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THE ECOLOGY AND DYNAMICS OF CORAL REEF COMMUNITIES IN AN EXTREME REEF ENVIRONMENT:

THE SOUTHERN PERSIAN GULF

Thesis submitted by
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Statement of contributions of others

This thesis included some collaborative work with Professor Morgan Pratchett, Dr. Andrew Baird, Dr. David Feary, Professor Bernhard Riegl, Dr. Scott Heron, Dr. John Burt and Dr. Georgenes Cavalcante. While undertaking these collaborations, I was responsible for the project concept and design, data collection, analysis and ecological interpretation, and the final synthesis of results into a form suitable for publication. My collaborators provided intellectual guidance, financial support, field assistance and equipment, technical instruction and editorial assistance. Aside from standardized formatting for the thesis, chapters two, three and five have been presented as published.

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"Sometimes a concept is baffling not because it is profound but because it is wrong."
---E.O. WILSON

Abstract

Coral reefs are among the most threatened ecosystem, partly due to the sustained and ongoing effects of global climate change. An important goal of a contemporary coral reef ecologist therefore, is to understand the dynamics of reefs corals subject to extremes of environmental conditions, and to determine limits to the capacity of coral populations to adapt to ongoing changes. A prerequisite for understanding reef dynamics in a rapidly warming ocean is to quantify population processes (i.e., reproduction, settlement, recruitment, growth, mortality) that regulate population densities through time. Changes to any one process may alter demographic rates, in turn affecting overall population dynamics and reef resilience. However, we still know little about sensitivities of coral at different life-stages to environment extremes. The purpose of this research was to quantify key ecological processes in the Persian Gulf, considered one of the most extreme environments for coral reefs, in order to understand the likely effects of climate change on the structure and dynamics of coral populations and communities.

The first step towards understanding possible effects of climate change on coral reefs is determining how the structure of coral assemblages (usually containing similar genus and/or species) vary along steep environmental gradients within a single geographical location. Chapter 2 provides a comprehensive regional examination of coral communities around the northeastern Arabian Peninsula (within the southern Persian Gulf, Strait of Hormuz, and Gulf of Oman), and a comparison of environmental variables considered important in structuring these communities. Multivariate analysis revealed distinct sub-regional coral communities among the southern Persian Gulf, Strait of Hormuz and Gulf of Oman, associated with considerable spatial heterogeneity in oceanic conditions. While temperature and salinity accounted for major differences in

the structure of coral assemblages among different locations, additional environmental parameters, including chlorophyll-*a*, surface currents and winds were also found to be important factors in structuring these assemblages. Aside from the strong spatial patterns, there have also been considerable temporal shifts in coral reef community structure throughout the northeastern Arabian Peninsula over the past two decades. Most dramatic are the apparent changes from *Acropora* dominated to poritid and faviid dominated communities, particularly in the southern Persian Gulf and the Strait of Hormuz, which is linked to taxonomic differences in susceptibility to extreme temperatures.

Extreme temperatures have significant direct effects on coral populations and communities, which are most apparent during multi-specific large-scale bleaching events. However, climate change is also likely to impact coral reproductive processes through modified thermal environments that may disrupt tightly regulated reproductive cycles or highly synchronized temporal spawning events. The aim of Chapter 3 was to: (1) determine whether corals in southern Persian Gulf (Dubai, UAE) are reproductively active, (2) determine the month(s) of spawning of six common coral species within this region, and (3) examine the reproductive biology of the three most abundant species: *Acropora downingi*, *Cyphastrea microphthalma* and *Platygyra daedalea*. Direct measures of the reproductive condition of coral colonies showed that coral reproduction was seasonal, with peak reproductive activity around the full moon in April. These results demonstrate that coral reproduction patterns within the region are highly seasonal and that multi-species spawning synchrony is highly probable. Moreover, *Acropora downingi*, *Cyphastrea microphthalma* and *Platygyra daedalea* were all hermaphroditic broadcast spawners with a single annual gametogenic cycle of between 7 and 9 months. Fecundity and mature oocyte sizes for all species were comparable to those in other

regions. Collectively these results demonstrate that the reproductive biology of corals in the southern Persian Gulf is similar to other regions, indicating that these species have adapted to the extreme environmental conditions in the southern Persian Gulf.

Coral settlement, a key ecological process in the maintenance, recovery and resilience of coral reef ecosystems, is also highly susceptible to increasing climate change. Elevated temperatures can affect coral larvae during early stages of development reducing rates of settlement, which in turn can have profound affects on overall reef dynamics. Chapter 4 investigated spatial and temporal patterns of coral settlement at six sites over two years using coral settlement tiles. Results from this thesis showed there is clear evidence of ongoing coral settlement in the southern Gulf, despite very high temperatures and high frequency disturbance events (i.e., bleachings). Coral settlement in the southern Gulf was low ($\approx$ 113 spat m^{-2} year^{-1}), but highly seasonal with peak settlement during the summer (June and August), when daily-mean temperatures approached 35°C, well above the critical thermal limit for coral larvae reported from other experimental studies. However, results also showed that peak settlement was recorded up to 4 months after the major spawning season in April and May suggesting either delayed larval settlement or spatial and/or taxonomic disparity between studies of reproduction and versus settlement. Furthermore, the composition of coral spat in the southern Gulf differed considerably from those reported on most reefs in the Indo-Pacific because there were few Acroporidae coral spat (11%), and no Pocilliporidae. Importantly, data from this thesis indicates that the observed long-term shifts in community structure of adult corals are likely being reinforced at the level of settlement, such that there is limited scope for recovery of former *Acropora*-dominated coral assemblages in the Gulf.

Fluctuations in a range of environmental variables (i.e. physical and chemical), mediated by changes in global climate, are predicated to directly affect the growth rates of corals and thus the overall size structure of coral populations. Chapter 5 tested for consistent differences in the size-structure of four different coral populations along established gradients of increasingly severe environmental conditions from the southern Persian Gulf (Dubai and Abu Dhabi) to the eastern Persian Gulf (western Musandam). Significant and consistent differences were observed in mean colony sizes and size distributions for all four coral species between locations. All corals in the southern Gulf, where sea surface temperatures, salinity, and the recent frequency of mass bleaching are all significantly higher, were smaller, and their size structure positively skewed. Differences in size structure between locations were more pronounced than differences between species at each location, suggesting that extreme differences in environmental conditions. Importantly, results suggest that even within regions, such as the Persian Gulf, where corals are considered particularly tolerant of environmental extremes, increased frequency of bleaching events will lead to persistent declines in the size of coral colonies. Overall, the fate of different corals will depend on the recurrence of major disturbance events relative to their capacity for recovery, which in turn depends on their capacity for individual and population growth.

This research shows at least some species of scleractinian corals can survive prolonged exposure to temperatures well above those (e.g., 32-34^{o}C) considered to be above the critical thermal limits of corals throughout much of the Indo-Pacific. Moreover, corals within the Persian Gulf (where temperatures range from <12°C in winter to >35°C in summer) are continuing to spawn, settle and grow. These results have far reaching implications, suggesting that there is capacity for corals to withstand sustained and ongoing climate change. However, corals within the Persian Gulf have become adapted to extreme temperature ranges and specific local conditions over thousands of years, and it is questionable whether corals in locations that have until now experienced much milder conditions posses (or can develop) similar capacity to withstand extreme environments. This largely depends upon the physiological or genotypic basis of increased temperature tolerance in corals from the Gulf, which requires considerable further research.

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Chapter 1: General Introduction

Coral reefs are one of the world's most productive and diverse ecosystems, largely due to the complex habitat provided by scleractinian corals (Jones et al. 1994, 1997; Bellwood et al. 2004). However, coral-dominated habitats have been effectively lost from one-third of the world's coral reefs, and up to 70% of reefs face similar fate within the next 50 years (Wilkinson 2008). Extensive loss of corals inevitably leads to declines in reef-associated plants and animals (i.e., species richness; Jones et al. 2004; Przeslawski et al. 2008), and contributes to the overall degradation of marine ecosystems (Bellwood et al. 2004; Wilson et al. 2006). The reduction of live coral cover, for example, causes rapid and pronounced declines in the abundance and diversity of reef fishes (e.g., Jones et al. 2004; Graham et al. 2006). Graham et al. (2006) found that climate change-driven losses of live coral in the Seychelles, and ultimately structural complexity, resulted in local extinctions, substantial reductions in species richness, reduced taxonomic distinctness, and a loss of species within key functional groups of reef fish. Overall, sustained and rapid degradation of the world's coral reef ecosystems is leading to severe depletion of many reef resources. Such declines are likely to have drastic consequences for the approximately half a billion people who depend on the many important ecosystem goods and services coral reefs provide (Moberg and Folke 1999). Importantly, despite these increasing impacts, human dependence on coral reefs continues to increase (Martínez et al. 2007).

Coral reefs are being degraded due to multiple disturbances (e.g., overfishing, pollution, coastal development, disease), which are becoming more frequent and severe, leading to increasing loss, as well as marked modification of these ecosystems (Hughes et al. 2003; Wilkinson 2008). Most importantly, enduring disturbances are now being compounded by the superimposed impacts of global climate change (Hoegh-Guldberg 1999, Hughes et al. 2003, Bellwood et al. 2004). Of particular concern for the persistence of tropical coral reefs are the rapid increases in atmospheric carbon dioxide concentrations ($[CO_2]_{atm}$), which contribute to both ocean warming and ocean acidification (Hoegh-Guldberg et al. 2007).

Comparative studies on the effects climate change on natural ecosystems report that coral reefs are among the susceptible ecosystems to observed and projected effects of climate change (Walther 2002; Parmesan 2006; Doney et al. 2012). Average tropical sea surface temperatures (SSTs) have increased by 0.28°C in recent decades (Lough 2012), with global SSTs predicted to increase 2–4°C within the next century (IPCC 2007). This has important implications because SST is the primary controlling factor of coral reef distribution (Ma 1959; Buddemeier and Kinzie 1976). Corals have already shown their sensitivity to the relatively small amount of warming observed so far, for example, more frequent climate-induced mortality events in many coral reef regions (e.g., Gardner et al. 2003; Wilkinson 2004; Bruno and Selig 2007; Baker et al. 2008). Established thermal thresholds of most corals will be chronically exceeded as the current rate of temperature increases because of the incessant accumulation of greenhouse gases in the atmosphere (Hoegh-Guldberg and Bruno 2010; Donner 2012). Moreover, progressive acidification of the oceans (due to dissolution of atmospheric CO_2 into the oceans) has caused surface pH to decline by 0.1 units since the 1950s (an increase in acidity of ~ 30%) (Raven et al. 2005; Feely et al. 2009), with further predicted decreases of up to 0.4 by 2100 (IPCC, 2007). Declines in pH are associated with reduced aragonite saturation (Ω), increasing the energetic costs associated with construction of aragonite skeletons for corals and other marine calcifiers (Raven et al 2005; Kleypas et al 2006; but see Wood et al. 2008).

Given that ecosystems typically exhibit non-linear (threshold) dynamics in response to slow (i.e., ocean acidification) and fast (i.e., increasing temperatures) drivers of change (Hughes et al. 2010), is likely to add to the complex behavior of ecological systems, thereby either reinforcing or triggering feedback loops (Hoegh-Guldberg and Bruno 2010). Consequently, the combination of elevated SSTs and ocean acidification are expected to ultimately lead to comprehensive loss of reef-building corals (Hoegh-Guldberg and Bruno 2010), however even now climate change is imposing strong selective pressures on the composition of coral assemblages and on population dynamics of highly susceptible species (Pandolfi et al. 2011; Hughes et al. 2012).

1.1 Elevated temperature and coral bleaching

Scleractinian corals are extremely sensitive to elevated temperature (Jokiel and Coles 1990; Glynn and D’Croz 1990; Kleypas et al. 1999), whereby even small increases in ocean temperatures (1–2°C above normal local limits) can have dramatic consequences for demographic rates and population dynamics. The most profound response of corals to temperature stress is of course “coral bleaching” whereby corals expel their symbiotic dinoflagellate algae (zooxanthellae). Established predictions suggest that coral bleaching occurs when seawater temperatures exceed normal summertime maximum by ≥1°C for a month or more (Goreau and Hayes 1994; Hoegh-Guldberg 1999, Berkelmans and Willis 1999). The accumulation of thermal stress in excess of coral bleaching thresholds is used to predict bleaching events (Fitt et al. 2001; Liu et al. 2003; Guest et al. 2012). These predictive tools are based on thermal stress algorithms and are commonly expressed as the accumulation of degree-heating-weeks (DHW; Eakin et al. 2009) degree-heating-months (DHM; Donner et al. 2005) or maximum monthly mean (MMM; Logan et al. 2012). In support of these predictions it has been suggested that increasing climate change will lead to massive loss of all corals (Hoegh-Guldberg 1999). However, this is based on the assumption that all corals respond identically to thermal stress, and that corals and their symbionts have low overall evolutionary potential to adapt to rising sea temperatures (Hughes et al. 2003; Hoegh-Guldberg 2007). Recent research has shown that bleaching thresholds in individual corals are not necessarily static over time because not all corals respond identically to thermal stress (McClanahan et al. 2007; Oliver and Palumbi 2011). Moreover, bleaching thresholds are not always simply related to a certain threshold of a DHM or DHW (Donner et al. 2011; Guest et al. 2012; Teneva et al. 2012), because they are often location specific or “best-fit” approximations applied over large spatial scales (from tens to 1000s of km) (Berkelmans 2009).

Recent experimental studies suggest that many reef organisms, including corals, are living very close to their critical thermal limits (Munday et al. 2008; Whalan et al. 2008; Donelson et al. 2010; Heyward and Negri 2010; Webster et al. 2011), such that increasing temperature anomalies in concert with sustained increases in the mean temperature may exceed the upper most temperatures that reef organisms are able to withstand. Evidence from these and other studies suggest some convergence toward an absolute threshold in the range 30–32°C, whereby higher temperatures will significantly compromise key physiological processes. For example, Heyward and Negri (2010) found that an upper temperature threshold of coral larvae of four broadcast spawning coral species was ≤32°C. If absolute thresholds and critical thermal limits are fixed, then we can expect localized extinctions of coral reef organisms in areas where temperatures are naturally highest, and/ or corresponding shifts in the distribution of organisms (e.g., Yamano et al. 2011) to escape the most severe temperatures. However, geographic variability in physiological stress does not always follow simple latitudinal gradients, but rather exhibit ‘mosaic’ patterns over geographic scales (Helmuth et al. 2002, 2006; Finke et al. 2007; Person et al. 2009), such that range shifts may not necessarily be possible for all species (Precht and Aronson 2004; Yomano et al. 2011). Furthermore, recent studies have documented geographic variability in physiological tolerance (Hughes et al. 2003; Donner et al. 2005; Pearson et al. 2009; and see review by Brown and Cossins 2011), reflective of adaptation to local environments (e.g., Kuo and Sanford 2009; Howells et al. 2012). These studies all suggest that a thorough understanding of the mechanisms underlying complex interactions between changes in the physical environment and organismal and ecological responses is vital if we are to predict future patterns of biodiversity, distribution and abundance, and that simple generalizations are not always effective as working null hypotheses (*sensu* Hoegh-Guldberg 1999).

It is now well understood that large-scale and multi-species bleaching and mortality events are mainly caused by high seawater temperatures and the accumulation of thermal stress, but may be exacerbated by high solar irradiance (Glynn 1996; Hoegh-Guldberg 1999; Mumby et al. 2001). However, it is also well demonstrated that bleaching variability in levels of susceptibility, adaptation and acclimatization also exists among species (Coles and Brown 2003). Importantly, absolute temperature at which corals bleach varies greatly within and among regions, mostly in accordance with normal maximum temperature experienced at each location (Coles et al. 1976; Berkelmans 2002). Upper thresholds limits within most tropical areas for coral bleaching and survival are remarkably consistent at 1–3°C above normal maxima regardless of location (Berkelmans 2001; Coles and Riegl 2012).

Given that corals are highly adapted to their local environments, including temperature regimes (Edmondson 1928; Coles et al. 1976), this has produced a large range of upper thermal limits of nearly 10°C across locations (Riegl et al. 2011; Coles and Riegl 2012). For example, cooler areas like Rapa Nui experience thermally induced bleaching at about 26°C whereas hotter regions like the Persian Gulf show thresholds as high as 35–36°C (Wellington et al. 2001; Coles and Riegl 2012). Consequently, corals in the Persian Gulf can live for extended period of times (i.e., several months) at temperatures that would immediately kill corals in most other regions (Sheppard 2003; Riegl et al. 2011).

Even at fine-scales bleaching is conspicuously patchy, and varies spatially, temporally, and taxonomically (Berkelmans and Willis 1999; Marshall and Baird 2000; Loya et al. 2001). For example, bleaching susceptibility varies between taxa (Marshall and Baird 2000; Loya et al. 2001), as well as within coral taxa containing different symbiont types (Berkelmans and van Oppen 2006; Sampayo et al. 2008). Because the extent of variability in bleaching thresholds itself varies among species, taxonomic differences in bleaching severity may vary among bleaching events (Baker et al. 2008; Pandolfi et al. 2011). Furthermore, the susceptibility of a given reef to bleaching also depends on the magnitude of thermal stress event (Kleypas et al. 2008), coral species composition (Marshall and Baird 2000) and levels of irradiance (Lesser and Farrell 2004). Other sources of stress, such as sedimentation, overfishing and ocean acidification also appear to interact with thermal stress to change bleaching thresholds (Baker et al. 2008; Anthony et al. 2008; Carilli et al. 2010).

The variable response of many coral species to thermal stress both within reefs and among regions suggests some potential for corals and their endosymbiotic algae to adapt or acclimate to increasing seawater temperatures (Douglas 2003; Hughes et al. 2003). Coral and their zooxanthellae may increase thermal tolerance through a variety of mechanisms, including but not limited to selective mortality (Loya et al. 2001), replacement of bleaching susceptible zooxanthellae by genetically distinct, thermally-resistant zooxanthellae (Rowan 2004; Baker et al. 2004) or by shifts in the dominant members of zooxanthellae populations in corals, which host multiple clades or types of algae (Berkelmans and van Oppen 2006). Coral and/or its symbionts (zooanthellae) might also increase thermal tolerance through physiological acclimatization. For example, corals may reduce bleaching susceptibility by producing stress proteins, antioxidants (Brown et al. 2000, 2002a), or photoprotective compounds (Salih et al. 2000). Importantly, both coral host and zooxanthellae affect the overall thermal tolerance of corals in influence bleaching susceptibility at elevated temperatures (Baird et al. 2009a).

There is also increasing evidence that suggests that the susceptibility of a given coral or reef to bleaching will also depend on the rate of environmental change, as well as the thermal history to which reef organisms have been exposed (McClanahan et al. 2007; Thompson and van Woesik 2009; Oliver and Palumbi 2011). Several studies have found that the thermal disturbance history of a reef/site can determine the level of resistance to bleaching and/or the resilience to bleaching and bleaching-related mortality (Coles and Jokiel 1978; Brown et al. 2002b; McClanahan et al. 2007). For example, corals exposed to successive thermal disturbances may have higher bleaching thresholds and lower rates of bleaching induced mortality (Maynard et al. 2008). Similarly, thermal history and previous exposure to thermal stress have been shown to determine bleaching responses to contemporary thermal stress (Thompson and van Woesik 2009). Bleaching susceptibility might also be related to past temperature variability (Kleypas et al. 2008, McClanahan et al. 2007). For example, following the 1997–1998 bleaching in the Western Indian Ocean coral mortality was lower in areas with higher historical SST variability (McClanahan et al. 2007; Ateweberhan and McClanahan 2010). Thus, thermal disturbance history and past temperature variability be a key critical factor in determining susceptibility to coral bleaching, and understanding the structure and resilience of reef ecosystems to rising ocean temperatures (Donner 2011).

As such, it is appropriate to examine and compare coral reefs already exposed to highly variable (i.e., extreme) environmental conditions with different background disturbance histories in order to understand how community structure (i.e., abundance, composition and size) could appear under future climates. Furthermore, if corals still have the capacity to adapt to elevated temperatures (Hughes et al. 2003), we would expect to find increases in thermal tolerance on reefs that have previously experienced major bleaching to exhibit the greatest increases in thermal tolerance (Maynard et al. 2008).

1.2 Elevated temperature and demographic rates

Aside from causing bleaching, elevated temperatures may reduce coral growth (De'ath et al 2009; Cantin et al. 2010), reproductive capacity (McClanahan et al. 2009), larval development and survivorship (Randall and Szmant 2009 Heyward and Negri 2010), and recruitment (Ritson-Williams et al. 2009; Albright and Mason 2013). Elevated temperatures also have strong effects on coral physiology, including: respiration, photosynthesis and metabolism (Coles and Jokiel 1977; Porter et al. 1999; Edmunds 2008), which can cascade in non-linear ways among different coral life stages (e.g., between juveniles and adults) (Edmunds 2005). Given the strong link between metabolic processes and temperature suggests that increasing sea temperatures are likely to continue exerting a wide range of sub-lethal affects for numerous processes within individuals, which in turn is likely to affect populations and communities (O'Connor et al. 2007). As such there has been increasing concern that affects of elevated temperatures on population processes, including coral growth, reproduction and early life history stages will have far-reaching consequences for coral population and communities (Fong and Glynn 1998, 2001; Edmunds 2005, Edmunds and Elahi 2007). Importantly, as temperatures begin to stabilize at higher values, the consequences for surviving corals will be mediated by their demographic responses to the sub-lethal effects of temperature (Edmunds 2005).

Seawater temperature has long been recognized as a primary controlling factor of coral growth, and the distribution of coral reefs (Ma 1959; Glynn and Stewart 1973; Kleypas et al. 1999). Significant correlations between coral growth parameters and temperature have been widely reported, though the particular component responses (i.e., linear extension, density and/or calcification rates) vary widely between and among species, and over multiple spatial and temporal scales (see review by Lough and Cooper 2011). Recent studies, however, indicate that a tipping point (i.e., threshold) has been reached with significant declines in coral growth rates (e.g., Cooper et al. 2008; De'ath et al. 2009; Bak et al. 2009; Cantin et al. 2010; Lough and Cooper 2011; and many more), primarily due to the effects of elevated temperatures over the past two decades. Elevated temperatures can affect the relationship between the coral host and its symbionts (zooxanthellae) suppressing the calcification rates of corals (De'ath et al. 2009). As seawater temperatures rise above mean summer time thresholds, the photosynthetic capacity of symbiotic algae declines (Jones et al. 1998), reducing the availability of algal-derived photosynthate that fuels light-enhanced calcification (Al-Horani et al. 2003). Importantly, it has been suggested that elevated temperatures can negatively affect calcification long before bleaching is evident (Cantin et al. 2010).

Similarly, seawater temperatures have also traditionally been considered the major seasonal cue in coral reproduction processes, partly because of the influence that temperature exerts on physiological processes, but also because many coral species in many locations broadcast spawn close to annual maxima (Harrison and Wallace 1990; Baird et al. 2009b). Not surprisingly, the timing of coral spawning seasons varies considerably among different regions (Baird et al. 2009b; Harrison 2011), as does the initiation of gametogenic cycles. Recent work, however, suggests that modified thermal regimes from climate change may have significant repercussions for reproductive success and phenology of many coral species, in particular coral species whose gametogenic cycles are tightly regulated by exogenous cues (i.e., temperature; Lawrence and Soame 2004), and for species that depend on seasonal cues for reproduction cycles (Olive et al. 1990). Changes in seasonal patterns of SST are also suggested to affect highly synchronized spawning events, i.e., multi-species spawning (Baird et al. 2009b), which could potentially effect population replenishment processes which are important following disturbances. Moreover, elevated temperatures have been shown to negatively effect reproductive capacity of corals, including: reduced polyp fecundity, reduced egg quality and lowered fertilization success (see reviews by McClanahan et al. 2009; Baird et al. 2009b).

Mounting evidence is also showing that high temperatures also impact early life history stages beyond the reproductive process (Edmunds et al. 2001; Bassim and Sammarco 2003; Putnam et al. 2008; Heyward and Negri 2010; Albright and Mason 2013). This has important implications given that many processes occurring early in life can greatly influence the number of individuals entering the adult population (Gaines and Roughgarden 1985; Caley et al. 1996). Recent studies reveal that thermal stress has a drastic and immediate effect on larval development (Edmunds et al. 2001; Bassim et al. 2002; Randall and Szmant 2009) rates of settlement (Nozawa and Harrison 2007), settlement choice (Putnam et al. 2008), larval survivorship (Bassim and Sammarco 2003; Baird et al. 2006; Randall and Szmant 2009), and time to reach competence (Heyward and Negri 2010). These factors can result in substantial changes to planktonic larval duration and disruption of normal larval dispersal patterns (Edmunds and Gates 2001; O'Connor and Bruno 2007; Shanks 2009; Weersing and Toonen 2009), which subsequently impact overall reef resilience. Collectively, negative effects of elevated temperatures acting on reproduction and various early life history stages could result in a critical failure of supply sided recruitment for many coral species (Putnam et al. 2008; Randall and Szmant 2009; Albright and Mason 2013).

Despite widely reported and geographically extensive increases in ocean temperatures (IPCC 2007; Lough 2012; Gupta and McNeil 2012), and knowledge about the effects of elevated temperatures on various population processes (e.g., coral growth, reproduction and early life history stages), we know very little about the consequences these impacts on the overall demographics of coral populations (Edmunds 2005; Edmunds and Elahi 2007; McClanahan et al. 2009; Madin et al. 2012). Moreover, within the existing literature there is limited agreement on the demographic implications of the effects of climate change on coral populations (Bak and Meesters 1999; Edmunds 2005; Nakamura and van Woesik 2001; Bena and van Woesik 2004; Shenkar et al. 2005). For example, Bak and Meesters (1999) proposed that elevated temperatures from climate change would likely produce coral populations, with fewer small colonies, lower variance, and more centralized distributions due to poor reproduction and recruitment. Similarly, Edmunds (2005) using ten-year matrix population projections suggested that sub-lethal increases in temperature would increase relative abundance of large colonies at the expense of smaller colonies and increase population size. In contrast, other research predicts that larger colony sizes may actually be deleterious when corals are exposed to thermal stress (Nakamura and van Woesik 2001), and coral recruits (<20 mm) in the field were unaffected by thermal stress (Mumby 1999). Thermal stress, which causes bleaching, can cause partial mortality and a number of studies show that smaller colonies survive better than larger ones (Loya et al. 2001; Nakamura and van Woesik 2001; Bena and van Woesik 2004; Shenkar et al. 2005). Moreover, a long-term study on Kenyan reefs found that bleaching reduced size of most coral taxa but that the size effect is within rather than between taxa (McClanahan et al. 2008).

Although there remains much uncertainty concerning the overall fate coral populations (Knowlton 2001, Buddemeier et al. 2004), there is a growing consensus that coral reefs will change rather than disappear entirely (Hughes et al. 2003), most likely through shifts in relative abundances of coral species (Pratchett et al. 2011; Pandolfi et al. 2011; Hughes et al. 2012), with some even altering their ecological ranges (Precht and Aronson 2004). Clearly, different coral populations are likely to respond differently to the affects of elevated temperatures from climate change, which is likely to result in variable geographic responses of demographic rates. As such coral reef scientists need an improved understanding of whether the current established thermal thresholds for corals are indeed fixed, and when and where absolute temperatures are likely to be exceeded or whether they will shift (Lough 2012). Given that corals are the major framework builders on reefs the capacity of coral species to either adapt or acclimatize to increasing episodes of thermal stress would greatly influence rates of reef degradation. Furthermore understanding how different population processes vary under different thermal stress regimes is important for us to understand how coral reefs will change over the next few decades and centuries

Central to understanding how coral communities will cope with future global climate change is knowledge of how coral ecosystems (usually containing similar genus and/or species found within tropical latitudes) persist within extreme environments. Coral communities in extreme environments may be better adapted (e.g., thermally adapted) for survival in an environment modified by increasing climate change, as a result of their existence in already stressed conditions (Glynn 1996; Riegl and Piller 2003). It is important to determine how various population processes function under these conditions, as similar and more extreme physical conditions may eventually become commonplace on a broad range of tropical coral reefs. Thus, studying coral communities in extreme environments may provide useful analogues for understanding the ecology of corals reefs subjected to deteriorating global conditions (Perry and Larcombe 2003), and may provide an opportunity to investigate specific ecological processes (e.g., reproduction, settlement, recruitment growth, species abundance and distribution) to determine how coral communities may respond to future climate changes (Kleypas et al. 1999).

1.3 The Persian Gulf

The Persian Gulf, also known as the Arabian Gulf or the “Inner Gulf” by the Regional Organization for Protection of the Marine Environment (ROPME), hereafter referred to as “the Gulf”, is located in a subtropical, hyper-arid region (see Chapter 2; Fig. 2.1). The Gulf is a young marginal epicontinental sea connected to the wider Indian Ocean through the narrow Straits of Hormuz (≈ 60 km wide) (Sheppard et al. 1992, 2010). Due to its high latitude position (24–30°N), shallow nature (≈ 35 m depth) and restricted water exchange, coral communities in the Gulf are exposed to extreme natural conditions (Chao et al. 1982; Sheppard et al. 1992; Riegl and Purkis 2012). The Gulf is characterized by the largest annual fluctuations of seawater temperatures of any reef region (Coles 1988, Coles and Fadlallah 1991). Sea surface temperatures (SSTs) can fluctuate >20ºC over the course of a single year, with temperatures ranging from summer highs of >35°C to winter lows <12°C (Coles and Fadlallah 1991; Sheppard and Loughland 2002; Sheppard et al. 2010). More importantly, Gulf corals exits in a thermal regime comparable to that predicted for most tropical oceans in 2100 (IPCC). Further, because of its enclosed nature and high net evaporation rates, the Gulf is a hyper-saline environment year-round with salinities regularly >40‰ (Sheppard et al. 1992). The Gulf also has high levels of turbidity and sedimentation (Riegl 1999), and relatively low levels of primary production (Nezlin et al. 2007). Collectively, these conditions put severe constraints on coral growth and reef formation within the Gulf, especially the southern Gulf, and, therewith, on biodiversity by restricting the number of corals that can survive in these conditions (Sheppard et al. 1992). Consequently, coral populations of the Gulf comprise only ca. 55–60 species (Sheppard et al. 2010, Riegl et al. 2012), or about 10% of the coral species that occur in the wider Indo-Pacific region (Coles 2003). Compared to most Indo-Pacific reefs, the comparatively younger coral communities in the Gulf (*ca.* 6000k) have a relatively higher representation of more stress tolerant taxa such as siderastreids, faviids and poritids while more sensitive acroporids are under-represented (Sheppard and Sheppard 1991; Veron 2000; Coles 2003; Riegl et al. 2012a).

Coupled with these extreme conditions, coral communities in the Gulf also experience frequent temperature-related mass mortality events (Shinn 1976; Coles and Fadlallah 1991; Riegl 1999; 2001; 2002; Riegl and Purkis 2009), which can cause temporal fluctuations in local species richness (Shinn 1976; Riegl 1999). For example, repeated cold-water temperature events during the winters of 1983, 1985, 1989 and 1992 caused extensive mortality of *Acropora* species, while portids, faviids and siderasteids were less affected (Coles and Fadlallah 1991; Fadlallah et al. 1995). Fadlallah et al. (1995) suggested that these events are particularly important for controlling coral-die off and expansion of faster growing coral species (e.g., *Acropora*) in the Gulf. More recently, coral communities in the Gulf have been exposed to recurrent severe thermal anomalies (35–37°C), which have resulted in high levels of coral bleaching and mortality throughout the region (Riegl 1999, 2002, 2003; Sheppard and Loughland 2002; Riegl and Purkis 2009; Riegl et al. 2011). Over the past 15 years, the Gulf region has suffered more severe bleaching events (1996, 1998, 2002, 2010 and 2011) than any other coral reef region in the Western Indian Ocean (Riegl et al. 2011; Riegl and Purkis 2012). While these bleaching events have led to significant declines of coral species such as *Acropora*, dominant reef-building corals (e.g., *Porites*, *Favia* and *Platygyra*) persist with mortality-rates much lower than would be predicted elsewhere in the Indo-Pacific (Riegl and Purkis 2009; Riegl et al. 2011). Furthermore, various levels of coral recovery, including most *Acropora* species, followed each of these severe bleaching events (Riegl 2002; Sheppard and Loughland 2002; Burt et al. 2008; Burt et al. 2011).

The fact that corals in the Gulf can persist at higher absolute temperatures and bleaching thresholds than anywhere else (e.g., Great Barrier Reef and Caribbean) (Sheppard, 2003; Riegl et al., 2011), and recover following severe bleaching events (Riegl, 2003; Riegl et al., 2011), indicates that corals and their algal symbionts have been able to acclimatize and selectively adapt to elevated sea temperatures (Baker et al. 2004; Obura 2009; Riegl et al. 2012b). Such genetic plasticity is concordant with recent observations that regions of maximal evolutionary potential exist on the geographic periphery of reef growth, such as the isolated high-latitude regime of the Gulf (Budd and Pandolfi 2010). Considering the dire predictions for reefs under projected increases in temperature due to global warming the existence of possible bleaching-resistant populations is clearly pertinent (Hughes et al. 2003; Veron et al. 2009). The Gulf therefore represents a potential source of temperature-capable corals, which mediated by oceanic currents, could spread through the Strait of Hormuz and into the adjacent Indian Ocean and impart the heat-adapted trait to reefs further afield through genetic connectivity (Riegl et al. 2011; Purkis et al. 2011). However, in order for this to occur, coral communities within the Gulf must sustain a large and healthy population into the future to provide enough larvae to nourish the migration (Purkis et al. 2011).

Recent populations models and field surveys verify that coral communities in the Gulf can survive repeated bleaching disturbances if several connected populations exist. (Riegl and Purkis 2009; Riegl et al. 2011). The models also confirms that bleaching recurrences at levels observed between 1995–2010 threaten at least *Acropora* in the southern Gulf (Riegl and Purkis 2009; Riegl et al. 2011), and unless well connected to another large population makes full recovery prior to the next bleaching mortality high unlikely. Connectivity among sites plays an important role in recovery dynamics in the Gulf, because connected populations can survive with lower per-capita fertility (Riegl and Purkis 2009). However, connectivity also depends on the amount of larvae available and suitable habitat for coral settlement and recruitment. A striking feature of coral assemblages in the Gulf is that, despite extensive coral growth, many (or most) do not appear to form proper reef frameworks (i.e., limited carbonate accretion), which limits the amount of suitable habitat they rely on for colonization (Purkis et al. 2005; Purkis and Riegl 2005). This has important long-term implications for Gulf corals, which are also threatened by chronic shortage of habitat, brought about by reduced hardground production caused by ocean acidification (Purkis et al. 2011). Thus, despite housing some of the world's most tolerant coral communities, with a history of high temperature variability and bleaching disturbance, coral communities in the Gulf may be less resilient to the effects of climate change than initially perceived (Riegl, 2002; Burt et al., 2008; Riegl et al., 2011).

Nonetheless, the remarkable temperature tolerance of corals in the Gulf suggest that coral physiology is indeed capable of adapting to high temperature, and offers some hope that coral adaptation can track continuously increasing temperatures (Riegl et al. 2012). As global temperatures continue to increase and environmental extremes become more pronounced, the study of Gulf reef systems gains increased relevance. Clearly important lessons can be learned from Gulf corals about environmental extremes that corals can survive and, given the high frequency of disturbances, maybe even lessons in adaptability (Riegl and Purkis 2012). Considering the harsh Gulf environment it has been presented as an ideal laboratory to evaluate coral reef persistence under global changing conditions (Riegl 2003). Yet, despite our recent advances in understanding this unique reef system (e.g., Riegl and Purkis 2009; Sheppard et al. 2010; Riegl and Purkis 2012; and many more), our knowledge of the mechanisms important for sustaining these coral communities, particularly the influence of extreme environmental conditions and recurring bleaching events on basic population processes (e.g., reproduction, larval settlement, recruitment, growth) that determine reef dynamics and resilience remains poorly understood (Riegl and Purkis 2009, 2012).

1.4 Research aims and objectives

Given the unique importance of coral reef ecosystems within the Gulf, especially in a time of rapid environmental change, the main objective of this thesis was to provide critical baseline information on the biology of corals from this location in order to improve our understanding of the likely effects extreme environmental conditions on the ecology and dynamics of future coral populations. This thesis is comprised of four independent chapters (Chapters 2-5), each focused on key processes that drive the structure and dynamics of coral populations or communities in the Gulf.

Chapter 2 provides a comprehensive regional comparison of coral communities within the northeastern Arabian Peninsula (within the southern Persian Gulf, Strait of Hormuz, and Gulf of Oman), testing for spatial and temporal changes in the relative abundance of corals due to marked changes in environmental conditions. This chapter quantified and compared the abundance, composition, diversity and richness of benthic and coral reef communities among 18 sites distributed around the northeastern Arabian Peninsula. A range of environmental variables, including temperature, salinity, productivity (inferred based on chl-*a*) and wave intensity, were quantified and related to observed differences in benthic communities.

Chapter 3 provides a quantitative assessment of the reproductive condition for six locally abundant coral species on patch reefs in the southern Persian Gulf (Dubai, United Arab Emirates) over two years to establish the timing (i.e., months) and degree of synchrony (i.e., multi-species) of coral spawning. Further, the reproductive biology of the three most common species: *A. downingi*, *C. microphthalma* and *P. daedalea* were examined to determine sexuality, mode of reproduction, gametogenic cycle and fecundity. The relationship between environmental parameters (e.g., SST, wind speed, tidal amplitude) and coral reproductive schedules is evaluated.

Chapter 4 quantifies the spatio-temporal variability of coral settlement at six sites over two years along the coast of Dubai. In doing so this study establishes spatial and temporal variability in rates of coral settlement and relates local variation in the taxonomic composition of settlers to local abundance and composition of adult corals.

Finally, **Chapter 5** examines the size structure of four locally abundant coral species, *Acropora downingi*, *Favia pallida*, *Platygyra daedalea*, and *Porites* spp. complex (*P. lobata*/*lutea*) in two distinct regions of the Gulf, the southern Gulf (Dubai and Abu Dhabi) and eastern Gulf (western Musandam, Oman) with contrasting environmental conditions to evaluate the importance of high temperature variability and recurrent bleaching events in structuring coral community size structure. The purpose of this study was to test for spatial variation in size-structure of corals, which may be reflective of marked differences in demographic rates (growth and mortality) of adult corals.

Results of the independent studies in each of the aforementioned chapters are then brought together and discussed in **Chapter 6**, considering the global importance of ongoing research in the Gulf, especially in a time of rapidly changing environmental conditions.

Chapter 2: Multiple environmental factors influence the spatial distribution and structure of reef communities in the northeastern Arabian Peninsula[2]

2.1 Abstract

Multivariate analysis revealed distinct sub-regional coral communities among the southern Persian Gulf, Strait of Hormuz, and Gulf of Oman. Differences in community structure among locations were associated with considerable spatial heterogeneity in oceanic conditions, and strong directional environmental gradients. Despite clear community differences, considerable changes to coral community structure have occurred throughout the northeastern Arabian Peninsula. Most dramatic of which are the apparent changes from *Acropora* dominated to poritid and faviid dominated communities, particularly in the southern Persian Gulf and Strait of Hormuz. Although temperature and salinity have previously been cited as the major environmental factors structuring coral communities around the region, additional environmental parameters, including chlorophyll-*a*, surface currents and winds are shown to be important in structuring reef communities throughout the northeastern Arabian Peninsula.

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2.2 Introduction

Irrespective of location, coral reef communities must respond to substantial variations in environmental conditions in order to successfully recruit, grow, reproduce and survive (Kleypas et al. 1999; Done 1999). On local and geographic scales, the structure and development of coral reef communities are subject to diverse and often interacting environmental variables (e.g., temperature, light, salinity, solar radiation, sedimentation, hydrodynamic factors) (Brown 1997; Kleypas et al. 1999; Done 2011). Collectively, these factors can affect the growth rate, growth form, reproduction, and the overall abundance, composition and diversity of communities (Brown 1997; Kleypas et al. 1999; Done 2011). However, fluctuations in a range of environmental variables (i.e., physical and chemical), mediated by changes in global climate, are predicted to directly affect the abundance, diversity, and composition of coral reef communities (Done 1999; Purkis and Riegl 2005; Baker et al. 2008), and may lead to further degradation of these reef systems globally (Hughes et al. 2003). Therefore, determining how different coral reef communities vary over their present range of environmental conditions, particularly reefs already surviving in extreme conditions, will be vital in understanding how these communities may respond to increasing changes in global climate (Kleypas et al. 1999).

The northeastern Arabian Peninsula is bounded by the Persian Gulf and the Gulf of Oman, two marginal seas distinguished by substantially different environmental and oceanographic conditions (Sheppard et al. 1992; Reynolds 2002). Due to its high-latitude position, shallow nature and restricted water exchange, the marine environment of the Persian Gulf is characterized by extremes in salinity and sea surface temperature (SST) (Sheppard et al. 1992; Coles 2003), with high levels of sedimentation and turbidity (Riegl 1999) and low levels of primary production (Nezlin et al. 2007). In contrast, the adjacent Gulf of Oman is well mixed by strong seasonal upwelling from the Arabian Sea (Reynolds 1993; Böhm et al. 1999), resulting in comparatively mild seasonal changes in SST (range 22–32°C) and salinity (35–37 psu) (Coles 1997; Schils and Wilson 2006), with relatively high primary production in the upper ocean as a response to seasonal winter monsoons (Piontkovski et al. 2011). Amid the Persian Gulf and Gulf of Oman, the Strait of Hormuz approximates a boundary between the two systems (Reynolds 1993). Water exchange and circulation patterns result in strong seasonal stratification (Thoppil and Hogan 2010), with SST and salinity comparatively lower in range than the Persian Gulf but higher than in the Gulf of Oman (Thoppil and Hogan 2009).

Several studies have shown that coral reef communities along the northeastern Arabian Peninsula are a distinct biogeographical subset, separated from communities in the wider Indo-Pacific and the Red Sea (Sheppard 1987, 1998; Sheppard and Sheppard 1991; Sheppard et al. 1992). Coral communities in this region support about 10% of the species that occur throughout the Indo-Pacific (Sheppard et al. 1992; Coles 2003). Compared to most Indo-Pacific reefs, coral reef communities in the Arabian region exhibit relatively low coral diversity, with few species in the family Acroporidae and a high representation of the families Siderasteridae and Faviidae (Veron, 2000; Coles 2003). Such dissimilarities between Arabian and Indo-Pacific reef communities have traditionally been related to extreme temperature and salinity regimes throughout the Arabian region. However, the majority of these studies only considered these variables in relative isolation (Sheppard 1987; Sheppard and Sheppard 1991; Sheppard et al. 1992; Coles 2003), with little consideration of other oceanic variables important in structuring reef communities (Brown 1997; Done 1999).

This paper provides a comprehensive regional examination of coral communities within the northeastern Arabian Peninsula, and the first in over two decades (Sheppard 1987; Sheppard and Sheppard 1991). Here we examined and compared the abundance, composition, diversity and richness of coral reef communities throughout the northeastern Arabian Peninsula. Moreover, we investigated and quantitatively compared the range of environmental variables considered important in structuring these communities between locations.

2.3 Materials and Methods

2.3.1 Benthic community surveys

Benthic reef communities were surveyed at 18 sites within the southern Persian Gulf, Arabian Peninsula side of Strait of Hormuz and Gulf of Oman from October to November 2008 (Fig. 2.1, see Appendix A for site details). At each site, surveys were conducted on eight 30 × 1 m belt transects at a depth of 6–8 m (Bauman et al. 2010). Along each transect benthic communities were surveyed within a 0.25 m^2 quadrat photographed at 3 m intervals (Bauman et al. 2010). Composition and percent cover of benthic taxa were quantified within each quadrat using 50 randomly distributed points within CPCe image analysis software, version 5 (Kohler and Gill 2006). Benthic cover were categorized into 8 major groups: (i) hard coral, (ii) soft coral, (iii) sponge, (iv) filamentous/fleshy algae (FFA), (v) coralline crustose algae (CCA), (vi) other live, (vii) recently dead coral (RDC), and (viii) sand, pavement and rubble (SPR). Hard coral were further identified to species level where possible (Veron

2000; Claereboudt 2006). Samples were standardized as percent of total cover.

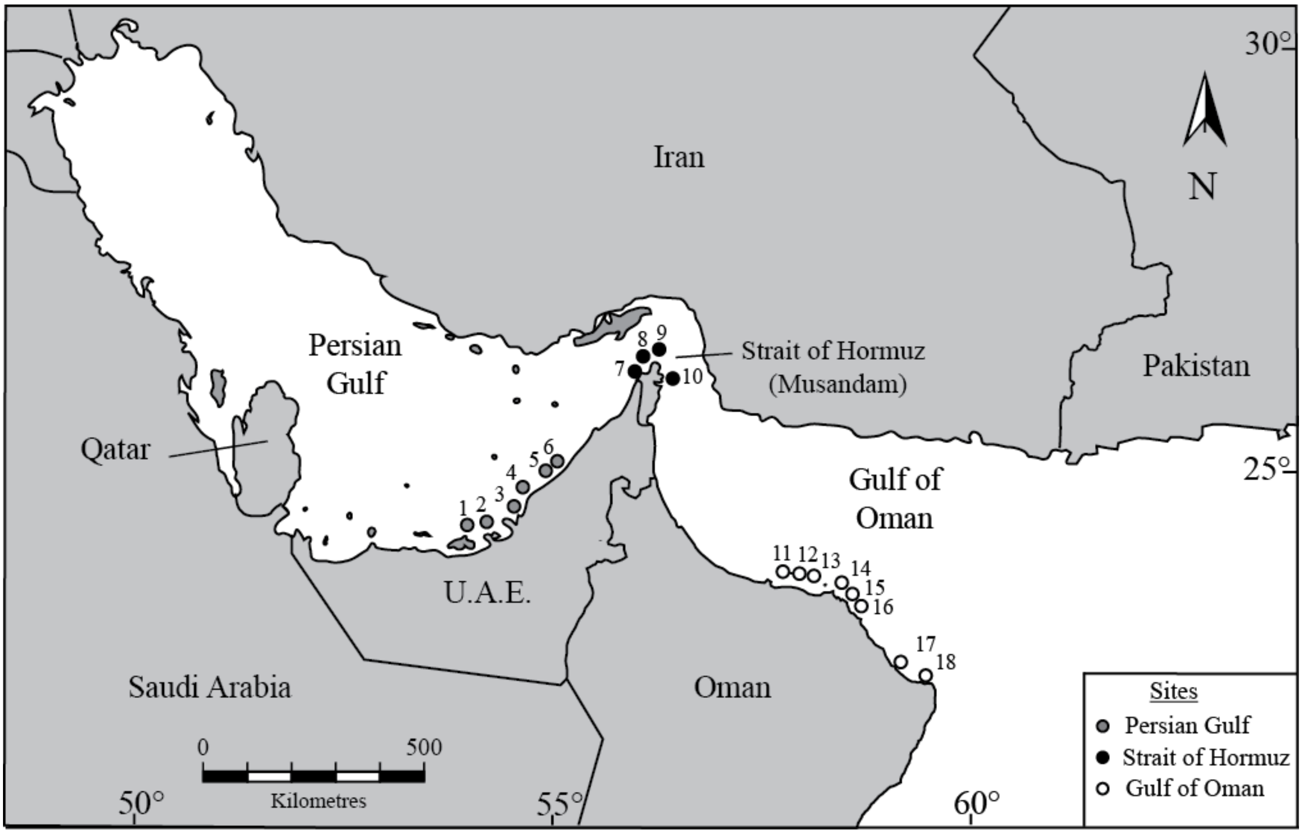

Fig. 2.1: Map of study sites around the northeastern Arabian Peninsula, with numbers indicating samples sites. Southern Persian Gulf (1. Bu Tinah 2. Al Hiel 3. Saadiyat 4. Ras Ghanada 5. Saih Shaib 6. Ras Hasyan); Strait of Hormuz (7. Khasab Reef 8. Coral Garden 9. Rashid Island West 10. E. Musandam); and Gulf of Oman (11. Al Ghattan 12. Al Jazeera 13. Fort Island 14. Qantab 15. Jussa West 16. Jussa Point 17. Al Heddla 18. Turtle Beach).

2.3.2 Environmental variables

Physical parameters of temperature, salinity and ocean currents (east and north components) for each location were obtained from a numerical ocean model: the 1/12° Global Hybrid Coordinate Ocean Model (HYCOM), maintained by the Naval Research Laboratory (NRL), Stennis Space Center (Metzger et al. 2010). The non-assimilative version (18.2) of the model was selected due to its extended time span

(2004–2009) as compared with the assimilative version (90.8, 2009-2010) and because comparisons during the one-year overlap indicated similar results at the study locations. At each site monthly temperature and salinity data were extracted and long-term mean, variability and annual range were calculated. Monthly ocean currents were binned into octants (45°), and the mean current and percentage of time within each octant was determined. Using shoreline direction, the mean current and percentage of time were also calculated for along-shore and cross-shore quadrants at each survey site.

To provide a comparison of primary productivity between the locations, 8-day composites of chlorophyll-*a* (chl-*a*) data at 0.05° resolution from MODIS Aqua were acquired for the period 4 July, 2002 to 20 July, 2010. Data were examined within a 5 × 5-pixel box centered at each survey location and the median value (of up to ~100 values) for each month calculated. This was undertaken to exclude data with contamination due to bottom-reflectance in shallow waters (see Cannizzaro and Carder 2006) in evaluating variation across the three locations.

Wind data for each site were acquired from 2002 to 2011 from the Blended Sea Winds product (http://www.ncdc.noaa.gov/oa/rsad/air-sea/seawinds.html). Monthly means of the east- and north-directed components were calculated. Mean wind speed and percentage of time in each 45° octant and for along- and cross-shore quadrants were determined at each survey site.

2.3.3 Data analysis

Non-metric multidimensional scaling (MDS) was used to examine benthic group patterns across locations (Clarke and Warwick 2001). Prior to analysis, mean benthic cover was obtained by pooling transect data across each site, and then categorizing sites within each location. All data were then arcsine square-root transformed. Analysis of similarity (ANOSIM) was then used to test the significance of differences between *a priori* defined 'benthic groups' and 'locations'. ANOSIM is a multivariate randomization test used to compare individual sites within locations based upon ranked benthic abundance data using Bray-Curtis dissimilarity matrices. The tests yield *R* statistics ranging between -1 and 1 that infer a degree of location separation. *R*-values close to zero suggest there are no differences among locations (i.e., the null hypothesis is true), while *R*-values of magnitude > 0.5 indicate a strong difference among locations (i.e. the null hypothesis is false) (Clarke and Warwick 2001). *P* values were then calculated for each *R* statistic using a permutation test of random rearrangement. Where there were significant differences in benthic cover between locations, a similarity percentage analysis (SIMPER) was performed to identify and quantify the contribution of benthic groups to community dissimilarity. SIMPER is a method for assessing which groups are primarily responsible for an observed difference between samples (Clarke and Ainsworth 1993) One-way ANOVA with post hoc Tukey's unequal-N HSD tests were then used to identify significant differences in benthic groups among locations.

Coral species composition and diversity patterns were compared between locations. ANOSIM analysis was used to test for differences in coral community composition between locations (Clarke and Warwick 2001). ANOSIM results were graphically interpreted using MDS, and SIMPER analysis was then used to determine which coral species contributed to community differences (Clarke and Warwick 2001). Only coral species found in more than 5% of sites were included in multivariate analyses to preclude the confounding effects of outliers (McCune and Grace 2002). Patterns of coral species diversity among location were then calculated using three diversity metrics, species richness (S), Shannon-Wiener diversity index (H') and Pielou's evenness (J') and analyzed using one-way ANOVA and post hoc unequal-N HSD tests.

Temperature, salinity and chl-*a* data were compared among locations using one-way ANOVA. Prior to analysis the data were square-root transformed. Where there were significant differences in each environmental variable between locations, unequal-N HSD Tukey's tests were used to identify differences. The BEST analyses (using the BIO–ENV procedure, PRIMER v6; Clarke and Gorley 2006) were used to assess the influence of environmental variables on patterns of benthic groups, and separately on coral community distribution patterns (Clarke and Ainsworth 1993; Clarke et al. 2008). The null hypothesis tested was that there was no relationship between environmental variables and benthic groups or coral community patterns among locations. Prior to analyses untransformed and log_e transformed environmental variables were normalized to account for different scales and units. Where possible, the range, mean maximum and mean minimum values of each environmental variable were used in the analysis. Environmental variables were pre-screened for multi-collinearity using draftsman plots (Clarke and Ainsworth 1993), and any subsets of variables strongly collinear (i.e., > 0.95) were reduced to a single representative variable. The BIO-ENV was run using Spearman rank correlations (ρ) and the significance of correlations was tested with the global BEST permutation tests (Clarke and Ainsworth 1993).

Environmental variables identified by BEST procedure were subsequently included as explicative variables in a linkage tree using LINKTREE (PRIMER v6 Clarke and Gorley 2006). This technique constructs a hierarchical tree that reflects how biotic samples from an underlying resemblance matrix are most naturally split into successively smaller groups for a set of observations (Clarke et al. 2008). The position of divisions on the vertical axis of the dendrogram indicates the absolute measure of group differences (*B*%) at that level. Quantitative thresholds for each division are provided for each relevant variable from the explanatory data. A similarity profile permutation test using $p > 0.05$ as the significance criterion (SIMPROF; Clarke et al. 2008) was used in conjunction with the LINKTREE for stopping unwarranted subdivisions at those links in which no significant multivariate structure was considered present among remaining biological samples.

2.4 Results

2.4.1 Benthic groups

MDS ordination indicated strong differences in benthic groups between the three locations (Fig. 2.2a). ANOSIM confirmed significant differences between locations ($R = 0.66$, $P < 0.001$) and for all three pair-wise comparisons (Persian Gulf × Gulf of Oman: $R = 0.63$, $p < 0.001$; Persian Gulf × Strait of Hormuz: $R = 0.67$, $p < 0.01$; Gulf of Oman × Strait of Hormuz: $R = 0.74$, $p < 0.001$). SIMPER showed that dissimilarity in benthic groups among locations was driven mainly by differences in hard and soft coral, and sand, pavement and rubble (SPR) (Table 2.1). Benthic groups in the Persian Gulf and Gulf of Oman were the most similar (26.9% dissimilar) (Table 2.1). SPR was the most common benthic group throughout locations, ([average cover ± SE], 41.3 ± 10.8 %), while hard coral (26.2 ± 8.6 %) and soft coral (9.25 ± 0.69 %) were the next most abundant benthic groups. All other benthic groups made up a relatively minor component of the reef communities (Fig. 2.3)

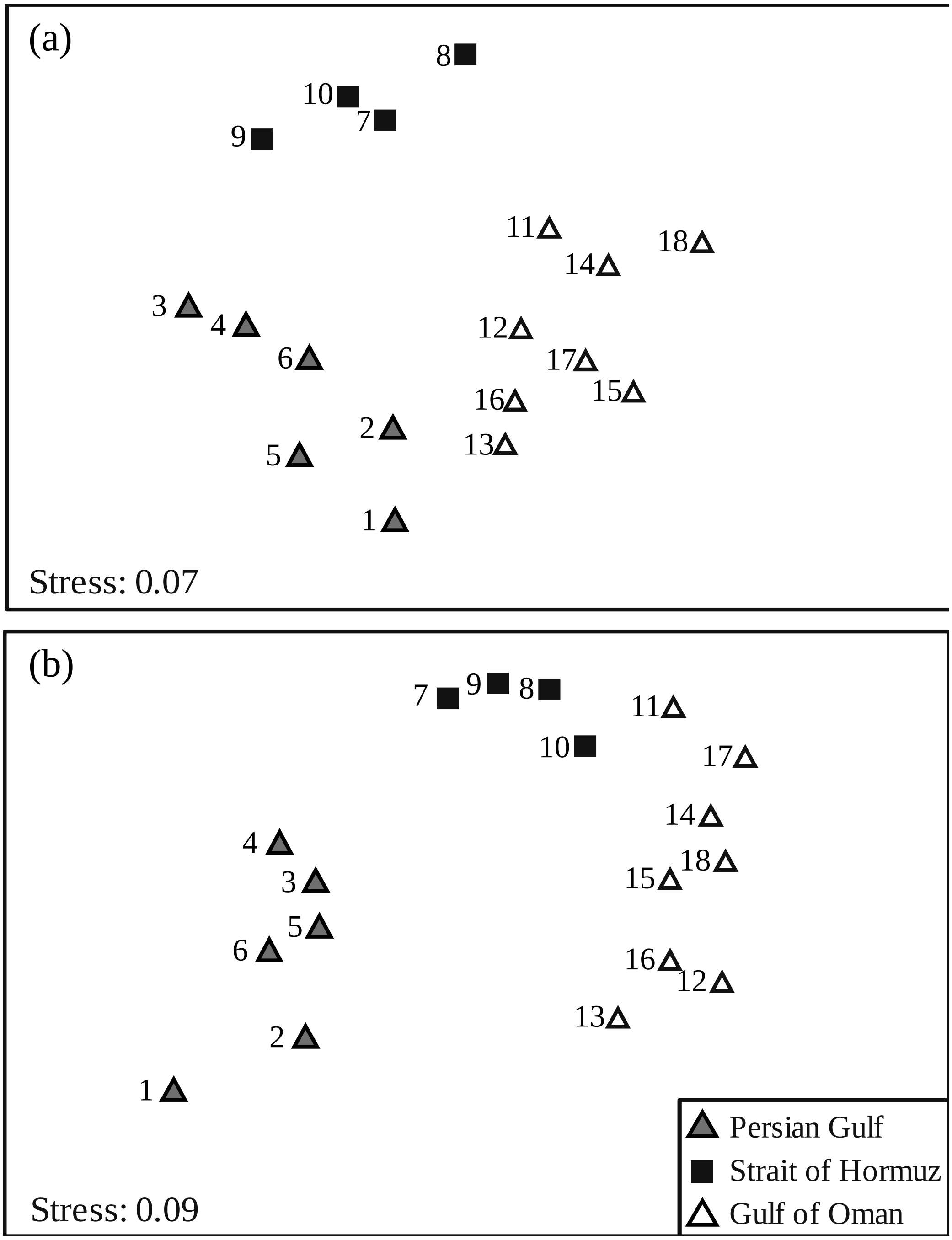

Fig. 2.2: MDS ordination plots of (a) benthic groups and (b) coral communities in the southern Persian Gulf, Strait of Hormuz and the Gulf of Oman. Each point represents the mean community at each of the 18 sites.

All benthic groups identified in the SIMPER analysis as driving regional community differences showed significant differences among locations in one-way ANOVAs (with the exception of sponge [ANOVA $F_{(2,141)} = 13.9$, $p = 0.68$], and soft

Table 2.1: Results of comparisons among benthic groups in the Persian Gulf, Strait of Hormuz and the Gulf of Oman, pooled for each location. The *R*-statistic and its *p*-value for comparisons among locations are shown, along with average percent dissimilarity (Mean δ%), individual and cumulative contribution (δ %) to dissimilarity from SIMPER. Where significantly different, percent cover of benthos that contributed >10% to dissimilarity are listed. CCA = crustose coralline algae; SPR = sand, pavement and rubble; FFA = filamentous/fleshy algae.

Benthic variable	Locations compared (% cover)		Contribution δ (%)	Cumulative δ (%)	*R*	*p*	Mean (δ %)
	Persian Gulf	Gulf of Oman					
Soft coral	0	14.3	25.98	25.98	0.63	<0.001	26.9
Hard coral	20.4	14.9	14.88	40.87			
Dead coral algae	6.8	0.86	12.53	53.40			
CCA	6.8	3.4	12.16	65.56			
	Persian Gulf	Strait of Hormuz					
SPR	54.1	19.9	25.83	25.83	0.67	<0.001	34.3
Hard coral	20.4	43.2	18.89	44.72			
Soft coral	0	13.4	15.92	60.64			
FFA	9.3	3.9	10.65	71.29			
	Gulf of Oman	Strait of Hormuz					
Hard coral	14.9	43.2	26.84	26.84	0.74	<0.001	35.1
SPR	49.1	19.9	20.31	47.16			
FFA	10.6	3.9	17.29	64.44			
CCA	4.3	11.5	11.90	76.34			

corals [ANOVA $F_{(2,141)} = 21.3$, $p = 0.37$]) (Fig. 2.3). Post hoc comparisons showed that hard coral and coralline algae cover were significantly higher in the Strait of Hormuz than the other locations ($p < 0.05$ for each comparison), while the Persian Gulf had significantly more recently dead coral (RDC; $p < 0.05$), and the Gulf of Oman had significantly higher percent of other live ($p < 0.05$; Fig. 2.3). The Persian Gulf and Gulf of Oman both had significantly higher cover of filamentous/fleshy algae and SPR than the Strait of Hormuz (Fig 2.3, $p < 0.05$ for each comparison, respectively).

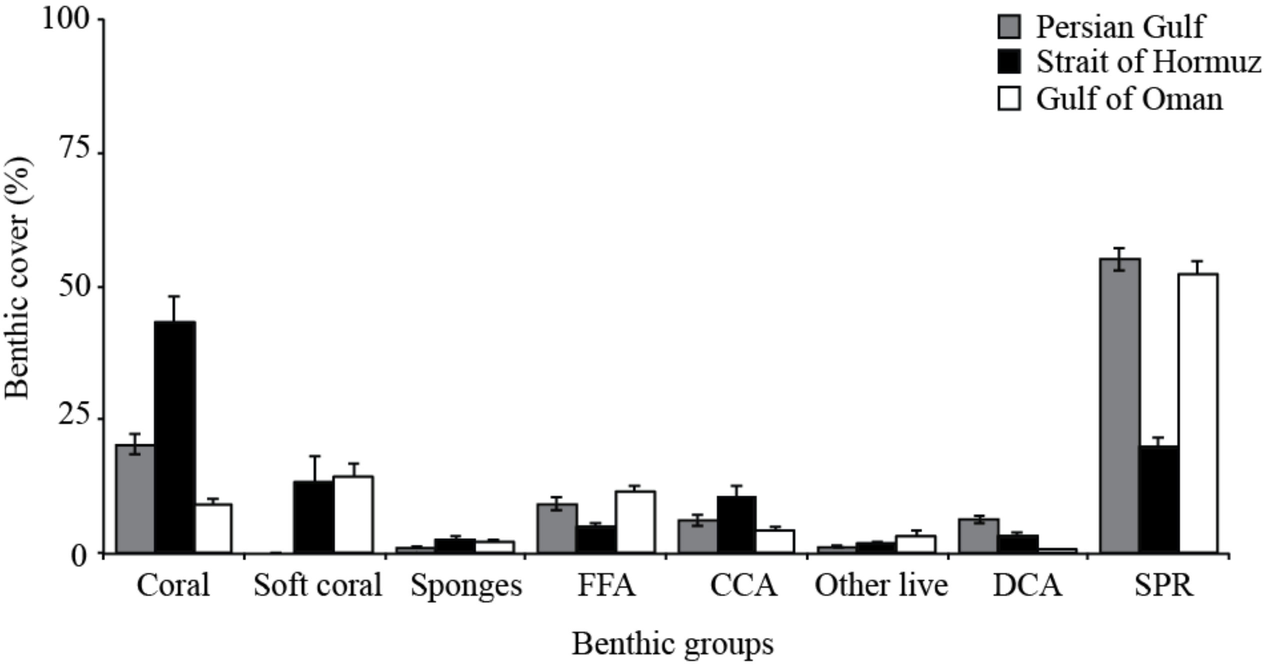

Fig 2.3: Benthic group patterns: percent cover of the major benthic categories at each location. FFA = filamentous/fleshy algae; CCA = crustose coralline algae; DCA = dead coralline algae; SPR = sand, pavement and rubble.

2.4.2 Coral communities

A total of 76 coral species from 30 genera were identified among the three locations (Appendix A 2.2 for complete species list). Species richness (*S*), Shannon-

Wiener diversity (*H'*) and Pielou's evenness (*J'*) all showed significant differences among locations (ANOVA $F_{(2,15)} = 12.63$, $F_{(2,15)} = 8.04$, and $F_{(2,15)} = 4.17$, respectively, $p < 0.05$ for each). Post hoc unequal-N HSD tests showed that the Persian Gulf had significantly lower total species richness and diversity than the Strait of Hormuz and Gulf of Oman ($p < 0.001$ each), while Gulf of Oman had significantly higher total species evenness than Persian Gulf and Strait of Hormuz ($p < 0.001$ each; Table 2.2). ANOSIM indicated significant differences in species composition between locations ($R = 0.58$, $p < 0.001$; Fig. 2b), although pair-wise comparisons showed no differences in species composition between Strait of Hormuz and the Gulf of Oman ($R = 0.11$, $p = 0.25$). In contrast, coral communities in the Strait of Hormuz and the Gulf of Oman were both significantly different from Persian Gulf (Persian Gulf × Gulf of Oman: $R = 0.81$, $p < 0.001$; Persian Gulf × Strait of Hormuz: $R = 0.71$; $p < 0.001$; Fig. 2b). SIMPER analysis indicated the highest dissimilarity in species composition between Persian Gulf and Gulf of Oman (76.6 % dissimilar), and relatively high dissimilarity between Persian Gulf and Strait of Hormuz (67.3 % dissimilar; Table 2.3). Of the coral species that predominantly contributed to dissimilarity in community structure between locations, 69% were more abundant in Strait of Hormuz and the Gulf of Oman; five of these species were absent from the Persian Gulf (Table 2.3).

The Persian Gulf and Strait of Hormuz were dominated by a relatively small number of coral genera, reflected by relatively low evenness values for both locations (Persian Gulf *E*: 0.42; Strait of Hormuz *E*: 0.47) (Fig. 2.4). In the Persian Gulf and Strait of Hormuz the genus *Porites* accounted for >50 % of total coral cover (Persian Gulf: 61.3 ± 1.41%; Strait of Hormuz: 51.2 ± 3.65%), while faviids represented >25% total coral cover in both locations. In contrast, Gulf of Oman coral communities held a relatively high number of coral genera, reflected in a high evenness value for this location (Gulf of Oman *E*: 0.83) (Fig 2.4). Within the Gulf of Oman four genera: *Platygyra* (19.2 ± 1.41%), *Porites* (15.8 ± 1.01 %), *Hydnophora* (13.1 ± 0.78%) and *Acropora* (12.2 ± 0.24%) accounted for approximately 60% of total coral cover.

Table 2.2: Coral richness (*S*), diversity (*H'*) and evenness (*J'*) from the southern Persian Gulf, Strait of Hormuz and the Gulf of Oman. *Indicates significant difference $p < 0.05$.

Location	Richness (*S'*)	Diversity (*H'*)	Evenness (*J'*)
Persian Gulf	29*	1.9 ± 0.19*	0.42 ± 0.03
Straits of Hormuz	49	3.1 ± 0.11	0.47 ± 0.02
Gulf of Oman	55	3.4 ± 0.09	0.83 ± 0.04*

2.4.3 Environmental variables

Although mean annual SST showed negligible differences among locations ($p = 0.412$), the mean annual range of SST varied considerably among locations (Table 2.4). Mean annual range of SST within the southern Persian Gulf was 4.6º C and 6.3º C greater than within the Strait of Hormuz and Gulf of Oman, respectively. Mean annual salinity differed significantly among locations ($F_{(2,15)} = 4.98$, $p < 0.05$), with significantly higher salinity in the southern Persian Gulf ($p < 0.05$; Table 2.4). The mean annual range in salinity also differed among locations, with the largest annual range in salinity apparent in the southern Persian Gulf (Table 2.4). Mean annual chl-*a* concentrations differed significantly among locations ($F_{(2,24)} = 4.51$, $p < 0.05$), with significantly higher chl-*a* concentrations in the Gulf of Oman ($p < 0.05$; Table 2.4). The annual range in mean chl-*a* also differed among locations, with the largest range

Table 2.3: Percentage dissimilarity (δ) of coral communities identified by SIMPER, with the contribution of the 10 most important species driving differences listed.

Species	Locations		Contribution of δ (%)	Cumulative δ (%)
	Persian Gulf	Gulf of Oman		
	76.6% dissimilarity			
Porites harrisoni	37.3	0.0	18.20	18.20
Porites lutea	15.7	2.5	9.38	27.59
Platygyra daedalea	10.7	19.1	6.81	34.40
Favia pallida	10.0	0.62	6.52	40.92
Cyphastrea microphthalma	8.6	1.4	5.93	46.85
Porites lobata	4.2	0.26	4.88	51.72
Porites sp.	3.4	13.7	4.12	55.84
Goniopora sp.	0.0	6.3	3.44	59.28
Hydnophora pilosa	0.0	13.4	3.29	62.58
	Persian Gulf	Straits of Hormuz		
	67.6% dissimilarity			
Porites sp.	3.4	26.9	13.25	13.25
Platygyra daedalea	10.7	22.7	10.23	23.48
Porites harrisoni	37.3	3.6	9.84	33.32
Porites cumulates	0.0	8.2	4.15	37.47
Favia pallida	10.0	0.14	4.03	41.50

Species	Locations		Contribution of δ (%)	Cumulative δ (%)
	continued			
Stylophora pistillata	0.0	4.5	3.89	45.39
Acropora valida	0.0	1.6	3.87	49.26
Symphyllia recta	0.0	1.9	3.69	52.95
Goniopora species	0.0	1.6	3.45	56.40
Montipora species	0.0	1.4	3.40	59.80
	Strait of Hormuz	Gulf of Oman		
	55.6% dissimilarity			
Hydnophora pilosa	13.4	0.0	12.23	12.23
Porites sp.	13.7	26.9	7.68	19.91
Porites lutea	2.5	8.2	6.34	26.25
Stylophora pistillata	0.2	4.3	4.24	30.49
Acropora khayranensis	4.8	0.8	4.03	34.52
Favites pentagona	4.2	0.8	3.87	38.39
Porites harrisoni	1.1	3.6	3.53	41.92
Acropora valida	3.5	1.6	3.22	45.14
Gonipora sp.	0.0	6.3	3.17	48.31
Montipora aequituberculata cf.	1.4	0.3	3.11	51.42

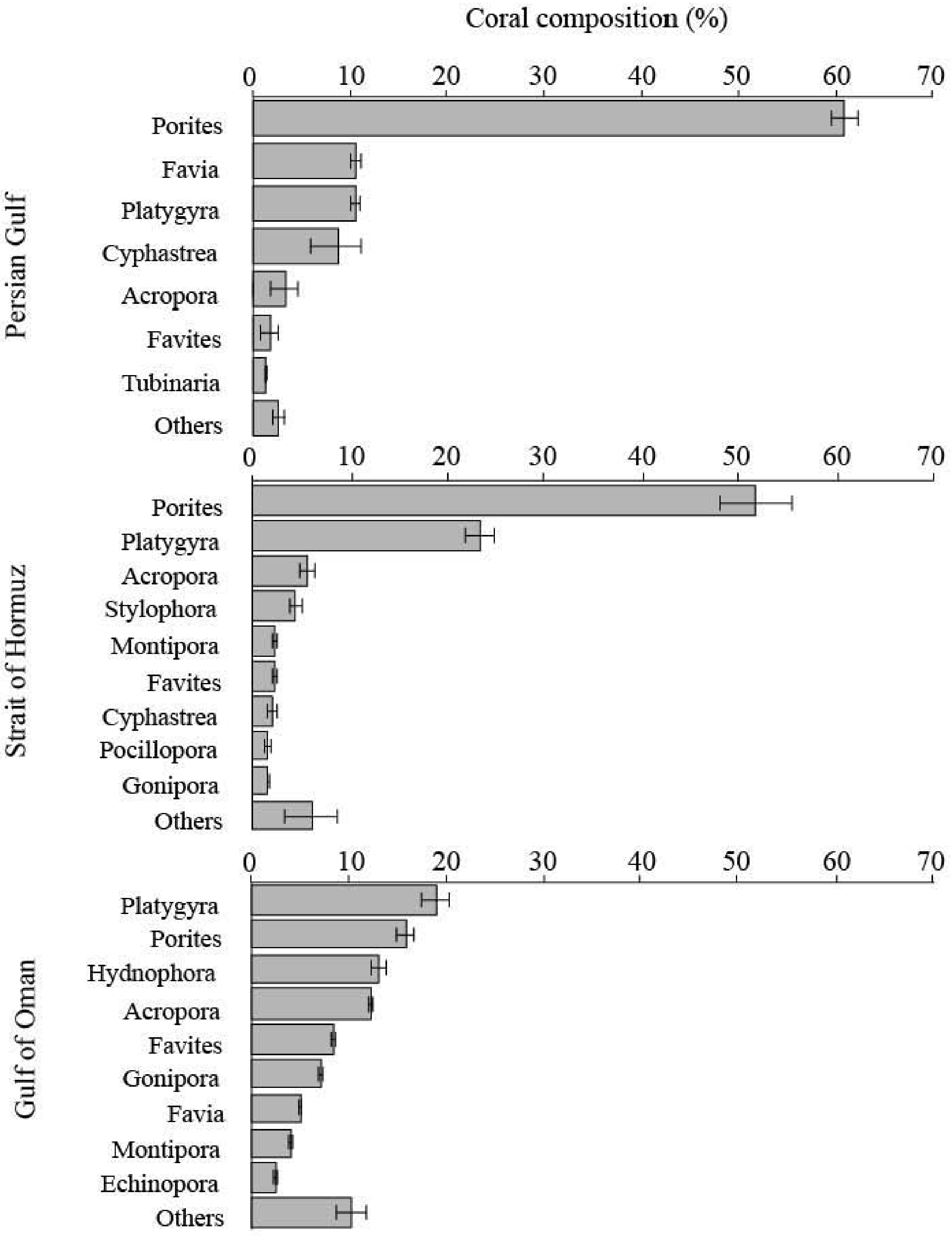

Fig. 2.4: Coral community patterns: percentage of coral at each location broken down by dominant genera: Persian Gulf (top), Strait of Hormuz (middle), and Gulf of Oman (bottom).

in chl-*a* concentration apparent within the Gulf of Oman (Table 2.4). The months of mean highest and lowest chl-*a* concentrations were identical for the Strait of Hormuz and Gulf of Oman (February = highest, May = lowest), in contrast to the southern Persian Gulf (September = highest, March = lowest). Importantly, these results are consistent with recent reports of seasonal changes of chl-*a* concentrations from the region (see Nezlin et al. 2010; Piontkovski et al. 2011).

Summaries of the currents and wind data are provided as rose plots for each location (Fig. 2.5), where direction indicates the motion for both parameters (i.e., oceanographic, not meteorological, convention). For most cases the most frequent directions of currents/wind also recorded the highest mean speeds; the exceptions to this were currents in the Gulf of Oman and the Strait of Hormuz, which is most likely related to variations in the orientation of the coast at sites in these locations. Currents in the southern Persian Gulf were predominantly southward, and winds were primarily offshore (Fig. 2.5). Within the Strait of Hormuz, surface currents were predominantly to the north and east but with a significant component to the west. Examination of individual sites in the Strait of Hormuz indicated that the dominant current pattern was along-shore and into the Persian Gulf. Additionally, winds within the Strait of Hormuz were predominantly to the north and east (Fig. 2.5). Gulf of Oman currents were the strongest across the three locations (Table 2.4) and were predominantly directed along-shore to the east and southeast (i.e., away from the Persian Gulf). Wind direction at this location was predominantly to the east and northeast (Fig. 2.5); however, the orientation of the coastline at individual sites meant that some sites were dominated by along-shore winds, while others were dominated by offshore winds.

Table 2.4: Physical metrics for the southern Persian Gulf, Strait of Hormuz and Gulf of Oman.

Location Position	Persian Gulf 55°E, 25°N	Strait of Hormuz 56°E, 26°N	Gulf of Oman 59°E, 23°N
SST (°C)			
Mean annual temperature	27.97 (± 1.49)	28.27 (± 1.03)	27.72 (± 0.79)
Mean warmest month	34.50 (± 0.04) Aug.	32.75 (± 0.22) July	31.37 (± 0.32) July
Mean coldest month	20.44 (± 0.17) Jan.	23.31 (± 0.07) Feb.	23.59 (± 0.05) Feb.
Annual temperature range	14.05	9.43	7.78
Salinity (psu)			
Mean annual salinity	40.86 (± 0.23)	37.15 (± 0.17)	36.67 (± 0.32)
Mean highest salinity month	42.07 (± 0.34) Feb.	37.54 (± 0.18) July	36.77 (± 0.04) July
Mean lowest salinity month	39.19 (± 0.65) May	36.76 (± 0.20) April	36.59 (± 0.01) Feb.
Annual salinity range	2.88	0.78	0.22
Chlorophyll-*a* (mg m^{-3})			
Mean annual chl-*a*	1.70 (± 0.65)	2.25 (± 0.17)	2.76 (± 0.44)
Mean highest chl-*a* month	2.44 (± 0.06) Sept.	3.19 (± 0.40) Feb.	8.17 (± 0.26) Feb.
Mean lowest chl-*a* month	1.07 (± 0.05) Mar.	1.06 (± 0.32) May	0.40 (± 0.03) May
Annual chl-*a* range	1.36	2.51	7.77
Currents (m s^{-1})			
Mean long-shore speed (m s^{-1})	0.024 (± 0.002)	0.04 (± 0.008)	0.06 (± 0.016)
Mean cross-shore speed (m s^{-1})	0.017 (± 0.001)	0.013 (± 0.004)	0.02 (± 0.006)
% time of along-shore current	48.8%	72.5%	80%
Winds (m s^{-1})			
Mean long-shore speed (m s^{-1})	1.97 (± 0.13)	1.80 (± 0.09)	2.98 (± 0.23)
Mean cross-shore speed (m s^{-1})	2.35 (± 0.06)	1.72 (± 0.09)	1.98 (± 0.08)
% time of cross-shore wind	66.3%	53.2%	40.5%

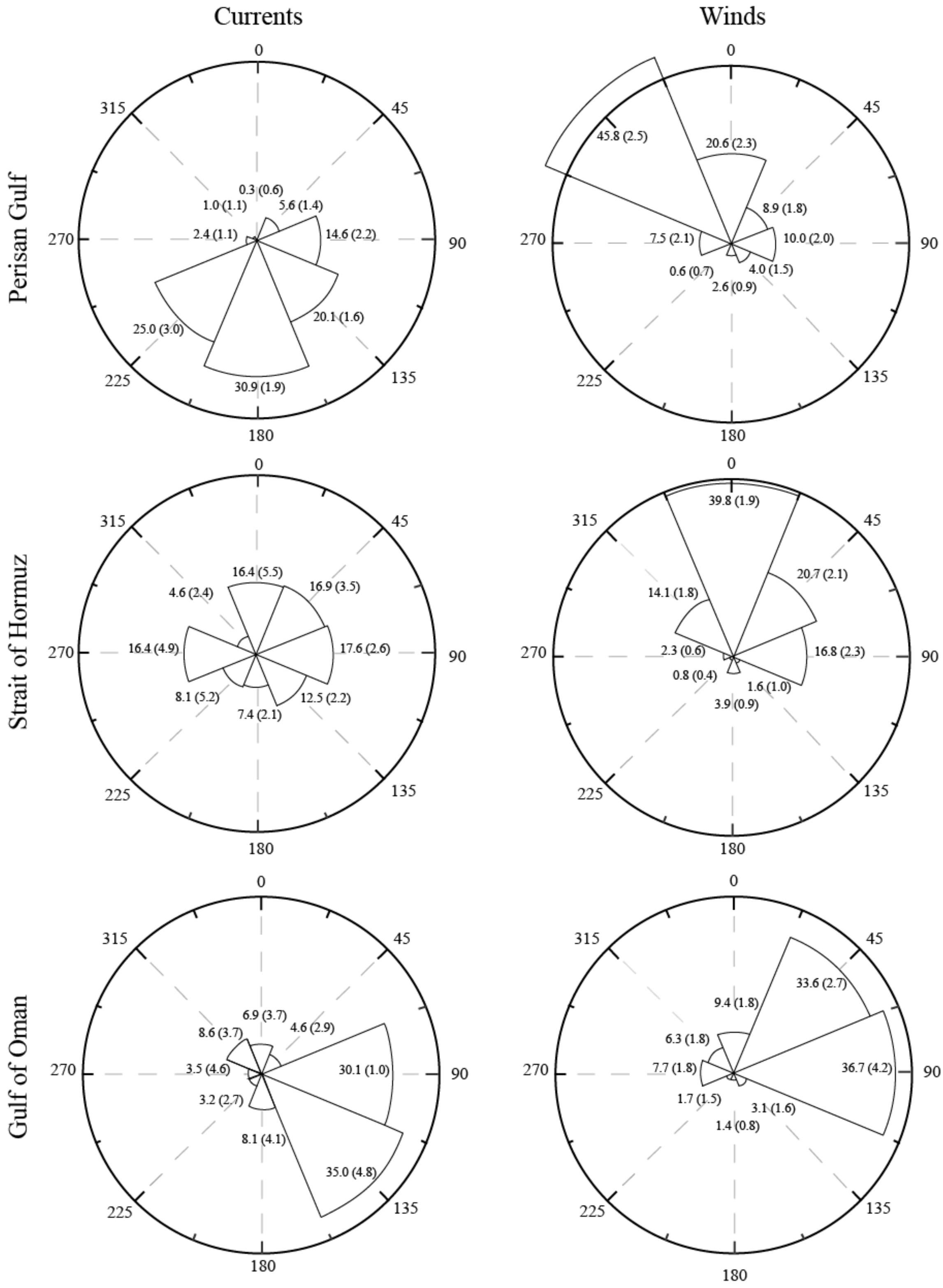

Fig. 2.5: Rose plot summaries of the currents and wind data for each location. The bearing indicates the direction of motion for both parameters (i.e., oceanographic, not meteorological, convention). The frequency in each quadrant is shown numerically and by the quadrant radius, where the outer circle represents 40%. Mean speed for each quadrant is parenthesized (cm s^{-1} for currents; m s^{-1} for wind).

2.4.4 Relationship between benthic groups, coral reef communities and environmental variables

Maximum chlorophyll-*a* concentration, maximum temperature, % time of along-shore currents, and mean cross-shore wind speeds best explained the spatial variation in benthic community patterns ($\rho = 0.587$, $p < 0.001$). These four variables explained 59% of the variation in benthic groups, while adding other variables did not improve the strength of the relationship. Maximum chl-*a* alone was the best single environmental predictor for differences in benthic groups ($\rho = 0.379$, $p < 0.01$). Other important variables explaining spatial variation in benthic group patterns when considered alone were maximum salinity ($\rho = 0.341$) and minimum chlorophyll-*a* ($\rho = 0.271$), and chlorophyll-*a* range (0.271).

LINKTREE analysis of benthic groups showed a first split (split 1; Fig. 2.6a) between two sites in the Strait of Hormuz (sites 8 and 9) from all other sites, associated with mean cross-shore wind speeds. The second split (split 2) separated all sites in the Persian Gulf and the remaining two sites in the Strait of Hormuz (sites 7 and 10) from all sites in the Gulf of Oman on the basis of differences in maximum chl-*a* concentration, and maximum temperatures (Fig 2.6a). The third split (split 3) distinguished sites 7 and 10 in the Strait of Hormuz based on measures of maximum chl-*a*, maximum temperature and mean cross-shore wind speeds, compared with all sites in the southern Persian Gulf. The fourth split (split 4) between sites in the southern Persian Gulf was associated with differences in mean cross-shore wind speed and % along-shore currents. Splits 5–7 on the dendrogram separated the sites in the Gulf of Oman from each other on the basis of differences in maximum chl-*a*, cross-shore wind speeds and % along-shore currents (Fig. 2.6a).

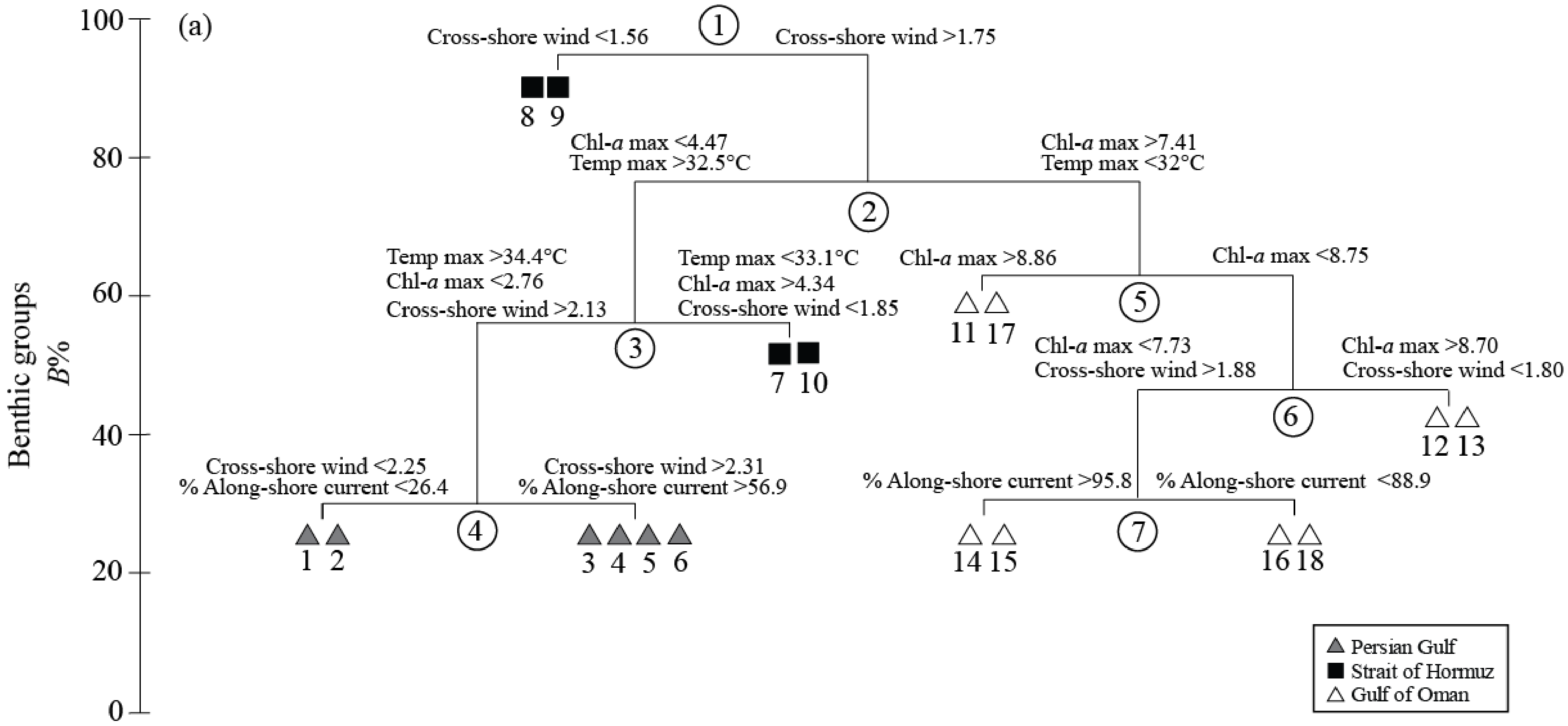

Fig. 2.6a: Linkage tree and associated physical and environmental variable thresholds that relate to the separation of benthic groups in the southern Persian Gulf, Strait of Hormuz and Gulf of Oman. Thresholds at the ends of each branch indicate that a left and right path, respectively, should be followed through the tree. B% is the absolute measure of group differences. Numbers under symbols correspond to sites on map (Fig. 2.1). Chl-*a* in mg m^{-3}, currents in cm s^{-1}, and winds in m s^{-1}.

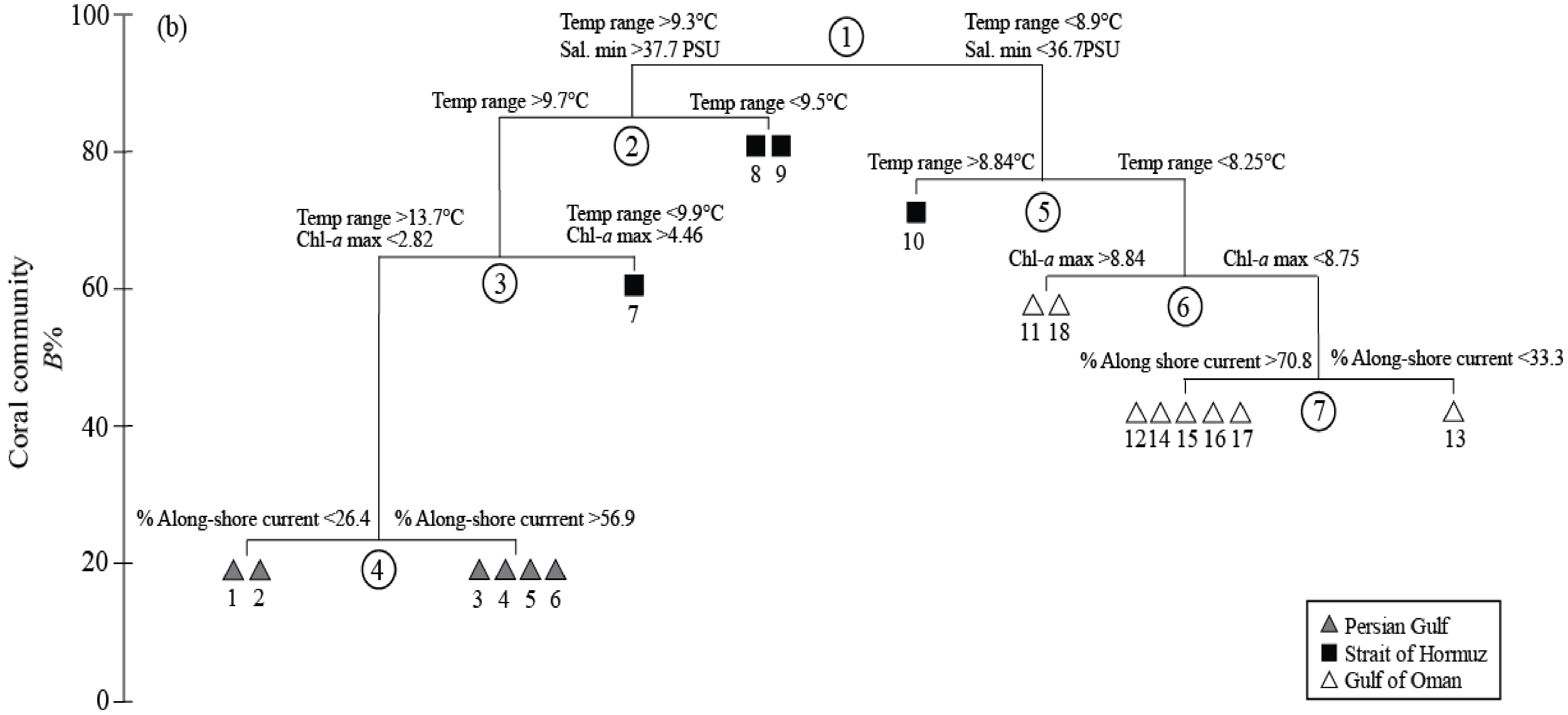

Fig. 2.6b: Linkage tree and associated physical and environmental variable thresholds that relate to the separation of coral communities in the southern Persian Gulf, Strait of Hormuz and Gulf of Oman. Thresholds at the ends of each branch indicate that a left and right path, respectively, should be followed through the tree. B% is the absolute measure of group differences. Numbers under symbols correspond to sites on map (Fig. 2.1). Chl-*a* in mg m^{-3}, currents in cm s^{-1}, and winds in m s^{-1}.

Temperature range, minimum salinity, maximum chl-*a*, and the % time of along-shore currents best explained the spatial variation in coral community structure among locations ($\rho = 0.683$, $p < 0.001$). These four variables explained 68% of the variation in coral community patterns among the locations. When the analysis was restricted to a single environmental variable, temperature range was the best predictor for differences in coral community patterns, and explained the majority of the variation between locations ($\rho = 0.543$, $p < 0.01$). Other important variables explaining the spatial variation in coral community patterns when considered alone were chl-*a* range ($\rho = 0.394$), maximum salinity ($\rho = 0.435$) and maximum temperature ($\rho = 0.479$); however the latter two showed significant correlations with each other.

LINKTREE analysis of coral communities showed a first split (split 1; Fig. 2.6b) dividing sites into those associated with a high temperature range and high minimum salinity (all southern Persian Gulf sites and Strait of Hormuz sites 7, 8 and 9) and those associated with a low temperature range and low salinity minimum (encapsulating all Gulf of Oman sites, and site 10 in Strait of Hormuz). On the left of the tree, the second split in the data was associated with a fine-scale change in temperature range, with sites 8 and 9 (Strait of Hormuz) associated with temperature range <9.5°C, while all Persian Gulf sites and Strait of Hormuz site 7 associated with temperate range >9.5 °C (split 2; Fig 2.6b). Higher maximum chl-*a* concentrations (i.e., greater primary productivity) and temperature range were important in differentiating coral communities at site 7 in the Strait of Hormuz from communities at all sites in the Persian Gulf (split 3; Fig. 2.6b). The distinction between communities in the Persian Gulf (split 4) was related to differences in % time of along-shore currents. On the right side of the tree, split 5 distinguished site 10 in the Strait of Hormuz from all sites in the Gulf of Oman on the basis of temperature range. Splits 6 and 7 differentiated the remaining Gulf of Oman sites on the basis of chl-*a* concentration and % time of along-shore current, respectively.

2.5 Discussion

Benthic groups and coral communities in the northeastern Arabian Peninsula differed significantly among the southern Persian Gulf, Strait of Hormuz, and the Gulf of Oman, associated with distinct sub-regional patterns in community structure. Similar to previous regional studies (e.g., Sheppard 1987; Sheppard and Sheppard 1991), there were substantial differences in the abundance, composition and species diversity within benthic groups and coral communities between locations. Community similarity values for corals were similar to previously reported values (Sheppard and Sheppard 1991; Sheppard et al. 1992), suggesting that coral community structure in the Strait of Hormuz and Gulf of Oman are most similar, and that southern Persian Gulf and Gulf of Oman communities the least similar. In contrast, benthic groups in the Strait of Hormuz showed higher community dissimilarity values compared with groups in the southern Persian Gulf and the Gulf of Oman.

Dissimilarities among benthic groups in the northeastern Arabian Peninsula were driven mainly by differences in the abundance of three benthic groups: hard coral; soft coral; and the combination of sand, pavement and rubble (SPR). Collectively, these three benthic groups contributed most to the dissimilarity between locations. Benthic groups in the southern Persian Gulf and Gulf of Oman were dominated by SPR, which accounted for more than 50% of the benthos. In contrast, less than 20% of the benthic groups in the Strait of Hormuz contained SPR. Such differences likely explain why benthic groups in the southern Persian Gulf and Gulf of Oman were less dissimilar (i.e., lower dissimilarity values) to each other, then when compared to groups in the Strait of Hormuz. Much of these two regions are dominated by uncolonizable soft substrates (i.e., sand and mud), compared to the Strait of Hormuz, which has substantial rocky substrate (Sheppard et al. 2000). Consequently, at sites around the northern and eastern Musandam (i.e., Strait of Hormuz), coral cover and the presence of true reefs is greater than anywhere else in the northeastern Arabian Peninsula (Sheppard and Salm 1988; Salm 1993).

Coral communities in the southern Persian Gulf were characterized by low species richness, diversity, and evenness, which likely reflect the severe constraints on coral survival in this region associated with extreme environmental conditions (Sheppard et al. 1992; Riegl et al. 2011). Several coral species, including *Montipora*, *Pocillopora* and *Stylophora*, that are common in the Strait of Hormuz and Gulf of Oman (Sheppard and Sheppard 1991; Claereboudt et al. 2006), were absent in the present survey. For example, no *Pocillopora* spp. were recorded, although *P. damicornis* is reported from neighboring reefs in Bahrain and Saudi Arabia (Fadlallah et al. 1993; Fadlallah et al. 1995). Additionally, *Stylophora pistillata*, which is dominant on many shallow reefs in Tarut Bay, Saudi Arabia (Fadlallah et al. 1995) were completely absent during surveys. Similar to recent studies (Burt et al. 2008; Riegl and Purkis 2009), reef communities in this study were dominated by poritids and faviids, which accounted for greater than 93% of the total coral cover surveyed. In contrast, *Acrpoora* species, which formerly dominated these reefs prior to recurrent bleaching events (Riegl 1999; George and John 2000; see also Riegl, 2002, 2003 and related references), represented less than 4% of total cover. Importantly, these findings provide additional evidence to support claims of long-term shifts in community structure in the southern Persian Gulf towards more robust coral species (*Porites* and faviids) that are more resistant to major disturbances (Riegl and Purkis 2009).

Coral communities in the Strait of Hormuz and Gulf of Oman were characterized by relatively high species diversity and richness, likely due to less extreme physical conditions in these locations (Sheppard 1987; Sheppard and Sheppard 1991; Glynn 1993). Nonetheless, each location represented a distinct community, with 56% dissimilarity in structure, associated with substantial differences in coral cover and community structure. The Strait of Hormuz had almost three times more coral cover than the Gulf of Oman, but had significantly lower species evenness, with communities dominated by poritids and faviids. In comparison, coral communities in the Gulf of Oman were relatively even, and held a much wider range of genera. This study also found that percent live coral cover within both locations was relatively similar with previous estimates (Sheppard and Salm 1988; Salm 1993; Glynn 1993). However, *Acropora* cover within the Strait of Hormuz was substantially lower than previously reported, while Gulf of Oman coral communities showed similar estimates of *Acropora* cover to previous work (Sheppard and Salm 1988). Sheppard and Salm (1988) reported extensive *Acropora* cover (50–85%) from several sites in the Musandam (i.e., Strait of Hormuz), while Maghsoudlou et al. (2008) reported in early 2007 that reefs in the Musandam had high coral cover in excess of 80% with *Pocillopora* and *Acropora* the dominant species. Both the Strait of Hormuz and the Gulf of Oman have been impacted by recent disturbance events, including Cyclone Gonu (2007) and a large-scale HAB event (2008), which had significant selective effects on branching species (e.g., *Acropora* spp.) (Maghsoudlou et al. 2008; Foster et al. 2008; Bauman et al. 2010). Such differences in *Acropora* cover between locations suggest that there has been substantial re-growth of *Acropora* species within the Gulf of Oman (Maghsoudlou et al. 2008), with limited recovery of these corals within the Strait of Hormuz.

Understanding how reef communities vary across environmental gradients is important for determining how communities will respond to changing environmental conditions (Kleypas et al. 1999). Results from this study showed considerable spatial heterogeneity in oceanic conditions among locations, with strong directional environmental gradients that operate from the Persian Gulf through the Strait of Hormuz to the Gulf of Oman (Reynolds 1993, 2002; Nezlin et al. 2007; Piontkovski et al. 2011). Interestingly, the combination of physical variables responsible for explaining differences between benthic groups and coral communities were relatively similar. Differences in benthic groups were best explained by maximum chlorophyll-*a* in combination with maximum temperature, % time of along-shore currents, and mean cross-shore wind speeds. In contrast, differences in coral community structure around the region were best explained by temperature range in combination with minimum salinity, maximum chlorophyll-*a*, and the % time of along-shore currents. Although BEST analysis selected temperature range and maximum chl-*a* as the single best environmental predictors for differences in patterns of benthic groups and coral community, these could effectively be replaced by the minimum, maximum or range in these parameters respectively, as these variables showed a similar gradient across the three locations.

Temperature and salinity are often cited as the two most important physical factors structuring benthic groups and coral communities around the northeastern Arabian Peninsula (Sheppard and Sheppard 1991; Sheppard et al. 1992; Reynolds 1993; Coles 2003). Results from this study support that finding but also indicated that chlorophyll-*a* concentrations, surface currents, and wind speeds, in addition to temperature and salinity, were important physical factors in structuring benthic groups and coral communities. It is worthwhile to note that differences in topography across the region may be responsible for coinciding associations between some of these variables. For example, it is reasonable that the much shallower enclosed southern Persian Gulf would experience increased values and ranges of temperature and salinity but not experience deep-water convective mixing or upwelling, whereas the sections of the coastline along the Strait of Hormuz and Gulf of Oman would experience less extreme values of temperature and salinity but could be exposed to enhanced chl-*a* values from convective mixing or upwelling of adjacent deep waters. Previous studies have indicated both higher temperature and salinity in the southern Persian Gulf (Sheppard et al. 1992, 2000), with higher chl-*a* in the Gulf of Oman and Strait of Hormuz due to seasonal upwelling and monsoonal events (Reynolds 1993; Piontkovski et al. 2011). Importantly this study has isolated specific environmental variables (i.e., chlorophyll-*a* concentrations, surface currents, and wind speeds) that, in addition to temperature and salinity, may influence the composition of benthic groups and coral communities. This has important implications for future ecosystem changes given the predicted long-term changes to multiple oceanic factors as a consequence of on-going climate changes (IPCC 2007).

Moreover, these factors are also considered likely correlates of resistance and resilience to bleaching events (West and Salm 2003; Maina et al. 2008), which are expected to become both more frequent and more severe in coming decades (e.g., Hoegh-Guldberg 1999). For example, recent studies suggest that chlorophyll-*a* may reduce the effects of light by absorbing and scattering thus creating a shading effect (Maina et al. 2008, 2011). Consequently, within regions that have high chlorophyll concentrations the severity and impact of bleaching events may be lower than in areas of low chlorophyll-*a* (McClanahan et al. 2003). Although the gradient in maximum chl-*a* increasing from the Persian Gulf to the Gulf of Oman likely influences coral community structure, it remains unclear whether this is indeed a causal relationship. Furthermore, areas with strong currents and high wind speed, which can enhance vertical mixing of the water column (Skirving et al. 2006), may potentially increase local and regional cooling, thereby reducing the effects of increased sea surface temperature, and the potential for disturbance mediated effects on coral reef communities (West and Salm 2003). Similar to previous studies, (Reynolds 1993, 2002; Piontkovski et al. 2011) results from this study indicate upwelling and stronger vertical mixing of the water column in both the Strait of Hormuz and along the coast of Oman. Interestingly, no coral bleaching was reported from either the Strait of Hormuz or Gulf of Oman during the 1998 large-scale coral bleaching event (Wilson and Claereboudt 2005) that heavily impacted most reefs around the world (see review Baker et al. 2008) and in the southern Gulf (Riegl 1999; 2002). Moreover, the southern Gulf has a much higher frequency, but also more recent occurrence, of bleaching events over the last three decades compared to the Strait of Hormuz or Gulf of Oman (Wilson and Claereboudt 2005; Sheppard and Loughland 2002; Baker et al. 2008).

2.6 Conclusions

Overall, this work has shown that considerable changes to coral reef community structure have occurred throughout the northeastern Arabian Peninsula over the past two decades. Most dramatic are the apparent changes from *Acropora* dominated to poritids and faviids dominated communities particularly in the southern Persian Gulf and Strait of Hormuz. Sustained and on-going disturbances throughout the region

(Maghsoudlou et al. 2008; Sheppard et al. 2010; Sale et al 2011; Riegl et al. 2011), associated with changing global climate, are likely to continue altering the structure of benthic groups and coral communities, and could potentially increase the deleterious effects on reef ecosystem function. Nonetheless, despite the stark contrasts between reef community structure in the southern Persian Gulf and other locations in this study, these do not necessarily apply to all regions within the Persian Gulf (e.g., coral areas along the coast of Iran, off-shore islands of UAE and Saudi Arabia). Furthermore, although temperature and salinity remain good proxies for distinguishing between coral reef communities across the region, they are not the only physical variables that correlate with the transition of community structure. This work clearly highlights that multiple environmental variables are related to reef community patterns throughout the northeastern Arabian Peninsula. As such there is a critical need to increase our understanding of the range of physical factors that influence the structure of reefs throughout the region, including different areas within the Gulf (e.g., off-shore islands and coast of Iran), and how these conditions may change with sustained climate change.

Chapter 3: Coral reproduction in the world's warmest reefs: southern Persian Gulf (Dubai, United Arab Emirates)[3]

3.1 Abstract

Despite extensive research on coral reproduction from numerous geographic locations, there remains limited knowledge within the Persian Gulf. Given that corals in the Persian Gulf exist in one of the most stressful environments for reef corals, with annual variations in sea surface temperature (SST) of > 12°C and maximum summer mean SSTs of 36°C, understanding coral reproductive biology in the Gulf may provide clues as to how corals may cope with global warming. In this study, we examined six locally common coral species on two shallow reef sites in Dubai, United Arab Emirates (UAE) in 2008 and 2009 to investigate patterns of reproduction, in particular the timing and synchrony of spawning. In total, 71% colonies in April 2008, and 63% colonies in April 2009 contained mature oocytes. However, the presence of mature gametes in May indicated that spawning was potentially split between April and May in all species. These results demonstrate that coral reproduction patterns within this region are highly seasonal and that multi-species spawning synchrony is highly probable. *Acropora downingi*, *Cyphastrea microphthalma* and *Platygyra daedalea* were all hermaphroditic broadcast spawners with a single annual gametogenic cycle.

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Furthermore, fecundity and mature oocyte sizes were comparable to those in other regions. We conclude that the reproductive biology of corals in the southern Persian Gulf is similar to other regions, indicating that these species have adapted to the extreme environmental conditions in the southern Persian Gulf.

3.2 Introduction

Over 25 years have passed since the discovery of multi-specific broadcast spawning of scleractinian corals on the Great Barrier Reef (GBR) (Harrison et al 1984). Since then there has been a substantial increase in research on coral reproduction globally. As a result, there has been a dramatic increase in the number of coral species for which reproductive schedules and traits are known, in particular from regions that were previously under-represented (reviewed by Baird et al. 2009b). However, despite this recent research, there remains limited information on coral reproductive processes in regions such as the Persian Gulf.

Coral assemblages in the Persian Gulf (24°N to 30°N) experience the highest annual variability in water temperatures of any coral reefs (Kinsman 1964; Sheppard 1988; Sheppard et al. 2000). Sea surface temperatures (SSTs) can fluctuate annually from winter lows < 12°C to summer highs > 36°C (Sheppard et al. 1992; Sheppard 1993). Moreover, the Persian Gulf has significant seasonal insolation fluctuations (Sheppard et al. 2010), and is a hyper-saline environment year-round with salinities regularly > 45 ppt (Sheppard et al. 1992). The persistence of reefs in the Persian Gulf indicates a potential to adapt to extreme environmental conditions (Coles and Fadlallah 1991; Coles and Brown 2003). The recovery of these coral assemblages following mortality induced by a number of recent temperature-related bleaching events (1996, 1998, and 2002) suggests these assemblages are also resilient to extreme fluctuations in water temperature (Riegl 1999, 2003; Burt et al. 2008). Considering that corals in the Persian Gulf survive in one of the most stressful physical environments encountered by any reef corals (Coles and Fadlallah 1991; Sheppard et al. 1992; Riegl 1999), understanding the process of coral reproduction under such extreme physical conditions may be crucial as similar conditions may eventually become commonplace on a broad range of coral reefs due to climate change.

Coral reproductive research in the Persian Gulf has been limited to a few coral species from two regions: Saudi Arabia (Fadlallah and Lindo 1988; Fadlallah et al. 1992; Fadlallah 1996) and Kuwait (Harrison 1995). In Saudi Arabia, a six-month gametogenic cycle in *Stylophora pistillata* was followed by synchronized release of planula in May and June, during a period of rapid temperature increase (Fadlallah and Lindo 1988). Synchronous release of gametes was also observed in *Acropora clathrata* both *in situ* and in aquaria, between 20:30 to 21:30, two days prior to the full moon in May 1993 (Fadlallah 1996). Synchronous spawning was also inferred from the disappearance of mature oocytes in colonies of *Acropora arabensis* and correlated with rapidly rising SST and increasing day length (Fadlallah 1996). In Kuwait, tagged colonies of *Acropora downingi* and *A. arabensis*, spawned both *in situ* and in aquaria 2-3 days prior to the full moon in May 1995, followed by more extensive spawning in the week following the full moon (Harrison 1995). In the same study, *Platygyra daedalea*, spawned after the full moon in June 1995 (Harrison 1995). Importantly, these observations demonstrate that coral species in the Persian Gulf spawn in a similar way to con-specifics elsewhere, however, other aspects of the reproductive biology, such as the length of the gametogenic cycles in species other than *S. pistillata*, and colony fecundity have yet to be examined.

Central to improving our understanding of how corals will be affected by climate change, is knowledge of how specific coral reproductive processes, such as gametogenic cycles and reproductive capacity (i.e., fecundity, reproductive effort), are likely to be affected under more extreme environmental conditions. As a consequence of on-going climate change, global SSTs are predicted to rise 2 to 3°C over the next century (Parry et al. 2007). Rising SSTs will likely have significant repercussions for reproductive phenology of coral species, in particular species whose gametogenic cycles are tightly regulated by exogenous cues (i.e., temperature) (Lawrence and Soame 2004; Baird et al. 2009b), and for species that depend on seasonal cues for reproduction cycles (Olive et al. 1990). Increases in SSTs will also likely affect coral populations biology by reducing reproductive capacity, at least in bleaching years (Baird and Marshall 2002; Mendes and Woodley 2002). The harmful effects of increased temperature on coral reproduction include reduced individual fecundity, reduced egg quality, lowered fertilization success and decreased larval survivorship (see review in McClanahan et al. 2009). Furthermore, changes in seasonal patterns of SST may affect highly synchronized temporal spawning events, i.e. multi-species spawning (Przeslawski et al. 2008; Baird et al. 2009b). Research focusing on reproductive processes in regions with extreme physical conditions is urgently needed as a baseline against which to test the effects of climate change on reproductive capacity.

In this paper, we present results of coral reproductive surveys conducted in the southern Persian Gulf (Dubai, UAE) in 2008 and 2009. The specific objectives were to: 1) determine whether corals in the southern Persian Gulf are reproductively active, 2) determine the month(s) of spawning of the six common coral species within this region and, 3) examine the reproductive biology of the three abundant species: *Acropora downingi*, *Cyphastrea microphthalma* and *Platygyra daedalea*.

3.3 Materials and Methods

3.3.1 Study sites and environmental variables

The reproductive conditions of six locally common coral species from the southern Persian Gulf were examined monthly from January 2008 to August 2009. Surveys were conducted at two shallow (< 5.0 m) near-shore reef sites in Dubai, UAE: Ras Hassan (24°97'N, 54°96'E) and Saih Al Shaib (24°92'N, 54°90'E). The two sites are approximately 0.5 - 1 km from shore and are composed of discontinuous coral patches associated with areas of early diagenetic limestone ('caprock') interspersed between areas of sand, rubble and mixed algal assemblages (Riegl 1999; Burt et al. 2008). This series of patch reefs extends approximately 12 km along the western coastline of Dubai.

Three environmental variables considered to be important influences on the reproduction of corals are also presented, seawater temperature, tidal amplitude and wind speed. Seawater temperature was recorded hourly throughout the study period from November 2007 to August 2009 using *in situ* temperature loggers (HOBO StowAway TidbiT), and mean daily averages were calculated. Tidal amplitude was calculated from a six-month hourly water level time series from Jebel Ali Port (24°59'N and 55°04'E), located ≈12 km northeast of the study sites. Wind data along the Dubai coastline were calculated through monthly averaged wind-speed data (m s^{-1}) derived from 2000 to 2009 using the 14 GHz channel scatterometer (microwave scatterometer SeaWinds) referred to as QuikScat (or QSCAT). The SeaWinds scatterometers are essentially radars that capture 25 km scatterometer orbital data pixels. The uncompressed QSCAT data files were downloaded from http://www.remss.com and loaded into MATLAB R2007B for analysis. The wind-field data were extracted 10 m above the water surface. A threshold of 6 m s^{-1} for wind velocity was chosen to allow a comparison with results from van Woesik (2010) and because significant waves begin to form when wind velocity is greater than 6 m s^{-1} (Pierson and Moskowitz 1964).

3.3.2 Field surveys to assess the reproductive condition of six common coral species

Field surveys were conducted 3 to 5 days prior to the full moon for 20 consecutive months (January 2008 – August 2009) to assess the reproductive condition of six common coral species: *Acropora downingi, A. clathrata, A. valenciennesi*, *Cyphastrea microphthalma*, *Favia pallida* and *Platygyra daedalea*. Colonies that contain visible, pigmented oocytes are generally considered to spawn on, or shortly after, the subsequent full moon (Harrison et al 1984). The maturity of oocytes in colonies was established by either breaking coral branches (i.e., *Acropora* colonies > 35 cm in diameter) or chiseling off small pieces (i.e., *Favia* colonies > 25 cm diameter) to expose developing oocytes (Harrison et al 1984). Colonies were classified into one of three reproductive conditions based on the color of oocytes: *mature* - oocytes pigmented; *immature* – oocytes white; *empty* - oocytes too small to see or absent (following Baird et al. 2002). For non-acroporid species, which typically have smaller oocytes than *Acropora* at maturity (Harrison and Wallace 1990), a 20X pocket magnifying glass was used *in situ* to detect immature oocytes. All species were sampled prior to the full moon, as previous research in the Persian Gulf suggests species will release their gametes shortly after the full moon (Fadlallah 1996). Colonies of the selected species were sampled haphazardly for 75 min on SCUBA at each site to ensure a minimum of 10 colonies of each species were sampled on each occasion. For the six species examined in 2008 and 2009, site data were pooled because there were no obvious site differences among species in reproductive condition. The timing of spawning was inferred by the disappearance of mature gonads between sampling periods. In addition, direct observations of coral spawning were made in Saih Al-Shaib (on SCUBA) between the hours of 18:00 and 22:00, starting on the night of the full moon, for 4 to 6 days in April and May 2009.

3.3.3 Dissections to further assess the reproductive biology of three species

To further investigate the reproductive biology of three abundant coral species within Dubai (*Acropora downingi, Cyphastrea microphthalma* and *Platygyra daedalea*), coral fragments were collected monthly, 3 - 5 days before the full moon, from August 2008 to August 2009 at Saih Al Shaib. For each species, three branches (≈ 6 cm long) or small fragments (≈10 cm^2 of tissue) were removed from each of 10 colonies. In most coral species, gametes typically develop with high synchrony among polyps (Harrison and Wallace 1990), and three fragments are generally sufficient to determine the reproductive condition of a colony.

Samples were fixed in 10% seawater formalin for at least 24 h then transferred to 30% ethanol in the laboratory. Fragments were then decalcified in 10% formic acid to yield soft sectionable tissues, and stored in 70% ethanol solution. The resulting tissue was then dissected and examined using a stereo dissecting microscope. For *A. downingi* and *C. microphthalma*, five polyps were haphazardly selected within each sample and removed intact to determine the presence of oocytes. In *P. daedalea*, where adjacent polyps share mesenteries, a portion of the decalcified tissue surrounding five randomly selected polyp mouths was removed and 6 to 8 mesenteries sub-sampled within each sample (following Mangubhai and Harrison 2008). Within all three species, each polyp within the sample containing oocytes was identified and photographed, and all visible oocytes were counted and measured (i.e., maximum diameter) using a calibrated eyepiece micrometer. Sexuality (gonochoric vs. hermaphroditic) and mode of reproduction (brooding vs. broadcast spawning) were also recorded.

3.4 Results

3.4.1 Spawning months in the coral assemblage in the Gulf

In situ examination of colonies from six local coral species, *Acropora downingi, A. clathrata, A. valenciennesi*, *Cyphastrea microphthalma, Favia pallida* and *Platygyra daedalea*, in 2008 and 2009 showed that all species contained the highest proportion of colonies with mature oocytes (henceforth referred to as mature colonies) prior to the full moon in April. In April 2008, 71% of colonies (*n* = 95) examined contained mature oocytes, while in April 2009, 63% of colonies (*n* = 99) contained mature oocytes. In May 2008 and 2009 following this peak in reproductive activity, there was a substantial decrease in the proportion of colonies containing mature oocytes to 21% (*n* = 107, *n* = 98, respectively). However, the majority of sampled species also had mature colonies in May in both years. Only *A. valenciennesi* colonies did not contain mature oocytes in May 2008, while *C. microphthalma* was the only species to contain mature oocytes in May of both years and in June 2008. All species had mature colonies for a 3 to 4 month period, generally from February to May.

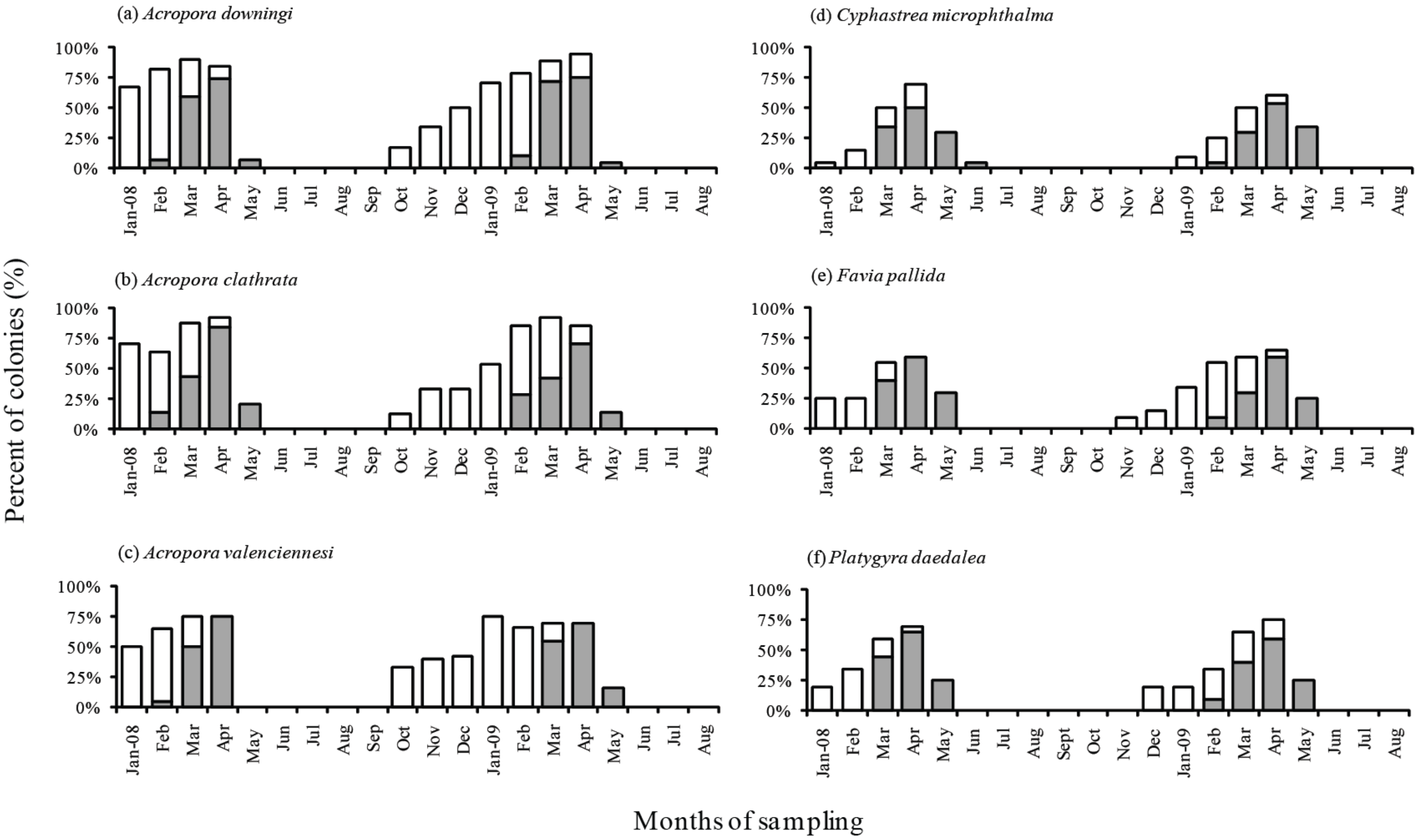
3.4.2 Spawning months inferred from in situ sampling

In *A. downingi* and *A. clathrata*, mature colonies were observed from February to May in 2008 and 2009 (Fig. 3.1a,b). The proportion of mature colonies peaked in April followed by a substantial decrease in mature colonies in May. In 2008, mature colonies of *A. valenciennesi* were observed February to April, in 2009 mature colonies from March to May (Fig. 3.1c). The proportion mature colonies peaked in April following which no oocytes were recorded in May 2008, but 17% of colonies were mature in May 2009.

In *C. microphthalma*, mature colonies were observed over four consecutive months in 2008 and 2009 (Fig. 3.1d). In 2008, mature colonies were observed from March to June, while in 2009 from February to May. The proportion of mature colonies peaked in April in both years. Following this peak reproductive period was a moderate decrease in the proportion of colonies with mature oocytes in May both years. Mature colonies were observed in *F. pallida* and *P. daedalea* from March to May in 2008, while in 2009 mature colonies were observed from February to May (Fig. 3.1e,f). Within both species the proportion of mature colonies peaked in April within both years followed by a decrease in mature colonies in May both years.

3.4.3 Reproductive biology of Acropora downingi, Cyphastrea microphthalma and Platygyra daedalea

All three species (*A. downingi*, *C. microphthalma* and *P. daedalea*) are simultaneous hermaphrodites that broadcast spawn their gametes. Mature oocytes and spermaries were observed in the same polyp on separate mesenteries in both *A. downingi* and *C. microphthalma* polyps prior to gamete release. In *P. daedalea* mature oocytes and spermaries were observed intermingled in the same mesentery prior to


(a) *Acropora downingi*

(b) *Acropora clathrata*

(c) *Acropora valenciennesi*

(d) *Cyphastrea microphthalma*

(e) *Favia pallida*

(f) *Platygyra daedalea*

Fig 3.1: Percent colonies with mature and immature oocytes in 2008 and 2009 for six coral species (a) *Acropora downingi*, (b) *A. clathrata*, (c) *A. valenciennesi*, (d) *Cyphastrea microphthalma*, (e) *Favia pallida* and (f) *Platygyra daedalea*. Shaded percent of colonies with mature gametes, white percent of colonies with immature gametes.

gamete release. *In situ* observations of the release of egg/sperm bundles in *C. microphthalma* and *P. daedalea* in April and May 2009 confirm these two species are broadcast spawners. Although spawning was not directly observed in *A. downingi*, the sudden disappearance of mature gametes from consecutive samples suggests that the majority of colonies broadcast spawned gametes around the full moon in April.

All three species have a single annual gametogenic cycle. In *A. downingi* and *P. daedalea*, the gametogenic cycles was 7 to 8 months, while the gametogenic cycle in *C. microphthalma* 8 to 9 months. Oocytes grew at relatively constant rates before reaching maturity in April. However, oocyte size varied considerably between species (Fig. 3.2). Mean fecundity increased in the early stages of gametogenesis after which it remained relatively constant until spawning (Fig. 3.3)

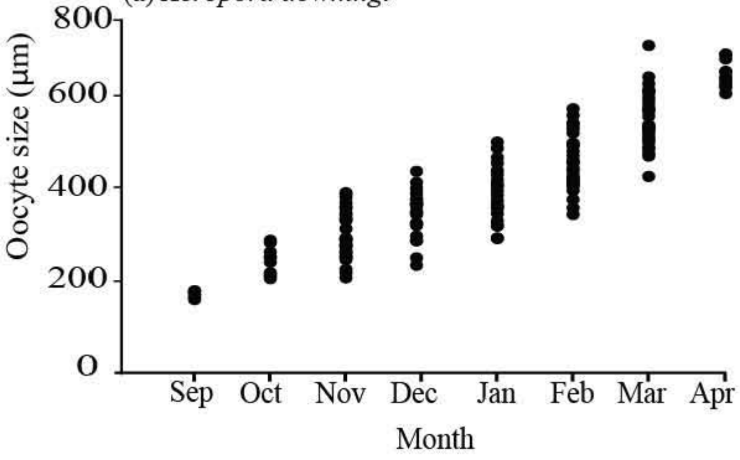
3.4.4 Spawning times

In situ observations confirmed that spawning in *C. microphthalma* and *P. daedalea* occurred in April and May 2009. Spawning was first observed on the full moon and continued for 2 to 4 consecutive days in April and May. In *C. microphthalma*, tan to light brown mature bundles (250–350 μm) were released from colonies nightly from 20:00 hrs to 22:00 hrs (2 to 4 hours after sunset). Whereas, in *P. daedalea*, pink mature bundles (350–400 μm) were released from colonies of nightly from 19:30 hrs to 22:00 hrs. Due to poor field conditions (i.e., high winds and high turbidity), *in situ* observations could not be conducted in March and June 2009.

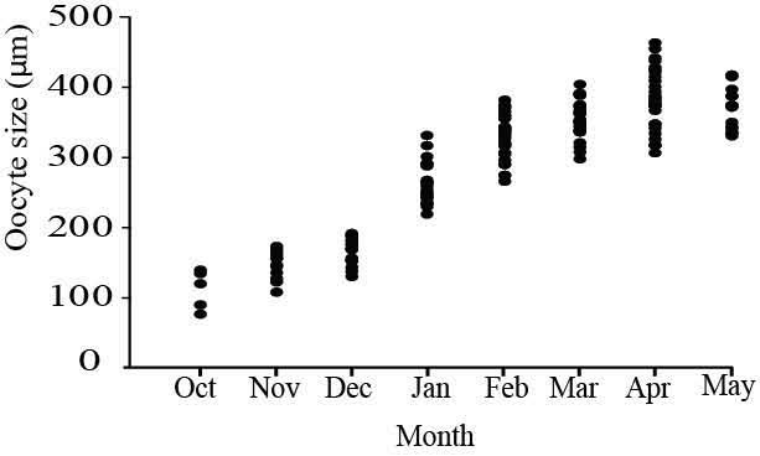
3.4.5 Environmental parameters

Spawning in *C. microphthalma* and *P. daedalea* was associated with rising SSTs,

(a) *Acropora downingi*



(b) *Platygyra daedalea*



(c) *Cyphastrea microphthalma*

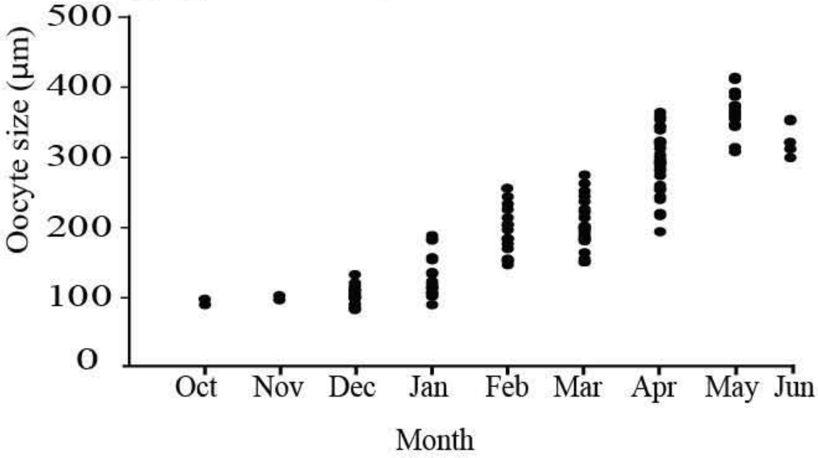
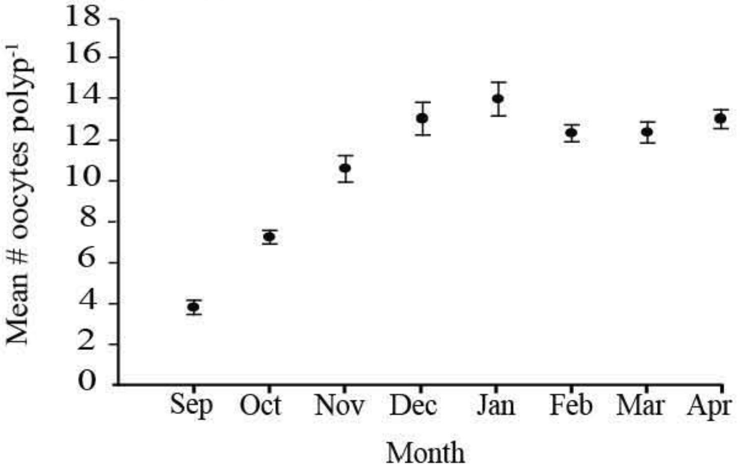
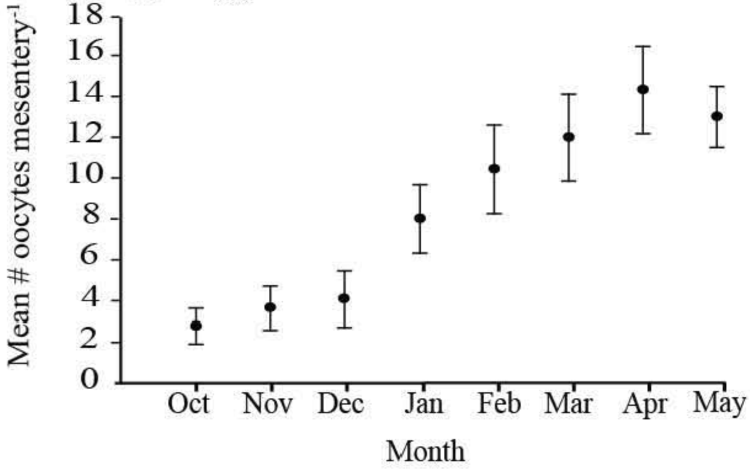


Fig 3.2: Mean monthly oocyte size (µm) during 2008/2009 for (a) *Acropora downingi*, (b) *Platygyra daedalea* and (c) *Cyphastrea microphthalma*

(a) *Acropora downingi*



(b) *Platygyra daedalea*



(c) *Cyphastrea microphthalma*

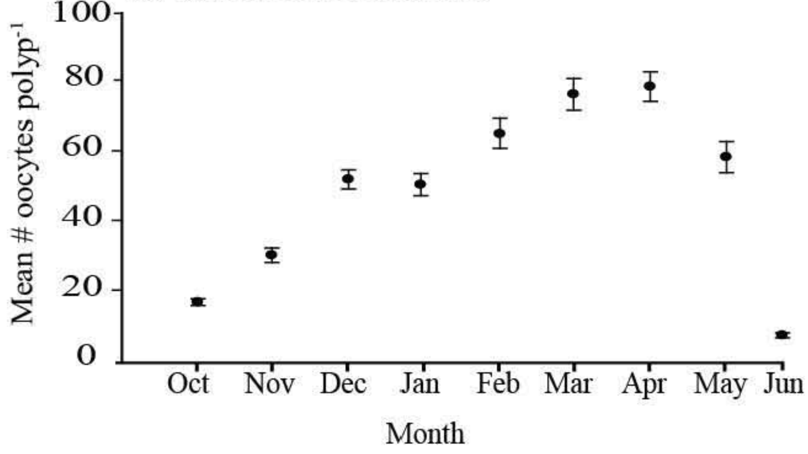


Fig 3.3: Mean number of oocytes per polyp/mesentery during 2008/2009 for (a) *Acropora downingi*, (b) *Platygyra daedalea* and (c) *Cyphastrea microphthalma*

temperatures between 26.5 °C to 31°C, spring tides, and wind velocities between 5.2 – 5.7 m s^{-1} (Electronic Supplemental Material, ESM; Appendix B). The other four species (*A. downingi*, *A. clatharata, A. valenciennesi* and *F. pallida*) are likely to have spawned under similar conditions, given the substantial decrease in the total proportion of colonies with mature gametes after April.

3.5 Discussion

The reproductive biology of these six coral species in the southern Persian Gulf was remarkably similar to con-specifics elsewhere in the Indo-Pacific (Baird et al. 2009b). Coral reproduction was seasonal, with peak reproductive activity in April, corresponding to rising mean SST above 26.5°C. Gametogenic cycles were between 7 to 9 months and polyp level fecundity was also similar to other regions (Table 3.1). Consequently, the reproductive biology of these species appears well adapted to extreme annual environmental fluctuations in the Gulf. Furthermore, the rapid recovery of *Acropora* assemblages in the Gulf following recurrent bleaching events in the Gulf (Burt et al. 2008), suggests that sexual reproduction remains the dominant reproductive strategy. The adaptive capacity of corals in the Persian Gulf is likely facilitated by a combination of short-term acclimation in individuals during acute environmental conditions (e.g., recurrent bleaching events) and long-term adaptation among coral populations to chronic environmental conditions (e.g., extreme temperatures). Clearly, these results from the Gulf demonstrate that coral populations can survive and proliferate in extreme conditions that are projected to occur in many other regions of the world by the end of this century. Nonetheless, it remains to be established whether populations can adjust in the short time span before such conditions prevail (Hoegh-Guldberg et al. 2007)

Gamete release in the southern Persian Gulf is inferred to occur in April and May (northern hemisphere spring), with the highest recorded proportion of mature colonies found in April in both years. Substantial decreases in the total proportion of colonies with mature gametes, between April (67%) and May (21%) suggest the majority of spawning activity occurs around the April full moon. Given the high proportion of mature colonies in April prior to the full moon it is highly probable that there would be some degree of multi-synchronous spawning, if these species behave like they do elsewhere in the Indo-Pacific. Furthermore the presence of mature gametes in May, following the spawning event in April, suggest some individuals also release gametes in around the May full moon. This inference was confirmed by *in situ* observations of *C. microphthalma* and *P. daedalea* spawning in consecutive months. Similar split spawning events, when coral populations divide spawning over two consecutive months, are common throughout the world including on the Great Barrier Reef (Willis et al. 1985; Baird et al. 2002), Thailand (Kongjandtre et al. 2010), and Japan (Baird et al. 2009c) and Venezuela (Bastidas et al. 2005). The alternative that mature unspawned gametes were reabsorbed after May is much less likely. The reabsorption of mature oocytes is uncommon (*cf*. Rinkevich and Loya 1979) except perhaps following disturbances such as coral bleaching (Sier and Olive 1994; Michalek-Wagner and Willis 2001) and coral fragmentation (Okubo et al. 2007).

Seasonal patterns of coral reproduction in the Gulf are generally consistent with other locations in region, including Saudi Arabia (Fadlallah and Lindo 1988; Fadlallah 1996), Kuwait (Harrison 1995) and the Red Sea (Hanafy et al. 2010).

Table 3.1: Comparisons of mean oocyte size and fecundity (oocytes polyp^{-1}/mesentery^{-1}) at different geographic locations for which data are available for Dubai, UAE (**bold**). For each species, data are ordered in decreasing mean oocyte size. (–) no data available. (*) indicates mean oocyte size and fecundity prior to the major spawning event in Kenya (i.e., bi-annual gametogenic cycles)

Family, Species	Location	Oocyte size (μm)	Fecundity	Source
Acroporidae				
A. downingi	United Arab Emirates	**543**	**14.2 polyp^{-1}**	Present study, first record
Faviidae				
C. microphthalma	Taiwan	301	–	Dai et al. 1992
	United Arab Emirates	**293**	**78.1 polyp^{-1}**	Present study
	Red Sea	290	105 polyp^{-1}	Shlesinger et al. 1998
P. daedalea	Taiwan	415	–	Dai et al. 1992
	United Arab Emirates	**368**	**14.2 mesentery^{-1}**	Present study
	Kenya*	259	7.9 mesentery^{-1}	Mangubhai and Harrison 2008

There were, however, subtle differences in spawning times between regions and among species (e.g. *Acropora* species and non-acroporids). For example, Fadlallah (1996) observed synchronous spawning in *A. clathrata* in early May, whereas some colonies of *A. downingi*, *A. clathrata* and *A. valenciennesi* were here inferred to have spawned in both April and May. Furthermore, *A. downingi* and *A. arabensis* spawned a few nights before the full moon in May, with more extensive spawning in the week following the full moon (Harrison 1995). Harrison (1995) also recorded spawning in *P. daedalea* after the full moon in June. Similarly, *C. microphthalma* in the present study contained mature oocytes in June prior to the full moon. Irrespective of such differences, evidence suggests that coral assemblages in the southern Persian Gulf exhibit similar synchronous spawning patterns at similar times of the year (i.e., rising SSTs, low wind speeds). Observed differences in reproductive timing possibly reflect localized environmental conditions, annual variation or delayed spawning due to latitudinal differences (Harrison and Wallace 1990).

Acropora and non-acroporid species exhibited similar seasonal patterns in the proportion of mature colonies through time. Mature gametes were present in the field 6 to 8 weeks prior to April spawning, and mature colonies were present over four months in most species (except *A. valenciennesi*), over at least one spawning season. Implicit in the assumption that most mature colonies (i.e., those containing pigmented oocytes) generally release their gametes around the subsequent full moon, is the expectation that the sum of the proportion of mature colonies throughout the season or the total proportion of colonies spawning should not exceed 100%. Interestingly, over both spawning seasons, the sum of the proportions of mature colonies within populations of all six species prior to the spawning in the spring exceeded 100%, suggesting that some colonies are either not releasing mature gametes or that some colonies are spawning twice.

This is not uncommon: for example individuals of *Montastraea faveolata* in the southern Caribbean spawn on up to three occasions, either on consecutive nights or in consecutive months (Bastidas et al. 2005) . Similarly, the total percentage of colonies within populations of *Acropora spicifera* and *Acropora hyacinthus* on Scott Reef in northwestern Australia with mature oocytes exceeded 100% over the summer months (Gilmour et al. 2009). Clearly, in some regions, the color of oocytes is not a perfect indicator that the entire colony is ready to spawn, perhaps because the maturation process may take longer in these regions, when compared to others

Despite our increased understanding of reproductive traits from a large number of coral species from more coral reef regions (Baird et al. 2009b), there remains the need for more descriptive coral reproductive studies from underrepresented regions (e.g., Persian Gulf). In the southern Persian Gulf, *A. downingi*, *C. microphthalma*, and *P. daedalea* are hermaphroditic broadcast spawners with single annual gametogenic cycles (i.e., 7 to 9 months), similar to con-specifics documented in many geographic locations (Willis et al. 1985; Shlesinger et al. 1998; Baird et al. 2009b). Importantly, mean fecundity and oocyte sizes prior to spawning for all three species are also similar to other regions (Table 3.1). These results have important implications given the known deleterious effects of temperature on reproductive output (e.g., reduced individual fecundity, egg size and quality) (McClanahan et al. 2009). The lack of significant differences in fecundity and gamete size between coral species in the Gulf and con-specifics elsewhere supports the idea that adaptation to environmental conditions projected under climate change is possible (Baird and Maynard 2008). Nonetheless, increases in SSTs, which are predicted to be more severe in high latitude regions, especially in the northern hemisphere (IPCC 2007; Strong et al. 2008), could push individual species and populations in the Gulf beyond local thermal thresholds thereby negatively effecting reproductive processes. Whether future coral populations in the southern Persian Gulf are capable of reproductive activities under more extreme environmental conditions as a result of climate change will likely depend on how quickly their able to adapt.

Overall, this work provides the first information on the timing of reproduction and spawning of a range of corals within the southern Persian Gulf, and confirms that corals are capable of reproductive activities under extreme environmental conditions. Importantly, such findings provide circumstantial evidence that coral can adapt to extreme environments, the question remains how quickly this capacity can evolve (Hoegh-Guldberg et al. 2007; Baird and Maynard 2008).

Chapter 4: Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates)[4]

4.1 Abstract

Coral settlement is a key ecological process in the maintenance, recovery and resilience of coral reef ecosystems. Given that coral reefs in the Persian Gulf survive in one of the most extreme environments, examining patterns of coral settlement in this region may provide important clues as to how settlement processes may be affected by ongoing climate change. Spatial and temporal patterns of coral settlement were examined at six sites in Dubai, United Arab Emirates using settlement tiles deployed and collected every three months for two years (2009/10 and 2010/11). Settlement was highly seasonal with highest settlement rates (3.2 spat tile^{-1} ± 0.21) between June and August, when summer sea temperatures approached 35°C. There was a smaller settlement pulse between September and November, but no settlement between December and May. Settlement was observed 1–4 months after the major spawning season (i.e., April and May), suggesting either delayed settlement of larvae, or spatial and/or taxonomic disparity between studies of reproduction versus settlement. Settlement rates varied significantly among sites, but spatial variation was

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[4] This chapter has been submitted to *Marine Ecology Progress Series*: Bauman AG, Baird AH, Burt JA, Pratchett MS, Feary DA (In Revision) Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates).

very consistent among years, suggesting strong effects of local environmental conditions or local coral assemblages. Poritidae and Acroporidae comprised only a small proportion of the coral spat (27% and 11%, respectively), while most abundant coral spat (61%) were categorized as others. These data indicate that observed long-term shifts in community structure of adult coral assemblages in the Gulf are being reinforced at the level of settlement, such that there is limited scope for recovery of former *Acropora*-dominated coral assemblages in the Gulf.

4.2 Introduction

Scleractinian corals are the primary habitat-forming species on coral reefs (Jones et al. 1994), but are declining in abundance in many coral reef provinces (e.g., Gardner et al. 2003; Bellwood et al. 2004). Sustained losses of scleractinian corals are attributed to multiple disturbances (e.g. over-fishing, coastal pollution and disease) that are being compounded by the more recent impacts of climate-induced coral bleaching from elevated temperatures (Hughes et al. 2003; Bellwood et al. 2004). Aside from significant losses of live coral cover (Gardner et al. 2003; Bellwood et al. 2004), increasing frequency, severity and diversity of disturbances are likely to cause marked shifts in community composition (Pandolfi et al. 2011; Hughes et al. 2012). In light of these recent concerns, there is an urgent need to understand how increasing sea temperatures from on-going climate change will affect early life history stages (Putnam et al. 2008; Albright et al. 2013) and the capacity of coral populations to replenish themselves (Diaz-Pulido et al. 2009).

For corals, most recent studies have focused on the effects of high sea temperature on the adult assemblage, with the goal of trying to understand the causes of thermal bleaching (Dove and Hoegh-Guldberg 2006) and differences in bleaching susceptibilities (e.g. comparative rates of mortality among adults; Marshall and Baird 2000). However, high sea temperatures caused by climate change are likely to affect biological and physiological processes that span multiple life history stages of corals (Putnam et al. 2008; Albright et al. 2013). Early life history stages of corals (i.e. larval development, survival and settlement) are extremely sensitive to environmental stresses, and especially high temperatures (Byrne 2011), the effects of which can have a greater biological significance than for adults (Gosselin and Qian 1997). Elevated temperatures, which cause bleaching, may also disrupt various early life history processes and greatly influence the number of individuals entering the adult population (McClanahan et al. 2009)

Population replenishment is an important demographic process for the persistence of all marine organisms (Gaines and Roughgarden 1985; Underwood and Keough 2001). The recovery of reefs following a disturbance (e.g. bleaching event) requires the replenishment of coral populations either by regrowth of surviving corals or the arrival and settlement of coral larvae and their post-settlement growth and survival (Hughes 1994; Hughes and Tanner 2000). However, the only means of restoring both coral cover and the genetic diversity of coral populations is through sexual recruitment (Baums et al. 2006). Successful coral recruitment is dependent upon many separate processes, including the fecundity of the local population (e.g. Hughes et al. 2000), rates of fertilization (e.g. Oliver and Babcock 1992), larval survivorship and dispersal (e.g. Graham et al. 2008), settlement (e.g., Hughes et al. 1999), and early post-settlement growth and survivorship (e.g. Ritson-Willams et al. 2009). Of these processes, coral settlement is widely recognized as one of the major determinant of adult assemblage structure on some reefs, reminiscent of a stock-recruitment relationship (Caley et al. 1996; Vermeij and Sandin 2008; but see Hughes et al. 1999; Edmunds 2000). Elevated temperatures can have dramatic effects on larval supply and settlement (Edmunds et al. 2001; Bassim and Sammarco 2003; Baird et al. 2006), and have profound affects on population dynamics (Harrison and Wallace 1990; Connell et al. 1997). Given that global sea surface temperatures (SSTs) are predicted to increase 2–4°C within the next century (IPCC 2007) it is important to understand how coral settlement will likely be affected under more extreme environmental conditions.

The Persian Gulf provides a novel and important setting for studying coral settlement. Corals in the Gulf persist in a naturally extreme environment (Sheppard et al. 1992), at temperatures predicted to occur on most tropical coral reefs by 2100 (IPCC 2007). Sea surface temperatures (SSTs) can fluctuate >20°C over the course of a single year, with summer daily-mean temperatures of >35°C while winter winds can chill water to <12°C (Sheppard 1992; Sheppard et al. 2010). Further, recent climate models suggest large-scale changes in sea surface salinity (SSS) (Durack et al. 2012), with increasing salinity at all latitudes in the Indian Ocean down to 150 m depth (Boyer et al. 2005). Corals in the Gulf survive in a hyper-saline environment year round with salinities regularly >42 ppt. In addition, corals in the Gulf are also subject to increasing pressure from anthropogenic impacts such as over-fishing, large-scale coastal development (Sheppard et al. 2010; Sale et al. 2011), and recurrent climate induced bleaching events (Riegl et al. 2011). Minimizing or reversing the continuing degradation of these reefs is critical to prevent significant erosion of ecosystem services and goods (Sheppard et al. 2010), but the recovery and resilience of coral populations in the Gulf will be very much dependent upon local levels of reproduction, settlement and recruitment.

Research of coral settlement in the Gulf has been limited to a few small-scale studies conducted mainly in the United Arab Emirates, (Burt et al. 2009, 2010). Burt et al. (2009) examined coral settlement at four sites (3 breakwaters and 1 patch reef) over one year in Dubai to determine whether different construction materials commonly used to build breakwaters influenced settlement. Coral settlement varied by an order of magnitude among sites, ranging from < 0.3 spat tile^{-1} year^{-1} to 4.9 spat tile^{-1} year^{-1}, possibly due to spatial variation in the abundance of adult corals and localized settlement (Burt 2009). However, there have not been any systematic studies of coral settlement to establish the seasonality in settlement, or explicitly testing for spatial variation in rates of settlement relative to local abundance and composition of adult corals. The specific objectives of this study were (1) to examine the spatio-temporal variability of coral settlement at six sites for eight seasons over two years along the coast of Dubai (United Arab Emirates) (2) determine the taxonomic composition of coral spat, and (3) explore the relationship between adult coral assemblages and coral spat among family.

4.3 Materials and Methods

4.3.1 Study area

This study was conducted in the southern basin of the Persian Gulf along the coast of Dubai, United Arab Emirates (Fig. 4.1). Most of the sea floor in this area is shallow (<10 m), and dominated by sand and silt substrates making it unsuitable for coral settlement (Sheppard et al. 1992; Riegl 1999). Suitable settlement substrate is restricted to small (<1,000 m^2) isolated areas of exposed limestone ‘caprock’, which occur mainly to the southwest of Dubai (Sheppard et al. 1992; Riegl 1999). In addition, breakwaters associated with coastal development in Dubai provide a substantial amount of hard substrate on which coral and other benthic fauna recruit (Riegl 1999; Burt et al. 2009). These breakwaters add over 65 km^2 of rocky sub-tidal habitat in an area where < 10 km^2 of natural hard-bottom habitat occurs (Burt et al. 2008). To test for spatio-temporal variation in coral settlement, 6 sites (5 breakwaters and 1 natural reef site) were selected across ~ 45 km of coastline in Dubai (Fig. 4.1).

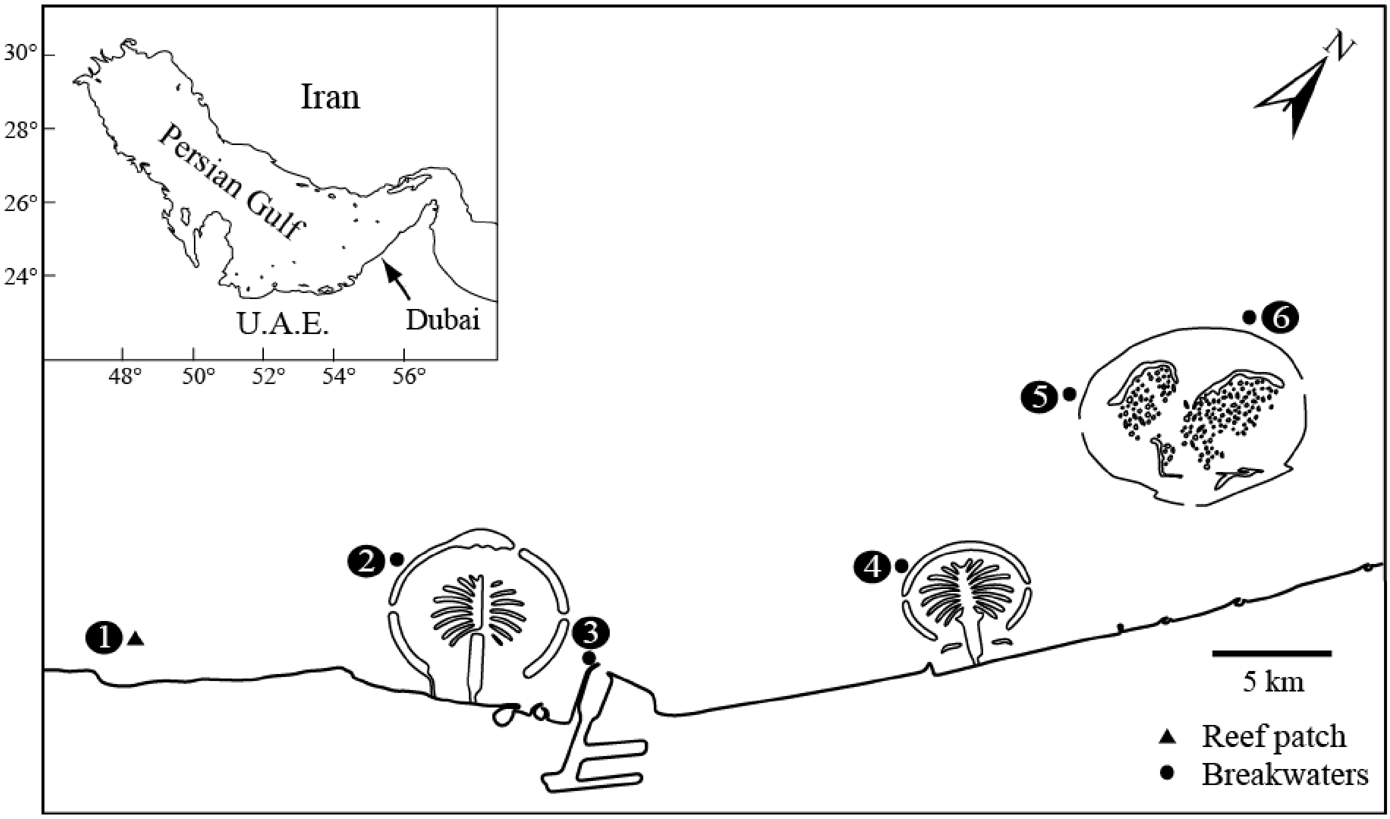

Fig. 4.1: Map of Dubai (United Arab Emirates) in the southern Persian Gulf showing the six coral settlement sites. Sites are organized from west to east: 1 = Jebel Ali Reserve, 2 = Palm Jebel Ali, 3 = Jebel Ali Port, 4 = Palm Jumeirah, 5 = The World West, and 6 = The World East.

All sites had comparable water depths that did not exceed 8 m and similar exposure to environmental conditions (e.g. wind and waves). Throughout the Dubai coastline winds and waves are predominantly from the northwest (Cavalcante et al. 2010), and settlement tiles were placed on exposed portions of the breakwaters and unsheltered coral patches. In Dubai, tides are mainly semi-diurnal and all sites experience similar tidal amplitude, ranging from 0.8 m neap to 1.95 m spring (Cavalcante et al. 2010). The prevailing coastal currents move from west to east, are relatively slow (0.25 – 0.40 m s^{-1}) and consistent throughout much of Dubai (Cavalcante et al. 2010).

4.3.2 Settlement patterns

To measure settlement, 25 unglazed settlement tiles were attached to the substrate at each site. Five tiles were attached to each of five 2 m long PVC poles (2.5 cm diameter). Tiles were spaced approximately 50 cm apart, and held in place with stainless steel bolts and wing nuts. A plastic washer was used to maintain each tile 5 mm above the substrate, following Mundy (2000). At each site, poles were bolted directly to the substrate with the aid of a pneumatic drill at ~ 5 m depth, and separated by a distance of 1–1.5 m.

Settlement tiles were deployed in the field starting in March 2009 before the coral spawning season, which in the southern Gulf occurs predominately between April and May (Bauman et al. 2011). Tiles were replaced every 3 months, thus defining 4 periods (hereafter referred to as seasons): March–May (spring), June–August (summer), September–November (autumn), and December–February (winter). This sampling procedure was repeated over a 2-year study period (March 2009–March 2011). Freshly collected tiles were soaked in diluted bleach for ~ 24–48 h to remove organic materials, and then rinsed and sundried before inspecting for coral spat. All coral spat were counted and identified on each tile using a dissecting microscope (40×

magnification). The majority of coral spat recorded were often single corallites <3 mm diameter. At this early stage of development, the morphology of the corallum is not sufficiently developed to allow high taxonomic resolution, and only three families (Acroporidae, Pocilloporidae, Poritidae) can be reliably distinguished (Babcock et al. 2003). All other coral spat were categorized as ‘others’. Coral spat that were too damaged to identify because of overgrowth by other organisms (e.g. barnacles, bryozoans, sponge) or during retrieval were listed as ‘unknown’.

4.3.3 Local coral assemblages

Prior to the deployment of settlement tiles, coral assemblages were surveyed at each site using photo-quadrats. At each site, six replicate 30 m long line transects were photographed at 3 m intervals using 0.25-m^2 quadrat for a total of 66 quadrats per site (or 16.5 m^2 of sampled area). Sampling was standardized to approximately 5 m depth, the same depth as settlement tiles. Images were analyzed using CPCe version 5 (Kohler and Gill 2006) using 50 randomly distributed points. Scleractinian (hard) corals underlying each point were identified to species. Data from images were then pooled for each transect at each site to provide a mean estimates of percent coral cover.

4.3.4 Seawater temperature

Seawater temperature was recorded at each site using Hobo Tidbit v2 water temperature loggers (± 0.2°C resolution). At each site, one logger was attached directly to the substrate at approximately the same depth as the settlement tiles. Loggers were set to record hourly, and were retrieved, downloaded, and changed each time settlement tiles were replaced (i.e., every 3 months). All six loggers were crosscalibrated prior to each deployment. Initial screening of the temperature data revealed that daily seawater temperatures (mean, high, and low) did not vary among sites, therefore temperature records were pooled across all sites and the overall daily mean temperature and range calculated.

4.3.5 Data analysis

Mean densities of coral spat on each 160-cm^2 tile were estimated seasonally for each site both years. To test for overall spatio-temporal variation in coral settlement, the density of spat was compared among sites, sampling seasons (spring, summer, autumn and winter), and years (2009/10 and 2010/11) using a 3-way fully factorial ANOVA. The densities of spat were log (x + 1) transformed prior to analysis to improve normality. Tukey's HSD post-hoc tests were used to compare multiple differences in settlement among the sites for each season, and between years. The density of spat for each family were also compared among sites for each season and year using 3-way ANOVAs when the data met parametric assumptions (i.e., others and Poritidae), or with Kruskal-Wallis non-parametric test when data were non-normally distributed (i.e., Acroporidae). Kendall's coefficient of concordance analysis (Poritidae and other spat) and Spearman's coefficient (Acroporidae) were used to determine whether relative ranks of sites according to mean settlement were consistent among seasons (Zar 2010). The relative abundance of coral cover was then compared among sites, and differences in percent live coral cover and abundance of dominant coral genera, were tested with one-way ANOVAs. Tukey's post-hoc tests were used to identify significantly different groups. Percent coral cover data were arcsine square-root transformed prior to analyses. The assumptions of normality and homogeneity of variance were tested through graphical analyses of residuals.

Spearman's rank-order correlation was used to analyze the relationship between mean percent coral cover and mean settlement for each family and spat categorized as other.

4.4 Results

4.4.1 Temporal and spatial coral settlement patterns

A total of 1,027 coral spat were observed over two years. The majority of spat (98.8%) were found on the bottom of the tiles, 1.2% on the sides, and no spat on the top. The mean number of spat per tile ranged from 0 (Mar.–May and Dec.–Feb. for all sites each year) to 8.61 (June-Aug. 2010 at site 4), and the maximum number of spat observed on one tile was 21. The most prominent patterns in total coral settlement were the strong seasonality with peak settlement in the summer followed by a smaller settlement pulse in the autumn while no coral spat were observed in the winter or spring in either year (Fig. 4.2). Also striking was the temporal consistency in the rank order among sites in total coral settlement; this despite the dramatic differences in the abundance of spat among seasons and less so between years. A three-way ANOVA showed that the total abundance of coral spat differed significantly among, sites, seasons and years but the spatial patterns were temporally confounded (ANOVA, Table 4.1). Coral settlement was highest in summer, at all except site 3 (Tukey's HSD test, $p < 0.001$ each), and in both years (Tukey's HSD test, $p > 0.05$, Fig. 4.2). In addition to differences among seasons, there were also differences in settlement among sites, and these varied seasonally (Fig. 4.2). Site 4 had the highest settlement of all sites during every season in which spat were observed, but this was significant only in the summer (Tukey's HSD test, $p < 0.05$). The total abundance of coral spat at site 4 (pooled between years) during the summer was 3-4 fold higher than spat on sites 1, 2, 5 and 6, and 17-fold higher than site 3. In contrast, site 3 consistently had the lowest settlement of all sites, and this was significant compared with the other sites during the peak settlement periods the summer 2009 and 2010 (Tukey's HSD test, $p < 0.05$). All other sites had comparable levels of settlement every season (Tukey's HSD test, $p > 0.05$, Fig. 4.2).

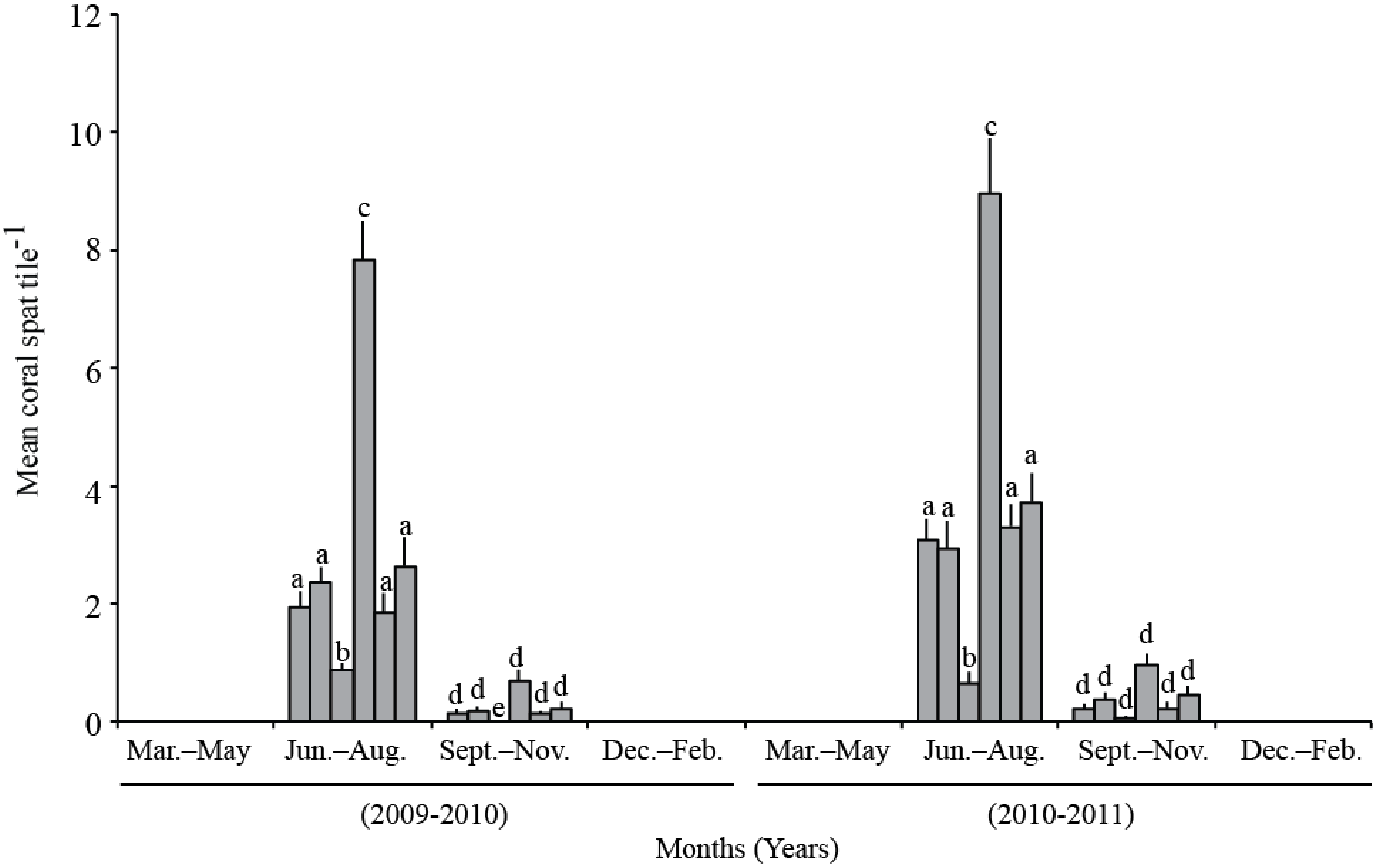

Fig. 4.2: Overall spatial and temporal variation in coral settlement at six sites in Dubai (arranged from west to east, see Fig. 4.1). Data are means ± SE, and different letters indicate significant differences (Tukey's test, $p < 0.05$).

The most common coral spat belonged to the taxa categorized as 'others' (61%) followed by the family Poritidae (27%) and Acroporidae (11%). No Pocilloporidae were observed, and damaged coral spat classified as 'unknown' accounted for < 1%. Coral spat categorized as 'others' were the most abundant spat in both seasons (summer and autumn) and years (i.e., pooled among sites; Fig. 4.3). Other spat were more abundant between June–Aug. than between Sept.–Nov., on all sites both years

Table 4.1: Summary of 3-way ANOVA results for comparisons of total spat densities among seasons (spring, summer, autumn, winter) sites (1–6) and years (2009/10 and 2010/11). Data were transformed log (x + 1) prior to analysis.

Source of variation	df	MS	F	*p*
Season	3	15.867	663.70	0.0001
Site	5	3.265	52.52	0.0001
Year	1	1.324	13.19	0.0023
Season × Site	15	0.935	30.70	0.0001
Season × Year	5	0.534	5.32	0.0012
Year × Site	3	0.007	0.27	0.9273
Site × Season × Year	15	0.006	0.25	0.9984
Error	1102	0.023		

(Fig. 4.4a). The abundance of other spat varied significantly among sites and seasons between years (ANOVA, Table 4.2). Mean settlement of ‘others’ was highest on site 4 (Tukey’s HSD test, $p < 0.001$), and second highest at site 6, all seasons (Fig. 4.4a). Site 4 had 2.4 to 3.6 times the mean settlement of site 6, and 3.3 to 3.9 times the mean settlement of the next highest site. Site ranks were concordant among all settlement seasons ($W_c = 0.97$, $(\chi_r^2)_c = 27.2$, $p = 0.0003$), however, a significant interaction between Season × Site indicates variation in the magnitude of differences among sites depending on time of year (Table 4.2). Settlement of Poritidae corals also varied significantly among sites and seasons between years (Table 4.2) Overall mean Poritidae settlement was highest on site 4 (Tukey’s HSD test, $p < 0.03$), and second highest at site 6 all seasons (Fig. 4.4b). Site 4 had 1.6 to 2.2 times the mean settlement of site 6, and 1.85 to 2.5 times the mean settlement of sites 1–3 and 5. Site ranks were

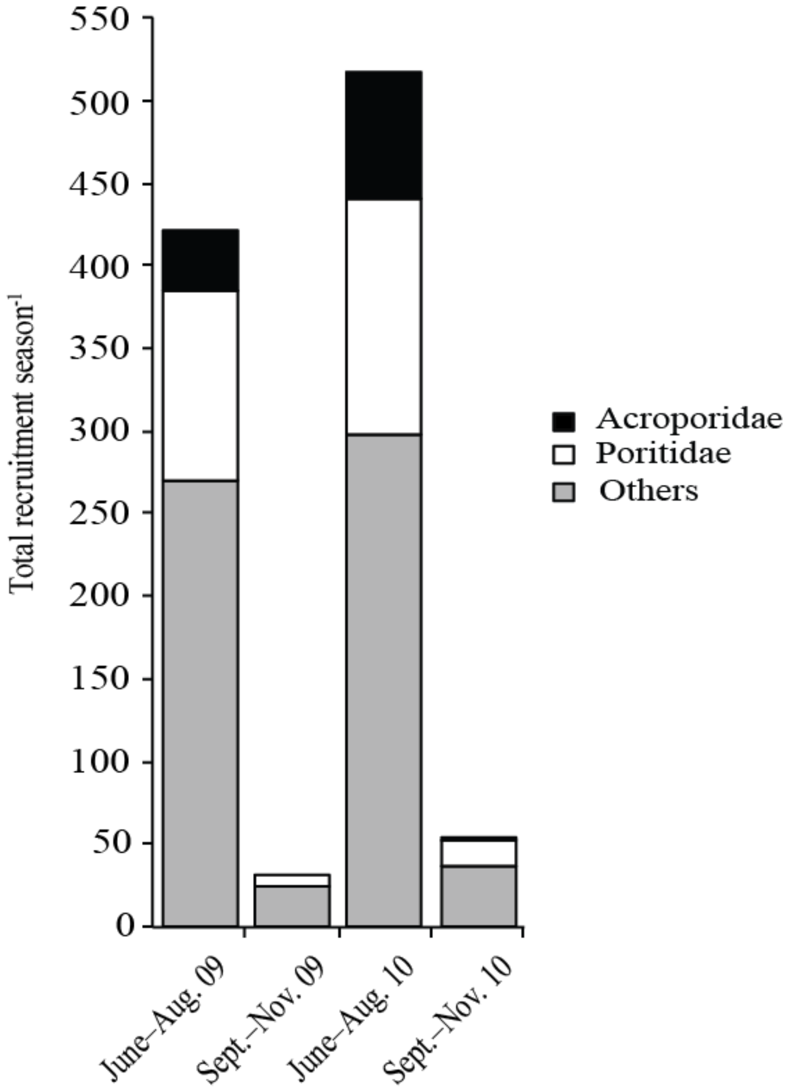

Fig 4.3: Total number of spat season^{-1} (summer and autumn only) and taxonomic composition of coral spat (pooled across sites) for 2009 and 2010.

concordant among all seasons ($W_c = 0.89$, $(\chi_r^2)_c = 27.2$, $p < 0.01$) however, a significant interaction between Season × Site indicates variation in the magnitude of differences among sites depending on time of year (Table 4.2). The family Acroporidae, the least abundant spat, differed significantly among sites from June–Aug. both years (Kruskal-Wallis $H \geq 21.67$, n = 22–25 tiles site^{-1} season^{-1} $p < 0.03$), but not between Sept.–Nov. ($p > 0.245$) when only a single coral spat was recorded (Fig. 4c). Acroporidae settlement was consistently higher at sites 1 and 2 than all other sites both years (ρ = 0.943, $p < 0.001$, Fig. 4.4c). Site 1 and 2 had between 2.7 to 5.6 times the mean settlement of sites 3, 4 and 6 and almost 13 times the mean settlement of site 5.

Table 4.2: ANOVA results comparing (a) 'others' and (b) Poritidae spat densities among seasons, sites and years. Data were transformed log (x + 1) prior to analysis.

Source of variation	df	MS	*F*	p
(a) Others				
Season	3	7.311	327.962	< 0.0001
Site	5	1.122	57.263	< 0.0001
Year	1	0.890	4.558	0.0329
Season × Site	15	0.712	36.323	< 0.0001
Season × Year	5	0.032	0.5755	0.7188
Year × Site	3	0.011	1.6825	0.1690
Site × Season × Year	15	0.011	0.5499	0.9126
Error	1102	0.019		
(b) Poritidae				
Season	3	2.606	170.99	< 0.0001
Site	5	1.168	11.06	< 0.0001
Year	1	0.721	4.73	0.029
Season × Site	15	0.117	7.71	< 0.0001
Season × Year	5	0.035	2.36	0.070
Year × Site	3	0.006	0.414	0.839
Site × Season × Year	15	0.004	0.256	0.998
Error	1102	0.015		

4.4.2 Local coral assemblage structure

Coral cover differed significantly among the sites (ANOVA $F_{(5,30)} = 191.45$, $p <$

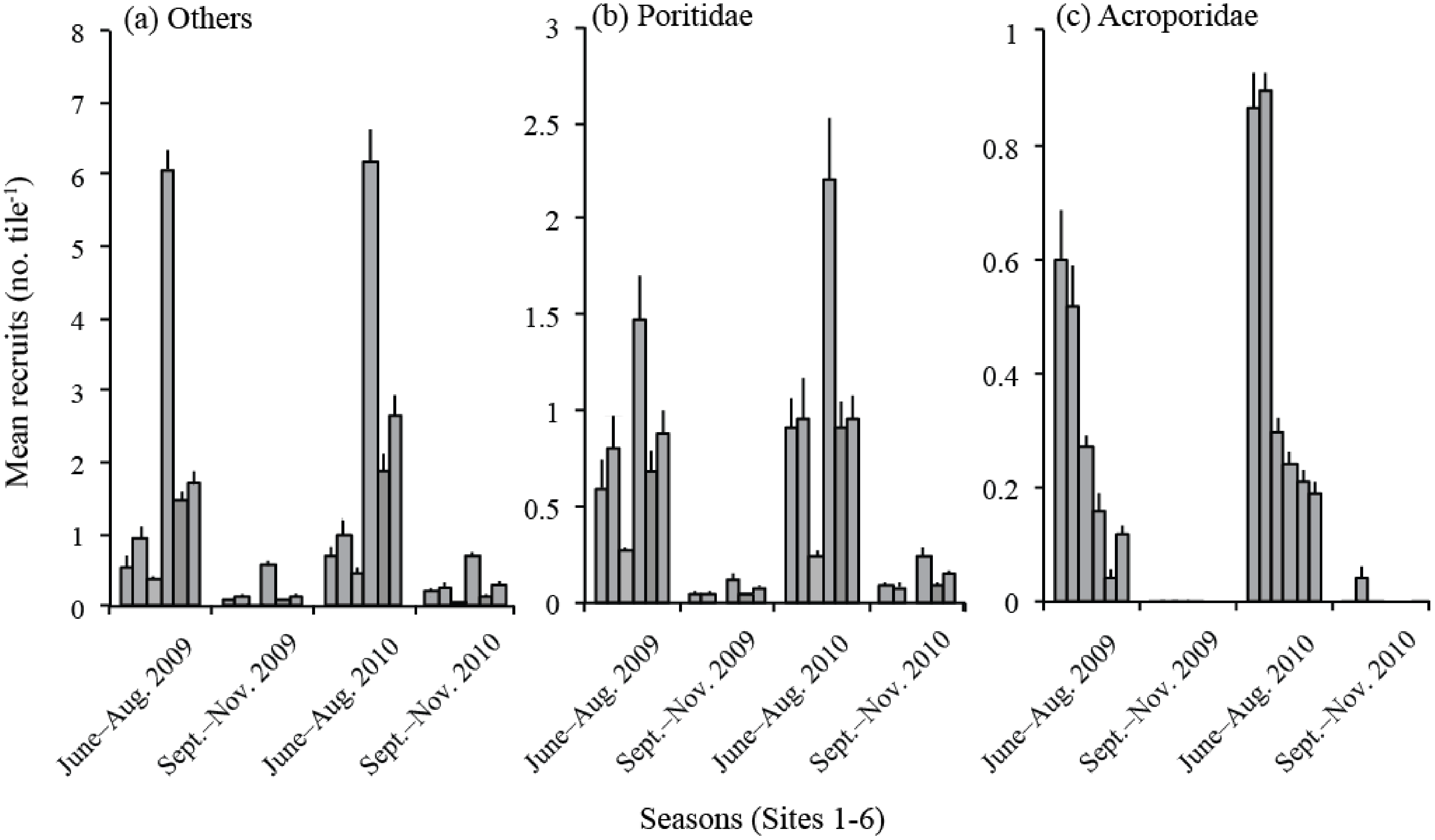

Fig. 4.4: Mean settlement ± SE (20–25 tiles site^{-1}) of 3 common spat (a) Others, (b) Poritidae, (c) Acroporidae for the 6 sites from June–Aug. and Sept.–Nov. in 2009 and 2010.

0.001), with significantly higher coral cover at sites 1 and 3 than all other sites (Fig. 4.5). The most common genera were *Porites* (35.7 ± 3.1%), *Cyphastrea* (25.3 ± 4.6%), *Platygyra* (18.1 ± 2.8%), *Acropora* (8.9 ± 1.0%), and *Favia* (9.8 ± 0.7%). Collectively, these five genera accounted for >96% of the total coral cover across all sites, while other genera accounted for <3% of total coral cover. Percent cover of the common coral genera differed significantly among all sites: *Porites* ($F_{(5,30)} = 53.70$, $p < 0.001$), *Cyphastrea* ($F_{(5,30)} = 167.77$, $p < 0.001$), *Platygyra* ($F_{(5,30)} = 112.59$, $p < 0.001$), *Acropora* ($F_{(5,30)} = 9.52$, $p < 0.001$), and *Favia* ($F_{(5,30)} = 23.65$, $p < 0.001$) (Fig.

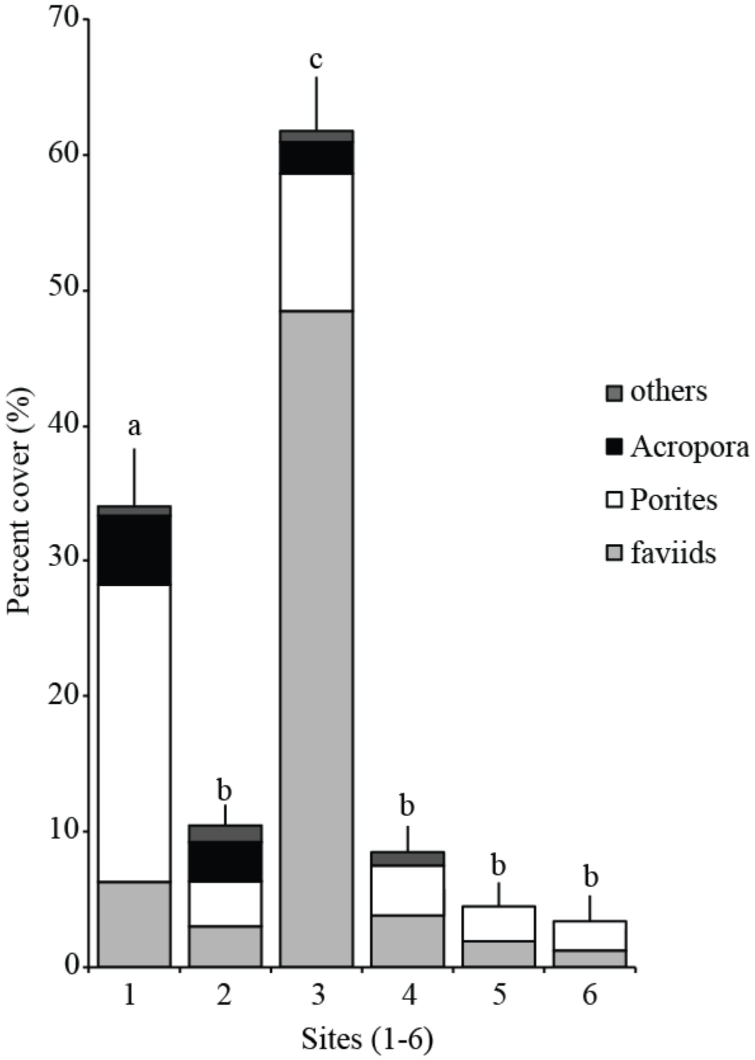

Fig. 4.5: Percent coral cover at each site broken down by the dominant genera. Data are means ± SE, and different letter indicate significant differences (Tukey's test, $p < 0.05$).

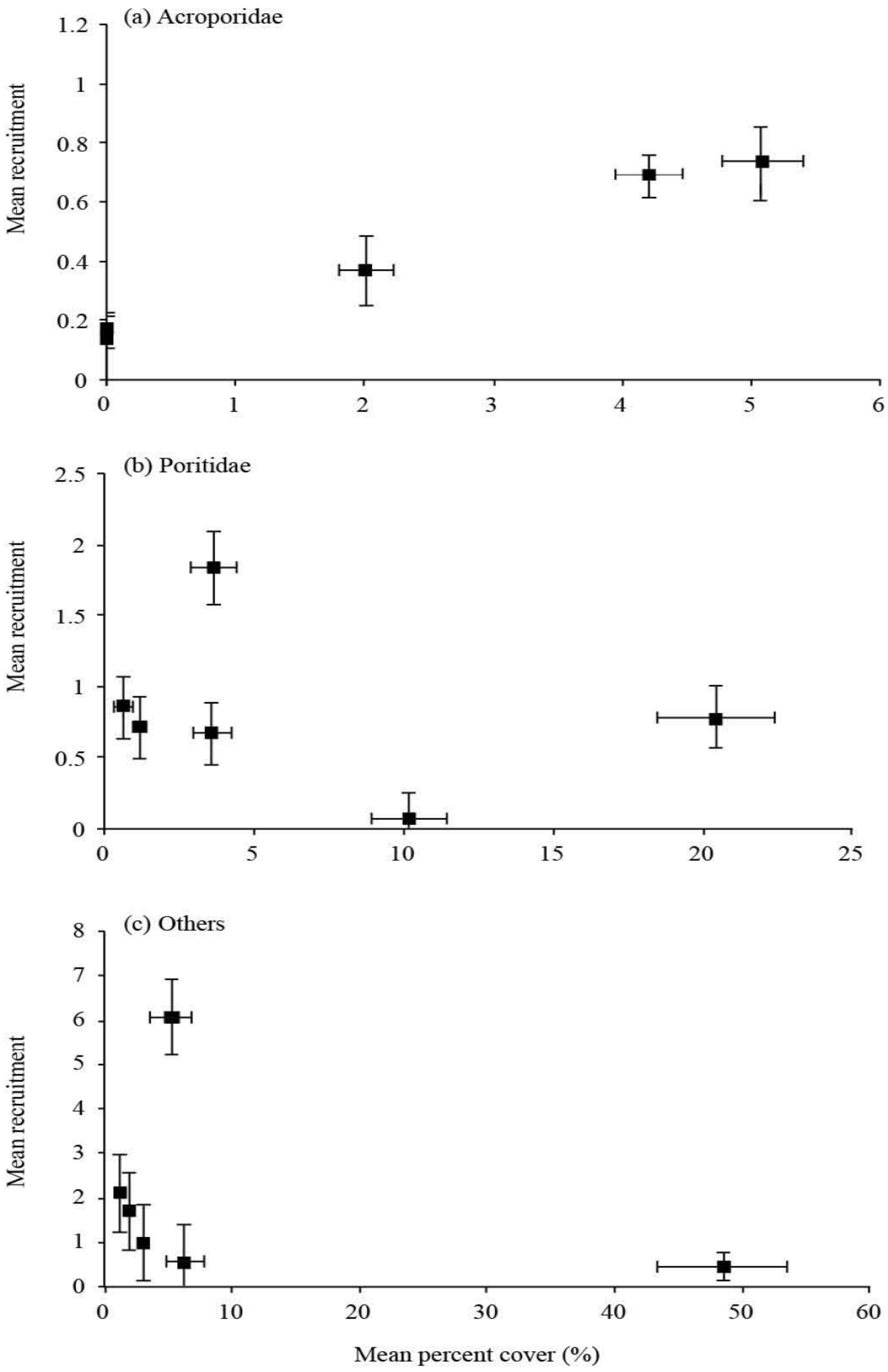

Fig. 4.6: Relationship between mean adult cover and mean settlement for (a) Acroporidae, (b) Poritidae, and (c) others.

4.5). Percent cover of *Porites* was highest on sites 1 (21.9 ± 2.3%) and 3 (10.2 ± 1.6%) than the other sites (2, 4–6) which all had < 4% cover. Faviids (including *Cyphastrea*, *Platygyra* and *Favia* spp.) were most abundant on site 3 (48.5 ± 4.6%) (Fig. 4.5), while *Acropora* cover was only recorded at sites 1–3 (Fig. 4.5).

Mean density of coral spat and mean percent coral cover at the family level were positively correlated in the family Acroporidae (Spearman's R = 0.625, *p* = 0.033, Fig. 4.6a). However, significant correlations were not observed at the family level for either Poritidae (Spearman's R = 0.431, *p* = 0.112) or spat identified as others (Spearman's R = 0.200, *p* = 0.606) (Fig. 4.6 b,c).

4.4.3 Seawater temperatures

Mean annual water temperatures pooled among sites in the southern Gulf showed negligible differences between years, 28.34°C (± 0.13 SE) between March 2009/10 and 28.51°C (± 0.18 SE) between March 2010/11, respectively. Mean annual temperature ranges varied considerably both years, ranging from 18.5–34.9°C between March 2009–10 and 18.3–35.2°C between March 2010–11. The mean warmest and mean coldest month in both years were identical with highest temperatures recorded in August (34.9°C in 2009 and 35.2°C in 2010) and the lowest temperatures recorded in February (18.5°C in 2010 and 18.3°C in 2011). Summer mean temperatures (i.e., June–August) when the majority of coral spat were observed was 34.11°C (± 0.11°C) in 2009, and 34.23°C (±0.14°C) in 2010 (Fig. 4.7). Moreover, temperature loggers recorded temperatures ≥35°C a total of 17 days in 2009, and 23 days in 2010 between July and August.

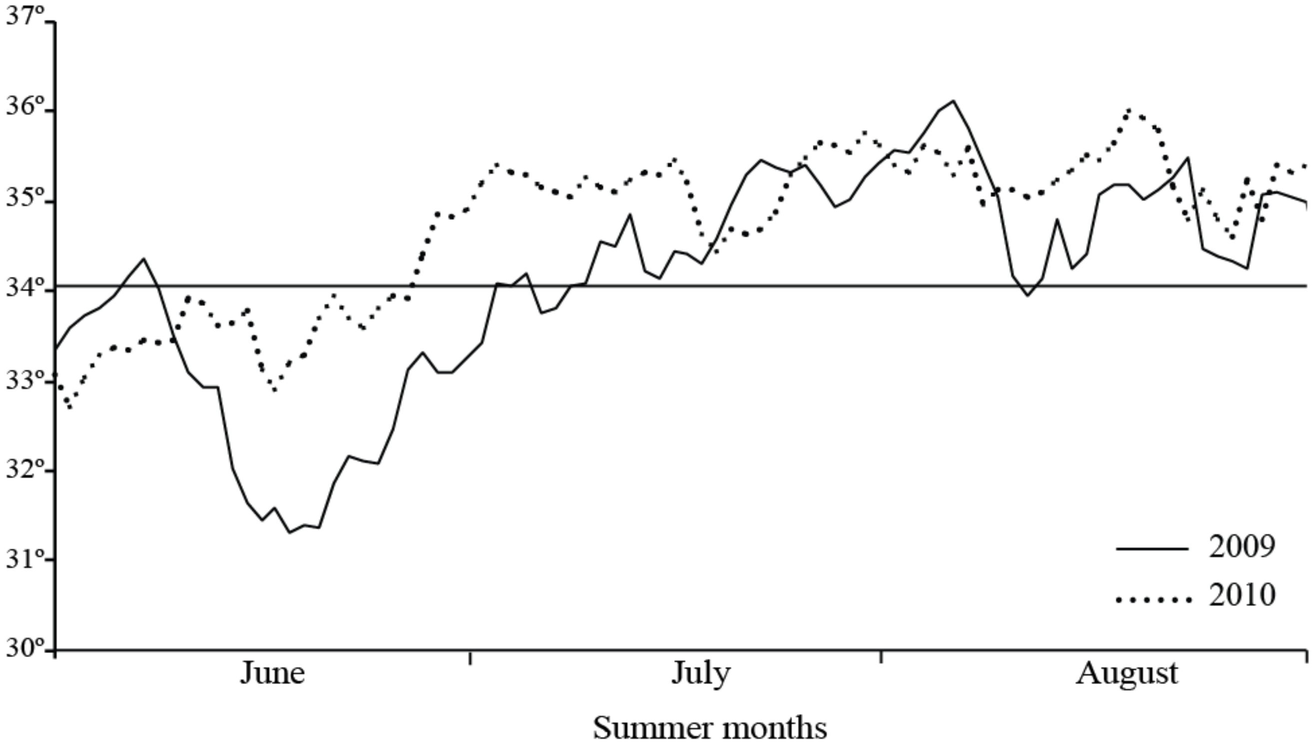

Fig. 4.7: Mean daily seawater temperatures in Dubai (~5m depth) during the summer months (June–August) for 2009 and 2010. Black bar indicates mean summer temperature.

4.5 Discussion

This study showed peak settlement in the southern Persian Gulf occurred during summer (June–August) when daily-mean temperatures were approximately 34°C, which is well above the critical thermal limit for coral larvae reported from experimental studies conducted in the Caribbean (Edmunds et al. 2001; Bassim and Sammaro 2003), Japan (Baird et al. 2006) and Taiwan (Putnam et al. 2008). Elevated seawater temperatures can affect coral larvae during early stages of development (Edmunds et al. 2001; Baird et al. 2006) reducing rates of settlement (Putnam et al. 2008) larval survivorship (Bassim and Sammarco 2003; Randall and Szmant 2009) and the time to reach competence (Heyward and Negri 2010). In particular, Baird et al. (2006) and Randall and Szmant (2009) showed that few coral larva can survive at seawater temperatures >32°C, in Japan and Caribbean, respectively. The fact that coral settlement is occurring at 34°C in Gulf is strong evidence for local adaptation.

Coral settlement in Dubai showed a high degree of spatio-temporal variation consistent with patterns reported from other marginal reef environments in the Indo-Pacific (Harriott and Banks 1995; Glassom et al. 2004; Nakamura and Sakai 2010). Overall, rates of coral settlement in Dubai were low (≈ 113 spat m^{-2} $year^{-1}$), but well within the range of values reported from other high-latitude marginal reefs, including: the Solitary Islands (132 spat m^{-2} yr^{-1}; Harriott and Banks 1995) and Taiwan (≈ 111 spat m^{-2} yr^{-1}; Soong et al. 2003). Coral settlement was highly seasonal with peak settlement in the summer followed by a much smaller settlement pulse in the autumn, while no settlement occurred during spring or winter.

Highly seasonal patterns of coral settlement are expected because the reproductive output of many coral species is highly seasonal (Baird et al. 2009). Coral species in the southern Gulf, (e.g. Acroporidae and Faviidae), also exhibit highly seasonal reproductive patterns (Bauman et al. 2011), however, no coral spat were observed during the peak reproductive period from April–May. Given that comparable coral spawning times have been reported from other locations in the region, including Kuwait (Harrison 1995) and Saudi Arabia (Fadlallah 1996), this was unexpected. Moreover, spawning slicks have been observed previously in April and May along the coast of Abu Dhabi southwest of Dubai (J. Burt pers. comm.). Nonetheless, higher rates of coral settlement outside major spawning events do occur (Babcock 1988; Soong et al. 2003). Babcock (1988), for example, found higher settlement of acroporid species between mid-January and March than in the months following the major spawning period on the central Great Barrier Reef (GBR), and suggested that the unusual patterns were caused by strong winds prevailing at the time of spawning that transported larvae off the reef. Likewise, coral larvae in Dubai may have been carried away from reefs due to strong offshore sea breezes generated during the springtime warming of the Arabian Desert (Sheppard et al. 1992; Riegl and Purkis 2012) or from sudden strong wind events known as Shamals. Historical wind records indicate a Shamal wind event (25–30 knots) occurred during the April 2009 spawning event in the Dubai Municipality (www.dubaicoast.ae). Short duration Shamal events (24–36 h) are considered important wave-generating winds that modify current-strength and flow patterns (Riegl and Purkis 2012).

Given that coral larvae can survive in the water column for periods exceeding 100 days (e.g., Graham et al. 2008), and still complete metamorphosis thereafter (e.g., Connolly and Baird 2010), coral spat observed June–August might have originated from corals that spawned in either April or May. Recent research has shown that coral larvae can extend their longevity in the plankton by rapidly reducing their metabolic rates shortly after competency (Graham et al. 2013a). Furthermore, delayed settlement of coral larvae has been shown to have no deleterious effects on post-settlement survival or growth (Graham et al. 2013b). Delayed larval settlement (i.e., the potential to remain in the water column for extended periods of time) is likely to have positive demographic consequences for broadcast-spawning reef-building corals because it increases larval dispersal potential, notably enhanced population connectivity (Graham et al. 2013b). Accordingly, it is also possible that the influx of coral spat June–August originated from coral populations on other reefs, such as the many offshore islands in the Gulf, where corals may spawn at slightly different times compared to those on coastal reefs. Well-developed coral populations on these islands appear well-connected to populations along the UAE coast, based on their position directly within the major current system of the Gulf (Riegl & Purkis 2012). Riegl et al. (2011) suggested that larvae from these populations are likely responsible for the strong regeneration of coral populations in Dubai and Abu Dhabi (Burt et al. 2008, Riegl & Purkis 2009) following recurrent severe bleaching and mortality events in 1996 and 1998. Nonetheless, we found marked differences in settlement rates among individual sites, corresponding in part with local abundance of adult corals. This would indicate that stock-recruitment relationships (*sensu* Caley et al. 1996) exist at very fine scales (> 1 km), especially for Acroporidae.

An alternative explanation for discrepancies between peak timing of settlement, relative to peak spawning (Bauman et al. 2011), may relate to differences in the corals considered in each of these studies. At least some corals in the Gulf may release gametes outside of predicted spawning periods (Baird and Guest 2009, Baird et al. 2009). For example, many *Acropora* species on the GBR spawn up two months later than previously documented (Baird and Guest 2009; Baird et al. 2009). Clearly, an extended reproductive season is likely to lead to an extended period of coral settlement, at least in some years. Similarly, reports from Dubai (Bauman et al. 2011) and Kuwait (Harrison et al. 1997) found that some species in the Gulf may have extended spawning seasons during late spring and early summer. Bauman et al. (2011) found mature colonies of *Cyphastrea microphthalma* prior to the full moon in June, while colonies of *Platygyra daedalea* were observed spawning in Kuwait after the full moon in June (Harrison et al. 1997). It is therefore likely that a proportion of the coral spat observed June–August in Dubai were the result of extended reproductive cycles in some species. Clearly, further research on the reproductive biology and larval ecology of coral species in the Gulf is necessary to improve our understanding of the temporal patterns of coral settlement in this area.

Aside from the apparent temporal patterns, results also showed strong, consistent spatial heterogeneity in coral settlement with marked variation in the abundance of coral spat among the six sites. Most interestingly, were the significantly higher numbers of coral spat at site 4 compared to the other sites, and its recurrence among all sampling seasons when spat were observed, suggesting that this is possibly a product of natural systematic processes rather than chance events (Fig. 4.2). Sites that receive consistently higher levels of settlement are known as “recruitment hotspots” (*sensu* Booth et al. 2000), and may be crucial to the persistence of populations (Eagle et al. 2012). Recent studies suggest that both deterministic and stochastic processes may affect settlement variation at these scales (Eagle et al. 2012). For example, Eagle et al. (2012) recently detected ‘hotspots’ in the lagoon and on the reef slopes at One Tree Island on the southern GBR for different coral families (i.e., Pocilliporidae, Poritidae, and Acroporidae). Results indicated that the rank order of settlement among sites at One Tree Island may be highly predictable, even though the magnitude of differences may vary from year to year (Eagle et al. 2012). Although there was congruence among hotspots for different families of coral spat, hotspots were associated with differences in water flow (i.e., hydrodynamics) and the abundance of adult conspecifics. Further work is required to determine the specific mechanisms behind the patterns of settlement observed at site 4, and whether this is an annual reoccurrence

The composition of coral spat in Dubai differed considerably from those reported on most reefs in the Indo-Pacific (Risk and Harriott 1990; Baird and Hughes 1997; Hughes et al. 2000) because there were few Acroporidae coral spat and no Pocilliporidae. Most coral assemblages in the Indo-Pacific are dominated by spat from the families Acroporidae Pocilloporidae, or Poritidae (e.g., Hughes et al. 1999;

Glassom et al. 2004). These differences are readily explainable by the adult assemblage structure in the southern Gulf, with Faviidae and Poritidae accounting for >89% of the total coral cover, while Acroporidae accounted for about 9%. Given the increasing incidence of severe bleaching events in the Gulf (Riegl & Purkis 2012), it is unlikely that *Acropora* species will increase in abundance any time soon. Another major difference between Dubai and Indo-Pacific reefs was the complete absence of spat from the family Pocilloporidae. Although Pocilloporidae is among the most wide-spread and ecologically tolerant coral families in the Indo-Pacific (Veron 2000), it is rare throughout most of the Gulf (Sheppard et al. 1992), and particularly the southern Gulf (Riegl 1999, Burt et al. 2008).

In summary, coral settlement rates in the Gulf are low but highly seasonal despite the extreme environmental conditions (i.e. seawater temperatures) and high frequency disturbance events (i.e. coral bleaching). Importantly, there is clear evidence of ongoing coral settlement. However, the composition of coral spat was highly distinct from other regions in the Indo-Pacific, reflecting the degraded condition of the adult assemblages (Riegl and Purkis 2009; Riegl et al. 2011). Further, the current patterns of settlement reinforce previous claims of long-term shifts in community structure away from formerly dominant *Acropora* species towards more robust coral species (Poritidae and Faviidae) that are more resistant to on-going disturbances (Riegl and Purkis 2009). Although corals in the Gulf have clearly adapted to the extremes experienced, it appears unlikely they can maintain the current assemblage structure in the face of sustained and ongoing disturbances.

Chapter 5: Variation in the size structure of corals is related to environmental extremes in the Persian Gulf[5]

5.1 Abstract

The size structure of coral populations is the culmination of key demographic events, including recruitment, mortality and growth, thereby providing important insights to recent ecological dynamics. Importantly, the size structure of corals reflects both intrinsic (inherent life-history characteristics) and extrinsic (enhanced mortality due to chronic or acute disturbances) forcing on local populations, enabling post-hoc assessment of spatial and taxonomic differences in susceptibility to disturbance. This study examined the size structure of four locally abundant corals (*Acropora downingi*, *Favia pallida*, *Platygyra daedalea*, and massive *Porites* spp.) in two regions of the Persian Gulf: the southern Gulf (Dubai and Abu Dhabi) and eastern Gulf (western Musandam). Significant and consistent differences were apparent in size-distributions between regions. The size structure of all coral species was more skewed and had higher kurtosis in the southern Gulf, compared to the eastern Gulf. Sea surface temperatures, salinity, and the recent frequency of mass bleaching are all higher, in the southern Gulf, suggesting higher mortality rates and/or slower growth in these populations. Differences in size structure between locations were more pronounced than differences between species at each location, suggesting that extreme differences

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in environmental conditions and disturbance events have a greater influence on population dynamics in the Gulf than inherent differences in their life-history characteristics.

5.2 Introduction

Scleractinian corals are fundamental to the biodiversity and function of coral reef ecosystems (Connell 1978; Done et al. 1996). Yet, coral reef ecosystems are among the most threatened aquatic ecosystems (Hoegh-Guldberg and Bruno 2010), and increasingly being degraded through multiple disturbances (e.g., over-fishing, coastal pollution, disease) that are becoming more frequent and severe (Hughes et al. 2003). Moreover, these enduring disturbances are now being increasingly compounded by the more recent impacts of global climate change (Hughes et al. 2003, Bellwood et al. 2004). Over the next century, global sea surface temperatures (SSTs) are predicted to increase by at least 2°C (Parry et al. 2007). Consequently, fluctuations in a range of environmental variables are predicted to affect the growth rate, growth form, reproductive capacity of corals (Brown 1997; Kleypas et al. 1999), which are likely to directly impact the overall abundance, composition and diversity of reef communities (Done 1999; Baker et al. 2008), and may lead to further degradation of these reef systems globally (Hughes et al. 2003). Unless corals are able to adapt to changing environmental conditions, and predicted increases in the frequency and severity of coral bleaching events (Donner et al. 2005), benthic reef assemblages may ultimately become dominated by macroalgae (Hughes et al. 2010) or other non-coral organisms (Norström et al. 2009).

Assessment of demographic consequences of time-varying influences of the environment, including the intensity and frequency of disturbance events requires long-term quantitative studies (Baird et al. 2009) and knowledge of key ecological processes important in structuring coral populations (Roth et al. 2010). However, traditional census techniques for measuring demographic rates (e.g., following the fate of individually tagged corals through time, or using permanent photo quadrats) are not always logistically feasible, particularly in remote geographic regions. In these cases, examining the size structure of coral reef assemblages may provide important insights into how local populations have been affected by local environmental conditions and/or recent disturbances (Bak and Meesters 1999; Meesters et al. 2001; Vermeij and Bak 2002). Examining size structure allows us to compare key demographics, or the interaction between size-specific growth, survival and fecundity, of populations to assess spatial and temporal changes from recent disturbance events (Bak and Meesters 1998, 1999; Meesters et al. 2001). Furthermore, information from size distributions enables inferences to be made about the future consequences of the observed changes, and provide some insight into past environmental events (Bak and Meesters 1998).

Colony size is an important life history trait for scleractinian corals because many life history processes, such as growth, fecundity and mortality, are strongly size-dependent (Connell 1973; Hughes and Jackson 1980; Hall and Hughes 1996). Marked differences in the size-structure of sympatric species reflect inherent differences in life histories among corals species (Hughes and Jackson 1985; Babcock 1991). However, within species differences in size structure are also expected to result from changes in growth, mortality regimes and recruitment (Meesters et al. 2001). Bak and Meesters (1999) suggested that changing global conditions will affect the size structure of coral populations, mainly due to selective effects on recruits and the smaller size classes, which would shift size frequency distributions towards larger size classes with lower variance and more centralized distributions. This is a readily testable hypothesis, by comparing size-frequency distributions of corals along established gradients of increasingly severe environmental conditions.

Coral communities in the Persian Gulf, especially in the southern Gulf, occur in naturally extreme environmental conditions, with annual variation in seawater temperatures > 20ºC, combined with very high salinities (> 42 ppt), and high levels of turbidity and sedimentation (Sheppard et al. 1992; Riegl 1999). Moreover, the Gulf region has suffered more frequent severe mass mortalities from coral bleaching events than any other region in the Western Indian Ocean (Wilson et al. 2002; Riegl et al. 2011). The persistence of reefs in the Gulf, following severe mass mortality events (Riegl 2003; Riegl et al. 2011), at temperatures exceeding those projected to affect other areas within decades (Sheppard 2003; Riegl et al. 2011), indicates that Gulf coral communities have shown the potential to acclimatize to extreme environmental conditions which would result in substantial mortality of coral communities in most other regions (Coles and Brown 2003; Riegl et al. 2011). Given the need to better understand coral reef resilience in the face of changing global conditions (McClanahan et al. 2007) the Gulf may be an ideal location to evaluate the role of extreme environmental conditions and recurrent disturbance events in structuring coral community size structure. In the present study, we examine the size structure of four locally abundant coral species, *Acropora downingi*, *Favia pallida*, *Platygyra daedalea*, and *Porites* spp. complex (*P. lobata*/*lutea*) in two regions of the Persian Gulf, the southern Persian Gulf (Dubai and Abu Dhabi) and eastern Persian Gulf (western Musandam) with contrasting environmental conditions (Riegl et al. 2011).

The purpose of this study was to test for consistent differences between locations in the size-structure of four different coral populations.

5.3 Materials and Methods

5.3.1 Study sites

Coral size structure was recorded for four locally abundant coral species: *Acropora downingi*, *Favia pallida*, *Platygyra daedalea*, and massive *Porites* spp., in October - November 2010, from the southern Persian Gulf (Dubai and Abu Dhabi) and eastern Persian Gulf (western Musandam) (Fig. 5.1). At each location, sampling was conducted in three replicate sites, separated by ~ 20–30 km. All sites were approximately 1.0 – 3.0 km from shore, and characterized by a mixture of discontinuous patch reefs and/or coral carpets (*sensu* Riegl 1999) interspersed between algal assemblages, sand and rubble. The size of patch reefs/coral carpets differed between sites, but generally exceeded 1,500 m^2. The two locations, which are < 250 km apart, differ considerably in their exposure to hydrodynamic forces including wind, tidal forces, circulation and mixing processes (Reynolds, 1993). However, despite such differences, the southern and eastern Gulf are located within the same zoogeographic region (Sheppard et al. 1992) and have relatively similar coral assemblage structures. Furthermore, coral assemblages in both locations, including all the sites in this study, have experienced severe temperature-related bleaching events over the past three decades (Salm 1993; Riegl 1999; Maghsoudlou et al. 2008; Riegl et al. 2011).

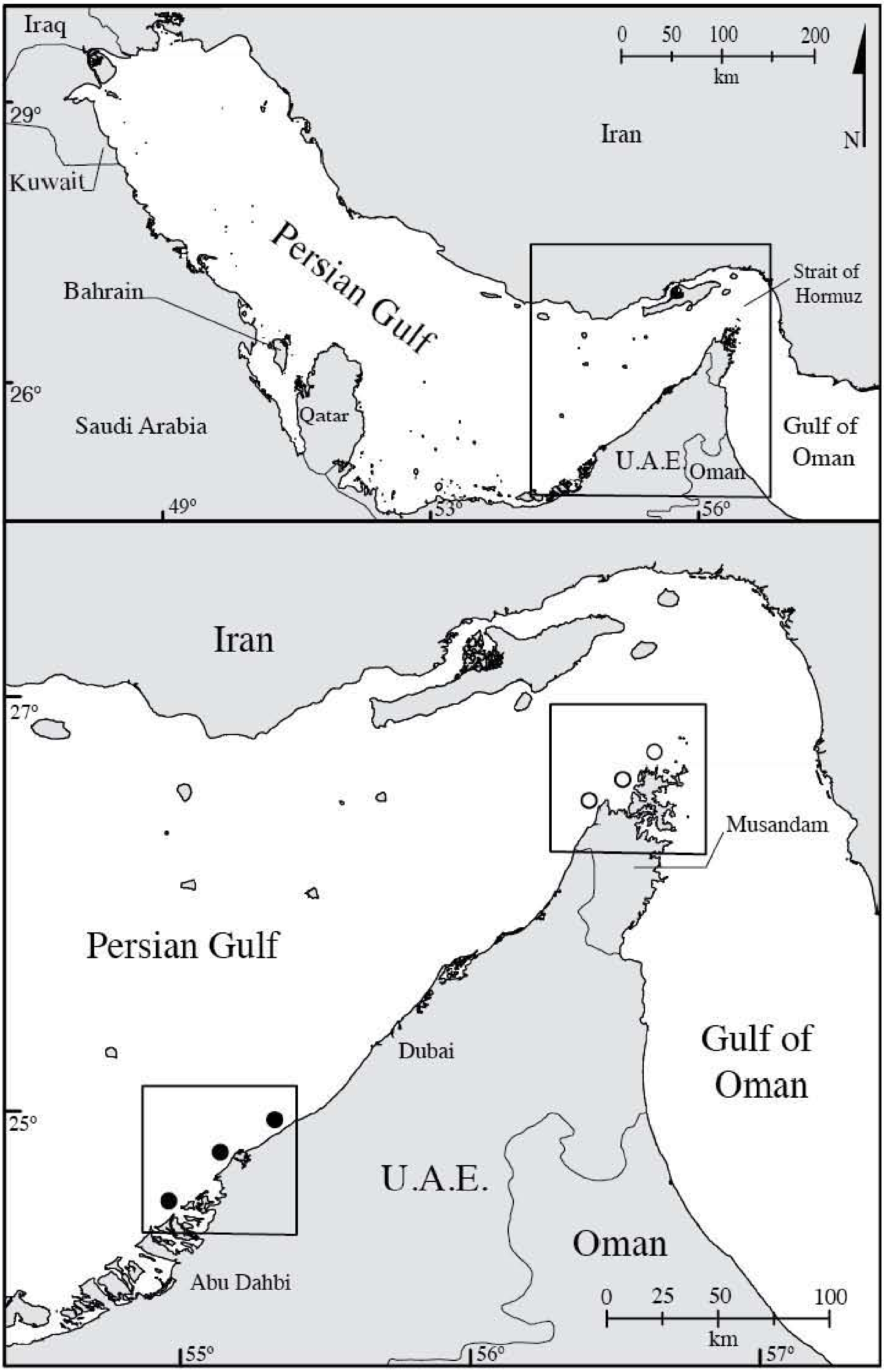

Fig 5.1: Map of study sites in the Persian Gulf, southern Persian Gulf (●) and eastern Persian Gulf (○).

5.3.2 Environmental data

Temperature and salinity are important determinants of reef growth in the Gulf (Sheppard et al. 1992) and are known to vary among locations. Historical SST data were obtained from the Retrospective Pathfinder version 5.0 dataset (Kilpatrick et al. 2001; Casey et al. 2010) for each site and averaged for each location, to examine mean annual temperature variations (i.e., range) and mean warmest and coldest months. The source data were acquired by Advanced Very High Resolution Radiometer (AVHRR) from satellite platforms of the US National Oceanic and Atmospheric Administration at ~ 4 km and daily resolution (Gleeson and Strong, 1995). Data are available for the period 1981–2009; however, there is a documented cold bias in coastal pixels early within the dataset from 1981–1984 (see http://www.nodc.noaa.gov/SatelliteData/pathfinder4km/ status.html). Therefore, we elected to use only the data from 1985 – 2009 (i.e., 25 years). Gapfilled, weekly composites of temperature data have been previously used in the study of coral reef ecosystems (see Heron et al. 2010).

Due to the dearth of spatiotemporally-extensive salinity observations in the Gulf, information on the seasonal variation and annual range in surface salinity between the southern and eastern Gulf was obtained from a numerical ocean model: the 1/12º Global HYbrid Coordinate Ocean Model (HYCOM) maintained by the Naval Research Laboratory, Stennis Space Center (Metzger et al. 2010). Monthly-mean salinity output from two model runs was acquired: a non-assimilative simulation spanning 2004–2009; and an assimilative (satellite surface temperature and height; in situ vertical profiles of temperature and salinity) hindcast spanning June 2009–September 2010. Both data assimilation and a longer dataset were preferable to examine seasonal variations of salinity. Comparisons between the surface salinity outputs from the model runs during the seven months of overlap suggested that the respective outputs were similar in both absolute value ($r^2 = 0.879$, SE y = 0.388 psu) and range ($r^2 = 0.746$, SE y = 0.135 psu) at survey locations. Based on the comparable nature of the output from the two model runs, though from a short period, and the application of the salinity information (to compare spatially the intra-annual variability and annual range between the southern and eastern Gulf), the longer-duration non-assimilative output was used for this study.

5.3.3 Size structure of corals

Size data were collected for all species using a timed swim method. Within each site, observers sampled each species for 75 min on SCUBA at 6–8 m depth. Observers swam in a uniform direction (generally, north to south) parallel to the shore and sampled every colony encountered. Individual colonies were defined as any autonomous, freestanding coral colonies with living tissue (*sensu* Bak and Meesters, 1998). Branching coral species (e.g., *A. downingi*) that shared a base were measured as a single colony. For each colony we measured, the maximum diameter (*L*), the perpendicular diameter (*l*), and the maximum colony height (*h*) of continuous areas of live tissue to the nearest cm with a flexible tape measure. The shape (e.g., hemispherical, spherical segment, disk) of each colony was also recorded. The projected surface area of live tissue for each colony (i.e., colony size) was calculated from maximum linear dimensions (*L*, *l,* and *h*) using appropriate geometric formulae (Meesters et al. 2001). For *F. pallida*, *P. daedalea*, and *Porites*, SA was calculated based on estimates of mean radius for a hemisphere or spherical segment, whereas the SA for *A. downingi* was calculated based on estimates of mean radius for a disk (i.e., circle).

5.3.4 Data analysis

Size-frequency distributions were constructed for each species, after calculating the projected colony surface areas (SA) of each colony. Prior to analyses, colony surface area data for each species were log transformed to normalize distributions and increase resolution among smaller size classes (*sensu* Bak and Meesters 1998; Vermeij and Bak 2002). Size data for each species were pooled among sites within each location to increase sampling densities after one-way ANOVAs with post hoc Tukey's unequal-N HSD tests showed no significant differences in mean colony sizes among sites within each location ($p > 0.05$ for each species, see Appendix C). Size classes consisted of aggregated bins (21 class sizes), based on log transformed colony size range for each species (Sokal and Rohlf 1995). Distributions were tested for normality by Kolmogorov-Smirnov (KS) one sample test and Lilliefors probabilities for significance. Size-frequency distributions were then compared to each other using the Kolmogorov-Smirnov (KS) two-sample comparison test, which is sensitive to differences in most distribution parameters.

Distribution parameters including mean colony size ($\bar{\chi}$), skewness (g_1), kurtosis (g_2), maximum colony size and the 95th-percentile were also calculated for each species. Differences in mean colony size within species between locations were compared using standard Student's t-test. Since size data among species were significantly non-normal (Shapiro-Wilk's $W = 0.49$, $P < 0.001$), non-parametric Kruskal-Wallis ANOVA was used to test differences in their coral colony sizes. Where significant differences were shown, pair-wise Mann-Whitney U-tests were performed to identify size differences between species. All statistical analyses were performed using Statistca 10.0 following Sokal and Rohlf (1995).

5.4 Results

5.4.1 Environmental data

Sea surface temperatures (SSTs) and salinities (psu) differed greatly between the southern and eastern Gulf (Fig. 5.2). Mean annual SSTs showed negligible differences between locations, however, mean annual temperature ranges varied considerably between southern and eastern Gulf (Fig. 5.2a). The mean annual SST range for the southern Gulf was 13.5ºC, considerably more variable than the mean annual SST range of 9.3ºC for the eastern Gulf. The mean warmest and mean coldest month in both locations were identical (i.e., August = warmest month, February = coldest month), however the mean SSTs within these months were both warmer and colder by > 2ºC in the southern Gulf. Furthermore, the relative rate of change in seawater temperature calculated per decade (ºC/decade) at both locations showed a positive trend of increasing seawater temperatures of 0.32ºC in the southern Gulf and 0.19ºC in the eastern Gulf, respectively (Fig. 5.3).

Mean annual salinities also differed substantially between locations (Fig. 5.2b), and the mean annual salinity range for the southern Gulf was approximately 4.12 psu while the mean annual salinity range for the eastern Gulf was 0.92 psu. The mean highest and mean lowest salinity months were also remarkably different between the southern and eastern Gulf (Fig. 5.2b). The mean highest salinity in the southern Gulf was February, while the mean highest salinity in the eastern Gulf was July. In contrast, the mean lowest salinity in the southern Gulf was May, while the mean lowest salinity in the eastern Gulf was April. Importantly, these results are consistent with previous reports of salinity from the Gulf (see Reynolds, 1993).

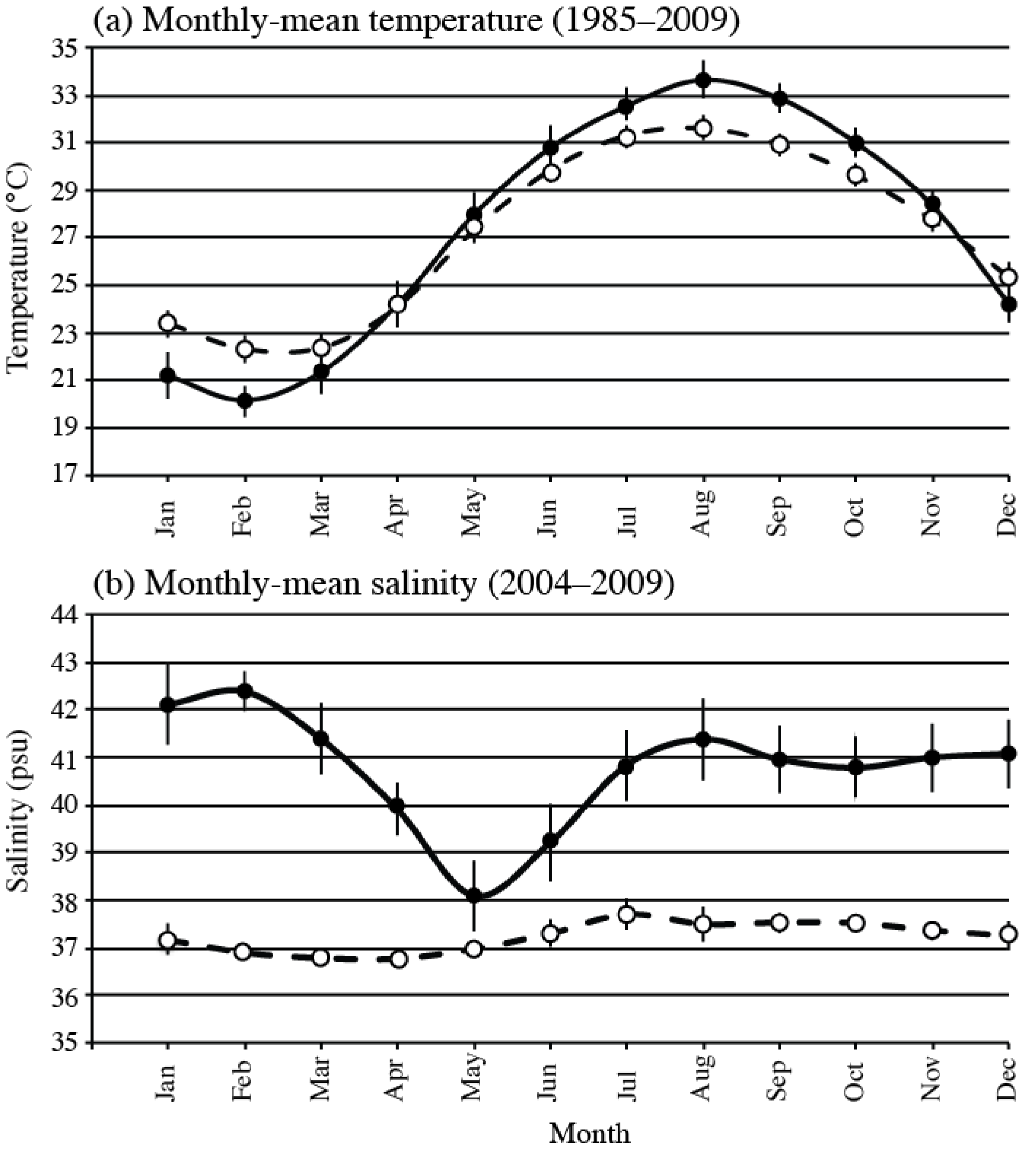

Fig. 5.2: Monthly-mean temperature output from Retrospective Pathfinder version 5.0 dataset spanning 1985–2009 (25 years), and monthly-mean salinity output from a non-assimilative simulation model spanning 2004–2009 (6 years) for southern (●) and eastern (○) Gulf, including standard error (±SE).

5.4.2 Size structure of corals

A total of 1,959 coral colonies were sampled during this study, including 407–536 of each coral taxa. Significant differences in size-frequency distribution (KS comparison $p < 0.05$ for each) and mean colony size (Kruskal-Wallis ANOVA $H_{(3,1959)} = 374.93$, $p < 0.001$) were recorded among species (Table 5.1). *Porites* spp. were larger (Mann-Whitney *U*-test, $p < 0.001$ each) and *F. pallida* were significantly smaller than all other species (Mann-Whitney *U*-test, $p < 0.001$ each). There was no significant difference in mean colony size between *A. downingi* and *P. daedalea* colonies (Mann-Whitney *U*-test, $p = 0.68$).

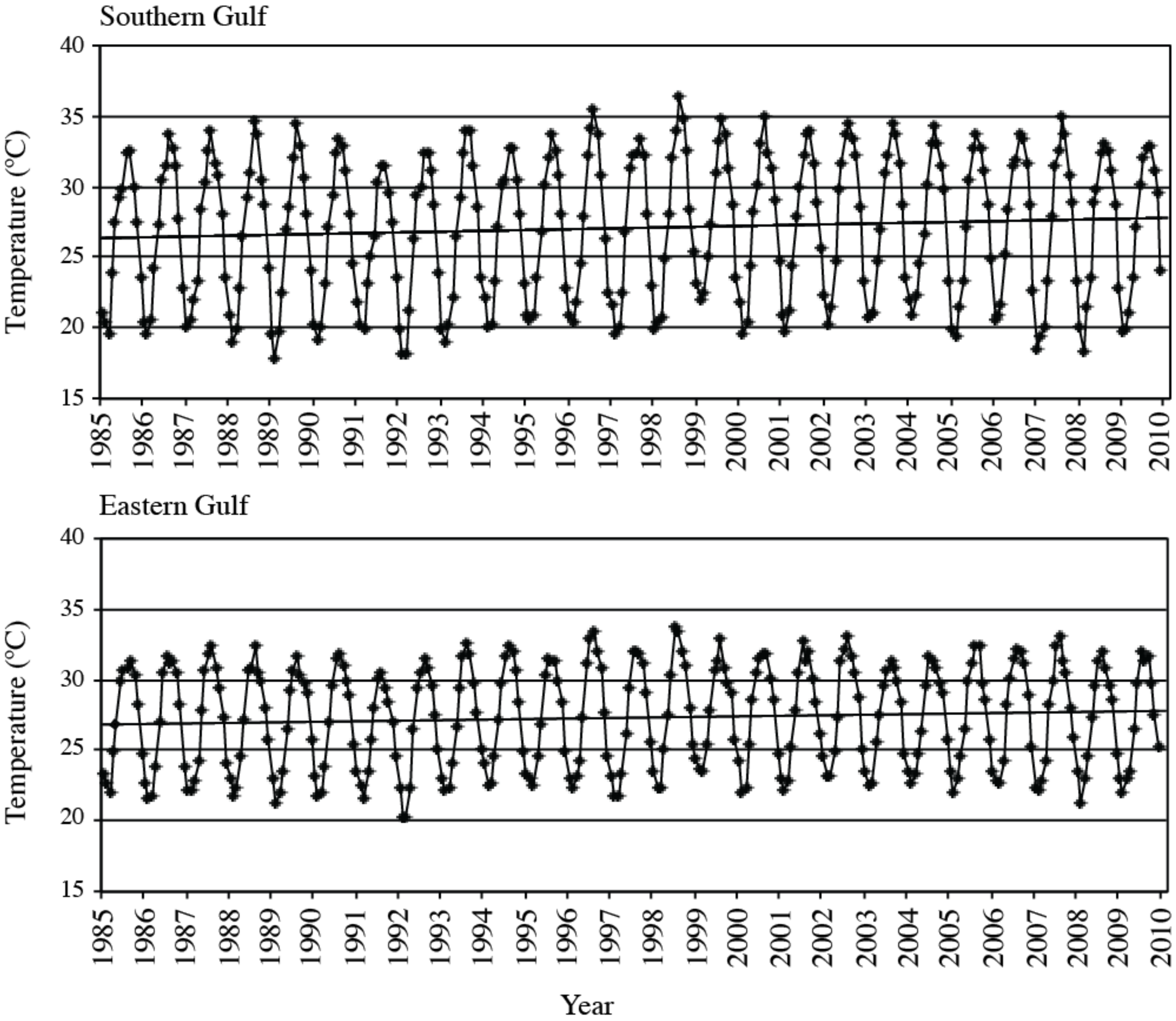

Fig 5.3: Sea surface temperature data sets for southern and eastern Gulf from Retrospective Pathfinder version 5.0 dataset spanning 1985–2009 (25 years) showing increasing temperatures in both regions.

Within the southern Gulf, size-frequency distributions of *Acropora downingi*, *Favia pallida*, *Platygyra daedalea*, and *Porites* spp. were all positively skewed ($+g_1$), reflecting a preponderance of colonies in smaller size classes. In contrast, size frequency distributions within the eastern Gulf were all negatively skewed ($-g_1$) indicating that the majority of coral colonies occur in the larger size classes with relatively fewer colonies in the smaller size classes (Table 5.1). Distributions differed significantly from normality (KS test $p < 0.05$ for each) and displayed variable kurtosis (i.e., both positive ($+g_2$) and negative ($-g_2$) kurtosis) although more leptokurtic in the southern Gulf (Table 5.1). Furthermore, there were significant differences in size-frequency distributions between the southern and eastern Gulf (KS comparison $p < 0.001$).

Such differences between species in size-frequency distribution were predominantly due to the higher proportion of small colonies in the southern Gulf than the eastern Gulf (Fig. 5.4). For example, the proportion of *A. downingi*, *P. daedalea* and *Porites* spp. colonies with surface areas < 1000 cm^2 accounted for > 50% of the total number of colonies surveyed for each species in the southern Gulf, compared to 27% (*A. downingi*), 22% (*P. daedalea*), and 19.5% (*Porites* spp.), respectively within the eastern Gulf (Fig. 5.4a,b,c). Similarly, the proportion of *F. pallida* colonies with surface areas ≤100 cm^2 accounted for 68% of the colonies sampled in the southern Gulf compared to only 27% in the eastern Gulf (Fig. 5.4d).

Mean colony size (χ) within species varied significantly between locations (Student's t-test within species, all $p < 0.001$, Fig. 5.4), due to colonies of each species being significantly smaller in the southern Gulf than the eastern Gulf (Table 5.1). The largest difference in mean colony size between locations was found in *P. daedalea* populations, which were three times smaller in the southern Gulf than the eastern Gulf (Table 5.1). Maximum size and the 95th percentile for all corals species were considerably smaller in southern Gulf compared to the eastern Gulf (Table 5.1).

Table 5.1: Size frequency distribution parameters for (a) *Acropora downingi*, (b) *Platygyra daedalea*, (c) massive *Porites* spp. and (d) *Favia pallida* within the southern and eastern Gulf, and combined total. n: total number of colonies measured; $\bar{\chi}$: mean projected surface area (×10^2 cm^2) of colonies (±SE); g_1: skewness and g_2: kurtosis are based on log-transformed size data. Max size: maximum colony size recorded; 95%: 95th-percentile

Species	Southern Gulf	Eastern Gulf	Combined
(a) *Acropora downingi*			
n	190	217	407
$\bar{\chi}$	10.6 (±1.72)	27.42 (±3.15)	20.04 (±1.89)
g_1	0.34	-0.29	-0.47
g_2	0.12	-0.39	-0.69
Max size	92.52	350.83	350.83
95%	37.91	109.35	73.60
(b) *Platygyra daedalea*			
n	258	278	482
$\bar{\chi}$	8.04 (±0.53)	26.02 (±1.84)	17.36 (±1.06)
g_1	0.23	-0.57	-0.68
g_2	2.19	0.88	-0.96
Max size	64.46	247.07	247.07
95%	23.27	75.83	58.19
(c) *Porites* spp.			
n	293	241	534
$\bar{\chi}$	13.86 (±1.11)	39.31 (±4.67)	25.90 (±2.25)
g_1	0.09	-0.15	-0.39
g_2	0.45	-0.73	-1.09
Max size	184.94	593.57	593.57
95%	49.62	179.54	88.51
(d) *Favia pallida*			
n	276	206	482
$\bar{\chi}$	2.75 (±1.25)	4.84 (±2.61)	3.64 (±1.41)
g_1	0.31	-0.17	-0.06
g_2	1.71	1.37	3.12
Max size	9.83	19.94	19.94
95%	6.10	15.44	10.22

5.5 Discussion

This study revealed marked differences in the size distributions of four locally abundant coral species (*Acropora downingi, Favia pallida, Platygyra daedalea*, and *Porites* spp.) between the southern Gulf (Abu Dhabi and Dubai) and eastern Gulf (western Musandam). All corals in the southern Gulf were significantly smaller, and their size structure positively skewed and relatively more leptokurtic (i.e., peaky) compared to the eastern Gulf. Notably, intraspecific differences in size structure (between locations) were more pronounced than interspecific differences (Table 5.1). These results differ from previous studies where taxonomic differences often have overriding importance because of differences in life-history traits among species (e.g., Bak and Meesters 1998, 1999; Meesters et al. 2001). For example, Meesters et al. (2001) found that size structure of the same coral species from degraded (i.e., urbanized areas) vs. control in sites in the Caribbean were more similar compared to the size structure of other sympatric species, indicating that population structure is highly species-specific. Intraspecific mean colony size also differed significantly among sites, however the pattern of differences was not consistent across all species (Meesters et al. 2001).

Interspecific differences in size frequency distributions among coral species are expected due to inherent differences in their life-histories (especially growth, Vermeij and Bak 2002). However, marked spatial differences in the size structure that are consistent across taxa are interesting because they reveal important differences in environment regimes and disturbance histories (Connell et al. 1997). Vermeij et al. (2007), for example, found generally smaller mean colony sizes in historically stressed marginal habitats (i.e., inland bays) compared to open reef environment sites in the Caribbean, and attributed these differences to higher partial mortality and post-

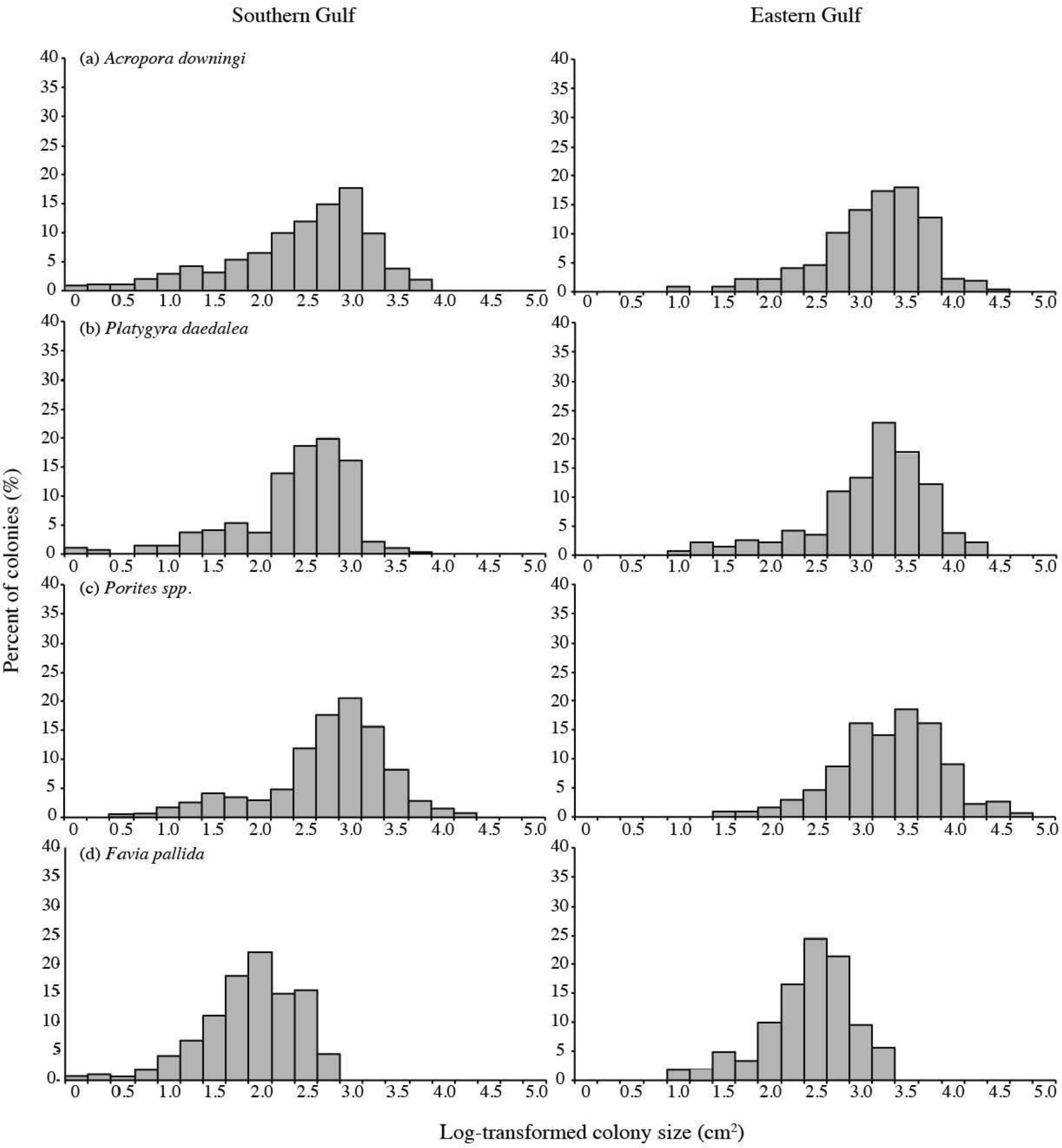

Fig 5.4: Size structure of (a) *Acropora downingi*, (b) *Platygyra daedalea*, (c) massive *Porites* spp. and (d) *Favia pallida* in the southern Gulf versus eastern Gulf.

settlement mortality. In our study, differences in size structure between locations relate to marked regional differences in both chronic (i.e., extreme environmental conditions) and acute disturbances (e.g., successive episodes of mass-bleaching. The combined effects, are likely to have resulted in much higher morality (i.e., partial and whole colony mortality), leading to reduced growth for corals in the southern Gulf.

High (but also variable) temperature and high salinity have long been suggested as the most important factors structuring coral populations in the Gulf, because of differences in species-specific tolerances (Sheppard et al. 1992). Therefore, we expected to find greater interspecific differences in size structure due to species-specific tolerances regardless of persistent environmental differences between locations. Chronic temperature and salinity stress both exert significant energetic costs on corals, affecting respiration and photosynthesis (Porter et al. 1999), leading to reduced growth, reproductive output, and/or survivorship (Coles and Jokiel 1992). STT and salinity are both much higher, but also more variable in the southern versus eastern Gulf (Fig. 5.2), which might account for the reduced size of corals in this region. However, differences in the size-structure of coral populations between regions are likely to have been exacerbated by acute mortality events, associated with temperature-induced bleaching and morality.

Bleaching has had a major impact on coral populations in the Gulf over the past 30 years (Salm 1993; Riegl 1999; Riegl et al 2011), but severe bleaching events have been more frequent in the southern Gulf (Wilson et al. 2002; Sheppard and Loughland 2002; Riegl et al. 2011). Bleaching can reduce growth and calcification, as well as survival rates of the affected corals (Cantin et al. 2010). Prior to our sampling, four major bleaching events (1996, 1998, 2002 and 2010) occurred in the southern Gulf (Riegl 1999, 2002; Riegl et al. 2011) compared to a single severe

Table 5.2: Recent severe bleaching events (1995–2010) in southern and eastern Gulf.

Location	Extreme bleaching event (Year)	Temperature (°C)	Duration	Reference
Southern Gulf	1996	+ 2.5	3 months	Riegl 1999
	1998	+ 2.5	4 months	Riegl 1999
	2002	+ 2.0	1 month	Riegl 2003
	2010	+ 2.5–3.0	3 months	Riegl et al. 2011
Eastern Gulf	2002	+ 1.0–2.0	3 months	Wilson et al. 2002, Wilson 2007

bleaching event in the eastern Gulf in 2002 (Wilson et al. 2002; Table 5.2). Such recurrent disturbances, may have persistent long-term effects on the structure and dynamics of coral communities (Connell 1997; Pratchett et al. 2011) and indeed have caused marked declines in the abundance of live coral, particularly *Acropora* spp. with > 90% mortality (Riegl 2002; Riegl et al. 2011), while more tolerant faviids and poritids suffered far less (Riegl 2002; Sheppard and Loughland 2002). But no mortality was reported from the single severe bleaching in the eastern Gulf (Wilson 2007), despite 60% bleaching of all colonies, including faviids and *Porites* (Wilson et al. 2002). Also, no bleaching was reported from the eastern Gulf during the 1998 event (Maghsoudlou et al. 2008) that heavily impacted reefs throughout much of the southern Gulf and the rest of the world. Clearly, the incidence of recent bleaching events within the Gulf, particularly in the southern Gulf, have had considerable affects on the coral community and left a measurable imprint on important population parameters.

Following a disturbance event, an increase in the incidence of partial mortality can greatly alter size-frequency distributions (Hughes and Jackson 1985). High rates of partial mortality will shift size-frequency distributions towards smaller colonies, especially if large intact colonies are divided into two or more daughter colonies. However, partial mortality is not a common characteristic of all corals, and can vary greatly within and among coral genera (Loya et al. 2001; Baird and Marshall 2002; McClanahan et al. 2008). On the Great Barrier Reef, for example, *Acropora* species were found to suffer higher rates of whole-colony compared to partial mortality following the 1998 bleaching (Baird and Marshall 2002). In contrast, rates of whole colony mortality were low in *Platygyra daedalea* and *Porites lobota*, and the majority of tissue loss was through partial mortality. Riegl (1999) reported similar patterns in the southern Gulf, with the virtual elimination of *Acropora* species, while faviids and *Porites* were less affected by whole-colony mortality. Recovery of partially bleached colonies was common (Riegl 1999; Sheppard and Loughland 2002). It is therefore likely that the reduced size of *Favia pallida*, *Platygyra daedalea*, and *Porites* spp. in the southern Gulf is due to increased rates of partial-mortality, but this is probably not the case for *Acropora*. In the case of *A. downingi*, reduced size may reflect size-specific mortality or overall increased rates of mortality in the southern Gulf.

Bleaching mortality is often size specific, with larger-sized colonies more susceptible than smaller-sized colonies (Mumby 1999; Loya et al. 2001; Shenkar et al. 2005; McClanahan et al. 2008). Strong size-based selectivity during mortality events will lead to marked declines in overall size, but recurrent bleaching (and high rates of associated mortality) will also shift the size structure towards juvenile and small colonies (Done 1999), regardless of increased vulnerability with colony size. The recent incidence of severe bleaching events in the southern Gulf, with limited opportunities for recovery in the intervening period, have almost certainly suppressed the size of corals across the Gulf, but more so in the southern Gulf. This would explain why faster growing *Acropora* corals exhibit less regional differences compared to the faviid and *Porites* corals. Moreover, these coral populations with drastically altered size-structure will also be vulnerable to future disturbances.

5.6 Conclusions

Overall, this study suggests that even within regions, such as the Gulf, where corals are considered particularly tolerant of environmental extremes (Sheppard et al. 1992) increased frequency of bleaching events will lead to persistent declines in the size of coral colonies (see McClanahan et al. 2008). Deleterious effects of ongoing climate change on the size-structure of corals were more pronounced for slow-growing corals (*Platygyra* and *Porites*), reflective of inherent constraints on recovery of different coral populations (Table 5.1). Overall, the fate of different corals will depend on the recurrence of major disturbance events relative to their capacity for recovery (Hughes et al. 2003), which in turn depends on their capacity for individual and population growth. This study provides important baseline data, from which to test for ongoing declines in the mean size and proportional abundance of large, reproductive colonies. However, this study also highlights a critical need for increased data and understanding of basic ecological processes (e.g., recruitment, post-settlement survival, partial and whole colony mortality) within the Gulf. This will require redefined research priority focused on longer-term demographic studies (e.g., colony tagging studies), and demographic modeling in order to identify life-history characteristics promoting resistance to extreme environmental conditions within the Gulf.

Chapter 6: General Discussion

Reef-building corals are generally considered to be highly sensitive to changes in environmental conditions, having adapted to a relatively narrow band of environmental optima (Kleypas et al. 1999; Couce et al. 2012). The environmental variability of the Gulf (minimal and maximal annual temperatures, hyper-salinity, high turbidity, etc.) is well beyond the range experienced on most tropical coral reefs (Sheppard et al. 1992, 2010; Riegl and Purkis 2012), testing both the physiological and ecological limits of coral reef organisms. Summer daily-mean temperatures are several degrees above the bleaching and mortality thresholds recorded for corals in the tropical Indo-Pacific (Riegl et al. 2011; Coles and Riegl 2012). While corals in the Gulf region have certainly suffered from recent and severe episodes of temperature-induced bleaching (Riegl 2002, 2003; Sheppard and Loughland 2002; Riegl and Purkis 2009) there remain many corals and coral reefs in this region. While links between environmental extremes (particularly high temperatures), recurrent bleaching events, and associated shifts in the composition of coral assemblages have been well documented for the southern Gulf (Riegl 1999, 2002, 2003; Sheppard and Loughland 2002; Burt et al. 2008; Riegl and Purkis 2009; Sheppard et al. 2010; Riegl et al. 2011; Coles and Riegl 2012), basic knowledge on key ecological processes (e.g., reproduction, settlement, recruitment and growth) that are important for regulating population dynamics and resilience to ongoing environmental change remains unclear.

Given the extreme temperatures that occur in the Gulf, studies of corals and reef ecosystems in this region are fundamental in understanding likely effects of increasing temperatures on coral reefs globally (Sheppard et al. 2010). However, there has been very limited research on key biological processes (e.g., growth and recruitment) for coral in the Gulf, which will determine the responses of corals to ongoing climate change. For example, Riegl and Purkis (2009) recently modeled the response of coral populations in the Gulf to accelerated bleaching and mass mortality events, but had to infer several key parameters (e.g., fertility, larval supply, and recruitment) based on studies conducted at other geographic locations outside the Gulf. The resultant model contributes to a better understanding which demographic processes are likely to have the greatest influence on coral persistence under predicted disturbances regime in the Gulf, but quantifying vital rates within the Gulf is critical not only to improving the accuracy of such models but our overall knowledge of how this coral assemblages are likely to respond to sustained and ongoing environmental change. Therefore, the data presented throughout this thesis provides important baseline data on several ecological parameters (e.g., reproduction, settlement, size structure), addressing an important knowledge gap.

6.1 Changing community structure in the Gulf

Elucidating the environmental limits of reef-building corals over their present range is central to understanding how coral colonies (individuals), populations, and communities may respond to sustained and ongoing climate change (Kleypas et al. 1999), and corresponding changes in disturbances regimes (Couce et al. 2012). The structure and development of coral reef communities are subject to diverse and often interacting environmental variables (e.g., temperature, light, salinity, sedimentation, hydrodynamic factors) (Brown 1997; Kleypas et al. 1999). These factors can differentially affect reproduction, settlement, recruitment, and/or growth, which in turn, affect the overall abundance, composition and diversity of communities (Brown

1997; Kleypas et al. 1999; Done 2011). Climate change is likely to cause fluctuations in a range of environmental variables (i.e., physical and chemical), which are predicted to directly affect the abundance, diversity, and composition of coral reef communities (Done 1999; Baker et al. 2008; Pratchett et al. 2011), and may lead to further degradation of these reef systems (Hughes et al. 2003; Bellwood et al. 2004).

Building on a growing body of literature aimed at understanding which environmental factors influence the structure of reef communities (*sensu* Kleypas et al. 1999), this thesis consolidates the view that multiple environmental factors, and the increasing frequency of major disturbances (i.e., bleaching events), influence the structure of reef communities in the northeastern Arabian Peninsula (Persian Gulf, Strait of Hormuz and Gulf of Oman) (Chapter 2). It is known, for example, that the community structure of coral assemblages and other benthic invertebrates varies greatly among sub-regions of the northeastern Arabian Peninsula in accordance with marked differences in the environmental and oceanographic conditions (Price 1982; Sheppard and Sheppard 1991; Sheppard et al. 1992). Such dissimilarities have traditionally been related to extreme temperature and salinity regimes throughout the Arabian region. However, the majority of these studies only considered these variables in isolation (Sheppard 1987; Sheppard and Sheppard 1991; Coles 2003), so any hierarchy of additional environmental variables and their respective effects on community structure and abundance remains unclear.

Similar to previous studies, multivariate analysis of benthic communities undertaken in Chapter 2, revealed distinct differences in the structure of coral assemblages and benthic groups among the southern Persian Gulf, Strait of Hormuz, and Gulf of Oman. Moreover, these differences in benthic communities correspond with sub-regional differences in oceanic conditions, temperature and salinity

(Sheppard 1987; Sheppard and Salm 1988; Sheppard and Sheppard 1991; Chapter 2). Differences in coral community structure around the region were best explained by temperature range in combination with minimum salinity, maximum chlorophyll-*a*, and the % time of along-shore currents (Chapter 2). Importantly, while temperature and salinity remain good proxies for distinguishing between coral communities across the region, results from this thesis indicate that chlorophyll-*a*, surface currents and wind speeds are also important physical factors in structuring reef communities throughout the region. Moreover, these factors are all considered likely correlates of resistance and resilience to bleaching events (West and Salm 2003; Maina et al. 2008), which are expected to become more frequent and severe in coming decades (e.g., Hoegh-Guldberg 1999). As such there is critical need to increase our understanding of the range of physical factors that influence the structure of reefs throughout the region, including different areas within the Gulf (e.g., off-shore islands and coast of Iran), and how these conditions may change with sustained climate change (Chapter 2).

Aside from strong spatial patterns, there have also been marked temporal shifts in the structure of coral assemblages over the past two decades (Sheppard 1987; Sheppard and Sheppard 1991). The most dramatic of these are the apparent changes from *Acropora* dominated to poritid and faviid dominated communities, particularly in the southern Persian Gulf and Straits of Hormuz (Chapter 2). These findings support claims of long-term shifts in community structure in the southern Persian Gulf towards more robust coral species (*Porites* and faviids) that are more resistant to major disturbances (Riegl and Purkis, 2009). These findings also suggest a potential trade-off exists between coral communities resistance to disturbance versus efficient recovery potential, and that incidents of disturbance events in the Gulf are likely to prevent effective recovery of even fast growing coral species (i.e., *Acropora*).

6.2 Coral reproduction under extreme conditions

Sexual reproduction by scleractinian corals is an important ecological process for enhancing genetic diversity, replenishing local populations, and connecting disparate populations (Harrison and Wallace 1990; Richmond and Hunter 1990; Baird et al. 2009b). Any reduction in the reproductive capacity of corals may threaten reef resilience, and especially the ability to recover in the aftermath of major disturbances (e.g., Gilmour et al. 2013). Coral reproductive processes are highly sensitive to a wide range of natural and anthropogenic stressors that may reduce fecundity, and/ or limit reproductive success (Harrison and Wallace 1990; Richmond 1993; Baird et al. 2009b; Harrison 2011). Increasing climate change, and especially altered thermal regimes, may disrupt tightly regulated reproductive cycles (e.g., gametogenic cycle) and affect highly synchronized temporal spawning events, which may limit larval settlement, post-settlement survival and recovery (Baird et al. 2009b; Harrison 2011). In addition, thermal stress from elevated seawater temperatures can negatively affect reproductive capacity of corals (Kojis and Quinn 1984; Edmunds et al. 2001; Nozawa and Harrison 2002, 2007; Bassim et al. 2002; and many more), by reducing individual fecundity, reduced egg quality, lowered fertilization success and decreased larval survivorship (see review McClanahan et al. 2009). Consequently, research focusing on reproductive processes in regions were extreme conditions are common, such as those in the Gulf, is urgently needed as a baseline against which to test the effects of climate change on corals reproductive capacities.

Despite the extreme environmental conditions in the southern Gulf the reproductive biology of six common coral species (*Acropora downingi*, *A. clathrata*, *A. valenciennesi*, *Cyphastrea microphthalma*, *Favia pallida* and *Platygyra daedalea*) was remarkably similar to conspecifics elsewhere in the Indo-Pacific (Chapter 3). Coral reproduction was highly seasonal with peak reproductive activity around the full moon in April, corresponding to rising mean SST above 26.5°C. Seasonal patterns of coral reproduction in the Gulf were generally consistent with other locations in region, including Saudi Arabia (Fadallah and Lindo 1988; Fadlallah 1996), Kuwait (Harrison 1995) and the Red Sea (Hanafy et al. 2010). Furthermore, given the high proportion of mature colonies prior to the full moon in April, it is highly probable that there would be some degree of multi-synchronous spawning (Chapter 3).

Likewise, the three most abundant corals in the southern Gulf (*Acropora downingi*, *Cyphastrea microphthalma* and *Platygyra daedalea*) were all hermaphroditic broadcast spawners with a single annual gametogenic cycles (i.e., 7–9 months) similar to conspecifics documented in many geographic locations (Willis et al. 1985; Shlesinger et al. 1998; Baird et al. 2009b). Mean fecundity and mature oocyte size prior to spawning for all three species were also similar to other regions (Chapter 3). Importantly, the lack of significant differences in fecundity and gamete size between coral species in the Gulf and conspecifics elsewhere supports the idea that adaptation to environmental conditions projected under climate change is possible (Baird and Maynard 2008).

Although these results clearly demonstrate that coral populations in the southern Gulf can survive and proliferate in extreme conditions projected to occur in many other regions by 2100 (IPCC 2007), further increases in seawater temperatures could exceed local thermal thresholds, leading to local reproductive failure, and undermining overall resilience of reefs in this region. Whether future coral populations in the southern Gulf are capable of similar reproductive activities under more extreme conditions as a result of climate change will likely depend on how quickly they are able to adapt.

6.3 Coral settlement under extreme conditions

The recovery of reefs following a disturbance (e.g. bleaching event) requires the replenishment of coral populations either by regrowth of surviving corals or the arrival and settlement of coral larvae and their post-settlement growth and survival (Hughes 1994, Hughes and Tanner 2000). Successful coral recruitment is dependent upon many separate processes, including the fecundity of the local population (e.g. Hughes et al. 2000), rates of fertilization (e.g. Oliver and Babcock 1992), larval survivorship and dispersal (e.g. Graham et al. 2008), settlement (e.g., Hughes et al. 1999), and early post-settlement growth and survivorship (e.g. Ritson-Willams et al. 2009). Species-specific rates of coral settlement ultimately constrain the abundance of corals, as well as influencing species composition (Hughes et al. 1999, Hughes and Tanner 2000, but see Edmunds 2000). Elevated temperatures can have dramatic effects on larval supply and settlement (Edmunds et al. 2001, Bassim and Sammarco 2003, Baird et al. 2006), and have profound affects on population dynamics (Harrison and Wallace 1990; Connell et al. 1997). Given that global sea surface temperatures (SSTs) are predicted to increase 2–4°C within the next century (IPCC 2007) it is important to understand how coral settlement will likely be affected under more extreme environmental conditions.

Overall, results from this thesis showed there is clear evidence of ongoing coral settlement in the southern Gulf (Chapter 4), despite very high temperatures. Coral settlement rates in the Gulf were low (113 spat m^{-2} yr^{-1}) but well within the range of values reported from other high-latitude marginal reefs, including: the Solitary Islands (Harriott and Banks 1995), Taiwan (Soong et al. 2003) and Hong Kong (Lam 2003). Furthermore, settlement was highly seasonal despite the extreme environmental conditions (i.e. high seawater temperatures) and high frequency disturbance events (i.e. bleaching). Peak settlement in the southern Gulf occurred during summer (June–August) when summer sea temperatures approached 35°C (Chapter 4), well above the critical thermal limit for coral larvae reported from most experimental studies (Edmunds et al. 2001; Bassim and Sammaro 2003; Baird et al. 2006; Putnam et al. 2008). The fact that coral settlement is occurring at around 35°C in Gulf is strong evidence for local adaptation, and further advances the idea that coral adaptation to rising sea temperatures is possible.

Peak settlement in the Gulf was recorded up to 4 months after the major spawning season in April and May. Elsewhere (e.g., on Australia's Great Barrier Reef), settlement tends to be highest following closely after the major mass-spawning season (Wallace and Bull 1981, Wallace 1985) reflective of rapid development and limited larval dispersal (Wilson and Harrison 1998; Hughes et al. 1999, 2002). The extended period between spawning and settlement in the Gulf suggests that either corals have an unusually protracted larval life-stage, or there is spatial and/or taxonomic disparity between studies of reproduction (Chapter 3) versus settlement (Chapter 4). The composition of coral spat recorded on tiles in the Gulf was very distinct from other regions in the Indo-Pacific. Most notably, there were few Acroporidae coral spat (11%) and no Pocilliporidae. The results show that reported shifts in community structure away from formerly dominant *Acropora* species and towards more robust coral species (Riegl 1999; 2002; Burt et al. 2008; Riegl and Purkis 2009; Riegl et al. 2011; Chapter 2) are being reinforced at the level of settlement, such that there is limited scope for recovery of *Acropora* dominant coral assemblages in the Gulf (Chapter 2, 4). Although corals in the Gulf have clearly adapted to the extremes experienced, it appears certain that the structure of coral assemblages has been forever changed due to climate change and other ongoing disturbances.

6.4 Variation in coral size structure in the Gulf

Examining size structure allows us to compare key demographics, or the interaction between size-specific growth, survival and fecundity, of populations to assess spatial and temporal changes from recent disturbance events (Bak and Meesters 1999; Meesters et al. 2001). Information from size distributions also enables inferences to be made about the future consequences of the observed changes, and provide some insight into past environmental events (Bak and Meesters 1998). Given the need to better understand coral reef resilience in the face of changing global conditions (McClanahan et al. 2007) the Gulf is an ideal location to evaluate the role of extreme environmental conditions and recurrent disturbance events in structuring coral community size structure.

This thesis found significant and consistent differences in mean colony sizes and size-distributions of four locally abundant coral species (*Acropora downingi*, *Favia pallida*, *Platygyra daedalea*, *Porites* spp.) between two regions in the Persian Gulf: the southern Gulf (Dubai and Abu Dhabi) and the eastern Gulf (western Musandam). All corals in the southern Gulf were significantly smaller, and their size structure positively skewed compared to corals in the eastern Gulf (Chapter 5). Sea surface temperatures, salinity and frequency of recent mass bleaching events are all higher in the southern Gulf, suggesting higher mortality and/or slower growth in these populations (Chapter 5). Moreover, differences in size structure between locations were more pronounced than differences between species at each location, suggesting that differences in environmental conditions and disturbance events have a greater influence on population dynamics in the Gulf than inherent differences in their life-history characteristics.

Following a disturbance event, an increase in in the incidence of partial mortality can greatly alter size-frequency distributions (Hughes and Jackson 1985). Clearly, the incidence of recent bleaching events within the Gulf, particularly in the southern Gulf, have had considerable affects on the coral community and left a measurable imprint on important population parameters. The fate of different corals will depend on the recurrence of major disturbance events relative to the their capacity for recovery (Hughes et al. 2003), which in turn depends on their capacity for individual and population growth (Chapter 5). Importantly, these results highlight that even within regions, such as the Gulf, where corals are considered particularly tolerant of environmental extremes, increased frequency of bleaching events will likely lead to persistent declines in the size of coral colonies (McClanahan et al. 2008; Chapter 5). Continuous disturbances and reduced size of corals is expected to reduce reproduction and recruitment from larval stages (Hall and Hughes 1996), could therefore impact recovery and overall reef resilience in the Gulf.

6.5 Global implications of this research

Gulf corals are unique in many respects, most notably because of their ability to withstand extreme temperatures (both highs and lows) and salinity (>40‰).

Importantly, corals in the southern Persian Gulf must withstand daily mean summertime temperatures well in excess of 34°C for 1–2 months (Riegl et al. 2011; Riegl and Purkis 2012). Given that world is getting warmer and extremes are becoming more pronounced, the study of such extreme reef systems gains increased relevance. The adaptive capacity of corals in the Gulf is likely facilitated by a combination of short-term acclimation in individuals during acute environmental conditions (e.g., recurrent bleaching events) and long-term adaptation among coral populations to chronic environmental conditions (e.g., extreme temperatures, salinities). Such information has much practical value, particularly the ability of how corals can increase their thermal tolerance (Brown and Cossins 2011), and acclimatize or adapt in a heating world (Sheppard 2003; Baker et al. 2004; Rowan 2004).

Nonetheless, while corals in the Gulf appear adapted to extreme environmental temperatures, spawning and settling at temperatures that would inhibit these processes in most regions of the world, the effects of climate change (i.e., seawater temperatures and bleaching events) are having a marked effects on the structure and dynamics of coral populations and assemblages. Coral assemblages in the southern Gulf have shifted away from formerly *Acropora* dominated communities to communities dominated by *Porites* and faviids, which are presently considered less susceptible to thermal stress (e.g., Marshall and Baird 2000; Loya et al. 2001; McClanahan et al. 2004). Previous studies have shown directional shifts in taxonomic structure of coral communities subject to a diverse range of disturbances (Berumen and Pratchett 2006; McClanahan et al. 2007; Pratchett et al. 2011). Pratchett et al. (2011), for example, showed that recent disturbance events on coral reefs in French Polynesia are reinforcing long-term shifts in the community structure, which have been ongoing since the early 1980s (Berumen and Pratchett 2006).

Thus, the question becomes whether observed shifts in community structure in the Gulf (i.e., *Acropora* to *Porites* and faviids) represent either (1) a new, stable and resilient community structure that will endure until there is a fundamental change in local conditions, or (2) a transitional community, indicative of either continuing degradation or recovery (Aronson et al. 2004; Riegl and Purkis 2009; Pratchett et al. 2011). In the southern Gulf, there has been limited recovery of *Acropora* species in small areas >15 years after the most severe mass mortality events on record occurred in the 1996 and 1998 (Purkis et al. 2009; Burt et al. 2008, 2011; Chapter 2). Conversely, on an isolated reef system in north Western Australia (Scott's Reef), where the coral assemblages also changed dramatically following the 1998 mass coral bleaching event, with marked declines in coral cover (especially *Acropora*) and the number of genera, took <12 years for coral cover and composition to return to pre-disturbance levels (Gilmour et al. 2013). Results from this work highlighted that a high proportion of the coral larvae that aided in the recovery of this reef were produced locally, settled and survived. Importantly, this study demonstrated that even corals reefs with a negligible supply of larvae (i.e., limited connectivity) could recover relatively quickly in the absence of chronic anthropogenic pressures.

Results from this thesis indicate the existence of a positive feedback mechanism is likely reinforcing and maintaining the altered coral community structure in the southern Gulf (Riegl and Purkis 2009; Chapters 2, 4 and 5). One indicator that this shift has occurred are differences in the taxonomic abundance of coral at the level of settlement were strongly reflective of patterns of local adult abundance in the Gulf, suggesting that there is limited scope of recovery for *Acropora* species. Penin et al. (2010) recently showed that taxonomic differences in juvenile abundance (cf. patterns of settlement) at sites around Moorea in French Polynesia are often reflected in subsequent patterns of abundance of adult abundance. Consequently the current community structure observed in the Gulf (i.e., faviids and *Porites* dominated) will likely persist until fundamental changes in local conditions. Congruent with this observation, recent population models from the Gulf predict that closely spaced bleaching events, such as those between 1996–2010, would not allow *Acropora* populations' time to recover and could possibly lead to local extinction in some areas (Purkis and Riegl 2009). However, when the time between bleaching events was prolonged (i.e., > 15 years) coral populations, particularly *Acropora* species in the model showed strong signs of recovery (Riegl and Purkis 2009).

Such changes are also likely being augmented by the community size structure, particularly in the southern Gulf. All corals in the southern Gulf were smaller, and their size structure positively skewed, compared to communities in the eastern Gulf. Sea surface temperatures, salinity and the frequency of recent bleaching events were all higher in the southern Gulf. Previous work has shown that in the absence of stress, corals are extremely fecund, and that fecundity increases exponentially with increasing colony size (Hall and Hughes 1996). Despite similar measures of coral fecundity to conspecifics elsewhere (Chapter 3), smaller colony sizes in the Gulf could eventually reduce sexual reproductive output, which is likely to further inhibit population recovery (i.e., *Acropora*) and adaptation potential. Thus, on-going climate change will not only lead to directional shifts in coral communities (i.e., taxonomically and size structure), but will reinforce these changes by modifying key ecological processes.

In addition to changes in temperature, fluctuations in a range of other environmental variables (i.e., physical and chemical), mediated by changes in the global change are predicted to occur. For example, recent study from Durack et al.

(2012) predict significant changes in sea surface salinity (SSS) will occur as a result of intensification of the global water cycle, with increasing salinity at all latitude in the Indian Ocean, including the Gulf, down to 150 m depth (Boyer et al. 2005). Chronic temperature and salinity stress can exert significant energetic costs on corals, affecting respiration and photosynthesis, leading to further reductions in growth, reproductive output and/or survivorship (Coles and Jokiel 1977; Porter 1999). Furthermore ocean temperatures are predicted to increase over the next several decades (IPCC 2007; Lough 2012), and these may exceed thermal tolerances, even within the Gulf. More importantly, however is whether corals elsewhere can adapt up to the temperatures that corals in the Gulf currently experience. The key question is how much heat is necessary to bleach, or even kill these apparently uniquely adapted corals, and whether corals in the Gulf can adapt further, by increasing their thermal tolerances. If they can, then it is fundamentally important that we continue to study population and community dynamics in the Gulf region.

6.6 Conclusions

While climate change poses an important and significant threat to the future structure and dynamics of coral reef communities, results from this thesis support the idea that climate change is likely to result in a reassortment of coral reef taxa rather than wholesale loss of entire reef ecosystems (*sensu* Hughes et al. 2012), with coral reefs exhibiting some flexibility in community composition. Thus, one could surmise that more severe climate induced bleaching events, coupled with on-going anthropogenic stress, will leave depauperate coral communities with a few very small robust species similar to the Gulf. Collectively, the results of this thesis emphasize the importance of understanding the affects of climate change on key ecological processes and demographics of reefs in the Gulf, and how these processes are likely to be affected on other reefs around the world. Furthermore, this study highlights the critical need for increased data and understanding of basic ecological processes (e.g., recruitment, pre- and post-settlement survival, partial and whole colony mortality) within the Gulf. This will require redefined research priority focused on longer-term demographic studies (e.g., colony tagging studies), and demographic modelling in order to identify life-history characteristics promoting resistance to extreme environmental conditions within the Gulf.

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Appendix A: Supplemental information for Chapter 2

Table A1: Locations, coordinates and coral cover (mean ± SE) at each study site, with site numbers corresponding to those in Fig. 2.1.

Site no.	Site name	Location	Body of Water	Latitude	Longitude	Coral cover
1	Bu Tinah	Abu Dhabi, UAE	Southern Persian Gulf	24°40.139N	53°03.820E	9.19 ± 1.7
2	Al Hiel	Abu Dhabi, UAE	Southern Persian Gulf	24°24.389N	53°12.243E	11.8 ± 2.1
3	Saadiyat	Abu Dhabi, UAE	Southern Persian Gulf	24°35.915N	54°25.915E	34.3 ± 5.2
4	Ras Ghanada	Abu Dhabi, UAE	Southern Persian Gulf	24°50.856N	54°41.415E	26.3 ± 3.9
5	Saih Shaib	Dubai, UAE	Southern Persian Gulf	24°55.375N	54°54.203E	11.8 ± 1.9
6	Ras Hasyan	Dubai, UAE	Southern Persian Gulf	24°58.303N	54°57.983E	28.7 ± 2.2
7	Khasab Reef	Musandam, Oman	Strait of Hormuz	26°14.469N	56°11.872E	42.7 ± 4.3
8	Coral Garden	Musandam, Oman	Strait of Hormuz	26°22.556N	56°24.895E	69.0 ± 5.5
9	Rashid Island West	Musandam, Oman	Strait of Hormuz	26°24.317N	56°29.712E	27.9 ± 6.4
10	Musandam East	Musandam, Oman	Strait of Hormuz	26°5.1160N	56°27.878E	32.5 ± 3.2
11	Al Ghattan	Al Sawadi, Oman	Gulf of Oman	23°47.682N	57°46.346E	24.9 ± 5.6
12	Al Jazeera	Al Sawadi, Oman	Gulf of Oman	23°47.491N	57°47.140E	6.6 ± 3.5
13	Fort Island	Al Sawadi, Oman	Gulf of Oman	23°47.269N	57°48.077E	6.1 ± 1.7
14	Qantab	Muscat, Oman	Gulf of Oman	23°33.870N	58°38.188E	9.7 ± 2.0
15	Jussa West	Muscat, Oman	Gulf of Oman	23°33.521N	58°38.756E	9.4 ± 2.1
16	Jussa Point	Muscat, Oman	Gulf of Oman	23°33.430N	58°39.678E	4.8 ± 1.4
17	Al Heddla	Ras Al Hadd, Oman	Gulf of Oman	22°45.422N	59°19.111E	7.6 ± 1.4
18	Turtle Beach	Ras Al Hadd, Oman	Gulf of Oman	22°31.958N	59°45.017E	6.2 ± 1.0

Table A2: Coral species list from each study location: + indicates presence in southern Persian Gulf (PG), Strait of Hormuz (SH), and Gulf of Oman (GO). Identifications follow Veron (2000) and Claereboudt (2006).

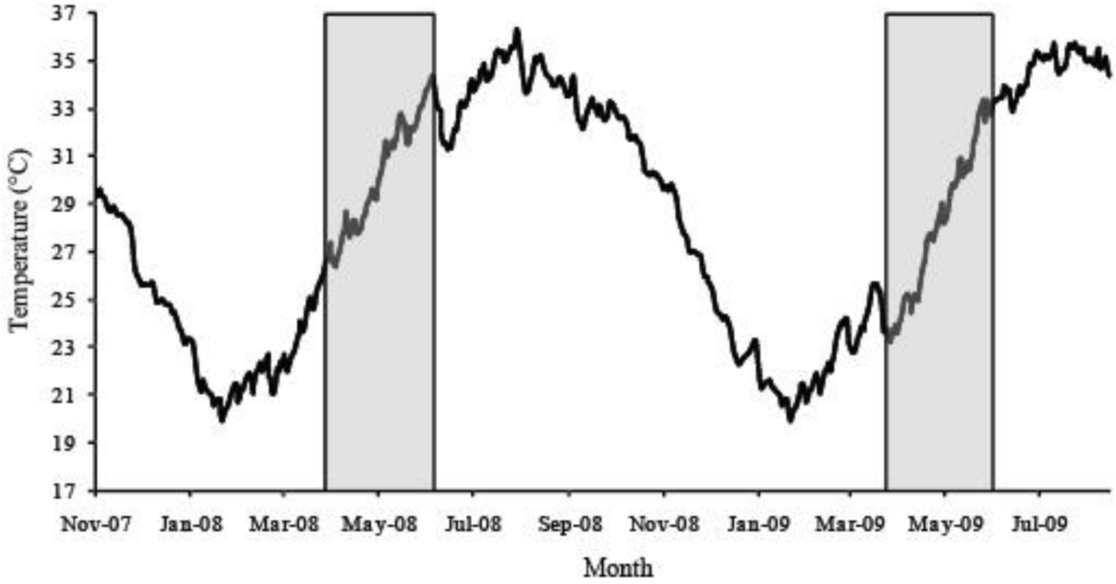
No. Species	Family	Species	PG	SH	GO
1	Astrocoeniidae	*Stylocoeniella guntherii*		+	
2	Pocilloporidae	*Pocillopora damicornis*		+	+
3		*Stylophora pistillata*		+	+
4	Euphyllidae	*Euphyllia divisa*		+	
5	Acroporidae	*Astreopora myriophthalma*			+
6		*Acropora arabensis*		+	+
7		*Acropora cf microphtalma*		+	
8		*Acropora clathrata*	+		
9		*Acropora downingi*	+	+	+
10		*Acropora gemmifera*			+
11		*Acropora khayranensis*		+	+
12		*Acropora nasuta*			+
13		*Acropora valenciennesi*	+		
14		*Acropora valida*		+	+
15		*Montipora aequituberculata*		+	+
16		*Montipora cf danai*		+	+
17		*Montipora stellata*		+	+
18	Agariciidae	*Pavona decussata*		+	+
19		*Pavona diffluens*		+	+
20	Siderastreidae	*Anomastraea irregularis*	+	+	
21		*Coscinaraea columna*			+
22		*Psammocora contigua*	+	+	+
23		*Psammocora interstinctus*			+
24		*Psammocora obtusanglulata*			+
25		*Psammocora superficialis*		+	+
26		*Pseudosiderastrea tayamai*	+	+	+
27		*Siderastrea savignyana*	+	+	+
28		*Coscinaraea monile*	+		
29	Poritidae	*Porites cumulatus*		+	
30		*Porites harrisoni*	+	+	+
31		*Porites lobata*	+	+	+
32		*Porites lutea*	+	+	+
33		*Porites mayeri*	+		
34		*Porites nodifera*	+	+	+
35		*Porites solida*	+		+
36		*Goniopora columna*			+
37		*Goniopora djiboutienis*			+
38	Faviidae	*Favia cf favus*	+	+	
39		*Favia matthaii*		+	+
40		*Favia pallida*	+		+
41		*Favia rotumana*	+		
42		*Favia speciosa*			+
43		*Favites abdita*	+	+	
44		*Favites chinensis*	+		+

45		*Favites complanata*		+	+
46		*Favites micropentagona*			+
47		*Favites pentagona*	+	+	
48		*Favites spinosa*		+	
49		*Platygyra crosslandi*			+
50		*Platygyra daedalea*	+	+	+
51		*Platygyra lamellina*	+		
52		*Platygyra sinensis*			+
53		*Plesiastrea versipora*	+		+
54		*Leptastrea bottae*		+	+
55		*Leptastrea purpurea*		+	+
56		*Leptastrea transversa*	+	+	+
57		*Cyphastrea microphthalma*	+	+	+
58		*Cyphastrea serailia*	+		+
59		*Parasimplastrea sheppardi*		+	+
60		*Echinopora grandicula*			+
61		*Echinopora hirsutissima*		+	
62		*Echinopora llamellosa*		+	+
63	Merulinidae	*Hydnophora exesa*			+
64		*Hydnophora micronos*		+	
65		*Hydnophora pilosa*		+	
66	Mussidae	*Blastomussa merletti*			+
67		*Symphyllia radians*		+	+
68		*Symphyllia recta*		+	+
69		*Acanthastrea echinata*	+	+	+
70		*Acanthastrea hillae*		+	
71		*Acanthastrea maxima*		+	+
72	Pectiniidae	*Echinophyllia aspera*		+	+
73		*Oxypora lacera*		+	
74	Dendrophylliidae	*Turbinaria mesenterina*			+
75		*Turbinaria peltata*	+	+	+
76		*Turbinaria reniformis*	+	+	+

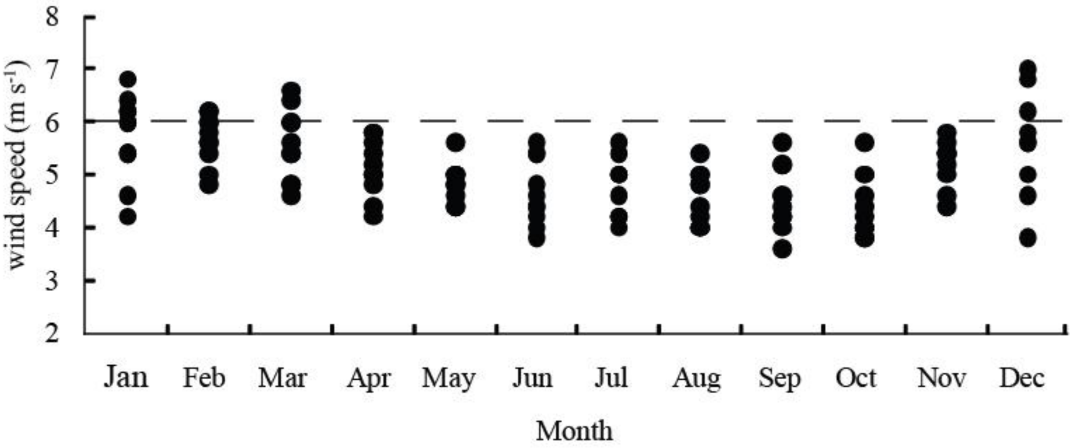
Appendix B: Supplemental information for Chapter 3

Fig. B1: (a) Mean daily water temperatures from November 2007 to August 2009 at Saih Al Shaib. Shaded areas indicate predicted coral spawning from April through May, and (b) monthly averaged wind-speed data (m s^{-1}) extracted from 2000 to 2009 for Dubai (24°N). Note that when winds are greater than or equal to 6 m s^{-1} that white caps form.

(a)



(b)



Appendix C: Supplemental information for Chapter 5

Table C1: Overview of size frequency descriptors for 4 coral species at 6 sites. Southern Gulf: Saih Al Shaib, Ras Ghanada, Saadiyat; Eastern Gulf: Khasab Reef, Coral Garden, Rashid Island. *n*: total number of colonies measured; Mean colony size: average size of colonies per species per site (cm^2) and standard error mean (±SE); 95 %: 95th percentile; g_1: skewness and g_2: kurtosis based on log-transform data.

Species (Site)	*n*	Colony size (cm^2)				
			Non-transformed		ln-transformed	
		Mean	±SE	95 %	g_1	g_2
Acropora downingi						
Saih Al Shaib	71	1072.2	289.7	3913.3	0.23	0.33
Ras Ghanada	52	911.6	157.4	2783.8	-0.06	1.12
Saadiyat	67	1216.8	371.8	4185.1	0.17	0.43
Khasab Reef	85	2711.3	197.6	3846.5	-0.68	0.62
Coral Garden	66	3055.6	301.2	6347.2	-0.07	-0.45
Rashid Island	66	2461.6	363.3	5477.4	-0.11	-0.77
Platygyra daedalea						
Saih Al Shaib	89	731.7	75.3	2143.1	0.11	0.49
Ras Ghanada	69	912.7	122.6	3315.6	0.19	0.26
Saadiyat	100	768.4	85.1	2195.0	0.44	1.03
Khasab Reef	104	3153.5	335.3	6666.2	-0.41	-0.66
Coral Garden	92	2213.9	512.4	4675.3	-0.45	-1.11
Rashid Island	82	2439.4	375.1	6538.9	-0.51	-0.41
Porites spp.						
Saih Al Shaib	93	1629.8	207.2	5043.4	0.33	0.76
Ras Ghanada	90	1419.4	231.1	5229.1	0.53	-0.39

Saadiyat	107	1414.2	176.8	4297.7	-0.67	-0.08
Khasab Reef	95	4543.4	411.5	7415.7	-0.39	-0.82
Coral Garden	66	3546.7	503.4	6921.4	-1.07	-0.93
Rashid Island	80	3805.3	398.1	7933.3	-0.63	-0.06
Favia pallida						
Saih Al Shaib	68	265.9	19.8	513.5	0.68	1.49
Ras Ghanada	132	296.9	21.5	605.8	1.13	0.87
Saadiyat	76	264.7	18.1	645.5	0.67	1.27
Khasab Reef	66	513.2	49.1	1404.3	-0.43	1.55
Coral Garden	58	543.6	47.1	1306.6	0.21	1.32
Rashid Island	82	469.8	39.9	1156.1	-0.33	-0.55

Appendix D: Publications from thesis

Publications from thesis chapters:

Bauman AG, Baird AH, Cavalcante GH (2011) Coral reproduction in the world's warmest reefs: southern Persian Gulf (Dubai, United Arab Emirates). Coral Reefs 30:405–413

Bauman AG, Pratchett MS, Baird AH, Riegl B, Heron SF, Feary DA (2013) Variation in the size structure of corals is related to environmental extremes in the Persian Gulf. Marine Environmental Research 84:43–50

Bauman AG, Feary DA, Heron SF, Pratchett MS, Burt JA (2013) Multiple environmental factors influence the spatial distribution and structure of reef communities in the northeastern Arabian Peninsula. Marine Pollution Bulletin doi.org/10.1016/j.marpolbul.2012.10.013.

Bauman AG, Baird AH, Burt JA, Pratchett MS, Feary DA (In revision) Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates). Marine Ecology Progress Series

Additional publications during candidature

Bauman AG, Burt J, Feary DA, Marquis E, Usseglio P (2010*)* Tropical harmful algal blooms*:* an emerging threat to coral reef communities? Marine Pollution Bulletin 60:2117–2122

Burt J, Bauman AG, Feary DA, Usseglio P, Sale P (2010) The influence of wave exposure on coral community development on large-scale man-made breakwater reefs, with a comparison to a natural reef. Bulletin of Marine Science 86:839–859

Feary DA, Burt J, Bauman AG, Usseglio P, Sale PF, Cavalcante GH (2010) Fish communities on the world's warmest reefs: What can they tell us about impacts of a climate change future? Journal of Fish Biology 77: 1931–1947

Burt JA, Feary DA, Bauman AG, Usseglio P, Cavalcante GH, Sale PF (2011) Biogeographic patterns of reef fish community structure in the northeastern Arabian Peninsula. ICES Journal of Marine Science 68:1875–1883

Cavalcante GH, Kjerfve B, Feary DA, Bauman AG, Usseglio P (2011) Water currents and water budget in a coastal mega-structure, Palm Jumeirah Lagoon in Dubai, UAE. Journal of Coastal Research 27:348–393

Sale PF, Feary DA, Burt JA, Bauman AG, Cavalcante GH, Drouillard KG, Kjerfve B, Marquis E, Trick C, Usseglio P, van Lavieren H (2011) The growing need for sustainable ecological management of marine communities of the Persian Gulf. Ambio 40:4–17

Mora C, Aburto-Oropeza O, Bocos AA, Ayotte PM, Banks S, Bauman AG, Beger M, Bessudo S, Booth DJ, Brokovich E, Brooks A, Chabanet P, Cinner J, Cortés J, Magaña AC, DeMartini E, Edgar GJ, Feary DA, Ferse SCA, Friedlander A, Gaston KJ, Gough C, Graham NAJ, Green A, Guzman H, Kulbicki M, Letourneur Y, Pérez AL, Loya Y, Martinez C, Mascareñas-Osorio I, Morove T, Nadon MO, Nakamura Y, Paredes G, Polunin N, Pratchett MS, Bonilla HR, Rivera F, Sala E, Sandin S, Soler G, Stuart-Smith R, Tessier E, Tupper M, Usseglio P, Vigliola L, Wantiez L, Williams I, Wilson SK, Zapata FA (2011) Human footprint on the linkages between diversity and function in reef fishes. PLoS Biology 9(4):e1000606. doi:10.1371/journal.pbio.1000606

Feary DA, Burt, JA, Cavalcante GH, Bauman AG (2012) Extreme physical factors and the structure of Gulf fish and reef communities. In Riegl BM, Purkis SJ (Eds) Coral Reefs of the Gulf, Adaptation to Climatic Extremes. Springer Science +Business Media, New York.

Burt JA, Feary DA, Bauman AG, Cavalcante G, Usseglio P (In press) Urban breakwaters as reef fish habitat in the Persian Gulf. Marine Pollution Bulletin doi.org/10.1016/j.marpolbul.2012.10.019

Pratchett, MS Hoey AS, Feary DF, Bauman AG, Burt JA, Riegl BM (In press) Functional composition of *Chaetodon* butterflyfishes at a peripheral and extreme coral reef location, the Persian Gulf. Marine Pollution Bulletin doi.org/10.1016/j.marpolbul.2012.10.014

Feary DA, Burt JA, Bauman AG, Hazeem SA, Abdel-Moati MA, Al-Khalifa KA, Anderson DM, Amos C, Baker A, Bartholomew A, Bento R, Cavalcante GH, Chen CA, Coles SL, Dab K, Fowler AM, George D, Grandcourt E, Hill R, John DM, Jones DA, Keshavmurthy S, Mahmoud H, Tapeh MMO, Mostafavi PG, Naser H, Pichon M, Purkis S, Riegl B, Samimi-Namin K, Sheppard C, Samiei JV, Voolstra CR, Wiedenmann J (In press) Critical research needs for identifying change in Gulf coral reef ecosystems. Marine Pollution Bulletin doi: 10.1016/j.marpolbul.2013.02.038.