesis below.

### **Functional traits of naturally stress-tolerant corals and the role of associated microbial communities**

Increasing our understanding of the adaptive capacity of corals to environmental extremes is key to predicting the future of coral reefs. Integral to ensuring a future for coral reefs is prioritizing the protection of existing biodiversity, which in turn provides ample genetic diversity for evolution to act on to promote rapid adaptation (Hume et al. 2016; Colton

et al. 2022). Thus, revealing the strategies that promote success under extreme conditions can inform proactive restoration initiatives and conservation management decisions (Colton et al. 2022). Previous work from other naturally extreme environments has demonstrated that the coral holobiont can adjust to environmental extremes utilizing diverse strategies (e.g., Jacquemont et al. 2022; Bay and Palumbi 2017; Lord et al. 2021). In this thesis, we found that inland bay corals differ from conspecifics from the fringing reefs in their host functional traits, symbiont, and bacterial communities, suggesting a significant role of all holobiont members in promoting increased tolerance to the extreme bay conditions.

We demonstrated that trophic plasticity and hosting thermally tolerant symbionts were key mechanisms underlying resistance of three species of bay corals (*Siderastrea siderea*, *S. radians*, and *Porites* sp.) to their native extreme, highly variable environmental conditions (Chapters 2 and 3). Other work has also shown that increased heterotrophy is a vital mechanism underlying recovery from thermal bleaching (Grottoli et al. 2006; Lange et al. 2023), but its role in promoting resistance to multiple co-occurring global and local stressors remains understudied. It has been hypothesized that corals from similar extreme habitats may rely on increased heterotrophy to compensate for increased energetic demand associated with living under more extreme conditions (Camp et al. 2017; Baumann et al. 2021). Our knowledge on metabolic demands of corals from extreme habitats is limited, with some studies reporting high metabolic demand in corals from extreme habitats relative to conspecifics from more stable habitats (Camp et al. 2017; Jacquemont et al. 2022), while other studies found no differences (Tanvet et al. 2023). Our measurements did not reveal consistently elevated respiration rates of bay native corals relative to reef native corals (Chapter 4), and hence our findings do not provide evidence of stress-induced elevated metabolic demands in bay corals. Therefore, while our results suggest that dynamic trophic strategies play a key role in allowing bay corals to adjust to seasonal changes in physicochemical conditions, we did not find clear evidence of heterotrophy as a compensatory mechanism related to increased metabolism (Chapter 2 and 4), as suggested in other studies (Camp et al. 2017; Baumann et al. 2021). Further investigation into the trophic strategies of corals from extreme habitats will help elucidate the role of heterotrophy in promoting adaptive capacity.

While bay and reef conspecifics had distinct bacterial communities, we also observed site-specific differences between the two inland bays and between the two reef sites. Interestingly, corals from the bays tended to host bacteria with diverse metabolisms (e.g., sulfur and nitrogen cycling), and unravelling their potential functional role in promoting tolerance to environmental extremes within the bays is a promising avenue for future research (Chapter 3). Overall, we found strong evidence that bay corals have optimized their energy acquisition strategies to match their more extreme environment, through high trophic plasticity, associating with heat-tolerant algal symbionts, and potentially harboring beneficial bacterial communities. These strategies underlie their ability to maintain high calcification rates and tissue biomass that are comparable to reef corals (Chapter 4). Our short-term comparison of these fitness metrics (calcification rates and tissue biomass) suggests minimal trade-offs at the colony scale, however, the reproductive success of bay populations relative to reef corals remains unknown. Coral cover within the bays is much lower than on the reefs, however, whether this is due to, for example, lower fecundity, low larvae survival, or lack of suitable settlement substrate is also unknown. Additional insights into the reproductive success of bay corals would provide further understanding of the fitness consequences associated with living under more extreme conditions. Nonetheless, our findings highlight that reefs of the future should consist of corals that will not only associate with thermally tolerant symbionts, but also have dynamic and highly mixotrophic energy acquisition strategies such that they can continuously adjust to environmental change.

### **Acclimatization to extreme bay conditions can enhance heat tolerance of reef corals**

The persistence of coral reefs as we know them today depends on, among other factors, their ability to acclimatize to increasingly extreme conditions and to rapidly acquire increased heat tolerance within a single generation (Logan et al. 2014; Torda et al. 2017; Drury 2020). However, it remains poorly understood which coral species have such adaptive capacity and the timescales involved in acquiring increased heat tolerance. A primary objective of this thesis was to investigate the acclimatization capacity of reef corals to the more extreme bay conditions and to assess their ability to gain heat tolerance after one year of exposure to bay conditions. We found that reef-origin corals transplanted into the bay (S.

*siderea* and *Porites* sp.) had high survival and growth by the end of the experiment and exhibited high phenotypic plasticity (Chapter 4). This acclimatization capacity provides some hope for their ability to persist under future, more extreme ocean conditions given their high phenotypic plasticity. Our findings agree with other similar studies on Caribbean corals that also demonstrated high phenotypic plasticity of corals when transplanted from cooler, more stable habitats into warmer, more variable inshore habitats (Baumann et al. 2021; Castillo et al. 2024; Kenkel et al. 2015). However, both species in our study faced energetic trade-offs within the bay habitat, as they could not fulfil daily energetic demand through photosynthesis alone following transplantation (low P:R ratios, Chapter 4). These energetic trade-offs agree with similar findings of corals from extreme mangrove lagoons in Bouraké, New Caledonia that also had lower P:R ratios than corals on the more stable reference reef (Camp et al. 2017). However, not all species from this mangrove habitat exhibit energetic deficits associated with living under extreme conditions (Jacquemont et al. 2022), and bay natives in our study also maintained P:R ratios similar to reef natives (Chapter 4). Chapter 2 showed that both species have high trophic plasticity, therefore, energetic deficits observed in corals transplanted from the reef into the bay (Chapter 4) may have been compensated through heterotrophy. Given the energetic trade-offs, our study illustrates that one year may not have been enough time for reef corals to fully adjust to the more extreme bay conditions, and outcomes could differ over longer time scales than one year. For example, *S. siderea* transplanted for 3.5 years from a relatively cooler, more stable offshore reef onto a warmer, more variable nearshore reef in Belize had growth rates and genotype expression profiles that closely resembled nearshore-natives (Castillo et al. 2024).

*Siderastrea siderea* showed remarkable ability to increase their heat tolerance by shuffling their algal communities to host more thermally tolerant symbionts (Chapter 5). Heat tolerant corals from thermally extreme habitats (e.g., Palumbi et al. 2014; Howells et al. 2020) and from extreme mangrove lagoons (Ros et al. 2021; Alessi et al. 2024) tend to host thermally tolerant algal symbiont communities. Yet, within some thermally extreme habitats, host mechanisms, such as increased gene expression plasticity, rather than symbiont community profiles have been attributed to conferring enhanced heat tolerance (Kenkel et al. 2016; Palumbi et al. 2014). In contrast to *S. siderea*, reef-origin *Porites* sp. did not acquire

enhanced heat tolerance despite hosting thermally tolerant symbionts, potentially due to prior exposure to *in situ* heat stress (Chapter 4). The findings of this thesis are consistent with other studies that demonstrated that gaining heat tolerance may be species-specific (Brown and Barott 2022; Ferrara et al. 2025) and highly dependent on past environmental stress loads (Klepac and Barshis 2020). Overall, reef *S. siderea* had high acclimatization capacity (Chapter 4) and potential to gain substantial heat tolerance (Chapter 5), demonstrating the adaptive capacity of this species through phenotypic plasticity and flexibility of symbiont associations. However, the degree to which reef corals in our study can retain this increased tolerance under, for example, chronically low pH or during periods of low dissolved oxygen remains unknown. Corals from an environmentally extreme mangrove lagoon on the Great Barrier Reef have been shown to have higher heat tolerance relative to conspecifics from a nearby, more stable reef, despite co-occurring warmer temperatures and highly variable and low pH and dissolved oxygen concentrations (Roper et al. 2025). Similarly, Alessi *et al.* 2024 demonstrated substantial heat tolerance of corals from a hot, acidified, low oxygen semi-enclosed lagoon of Bouraké, New Caledonia, but only in corals that are associated with certain algal symbiont profiles. In Palau's Rock Islands, corals exhibited higher heat tolerance compared to outer reef corals despite exposure to warmer, more acidic and highly variable temperature and pH (Rivera et al. 2022). In contrast, in Rathbone *et al.* 2022, corals from a habitat with highly variable temperature and pH did not have increased tolerance to future warming and acidification relative to corals from a more stable reef. Significant knowledge gaps remain on the capacity for corals to gain heat tolerance in the presence of co-occurring stressors, but it is a crucial consideration for understanding reef corals' capacity to adjust to climate change (Gunderson et al. 2016; Pendleton et al. 2016). Additionally, as marine heatwaves increase in frequency and severity (e.g., Frölicher and Laufkötter 2018), their ability to withstand annual and cumulative heat stress must be evaluated (Grottoli et al. 2014).

### **Hotspots of resilience – bay corals have higher heat tolerance than reef corals**

In Chapter 5, we found that bay corals of both species naturally had higher heat tolerance compared to fringing reef conspecifics, which was at least in part supported by hosting thermally tolerant symbionts (Chapters 3

and 5). The inland bays are thus “hotspots of resilience”, a term proposed in Camp (2022) to broadly describe areas of high coral stress resilience. Importantly, given the decline in coral populations in the bays through time (Debrot et al. 1998), this term does not imply that bay corals have historically been resilient to environmental pressures, but rather that selective pressures through time have promoted increased tolerance (relative to conspecifics on the reef) for a subset of corals that remain today. Hotspots of thermal resilience, such as the inland bays, can support many proactive coral reef management opportunities, such as selective breeding of naturally heat tolerant corals and inclusion in spatial marine protected area planning. These protective services are outlined in Camp (2022), and discussion of the utility of inland bay corals for restoration initiatives is continued in the next section. Several other studies have also demonstrated that corals from naturally warmer and/or more thermally variable environments have increased heat tolerance compared to conspecifics from more thermally stable environments (e.g., Palumbi et al. 2014; Schoepf et al. 2015; Safaie et al. 2018). Coral heat tolerance in such environments has been attributed to a range of mechanisms involving a strong role of both hosts *and* symbionts, including hosting thermally tolerant symbionts (e.g., Howells et al. 2011; Hume et al. 2015), host adaptations that allow them to cope with oxidative stress (e.g., Howells et al. 2016), and increased gene expression plasticity (Roper et al. 2025; Palumbi et al. 2014; Castillo et al. 2024). Further investigation of the potential genetic component of bay corals’ heat tolerance is needed to fully understand the mechanisms underpinning their increased heat tolerance.

In many systems, coral thermal tolerances are determined by local thermal regimes (e.g., Palumbi et al. 2014; Howells et al. 2016; Schoepf et al. 2015), and limited evidence suggests that heat tolerance can be gained in the presence of other extreme conditions, such as lower and/or highly variable pH and dissolved oxygen concentrations (Alessi et al. 2024; Roper et al. 2025; Rivera et al. 2022). Given the warmer and more variable temperatures of the bay compared to the reef and the higher heat tolerance of bay corals, our results support a strong role of thermal regimes in determining heat tolerance. Interestingly, exposure to local stressors such as increased nitrogen pollution (nitrate and ammonium) can impair thermal tolerances (Donovan et al. 2020; Vega Thurber et al. 2014), however, bay corals still had higher tolerance than reef corals despite

chronic exposure to higher inorganic nutrients (Govers et al. 2014; de Jong et al. 2025). In Chapter 2, we posited that the higher concentrations of inorganic nutrients in the bays may even boost the productivity of their thermally tolerant algal symbionts, stimulating autotrophy in bay corals, thereby providing them with an energetic advantage. Further, corals from extreme mangrove lagoons and inland bays may also be exposed to higher dissolved organic nutrients (e.g., Kristensen et al. 2008; Maggioni et al. 2021), which they could be taking up under thermal stress to improve their resistance to and/or recovery from bleaching (Camp et al. 2017; Lange et al. 2023; Grottoli et al. 2006). Given that bay corals exhibit seasonal trophic plasticity, it seems evident that they can opportunistically capitalize their energetic gains using a dynamic combination of autotrophy and heterotrophy, which may stabilize the symbiotic relationship between hosts and symbionts under heat stress (Solomon et al. 2025; Tremblay et al. 2016). Our study demonstrated that despite chronic exposure to warmer and inorganic nutrient rich conditions, and highly variable temperatures, pH, and dissolved oxygen concentrations, corals from the inland bay (Spanish Water Bay) still had higher heat tolerance than reef corals (Chapter 5). However, as previously emphasized, the heat tolerance of these corals under chronically lower pH and dissolved oxygen levels should be assessed to further predict their prospect to serve as adaptive refugium under future climate change (Keppel and Wardell-Johnson 2012; Kapsenberg and Cyronak 2019). The higher heat tolerance and life-long exposure to high diel variability of pH and dissolved oxygen may also confer increased tolerance to ocean acidification (Cornwall et al. 2018) and/or hypoxia (Lucey et al. 2025). Thus, a deeper look into how multiple chronic stressors interact to affect various environmental tolerances of these corals and the potential role that nutrient availability (e.g., dissolved organic matter, inorganic nutrients) is a worthwhile direction for future work.

### **Local adaptation, environmental memory, and limits to acclimatization capacity – are bay and reef corals candidates for proactive restoration initiatives?**

Naturally stress-tolerant corals may be highly useful for building reef resilience through larval propagation, assisted evolution, assisted gene flow, and other proactive restoration initiatives (Caruso et al. 2021; Baker et al. 2025). Inland bay corals investigated in this thesis are thermally

tolerant and potentially climate-change resistant corals, but should they be used in restoration? Their utility under a restoration context depends on their ability to retain their stress tolerance when moved to novel environments. In Chapter 4, bay corals transplanted to the reef grew slower and suffered partial tissue mortality, but nonetheless retained their heat tolerance. Some naturally heat-tolerant corals from extreme environments have reduced ability to cope with thermal stress under novel conditions due to, for example, local adaptation to native conditions or changes in gene expression following acclimatization to more benign conditions (Palumbi et al. 2014; D'Angelo et al. 2015). However, there is also evidence that some corals can retain their “environmental memory” such that prior exposure to abiotic stress primes, or stress-hardens them to have enhanced tolerance to future disturbances (Brown et al. 2015; Hackerott et al. 2021). Therefore, two key aims of this thesis were to determine if local adaptation limits acclimatization capacity to novel environmental conditions and to investigate changes in the thermal tolerances of bay corals following acclimatization to less extreme conditions. In Chapter 4, we did not find strong evidence of local adaptation of bay corals, and they maintained their heat tolerance following one year of exposure to reef conditions. Bay corals retained a high proportion of thermally tolerant symbionts, despite acclimatization to cooler, more benign reef conditions, thereby retaining their environmental memory. Nonetheless, there were trade-offs associated with living on the reef, including reduced growth rates and higher partial tissue mortality. These findings suggest that they are locally specialized to thrive under bay conditions, which limits their acclimatization capacity to novel environmental conditions (Chapter 4). In addition to environmental specialization that limited their acclimatization potential, bay corals transplanted onto the reef may have been exposed to stress-inducing factors that we did not measure, such as novel pathogens (e.g., Casey et al. 2015), as bay and reef corals were found to have distinct bacterial communities (Chapter 2). Bay corals may have also experienced resource limitation on the reef that led to growth trade-offs, such as reduced availability of dissolved organic matter, an important source of nutrition to corals (e.g., Houlbrèque and Ferrier Pagès 2008), which has not been directly measured in the bays, however, de Jong et al. 2025 found relatively higher organic content within sediment traps. Whether or not such a reduction in growth is an acceptable trade-off for increased heat tolerance

for corals included in restoration initiatives remains unresolved (Banaszak et al. 2023; Caruso et al. 2021; Vogt-Vincent et al. in review). It remains unknown if bay corals can retain their heat tolerance in novel environments beyond the time scales involved in our experiment (1 year). Therefore, future work should not only investigate the potential genetic mechanisms underlying heat tolerance, but also their capacity to retain their environmental memory. Regardless, given the urgent and mounting pressure on coral reefs, I suggest that the utility of bay-origin corals in restoration is promising, which will be discussed more below.

In Chapter 5, we demonstrated that exposure of reef-origin *S. siderea* to extreme, highly variable conditions can prime them to have enhanced heat tolerance, making corals from this population viable candidates for restoration projects that involve stress-hardening regimes (e.g., Banaszak et al. 2023). This finding is especially relevant given that the ability to gain environmental tolerance through stress-hardening via exposure to warmer and/or more variable temperature regimes is species-specific (Brown and Barott 2022; Ferrara et al. 2025). Our results that branching *Porites* sp. did not gain heat tolerance supports this, and it may be due to species-specific trade-offs associated with higher heat tolerance (e.g., Ferrara et al. 2025; Hackerott et al. 2021). While not observed in our study, another possible outcome of prior exposure to elevated and/or more variable temperatures is increased sensitization to heat, where corals can become even more susceptible to thermal bleaching (Grottoli et al. 2014; Brown and Barott 2022). Further, while there have been promising examples of corals that can gain heat tolerance through stress-hardening, these protective priming effects may not persist as marine heatwaves intensify (Ainsworth et al. 2016). Nonetheless, our results support that reef-origin *S. siderea* can be stress-hardened using the inland bay as a nursery and has potential to be stress-hardened within *ex situ* nurseries (e.g. Ferrara et al. 2025), making them viable candidates for restoration initiatives in Curaçao.

Given that our study found evidence of potential metabolic trade-offs where their daily metabolic demand exceeded or nearly exceeded photosynthetic gains (P:R ratios <1; Chapter 4), the long-term health of the *S. siderea* reef population could be compromised, especially under annual and cumulative heat stress (e.g., Levas et al. 2018). Furthermore, bay-origin corals also demonstrated significant trade-offs on the reef, including high

partial mortality. Therefore based on our results, it is still hard to say whether corals from the reef or corals from the bay would be better candidates for reef restoration initiatives and using both may promote increased genetic diversity within restoration nurseries. In both cases, the population-specific risks and trade-offs discussed in this synthesis should be considered. A closer look at other traits that may convey environmental tolerance is needed to assess their performance under future ocean conditions, such as their disease susceptibility (e.g., Klein et al. 2024), ability to utilize dissolved organic nutrients under heat stress (e.g., Lange et al. 2023), mechanisms that reduce oxidative stress (e.g., Howells et al. 2016; Roper et al. 2025), and gene expression plasticity (e.g., Roper et al. 2025; Castillo et al. 2024). Further, our study did not address how acclimatization to novel conditions may impact other key fitness metrics, such as reproductive output (Brown and Barott 2022). A better understanding of which population of *S. siderea* (bay- vs. reef-origin) may have higher fitness could inform such a decision.

### **Genetic connectivity of bay and reef habitats, conservation management implications, and the potential for cryptic species**

To support the adaptive potential of coral reefs, conservation management plans should prioritize protecting networks of coral habitats with diverse, heterogeneous characteristics (Webster et al. 2017; Camp, 2022; Colton et al. 2022). This approach can help to protect as much genetic diversity that natural selection can act on and facilitate the evolutionary adaptation to climate change (McLeod et al. 2019; Wilson et al. 2020; Colton et al. 2022). Habitats that harbor corals that are naturally tolerant to extreme conditions (e.g., higher temperatures, lower pH and dissolved oxygen) should be included in such adaptive networks to enhance coral adaptive capacity, as they are sources of potentially climate-change resistant genotypes (Camp, 2022; Colton et al. 2022). For example, at local and regional scales, corals from cooler, more benign habitats may be able to increase their environmental tolerances through evolutionary rescue via exchange of heat-resistant genes from warmer, more extreme habitats (Bell and Gonzalez 2009; Colton et al. 2022). Inland bay corals may be sources of heat tolerant genes and/or genetic diversity that can support rapid evolution of reef corals in Curaçao. However, the heritability of heat tolerance observed in bay corals (Chapter 5), larval dispersal patterns, and genetic connectivity (gene flow) between the inland bays and surrounding

fringing reefs are unknown. In other extreme environments, gene flow between distinct habitats (e.g., highly variable lagoons and stable reefs) can be relatively high, but selection pressures are stronger, contributing to local adaptation (e.g., Bay and Palumbi et al. 2014; Thomas et al. 2022; Savolainen et al. 2013). Thus, local adaptation of corals within more extreme habitats (Scucchia et al. 2023; Leiva et al. 2025) is associated with fitness costs in other environments (Kenkel et al. 2015; Howells et al. 2013; Bay and Palumbi 2017). Our finding that bay corals had higher heat tolerance, but grew slower on the reef agrees with this pattern, and suggests that even with high larval connectivity between bays and reefs, high selection pressures may limit gene flow (Thomas et al. 2022; Savoleine et al. 2013). Regardless, given that the inland bays are hotspots of thermal resilience, reducing the anthropogenic impacts on inland bays should be prioritized to prevent further decline of coral health in these valuable ecosystems (Debrot et al. 1998; de Jong et al. 2025). Further insights into the potential role that inland bay corals may play in promoting increased resilience of reefs to climate change through gene flow can inform conservation management plans focused on protecting the evolutionary capacity of vulnerable populations (Colton et al. 2022).

The amount of genetic diversity of corals within the bays has never been assessed, however, the findings from this thesis demonstrate that bay corals are specialized to cope with highly variable, extreme conditions (Chapter 4). Our finding that bay corals are locally specialized while reef corals have a more generalist strategy (Chapter 4), suggests that these are distinct populations. Throughout this thesis, we rely on comparisons of physiology and microbial associations of conspecifics in the bays and reefs to understand how a given species may acclimatize to increasingly stressful conditions. However, an unexpected amount of cryptic diversity, or genetically distinct lineages, of corals has recently been revealed (Grupstra et al. 2024). Therefore, it is possible that differences in holobiont traits observed between bay and reef habitats are due to cryptic genetic divergence (Rippe et al. 2021; Grupstra et al. 2024b; Aichelman et al. 2025). For example, three cryptic lineages of *S. siderea* were identified in Bocas del Toro, Panamá, which differed in their distributions across a similar environmental gradient as the bays and reefs (inshore vs. offshore), as well as in key phenotypic traits, microbial associations, and heat tolerances (Aichelman et al. 2025). Further insights into mechanisms of

heat tolerance, such as heritable genetic adaptations or differential gene expression, are necessary to better understand the role of the host versus symbiont in bleaching resistance in bay corals. Therefore, investigating the genetic connectivity between bay and reef habitats and identifying cryptic lineages with distinct holobiont traits can increase our ability to predict species' responses to climate change.

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