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The ecological response of reef communities to an extreme environment: implications for climate change

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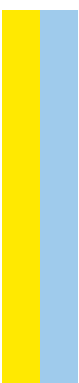RITA COSTA SAN MIGUEL BENTO CAVALCANTE

THE ECOLOGICAL RESPONSE OF REEF COMMUNITIES TO AN EXTREME ENVIRONMENT: IMPLICATIONS FOR CLIMATE CHANGE

Tese de Candidatura ao grau de Doutor em Ciências Biomédicas submetida ao Instituto de Ciências Biomédicas Abel Salazar da Universidade do Porto.

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Author Statement

This doctoral thesis includes two articles that have been published in peer-review international journals, as listed below. Both of these articles are included in Chapter 2 and Chapter 3, and the remaining Chapters, 4 and 5, are formatted with the intuition of publishing shortly. Chapters from 2 to 5 are preceded with an introductory text and the highlights of the respective findings. The candidate was responsible for all data collection needed for the completion of this thesis, as well as the analyses and writing process of all chapters. All the work process was in close cooperation with, and reviewed by, the supervisors as well as other researchers.

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Acknowledgments

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Abstract

Detrimental effects of climate change on socioeconomically and biologically important coral reef ecosystems are apparent globally. Increasingly recurrent bleaching events have reduced coral cover and structural complexity, with changes resulting in shifts from coral to macroalgal-dominated states and concomitant adjustments in the reef communities. Predicted increases in the frequency and severity of globally relevant bleaching events highlight the need to understand how reef communities are structured in naturally extreme environments. The current study aims to explore how reef communities, including both benthic and fish communities, are structured by focusing on the environmentally extreme Arabian/Persian Gulf, comparing these communities with those found in the more environmentally benign conditions within the neighboring Musandam and Sea of Oman. The Chapter 2 of this study explores the reef benthic community structure within the three regions, during a three-year period, and shows that coral communities might persist under an increasingly disturbed future environment, although in a more structurally simple configuration. Chapter 3 examines seasonal and spatial variability in the composition of new colonists among regions, with results revealing a meager rate of coral settlement in the region, suggesting that reefs are likely to recover slowly from disturbances. Chapter 4 explores spatial and seasonal variation on the density, biomass, size structure, and functional composition of small site-attached reef fish communities within the three regions, finding spatial differences in community composition, as well as lower biomass and density in the Arabian/Persian Gulf. Chapter 5 investigates, through the use of experimental tiles, the rates of herbivory and identifies key herbivores species in the Arabian/Persian Gulf and the Sea of Oman, with findings showing that one single abundant omnivore angelfish acts as a functionally important herbivore in the Arabian/Persian Gulf. Altogether, the results of this work has shown that coral reef fauna can occur in extreme environmental conditions predicted to arise as a consequence of future global warming, but that there are incredible ramifications on the diversity and functional ecology of these ecosystems. These results provide insights into changes we may expect on reefs elsewhere in the future.

Resumo

Os efeitos prejudiciais das mudanças climáticas em ecossistemas de recifes de coral de elevada importância socioeconómica e biológica são globalmente visíveis. Episódios de branqueamento, cada vez mais frequentes, têm vindo a reduzir a extensão e a complexidade estrutural dos corais, resultando em mudanças no domínio de corais para macroalgas e respectivos ajustes nas comunidades dos recifes. Aumentos previstos globalmente na frequência e gravidade de episódios de branqueamento destacam a necessidade de entender como as comunidades de recifes são estruturadas em ambientes naturais extremos. O presente estudo tem como objetivo explorar como as comunidades de recifes, incluindo comunidades bentónicas e de peixes, são estruturadas no Golfo Arábico/Pérsico, comparando com comunidades em condições ambientalmente mais benignas de Musandam e do Mar de Omã. O capítulo 2 deste estudo explora a estrutura da comunidade bentónica dos recifes destas três regiões, durante um período de três anos, verificando-se que as comunidades de corais podem persistir sob um ambiente futuro cada vez mais alterado, embora numa configuração estruturalmente mais simples. O capítulo 3 examina a variabilidade sazonal e espacial na composição de novos recrutas entre as regiões, revelando uma escassa taxa de fixação de corais na região, sugerindo uma lenta recuperação dos recifes a ocorrências adversas. O capítulo 4 estuda as variações espaciais e sazonais da densidade, biomassa, estrutura das classes de tamanho e composição funcional das comunidades de peixes de recife nas três regiões, encontrando-se diferenças espaciais na composição da comunidade, bem como menor biomassa e densidade na região do Golfo Arábico/Pérsico. O capítulo 5 investiga, através do uso de telhas experimentais, as taxas de herbivoria e identifica espécies-chave de herbívoros no Golfo Arábico/Pérsico e no Mar de Omã, com descobertas mostrando que uma única espécie de peixe-anjo omnívoro, abundante na região, age como o principal herbívoro no Golfo Arábico/Pérsico. Em conjunto, os resultados deste trabalho demonstram que a fauna de recifes de coral pode ocorrer em condições ambientais extremas, previstas no futuro como consequência do aquecimento global, mas que existem diversas ramificações

na diversidade e ecologia funcional desses ecossistemas. Estes resultados fornecem informações sobre mudanças previstas nos recifes de coral no futuro.

Chapter 1 Introduction

Coral reefs occupy less than 0.1% of the marine environment but are home to over a quarter of all marine biodiversity (Veron et al., 2009). These marine ecosystems are extremely diverse, ecologically complex and function as important breeding, spawning, nursery, shelter and feeding areas for a multitude of organisms (Moberg and Folke, 1999). In addition to its importance to biodiversity, reefs also provide essential economic revenues for coastal populations around the world; an estimated 350,000 int$/year/ha in goods and services are produced annually, directly supporting tens of millions of people living in developing countries that border coral reefs through food, coastal protection, building materials, medicines, and economic value from tourism and fisheries (Moberg and Folke, 1999; Martínez et al., 2007; Sheppard et al., 2009; De Groot et al., 2012; Spalding et al., 2017).

Coral reefs under threat

Despite their importance, coral reefs are globally under threat from anthropogenic impacts of overfishing, pollution, coastal development, destructive tourism activities, and climate change (Moberg and Folke, 1999). Due to the thermal sensitivity of reef-building corals, coral reefs worldwide have undergone mass bleaching events, where increases of sea surface temperatures (SSTs) causes corals to expel their symbiotic algae (zooxanthellae, *Symbiodinium* spp.) (Rowan, 2004). Depending on the severity and duration of the thermal stress that reefs face, the impacts of such bleaching can vary from changes in the species composition and functional traits structure of coral assemblages, with coral communities transitioning from more sensitive branching corals to more resilient massive species (Marshall and Baird, 2000; McClanahan et al., 2007; Hughes et al., 2018b) to almost total loss of the coral population and shifts to an algal dominated stable state (termed 'phase shift') (Hughes, 1994; Pandolfi et al., 2003).

Given the slow growth rates of corals and their sensitivity to stress, phase shifts can cause substantial impacts to the ecological and economic integrity of reef systems (Knowlton, 1992; Moberg and Folke, 1999; Scheffer et al., 2001). Numerous studies have shown that phase-shifts from coral to algal dominated systems can occur rapidly after disturbance (i.e., several months following disturbance) and can persist

over long time periods (such as 15 years) (Hughes, 1994; Hughes et al., 2007; Cvitanovic and Bellwood, 2008; Diaz-Pulido et al., 2009; Cheal et al., 2010). In addition, recent climate change models have predicted an increase in the frequency and severity of mass coral bleaching events as a reaction to the rise of ocean temperatures (Teneva et al., 2011; Frieler et al., 2013; Hughes et al., 2018a). As a consequence, it is expected that there will be an increase in coral mortality globally accompanied by a phase-shift towards an algae-dominated system (Ledlie et al., 2007; Diaz-Pulido et al., 2009). These phase-shifts produce a cascade of effects within coral reef assemblages, from declines in coral recruitment, to subsequent impacts on other species that are dependent on corals, which leads to a degradation of reefs (Wilson et al., 2006; Munday et al., 2008).

Reef communities' responses to hostile conditions

Benthic communities

Reef recovery from disturbances depends significantly on the supply of available colonists that can settle on the substrate made available by the death of corals (Gilmour et al., 2013). This new open-space can be either colonized by new coral larvae (Hughes and Tanner, 2000), turf and/or coralline algae (Gilmour et al., 2013) or other organisms that can exclude and outcompete corals, such as macroalgae and sponges (Diaz-Pulido and McCook, 2002; Norström et al., 2009). Whether there is a long-term shift into a new stable state community (Roff et al., 2015) or a rapid return to the pre-disturbance assemblage (Halford et al., 2004; Adjeroud et al., 2009) will depend on both stochastic and deterministic processes (Lillis et al., 2016). While the supply of potential larval colonists is predominantly affected by stochastic processes (e.g. currents, predation (Keough and Downes, 1982; Siegel et al., 2008)), deterministic processes such as habitat availability, larval substratum preference, and interactions with existing community members underlie much of the settlement process occurring on reefs (Lillis et al., 2016). After settlement, final community structure will depend on post-settlement processes (Caley et al., 1996).

Small-bodied reef dependent fish community

Decreases in coral species diversity and a reduction in the three-dimensional reef complexity after disturbance can have immediate impacts on the associated fauna

(Berumen and Pratchett, 2006). Reef fish populations that depend on the reef for food and shelter can be directly affected by shifts in coral communities, resulting in reductions in abundance, diversity and size structure of fishes (Wilson et al., 2006; Pratchett et al., 2008; Bonin et al., 2011; Bellwood et al., 2012; Rogers et al., 2014). Most impacted by changes in the structure of coral reef communities are small-bodied, site-attached fish species. These species constitute a substantial numerical proportion of reef fish communities, and are inherently associated with the reef matrix and reliant on fine-scale habitat structure (Munday and Jones, 1998; Ferreira et al., 2001). In parallel with their habitat dependence, the limited regenerative capacity and short life-spans of small-bodied site-attached fish species (Bellwood et al., 2006) makes them extremely responsive to environmental change and particularly useful for investigating reef fish responses under extreme environments (Depczynski and Bellwood, 2004; Pratchett et al., 2008).

The importance of herbivory on reef resilience

There is increasing evidence to show that a range of fish functional groups may promote resilience of coral reef communities by controlling the benthic algae, sponges and coral growth, potentially affecting reef trajectories following disturbance (Burkepile and Hay, 2008; Cole et al., 2009; Pawlik et al., 2013). Many factors can promote ecosystem vulnerability and trigger a shift from coral to macroalgal-dominance (Hughes et al., 2007), but the reduction or disappearance of critical functional groups such as herbivores are considered vital components of this process (Scheffer et al., 2001; Hughes et al., 2007; Ledlie et al., 2007). One of the primary factors suggested to control the transition from coral to algal dominance is the grazing action of herbivorous fish and invertebrates (Burkepile and Hay, 2008; Ceccarelli et al., 2011). Herbivores regulate the competitive relationship between macroalgae and coral communities by removing competitive dominant algae that can inhibit coral growth, while also opening suitable space for the settlement of coral spat (Hughes, 1994; Lirman, 2001; Jompa and McCook, 2002; Bellwood et al., 2004; Burkepile and Hay, 2008; Green and Bellwood, 2009). Herbivorous grazing may be an essential factor affecting coral recovery following major disturbances such as bleaching events, with grazers then acting as regulators of both community structure and function (Lessios, 1988; Moberg and Folke, 1999; Nyström and Folke, 2001; Bellwood et al., 2004).

It is likely that herbivores will play a crucial role in the resilience and recovery potential of coral reefs amid climate change increases in the degradation of reef habitats (Diaz-Pulido et al., 2009). However, the magnitude and extent of the importance of herbivores under increasing sea surface temperatures, as well as changes in the structure of the reef-dependent community, is not well understood (Feary et al., 2010; Pratchett et al., 2013; Hoey et al., 2016). As such, it is appropriate to examine the role of herbivory in structuring benthic communities in areas currently exposed to naturally high sea-surface temperatures in order to develop an understanding of the potential role of herbivores in structuring reef communities under future climate change.

Reef resilience will be, in part, determined by the localized environmental context in which communities occur (Hoegh-Guldberg, 1999; Coles and Riegl, 2013). Environmental factors, such as, temperature, salinity, and light, can strongly influence the growth, mortality, fecundity, and settlement of corals (Hoegh-Guldberg, 1999; Baird and Marshall, 2002; Riegl and Purkis, 2012), and hence their capacity to re-assemble following disturbances (Hoegh-Guldberg et al., 2007), control recruitment and settlement of other reef benthos (Chan and Williams, 2003; Saunders and Metaxas, 2007; Przeslawski et al., 2008) as well as influence the reef fish community (Munday et al., 2008; Wilson et al., 2010; Burt et al., 2011; Richards et al., 2012).

The Gulf

While reefs commonly exist in relatively stable and thermally optimal environmental conditions, reefs throughout the Arabian Peninsula occur in what is regarded as an extreme environment and can serve as a gateway to show us possible future changes and acclimation of the reef community to future climate-change induced warm-water anomalies (Feary et al., 2012; Burt et al., 2014; Shraim et al., 2017). The Persian/Arabian Gulf (hereafter 'the Gulf') has been known in the scientific community as a natural laboratory where the study of the effects of climate change is possible to do in situ (Feary et al., 2010; Pratchett et al., 2013; Burt et al., 2014; Shraim et al., 2017).

The Gulf is a small, semi-enclosed shallow marine environment with maximum depth 90m (Sheppard et al., 2010a). This semi-enclosed basin has a restricted water

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exchange due to the narrow 50 km connection with the Sea of Oman and the Arabian Sea through the Strait of Hormuz (Sheppard et al., 1992; Reynolds, 1993; Coles, 2003). The water enters along the Iranian coast at surface levels, reaching the Arabian coast after in an anti-clockwise broad circulation pattern (Sheppard et al., 2010a). Due to its location, in an arid subtropical environment, with very little river inflow or fast oceanic water circulation refill, seawater temperatures and salinity have normal extremes values (B. M. Riegl and Purkis, 2012). Although being a sub-tropical region, located above the Tropic of Cancer, it presents a more tropical climate in the summer and a more temperate one in the winter than in other areas at the same latitude (Sheppard, 1993; Sheppard et al., 2010a). For example, SST values observed in the Gulf are the widest range encountered worldwide on reefs, with average annual temperature range of 24°C, varying from 12°C in the winter months to 36°C during the summer (Price et al., 1993; Riegl, 2001; Sheppard and Loughland, 2002; Coles, 2003). This is in comparison with other tropical regions, where the range in SST is usually limited to ~19°C, being often the upper limits between 33ºC and 34ºC and the lower limits reaching 13 to 16ºC (Coles, 2003).

High temperatures in the summer, together with dry winds in the winter and little precipitation results in an average of 1 to 2 m evaporation per year in the Gulf (Sheppard et al., 2010a). Salinity values in the Gulf usually are higher than 39 psu (Sheppard et al., 2010a; Sheppard et al., 2012), reaching values as high as 70 psu in the Bahrain embayments (Sheppard et al., 2010a) and 50 psu in some coral areas (Coles, 2003). These salinity values experienced in the Gulf exceed the optimum range of coral reefs in other tropical regions (i.e., within the Atlantic and Pacific) that generally have a salinity interval of 35 to 37 and an upper tolerance range between 40 and 45 (Price et al., 1993; Coles, 2003).

Strong variation in SST and high salinity values within the Gulf substantially influence water density, currents, water mixing, and a host of other environmental parameters, and therefore species composition (Price et al., 1993; Riegl, 2001; Coles, 2003). These conditions make the Gulf an ideal location to study the effects of climate change on oceanic processes and to develop an understanding of potential changes in coral reefs and coral communities in the future under climate change effects (Sheppard and Loughland, 2002; Baker et al., 2004; Feary et al., 2010; Sheppard et

al., 2010b). To understand these effects entirely, it is essential to compare studies conducted in the Gulf with a biogeographically similar areas that have more favorable conditions.

The Gulf is bordered to the east by the Sea of Oman, part of the Arabian Sea and the Indian Ocean (Sheppard et al., 1992). The Gulf and the Sea of Oman are biogeographically connected with one another through the Strait of Hormuz, and although both share close taxonomic affinities, each represents very different environmental conditions (Carpenter et al., 1997; Coles, 1997; 2003; Feary et al., 2010). The Sea of Oman contains deeper waters that are well mixed, with mild seasonal changes in SSTs, ranging from 32°C in the summer to 20°C in winter, as well as in salinity, presenting values between 35 and 37 (Coles, 1997; Böhm et al., 1999; Coles, 2003; Foster et al., 2012). Both the Sea of Oman and Straits of Hormuz have substantial vertical mixing of the water (Bauman et al., 2013). As such, the Gulf and the Sea of Oman make an ideal natural experimental area to study the effects of climate change in marine ecological processes, and these two areas can be compared using observational and manipulative studies in order to examine the importance of herbivory under different climatic conditions.

Reef communities in an extreme environment

Although the Gulf is a harsh environment, the coral reefs of this region can survive in what is considered extreme conditions in other areas of the globe (Sheppard et al., 1992). As a result of these extreme conditions, the region represents a less complex and less diverse reef ecosystem when compared to other reefs in the Indo-Pacific (Sheppard et al., 1992). Different physical factors influence the structure of the benthic community in the northeastern Arabian Peninsula. These factors include extreme temperatures, high salinities, macroalgal competition, and geographic isolation (Coles, 2003). Temperatures extremes and high salinity are the two most important factors, but chlorophyll-a concentrations, surface currents and wind speeds have been recently shown to play also a significant role (Bauman et al., 2013). Changes in the actual topography of these reefs have influenced different organisms that inhabit the Gulf and their metabolism; such as fish feeding habits (Burt et al., 2011; Pratchett et al., 2013), and benthic communities diversity.

Research aims

The purpose of this dissertation was to understand how reef communities within the Gulf are structured within the naturally extreme variations in sea-surface temperatures and salinity, as well as under increasing environmental disturbances, and compare these with reef communities in more benign environmental conditions. This study analyses responses from benthic communities (corals and non-corals) and small-bodied reef-dependent fish communities to extreme environments as it also looks at the main functional group of fishes, herbivores, responsible for the reef resilience. The first chapter of this dissertation explores how benthic coral ecosystems are structured within extreme environments with recurrent disturbances, showing that although coral communities may persist under such stress, a much more structurally simple configuration is expected. As the recovery of reefs is strongly dependent on the benthic organisms settling after disturbances, in the second chapter, I examine the spatial and seasonal patterns in settlement of benthic reef organisms, with results indicating that these reefs are likely to recover at a slow rate from on-going and future disturbances due to the low rates of larval coral settlement to these reefs. In the third chapter, I study how the community structure of small-bodied reef fish is impacted by the extreme seasonal variation of different environmental factors, with results showing fundamental impacts in density and biomass, as well as substantial changes in the associated fish community's functional composition which are likely to happen on reefs as global climate continues to change. In the final chapter, I conduct a manipulative experiment to elucidate the role of macro-herbivores in the removal of macroalgae in an extreme reef environment (the Gulf) compared with a more benign environment (the Sea of Oman), with results showing different taxa being responsible for herbivory within each environment. Surprisingly, the key species responsible for algae removal in the Gulf was not the expected local herbivores, but a single hyper-abundant omnivore species (an angelfish), while sea urchins were the active herbivores in the Sea of Oman. Together, these studies provide profound insights into how reefs around the world may react to increasing climate change and anthropogenic pressure and will help to identify the main herbivorous groups that are predicted to play an important role in the resilience and recovery of reefs in future environments with extreme conditions. The extrapolation of these results can help in predicting

alterations that are likely to occur in other regions worldwide as a consequence of climate change.

References

Adjeroud, M., Michonneau, F., Edmunds, P.J., Chancerelle, Y., Lison de Loma, T., Penin, L., et al. (2009). Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs* 28(3)**,** 775-780.

Baird, A.H., and Marshall, P.A. (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* 237**,** 133-141.

Baker, A.C., Starger, C.J., McClanahan, T.R., and Glynn, P.W. (2004). Coral reefs: corals' adaptive response to climate change. *Nature* 430(7001)**,** 741.

Bellwood, D.R., Baird, A.H., Depczynski, M., Gonzalez-Cabello, A., Hoey, A.S., Lefevre, C.D., et al. (2012). Coral recovery may not herald the return of fishes on damaged coral reefs. *Oecologia* 170(2)**,** 567-573.

Bellwood, D.R., Hoey, A.S., Ackerman, J.L., and Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* 12(9)**,** 1587-1594.

Bellwood, D.R., Hughes, T.P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. *Nature* 429(6994)**,** 827-833.

Berumen, M.L., and Pratchett, M.S. (2006). Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. *Coral Reefs* 25(4)**,** 647-653.

Böhm, E., Morrison, J.M., Manghnani, V., Kim, H.S., and Flagg, C.N. (1999). The Ras al Hadd Jet: remotely sensed and acoustic Doppler current profiler observations in 1994-1995. *Deep Sea Research Part II: Topical Studies in Oceanography* 46(8-9)**,** 1531-1549.

Bonin, M.C., Almany, G.R., and Jones, G.P. (2011). Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* 92(7)**,** 1503-1512.

Burkepile, D.E., and Hay, M.E. (2008). Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences* 105(42)**,** 16201-16206.

Burt, J., Van Lavieren, H., and Feary, D.A. (2014). Persian Gulf reefs: an important asset for climate science in urgent need of protection. *Ocean Challenge* 20**,** 49-56.

Burt, J.A., Feary, D.A., Bauman, A.G., Usseglio, P., Cavalcante, G.H., and Sale, P.F. (2011). Biogeographic patterns of reef fish community structure in the northeastern Arabian Peninsula. *ICES Journal of Marine Science* 68(9)**,** 1875-1883.

Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., and Menge, B.A. (1996). Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27(1)**,** 477-500.

Carpenter, K.E., Krupp, F., Jones, D.A., and Zajonz, U. (1997). *The living marine resources of Kuwait, Eastern Saudi Arabia, Bahrain, Qatar, and the United Arab Emirates.* Rome: Food & Agriculture Org.

Ceccarelli, D.M., Jones, G.P., and McCook, L.J. (2011). Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. *Journal of Experimental Marine Biology and Ecology* 399(1)**,** 60-67.

Chan, B.K.K., and Williams, G.A. (2003). The impact of physical stress and molluscan grazing on the settlement and recruitment of Tetraclita species (Cirripedia: Balanomorpha) on a tropical shore. *Journal of Experimental Marine Biology and Ecology* 284(1-2), 1-23.

Cheal, A.J., MacNeil, M.A., Cripps, E., Emslie, M.J., Jonker, M., Schaffelke, B., et al. (2010). Coral–macroalgal phase shifts or reef resilience: links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. *Coral Reefs* 29(4), 1005-1015.

Cole, A.J., Pratchett, M.S., and Jones, G.P. (2009). Effects of coral bleaching on the feeding response of two species of coral-feeding fish. *Journal of Experimental Marine Biology and Ecology* 373(1), 11-15.

Coles, S.L. (1997). Reef corals occurring in a highly fluctuating temperature environment at Fahal Island, Gulf of Oman (Indian Ocean). *Coral Reefs* 16(4), 269-272.

Coles, S.L. (2003). Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific Region. *Atoll Research Bulletin* 507, 1-19.

Coles, S.L., and Riegl, B.M. (2013). Thermal tolerances of reef corals in the Gulf: a review of the potential for increasing coral survival and adaptation to climate change through assisted translocation. *Marine Pollution Bulletin* 72(2), 323-332.

Cvitanovic, C., and Bellwood, D.R. (2008). Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral Reefs* 28(1), 127-133.

De Groot, R., Brander, L., Van Der Ploeg, S., Costanza, R., Bernard, F., Braat, L., et al. (2012). Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services* 1(1), 50-61.

Depczynski, M., and Bellwood, D.R. (2004). Microhabitat utilisation patterns in cryptobenthic coral reef fish communities. *Marine Biology* 145(3), 455-463.

Diaz-Pulido, G., and McCook, L.J. (2002). The fate of bleached corals: patterns and dynamics of algal recruitment. *Marine Ecology Progress Series* 232, 115-128.

Diaz-Pulido, G., McCook, L.J., Dove, S., Berkelmans, R., Roff, G., Kline, D.I., et al. (2009). Doom and boom on a resilient reef: climate change, algal overgrowth and coral recovery. *PLoS ONE* 4(4), e5239.

Feary, D.A., Burt, J.A., Bauman, A.G., Usseglio, P., Sale, P.F., and Cavalcante, G.H. (2010). Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future? *Journal of Fish Biology* 77(8), 1931-1947.

Feary, D.A., Burt, J.A., Cavalcante, G.H., and Bauman, A.G. (2012). "Extreme physical factors and the structure of Gulf fish and reef communities," in *Coral Reefs of the Gulf,* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 163-170.

Ferreira, C.E., Goncalves, J.E., and Coutinho, R. (2001). Community structure of fishes and habitat complexity on a tropical rocky shore. *Environmental Biology of Fishes* 61(4), 353-369.

Foster, K., Foster, G., Al-Cibahy, A.S., Al-Harthi, S., Purkis, S.J., and Riegl, B.M. (2012). "Environmental setting and temporal trends in southeastern Gulf coral communities," in *Coral Reefs of the Gulf,* eds. B. Riegl & S. Purkis. (Dordrecht: Springer), 51-70.

Frieler, K., Meinshausen, M., Golly, A., Mengel, M., Lebek, K., Donner, S.D., et al. (2013). Limiting global warming to 2 C is unlikely to save most coral reefs. *Nature Climate Change* 3(2)**,** 165-170.

Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H., and Pratchett, M.S. (2013). Recovery of an isolated coral reef system following severe disturbance. *Science* 340(6128)**,** 69-71.

Green, A.L., and Bellwood, D.R. (2009). *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific Region.* Gland, Switzerland: IUCN.

Halford, A., Cheal, A.J., Ryan, D., and Williams, D.M. (2004). Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85(7)**,** 1892-1905.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50(8)**,** 839 - 866.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., et al. (2007). Coral reefs under rapid climate change and ocean acidification. *Science* 318(5857)**,** 1737-1742.

Hoey, A.S., Feary, D.A., Burt, J.A., Vaughan, G., Pratchett, M.S., and Berumen, M.L. (2016). Regional variation in the structure and function of parrotfishes on Arabian reefs. *Marine Pollution Bulletin* 105(2)**,** 524-531.

Hughes, T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265(5178)**,** 1547-1551.

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., et al. (2018a). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359(6371)**,** 80-83.

Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., et al. (2018b). Global warming transforms coral reef assemblages. *Nature* 556(7702)**,** 492.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., et al. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17(4)**,** 360-365.

Hughes, T.P., and Tanner, J.E. (2000). Recruitment failure, life histories, and long-term decline of Caribbean corals. *Ecology* 81(8)**,** 2250-2263.

Jompa, J., and McCook, L.J. (2002). Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology* 271(1)**,** 25-39.

Keough, M.J., and Downes, B.J. (1982). Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54(3)**,** 348-352.

Knowlton, N. (1992). Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32(6)**,** 674-682.

Ledlie, M.H., Graham, N.A.J., Bythell, J.C., Wilson, S.K., Jennings, S., Polunin, N.V.C., et al. (2007). Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* 26(3)**,** 641–653.

Lessios, H.A. (1988). Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Annual Review of Ecology and Systematics* 19(1)**,** 371-393.

Lillis, A., Bohnenstiehl, D., Peters, J.W., and Eggleston, D. (2016). Variation in habitat soundscape characteristics influences settlement of a reef-building coral. *PeerJ* 4**,** e2557.

Lirman, D. (2001). Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19(4)**,** 392-399.

Marshall, P.A., and Baird, A.H. (2000). Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19(2)**,** 155-163.

Martínez, M.L., Intralawan, A., Vázquez, G., Pérez-Maqueo, O., Sutton, P., and Landgrave, R. (2007). The coasts of our world: Ecological, economic and social importance. *Ecological Economics* 63**,** 254-272.

McClanahan, T.R., Ateweberhan, M., Graham, N.A.J., Wilson, S.K., Sebastián, C.R., Guillaume, M.M.M., et al. (2007). Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series* 337**,** 1-13.

Moberg, F., and Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecological Economics* 29(2)**,** 215-233.

Munday, P.L., and Jones, G.P. (1998). "The ecological implications of small body size among coral-reef fishes," in *Oceanography and Marine Biology: An Annual Review,* eds. A.D. Ansell, R.N. Gibson & M. Barnes. UCL Press), 373-411.

Munday, P.L., Jones, G.P., Pratchett, M.S., and Williams, A.J. (2008). Climate change and the future for coral reef fishes. *Fish and Fisheries* 9(3)**,** 261-285.

Norström, A.V., Nyström, M., Lokrantz, J., and Folke, C. (2009). Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Marine Ecology Progress Series* 376**,** 295-306.

Nyström, M., and Folke, C. (2001). Spatial Resilience of Coral Reefs. *Ecosystems* 4(5)**,** 406-417.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., et al. (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301(5635)**,** 955-958.

Pawlik, J.R., Loh, T.-L., McMurray, S.E., and Finelli, C.M. (2013). Sponge communities on Caribbean coral reefs are structured by factors that are top-down, not bottom-up. *PLoS ONE* 8(5)**,** e62573.

Pratchett, M.S., Hoey, A.S., Feary, D.A., Bauman, A.G., Burt, J.A., and Riegl, B.M. (2013). Functional composition of Chaetodon butterflyfishes at a peripheral and extreme coral reef location, the Persian Gulf. *Marine Pollution Bulletin* 72(2)**,** 333-341.

Pratchett, M.S., Munday, P.L., Wilson, S.K., Graham, N.A.J., Cinner, J.E., Bellwood, D.R., et al. (2008). Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences. *Oceanography and Marine Biology* 46**,** 251-296.

Price, A.R.G., Sheppard, C.R.C., and Roberts, C.M. (1993). The Gulf: its biological setting. *Marine Pollution Bulletin* 27**,** 9-15.

Przeslawski, R., Ahyong, S., Byrne, M., Wörheide, G., and Hutchings, P.A.T. (2008). Beyond corals and fish: the effects of climate change on noncoral benthic invertebrates of tropical reefs. *Global Change Biology* 14(12)**,** 2773-2795.

Reynolds, R.M. (1993). Physical oceanography of the Gulf, Strait of Hormuz, and the Gulf of Oman - Results from the Mt Mitchell expedition. *Marine Pollution Bulletin* 27**,** 35-59.

Richards, B.L., Williams, I.D., Vetter, O.J., and Williams, G.J. (2012). Environmental factors affecting large-bodied coral reef fish assemblages in the Mariana Archipelago. *PLoS ONE* 7(2)**,** e31374.

Riegl, B. (2001). Inhibition of reef framework by frequent disturbance: examples from the Arabian Gulf, South Africa, and the Cayman Islands. *Palaeogeography, Palaeoclimatology and Palaeoecology* 175(1-4), 79-101.

Riegl, B.M., and Purkis, S.J. (2012). "Environmental constraints for reef building in the Gulf," in *Coral Reefs of the Gulf,* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 5-32.

Roff, G., Doropoulos, C., Zupan, M., Rogers, A., Steneck, R.S., Golbuu, Y., et al. (2015). Phase shift facilitation following cyclone disturbance on coral reefs. *Oecologia* 178(4), 1193-1203.

Rogers, A., Blanchard, J.L., and Mumby, P.J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology* 24(9), 1000-1005.

Rowan, R. (2004). Coral bleaching: thermal adaptation in reef coral symbionts. *Nature* 430(7001), 742.

Saunders, M., and Metaxas, A. (2007). Temperature explains settlement patterns of the introduced bryozoan Membranipora membranacea in Nova Scotia, Canada. *Marine Ecology Progress Series* 344, 95-106.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., and Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature* 413(6856), 591-596.

Sheppard, C., Al-Husiani, M., Al-Jamali, F., Al-Yamani, F., Baldwin, R., Bishop, J., et al. (2010a). The Gulf: a young sea in decline. *Marine Pollution Bulletin* 60(1), 13-38.

Sheppard, C., Al-Husiani, M., Al-Jamali, F., Al-Yamani, F., Baldwin, R., Bishop, J., et al. (2010b). The Gulf: A young sea in decline. *Marine Pollution Bulletin* 60, 13-38.

Sheppard, C., Al-Husiani, M., F. Al-Jamali, Al-Yamani, F., Baldwin, R., Bishop, J., et al. (2012). "Environmental concerns for the future of Gulf coral reefs," in *Coral Reefs Gulf.: Adaptations to Climatic Extremes,* eds. B. Riegl & S.J. Purkis.), 349–368.

Sheppard, C., and Loughland, R. (2002). Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. *Aquatic Ecosystem Health and Management* 5(4), 395-402.

Sheppard, C., Price, A., and Roberts, C. (1992). *Marine ecology of the Arabian Region: patterns and processes in extreme tropical environments.* Toronto: Academic Press.

Sheppard, C.R. (1993). Physical environment of the Gulf relevant to marine pollution: an overview. *Marine Pollution Bulletin* 27, 3-8.

Sheppard, C.R.C., Davy, S.K., and Pilling, G.M. (2009). *The biology of coral reefs.* Oxford University Press.

Shraim, R., Dieng, M.M., Vinu, M., Vaughan, G., McParland, D., Idaghdour, Y., et al. (2017). Environmental extremes are associated with dietary patterns in Arabian Gulf reef fishes. *Frontiers in Marine Science* 4, 285.

Siegel, D.A., Mitarai, S., Costello, C.J., Gaines, S.D., Kendall, B.E., Warner, R.R., et al. (2008). The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences* 105(26), 8974-8979.

Spalding, M., Burke, L., Wood, S.A., Ashpole, J., Hutchison, J., and zu Ermgassen, P. (2017). Mapping the global value and distribution of coral reef tourism. *Marine Policy* 82, 104-113.

Teneva, L., Karnauskas, M., Logan, C.A., Bianucci, L., Currie, J.C., and Kleypas, J.A. (2011). Predicting coral bleaching hotspots: the role of regional variability in thermal stress and potential adaptation rates. *Coral Reefs* 31(1)**,** 1-12.

Veron, J.E., Hoegh-Guldberg, O., Lenton, T.M., Lough, J.M., Obura, D.O., Pearce-Kelly, P., et al. (2009). The coral reef crisis: the critical importance of<350 ppm CO2. *Marine Pollution Bulletin* 58(10)**,** 1428-1436.

Wilson, S.K., Adjeroud, M., Bellwood, D.R., Berumen, M.L., Booth, D., Bozec, Y.M., et al. (2010). Crucial knowledge gaps in current understanding of climate change impacts on coral reef fishes. *The Journal of Experimental Biology* 213(6)**,** 894-900.

Wilson, S.K., Graham, N.A., Pratchett, M.S., Jones, G.P., and Polunin, N.V. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* 12(11)**,** 2220-2234.

Chapter 2 "The implications of recurrent disturbances within the world's hottest coral reef"

Preface

The first publication of this dissertation compares benthic assemblages, of the Gulf, Musandam and the Sea of Oman, over a period of time that included several large-scale disturbances. The results gathered in this study provide insights into how coral communities may respond to disturbance under environmental extremes associated with future climate change.

Highlights

- Coral communities shaped by local environmental conditions and disturbance history;

- Gulf reefs dominated by stress-tolerant corals and resilient to disturbances;

- Musandam and Sea of Oman reefs dominated by stress-sensitive corals;

- Harsh conditions and ongoing disturbances likely to lead to novel coral assemblages.

The implications of recurrent disturbances within the world's hottest coral reef

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ABSTRACT

Determining how coral ecosystems are structured within extreme environments may provide insights into how coral reefs are impacted by future climate change. Benthic community structure was examined within the Persian Gulf, and adjacent Musandam and northern Oman regions across a 3-year period (2008–2011) in which all regions were exposed to major disturbances. Although there was evidence of temporal switching in coral composition within regions, communities predominantly reflected local environmental conditions and the disturbance history of each region. Gulf reefs showed little change in coral composition, being dominated by stress-tolerant Faviidae and Poritidae across the 3 years. In comparison, Musandam and Oman coral communities were comprised of stress-sensitive Acroporidae and Pocilloporidae; Oman communities showed substantial declines in such taxa and increased cover of stress-tolerant communities. Our results suggest that coral communities may persist within an increasingly disturbed future environment, albeit in a much more structurally simple configuration.

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1. Introduction

Coral reefs are one of the worlds' most biodiverse ecosystems, and provide coastal populations with economically valuable goods and services (Moberg and Folke, 1999; Sheppard et al., 2009). However, coral reefs are in global decline. The combined effects of eutrophication, sedimentation, overfishing, outbreaks of disease and predation, and recurrent bleaching events associated with elevated sea temperatures are having a marked effect on the structure and functioning of reef systems (Hoegh-Guldberg, 1999; Hughes et al., 2003; Riegl et al., 2009). The capacity for reefs to resist change and/or recover from these escalating threats (i.e., resilience, sensu Walker et al., 2004) will be, in part, determined by the localised environmental context in which communities occur (Coles and Riegl, 2013; Hoegh-Guldberg, 1999). Abiotic factors, in particular temperature, salinity, and light, can strongly influence the growth, mortality, fecundity, and settlement of corals (Baird and Marshall, 2002; Hoegh-Guldberg, 1999; Riegl and Purkis, 2012b), and hence their capacity to re-assemble following disturbance (Glynn, 1996; Hoegh-Guldberg et al., 2007). Corals and associated organisms that occur in highly variable physical environments are physiologically acclimated and/or genetically adapted to the extreme conditions to

which they are exposed, allowing them to persist in environments that are often outside the physiological thresholds for most communities (Hoegh-Guldberg, 1999; Rowan, 2004; Sheppard, 2003). Understanding how benthic communities in extreme environments respond to disturbances may therefore provide important insights into how reefs in other regions may respond to future disturbance under increasing climate change and anthropogenic pressure (Brown, 1997; Burt et al., 2011a).

The Persian Gulf is among the most physically hostile environment in which coral reefs currently exist (Coles and Riegl, 2013; Sheppard et al., 1992). The Persian Gulf is a small, shallow sea (mean depth < 30 m) that has relatively restricted water exchange with the wider Indian Ocean (Riegl and Purkis, 2012a). As a result, the physical environment is characterised by thermal extremes, with sea surface temperatures (SSTs) ranging over 22 °C every 6 months; from < 13 °C in winter to > 35 °C in summer (Coles, 2003). This is the largest thermal range and highest maximum temperature experienced by extant coral reef communities (Coles, 2003; Sheppard et al., 1992; Sheppard and Loughland, 2002). In addition, limited freshwater input and the arid nature of the surrounding landscape causes high evaporation, and as a result salinity regularly exceeds 42 psu on reefs in the region (Coles, 2003; Riegl and Purkis, 2012b). Despite these extreme conditions, there are extensive reef systems in shallow coastal areas throughout the Persian Gulf, and these offer a 'natural laboratory' in which to study the impact

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of extreme and variable environmental conditions on the structure and function of coral reef fauna (Foster et al., 2012; Sheppard et al., 2012).

The Gulf of Oman is biogeographically connected to and at the same latitude as the Persian Gulf. The Gulf of Oman is deep (mean depth > 1000 m) and well mixed with the wider Indian Ocean, resulting in relatively benign environmental conditions (SST: 22–32 °C, salinity: 35–37 psu; Böhm et al., 1999; Coles, 1997, 2003), making these regions ideal for comparative studies of the role of environmental extremes in structuring reef communities (Burt et al., 2011b; Feary et al., 2010).

Coral communities around the Arabian Peninsula, like reefs in other regions, have been subject to an increasing frequency and/or intensity of disturbances in recent years (Burt et al., 2011a; Riegl and Purkis, 2012a; Sheppard et al., 2012). In 2007, category 5 cyclone Gonu, the strongest cyclone ever recorded for the Arabian Peninsula, caused extensive damage to reefs in the Gulf of Oman (Coles et al., 2015; Foster et al., 2011; Fritz et al., 2010). This was followed by a widespread harmful algal bloom (HAB) in 2008/2009 that resulted in mass coral mortality in both the Persian Gulf and Gulf of Oman (Bauman et al., 2010; Riegl et al., 2012c), and recurrent large-scale bleaching events in 2010 and 2011 (Riegl and Purkis, 2012b). The objective of this study was to examine temporal changes in benthic reef communities in three locations around the Arabian Peninsula: the Persian Gulf (Abu Dhabi), the Gulf of Oman (Fujairah), and the Straits of Hormuz (Musandam Peninsula, which connects the two Gulfs). By comparing benthic assemblages over a period that included several large-scale disturbances this study may provide insights into how reefs may respond to disturbance under environmental extremes associated with future climate change.

2. Methods

Benthic coral reef communities were surveyed at six sites around the Arabian Peninsula, with two sites surveyed at each of three locations; the Gulf of Oman (Al Aqa, Dibba), Persian Gulf (Saadiyat, Ras Ghanada) and Musandam Peninsula in the Straits of Hormuz (Al Harf, Coral Garden) (Fig. 1). Sites within each location were separated by 13–33 km. All sites were initially surveyed in September/November 2008, at the start of a widespread harmful algal bloom (HAB) event, and resurveyed 3 years later (2011). The HAB started at Dibba in the

Gulf of Oman in August 2008 and lasted until May 2009, initially expanding north to the Straits of Hormuz, before spreading westward and southward through coastal areas of Iran, Qatar, and the United Arab Emirates (Richlen et al., 2010). A total of 1200 km of coastline was affected by the HAB, with extensive fish kills and/or coral damage recorded in Oman, Fujairah, Iran, Dubai, Abu Dhabi, and Ajman (Bauman et al., 2010; Coles et al., 2015; Richlen et al., 2010). In 2010, a major bleaching event was also observed in the Persian Gulf, where corals were exposed to the highest temperatures recorded in the region (>35 °C) for a period of 3 weeks (Riegl et al., 2011, 2012a). A second major bleaching event was recorded in coastal UAE reefs in 2011 (Riegl et al., 2012c).

At each site the benthic community was quantified along six randomly placed 30-m transects at depths of 2–8 m. The depth of the surveys was determined by the reef topography and available hard substrata at each site, and depths surveyed were consistent between years. Transects were placed parallel to each other with a minimum of 3 m between adjacent transects. Along each transect eleven 0.5×0.5 m (i.e. 0.25 m^2) quadrats were placed at 3 m intervals and photographed (n = 66 quadrats per site per year). The substratum-type and coral composition within each quadrat was quantified under 50 random points using Coral Point Count with Excel Extensions (CPCe) software (Kohler and Gill, 2006). Substratum type was categorised into seven broad groups: (i) live scleractinian coral, (ii) fleshy and turf algae, (iii) crustose coralline algae (CCA), (iv) other live organisms (which encompassed all live benthic organisms that do not belong to the former groups; primarily barnacles, bivalves, sponges, and urchins), (v) dead coral framework, (vi) terrestrial derived rock, and (vii) unconsolidated substrata (i.e., sand and rubble). To quantify the composition of coral assemblages all live corals recorded were identified to genus (Riegl et al., 2012b; Veron, 2000). Percent cover of all benthic categories were then pooled to the transect level, and the relative abundance for each transect within each site calculated.

Two non-metric multi-dimensional scaling (nMDS) analyses and Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson et al., 2008) were used to investigate variation in (i) benthic community composition and (ii) scleractinian coral composition among regions (Persian Gulf, Musandam, Gulf of Oman) and years
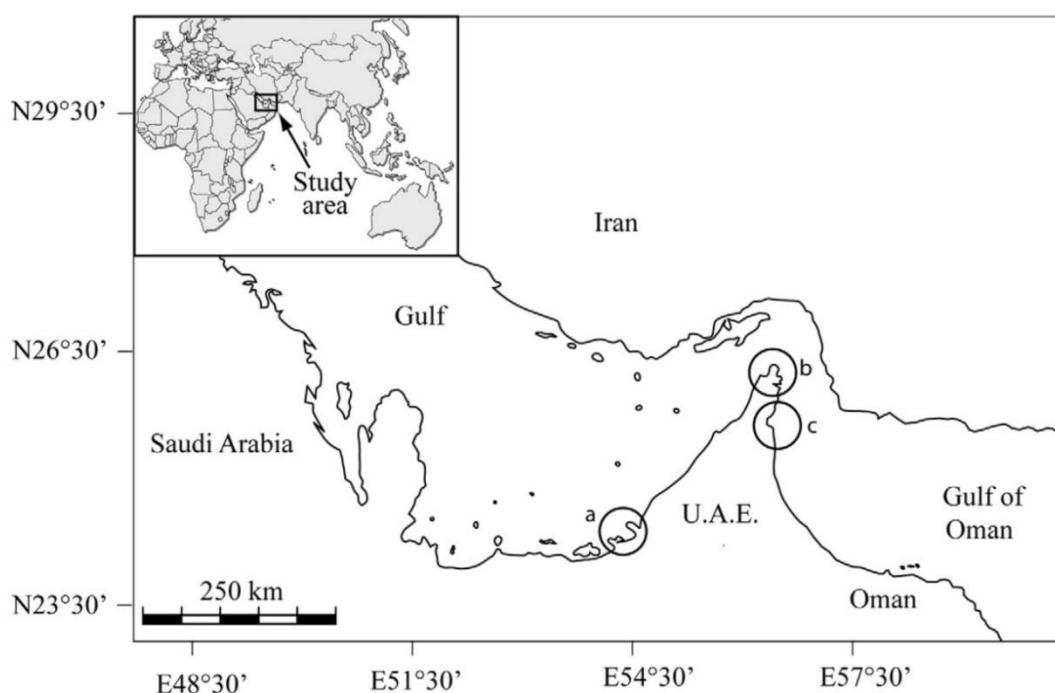
Fig. 1. Map of the Arabian Peninsula showing the geographic position of the three locations where the benthic communities were surveyed. a) Persian Gulf (Saadiyat and Ras Ghanada), b) Musandam (Al Harf and Coral Garden), and c) Gulf of Oman (Dibba and Al Aqa).

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(2008 vs. 2011). The analyses were based on the mean proportion of each substratum category and coral family, respectively at each site within each year. The analyses were based on Bray–Curtis similarities of arcsin-square root transformed data.

A series of 3-factor ANOVA's were used to determine the effect of region, year, and site (nested within region) on the relative abundance of each of the benthic substratum categories, and coral families. Assumptions of the ANOVA were examined by residual analysis. Prior to analyses the proportional cover of each of the benthic categories and coral families was arcsine–square root transformed, and coral genus richness log_{10} transformed, to improve normality and homoscedasticity. Fishers LSD tests were used to identify which means contributed to any significant differences detected.

3. Results

### 3.1. Changes in benthic composition

The nMDS of benthic community composition showed some separation between regions and years (Fig. 2A), and these differences were supported by the PERMANOVA (region: pseudo-F = 18.63, p = 0.001, year: pseudo-F = 8.87, p = 0.001). Overall, the Musandam and Persian Gulf sites were separated from the Gulf of Oman sites along the first dimension of the nMDS. The Musandam and Persian Gulf sites were characterised by a relatively high cover of live coral, dead coral and sand and rubble, while the Gulf of Oman sites were characterised by a high cover of rock, 'other' live organisms, and algae (Fig. 2B). In addition to spatial variation, there was also a separation of benthic communities between years at the Musandam and Persian Gulf sites, with the cover

of live coral being generally greater in 2011 than 2008. In contrast, the Gulf of Oman sites had lower cover of live coral and higher cover of rock in 2011 than in 2008 (Fig. 2).

The distribution of all benthic categories, except dead coral, was influenced by an interaction between region and year, indicating that temporal changes in the cover of each category was not consistent among regions (live coral: ANOVA $F_{2,60}$ = 7.81, p = 0.001, algae: $F_{2,60}$ = 3.43, p = 0.039, CCA: $F_{2,60}$ = 16.76, p < 0.001, 'other' live organisms: $F_{2,60}$ = 46.94, p < 0.001, rock: $F_{2,60}$ = 12.69, p < 0.001, sand and rubble: $F_{2,60}$ = 17.77, p < 0.001; Table S1). Live coral cover increased significantly in the Persian Gulf (2008: 31.7%, 2011: 56.1%, Fishers LSD: p < 0.001, Fig. 3A) and Musandam regions (2008: 46.9%, 2011: 58.5%, Fishers LSD: p = 0.037, Fig. 3B), while there was a small but non-significant decline in live coral cover within the Gulf of Oman (Fishers LSD: p = 0.17, Fig. 3C). The increase in coral cover within the Persian Gulf was accompanied by relatively small increases in the cover of algae and 'other' live organisms, and decreases in CCA, dead coral and sand/rubble (Fig. 3A). In contrast, the increase of live coral in the Musandam region was accompanied by an increase in sand/rubble, and decreases in the cover of CCA, 'other' live and rock (Fig. 3B).

3.2. Changes in coral composition

A total of 29 coral genera from 11 families were recorded across all surveys, with 4 families (Acroporidae, Faviidae, Pocilloporidae, and Poritidae) accounting for 97% of all corals surveyed. The composition of coral assemblages varied markedly between regions (PERMANOVA: pseudo-F = 15.23, p = 0.001), but displayed less variation between years (PERMANOVA: pseudo-F = 2.81, p = 0.042; Fig. 4). The
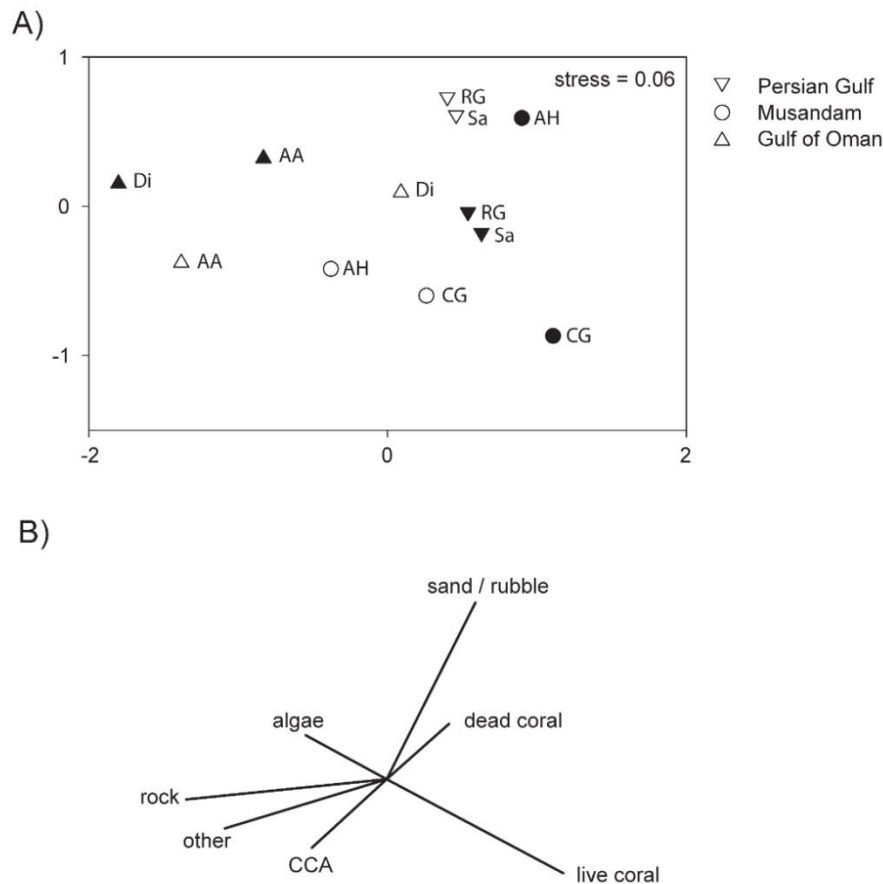
Fig. 2. Spatial and temporal variation in benthic communities around the Arabian Peninsula. A) Non-metric multi-dimensional scaling (nMDS) of benthic assemblages at two sites within each of the Persian Gulf (inverted triangle), Musandam (circle) and Gulf of Oman (triangle) in 2008 (open symbols) and 2011 (filled symbols). Letters indicate the individual sites (Di: Dibba, AA: Al Aqa, AH: Al Harf, CG: Coral Garden, Sa: Saadiyat, RG: Ras Ghanada). B) Vectors represent the partial regression coefficients of the original variables (benthic categories) with the two dimensions. Lengths of the vectors are proportional to the squared multiple correlation coefficient.

A) Persian Gulf

B) Musandam
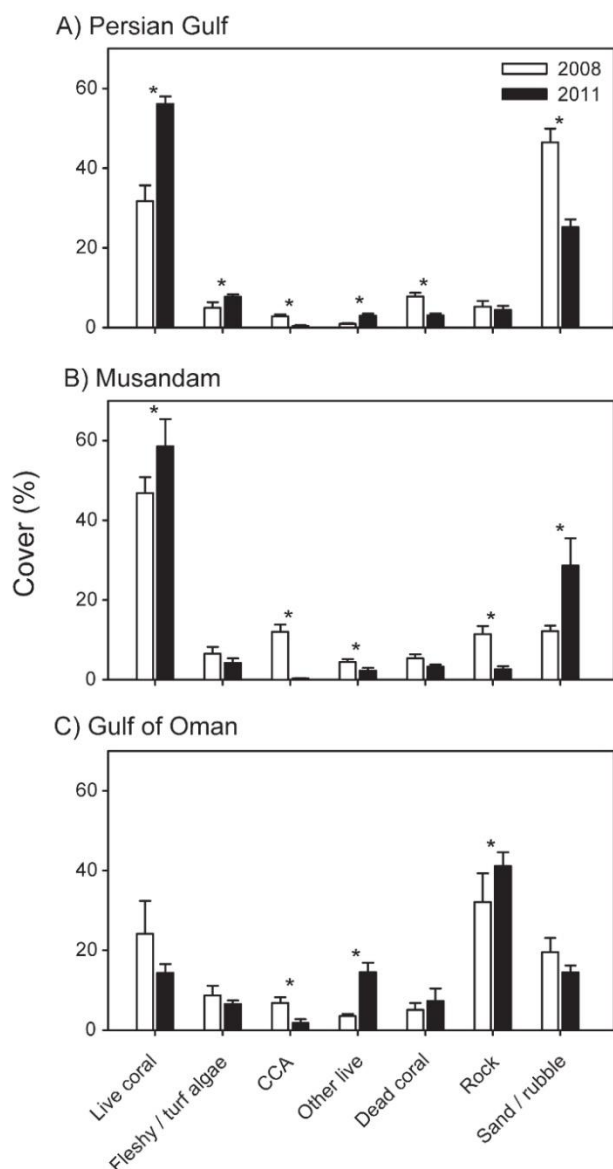
C) Gulf of Oman

Fig. 3. Temporal variation in benthic components within (A) the Persian Gulf, (B) Musandam, and (C) Gulf of Oman before the beginning of a harmful algal bloom (2008), and 3 years after (2011). Bars represent mean percentage cover (± standard error). * indicates significant (p < 0.05) difference identified by Fishers LSD test.

composition of coral assemblages was relatively consistent among sites and years within Musandam and the Persian Gulf, with both being characterised by a relatively high cover of Poritidae and Faviidae (Fig. 4). The Musandam sites were also characterised by high cover of Acroporidae (Fig. 4). Coral assemblages were more spatially variable within the Gulf of Oman with one site (i.e., Dibba) being characterised by a high cover of Pocilloporidae, and the other site (i.e., Al Aqa) by a relatively high cover of Pectinidae and Mussidae (Fig. 4).

Comparisons of the cover of the four most abundant coral families revealed that the distribution of three of these families were influenced by an interaction between region and year (Faviidae: ANOVA $F_{2,60}$ = 11.96, p < 0.001; Pocilloporidae: $F_{2,60}$ = 4.47, p = 0.01; Acroporidae: $F_{2,60}$ = 5.28, p = 0.01; Table S2). The cover of poritid and faviid corals increased significantly at the two Persian Gulf sites from 2008 to 2011 (Fig. 5A), yet displayed no change or small decreases in cover at the Musandam and Gulf of Oman sites (Fig. 5B, C). The cover of Pocilloporidae decreased significantly over the same time at the Gulf of Oman sites and did not change at the Musandam sites; this family was absent from the Persian Gulf sites in both years (Fig. 5). The cover

of Acroporidae increased significantly at the Musandam sites from 2008 (4.9%) to 2011 (16.4%), but was rare in the Gulf of Oman and Persian Gulf (Fig. 5). See Tables S3 and S4 for complete details of benthic categories and coral composition among regions, sites, and years.

4. Discussion

Coral reefs are being increasingly impacted by a suite of anthropogenic and natural stressors, with these effects being greatly compounded by climate change (Bellwood et al., 2004; Gardner et al., 2003). Future predictions of increased frequency and/or intensity of disturbances paint a bleak picture of accelerated declines and coral loss (Carpenter et al., 2008; De'ath et al., 2012; Hoegh-Guldberg, 1999; Hughes et al., 2003; Pandolfi et al., 2003; Riegl, 2003). Despite the extreme environmental conditions (e.g., high and variable SST and salinity) and numerous acute and chronic stressors (e.g., coral bleaching, HAB, intensive coastal development) impacting reefs around the north-eastern Arabian Peninsula during the course of this study, there were no significant declines in coral cover over the 3-year period (2008–2011) with coral cover actually increasing at two of the three locations (Persian Gulf and Musandam). There were, however, temporal changes in the composition of coral communities, and consistent differences in the composition of the overall benthic communities and scleractinian coral communities between the three locations. This spatial variation likely reflects the local environmental conditions (e.g., Bauman et al., 2013; Fishelson, 1973; Maina et al., 2011); and disturbance history of each location (e.g., Berumen and Pratchett, 2006; Hughes, 1989).

Coral communities within the Persian Gulf were dominated by massive and submassive Poritidae and Faviidae, which collectively accounted for over 95% of all corals recorded on these reefs. Poritid and faviid corals are generally viewed as being relatively tolerant to a range of stressors, including thermally-induced bleaching, predation by Crown-of-Thorns starfish, and storms (Baird and Marshall, 2002; Baird et al., 2013; Guest et al., 2012; Loya et al., 2001; Madin and Connolly, 2006; McClanahan et al., 2007). Consequently, coral assemblages dominated by these stress tolerant taxa are often indicative of a disturbed system. Indeed historical accounts of coral communities within the Persian Gulf describe these reefs as being dominated by *Acropora*, such as the tabular *Acropora clathrata* and *Acropora downingi*, up until the mid-1990s (George and John, 1999; Shinn, 1976). However, recurring bleaching events and coral mortality in 1996, 1998, 2002, 2010, and 2011 (Burt et al., 2008; George and John, 1999; Riegl, 1999, 2003; Sheppard and Loughland, 2002; Riegl and Purkis, 2012a), coral disease (Riegl et al., 2012c), and extensive coastal development and modification (Burt, 2014; Sale et al., 2011), over the past two decades have shifted these reefs from an *Acropora*-dominated configuration to a poritid- and faviid-dominated community (Bauman et al., 2013; Burt et al., 2011a; Riegl and Purkis, 2012b; Sheppard et al., 2012). Similar shifts in coral species composition have been recorded in response to disturbances in other regions (e.g., Indian Ocean: Ateweberhan et al., 2011; French Polynesia: Berumen and Pratchett, 2006; Pratchett et al., 2011; Kenya: McClanahan and Graham, 2005; Western Australia: Speed et al., 2013; Taiwan: Kuo et al., 2012) and has led to suggestions that in the face of continuing or increasing disturbances reefs will persist in these altered, or novel, states (Darling et al., 2013; Graham et al., 2014).

Although there has been a marked shift in coral assemblages in the Persian Gulf over the past two decades, the current poritid and faviid-dominated assemblages appear to be relatively insensitive to stressors. Multiple disturbances within the Persian Gulf during 2008–2011 had minimal impacts on coral assemblages at our study sites, with the cover of poritid and faviid corals not only being maintained but exhibiting a >60% increase. The apparent resilience of these assemblages is remarkable given the 2010 thermal anomaly was the highest on record for the region (>35 °C for 3 weeks; Riegl et al., 2011,
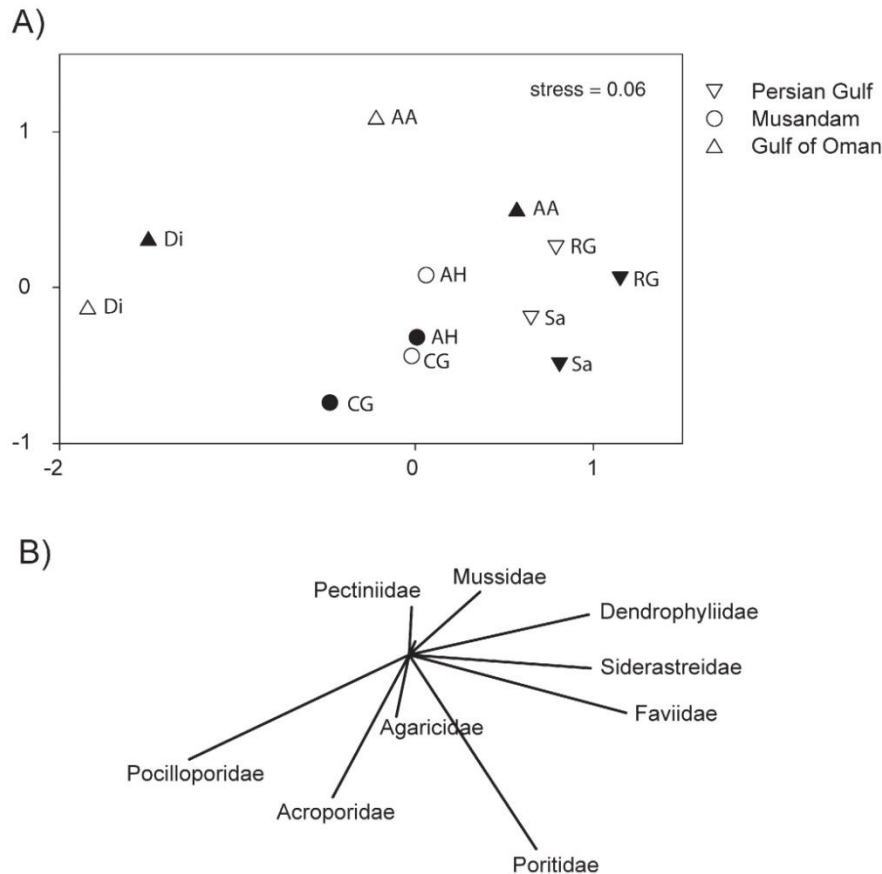
Fig. 4. Spatial and temporal variation in coral family composition around the Arabian Peninsula. A) Non-metric multi-dimensional scaling (nMDS) of coral families composition at two sites within each of the Persian Gulf (inverted triangle), Musandam (circle) and Gulf of Oman (triangle) in 2008 (open symbols) and 2011 (filled symbols).). Letters indicate the individual sites (Di: Dibba, AA: Al Aqa, AH: Al Harf, CG: Coral Garden, Sa: Saadiyat, RG: Ras Ghanada). B) Vectors represent the partial regression coefficients of the original variables (coral families) with the two dimensions. Lengths of the vectors are proportional to the squared multiple correlation coefficient.
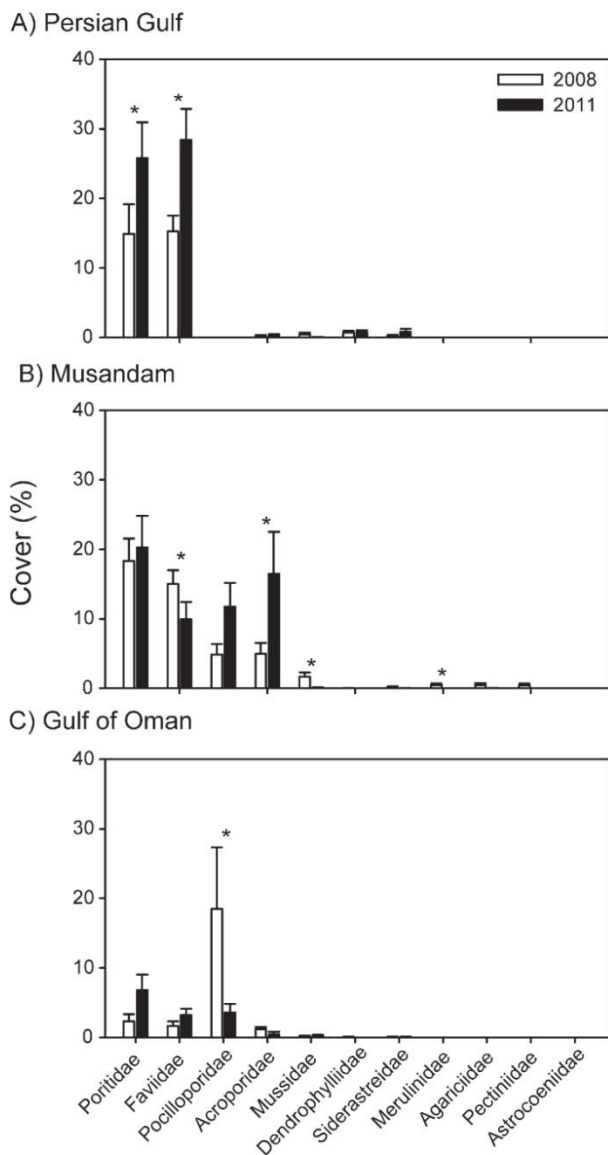
2012a), and several degrees higher than has been shown to cause extensive bleaching elsewhere (Coles, 2003; Riegl et al., 2012a). The cover of *Acropora* remains low on reefs in this region (<1% cover, Burt et al., 2008; Foster et al., 2012; present study) and given the limited input from larval sources (Bauman et al., 2014) recovery seems unlikely. Recent observations using artificial substrata (i.e., settlement tiles) demonstrated that newly-settled corals in the Persian Gulf were dominated by poritids and 'other' corals, with few *Acropora* and no *Pocillopora* recorded (Bauman et al., 2014). This is in marked contrast to similar studies elsewhere in which *Acropora* dominate assemblages of coral recruits (e.g. Hughes et al., 1999; Penin et al., 2010; Gilmour et al., 2013). Further, field-based fecundity estimates and demographic modelling predicts that acroporids will remain functionally extinct in the southern Persian Gulf under the current disturbance regime (Riegl and Purkis, 2009; Howells et al., 2016). The current poritid and faviid-dominated assemblages, although less diverse and structurally complex than the previous *Acropora*-dominated assemblages (Burt et al., 2011a; Burt et al., 2008), appear to be resilient to the extreme environmental conditions and frequent disturbances of this region.

In contrast to the Persian Gulf, reefs within the Musandam Peninsula and Gulf of Oman typically experience less extreme and less variable environmental conditions (Bauman et al., 2013) and have been subjected to fewer major disturbances in recent years (Riegl et al., 2012a,c). It is perhaps not surprising that reefs in these regions support a higher diversity of coral families, including the stress-sensitive Acroporidae and Pocilloporidae. Reefs in the Musandam Peninsula displayed a ca. 20% increase in overall coral cover from 2008 to 2011, which was primarily driven by increases in pocilloporid and acroporid corals. Increased coverage of these fast growing but stress-sensitive corals reflect the lack of major disturbances in the region.

Reefs in the Gulf of Oman, although having the least variable environmental conditions of the three regions examined (Bauman et al., 2013), experienced a ca. 75% decline in cover of pocilloporid corals over the study period. This decline in cover was largely offset by small, but non-significant increases in portiid and faviid corals, resulting in limited change in overall live coral cover from 2008 to 2011. Historically, the Gulf of Oman has had little documented exposure to substantial disturbances (Coles et al., 2015; Richlen et al., 2010), however a region-wide harmful algal bloom (HAB) that initiated in the Gulf of Oman and extended into the Persian Gulf in 2008–9, had its most severe impacts on reefs in the northern Gulf of Oman (Richlen et al., 2010; Riegl et al., 2012c). The HAB caused >80% mortality of corals (including acroporids, pocilloprids, faviids, and poritids) on reefs in the northern Gulf of Oman, including those in the present study (Bauman et al., 2010; Foster et al., 2011, 2012). It is likely that the decline in Pocilloporidae in the present study was directly related to the impact of the HAB. The similarity in the magnitude of coral mortality immediately following the HAB (Bauman et al., 2010) and the reduction in the cover in the present study suggest there has been little, if any, recovery of the previously dominant pocilloporid populations 3 years after the HAB. Interestingly, poritids and faviids also experienced mortality from the HAB (Riegl et al., 2012c) but appear to have recovered, and even increased in cover in the subsequent 3 years. The shift in coral composition, therefore, may be related to the differential recovery of coral populations, rather than differential mortality. It remains to be seen if this represents a long-term shift in community structure or a transitional configuration. Several studies have reported variable

A) Persian Gulf

and frequent disturbances, the stability of faviid and poritid-dominated reef in the Persian Gulf is remarkable and may provide a window into the future configuration of reefs under climate change. Although this may be a cause for some optimism, these novel configurations are structurally simple and will invariably lead to reductions in the diversity and abundance of reef associated fishes (Pratchett et al., 2014) and the goods and services they provide.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marpolbul.2015.10.006.

Fig. 5. Temporal variation in the cover of the eleven most abundant coral families within (A) the Persian Gulf, (B) Musandam and (C) the Gulf of Oman. Bars represent mean percentage cover ($\pm$ standard error). * indicates significant ($p < 0.05$) difference identified by Fishers LSD test.

timeframes for recovery of coral populations following disturbances, with the rate of recovery being dependent on a range of factors including the supply of larvae, connectivity, and competition with other benthic organisms (e.g., Ceccarelli et al., 2011; Gilmour et al., 2013). Pocilloporids are often abundant on marginal or subtropical coral reefs (e.g., Hoey et al., 2011), however being brooding spawners larval supply for this coral species is tightly linked to local adult abundance, and is likely to lead to protracted population recovery within the Gulf of Oman.

Understanding how coral reefs in extreme environments respond to disturbance may provide insights into how reefs in other regions may respond to disturbance under ongoing climate change (Sheppard et al., 2012). Although there have been some suggestions that accelerating climate change and anthropogenic stressors will cause coral reefs to decline to such an extent that they will be largely unrecognizable by the middle of this century (Caldeira and Wickett, 2003; Donner, 2009; Donner et al., 2005; Hoegh-Guldberg, 1999, 2005; Hoegh-Guldberg et al., 2007; Orr et al., 2005; Veron et al., 2009), it appears more likely that reefs will persist, albeit in a different configuration (Graham et al., 2014). Set against a backdrop of extreme environmental conditions

References

Anderson, M., Gorley, R.N., Clarke, R.K., 2008. PERMANOVA+ for primer: guide to software and statistical methods. Primer-E, Plymouth.

Ateweberhan, M., McClanahan, T.R., Graham, N.A.J., Sheppard, C.R.C., 2011. Episodic heterogeneous decline and recovery of coral cover in the Indian Ocean. Coral Reefs 30, 739–752.

Baird, A.H., Marshall, P.A., 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Mar. Ecol. Prog. Ser. 237, 133–141.

Baird, A.H., Pratchett, M.S., Hoey, A.S., Herdiana, Y., 2013. *Acanthaster planci* is a major cause of coral mortality in Indonesia. Coral Reefs 32, 803–812.

Bauman, A.G., Burt, J.A., Feary, D.A., Marquis, E., Usseglio, P., 2010. Tropical harmful algal blooms: an emerging threat to coral reef communities? Mar. Pollut. Bull. 60, 2117–2122.

Bauman, A.G., Feary, D.A., Heron, S.F., Pratchett, M.S., Burt, J.A., 2013. Multiple environmental factors influence the spatial distribution and structure of reef communities in the northeastern Arabian Peninsula. Mar. Pollut. Bull. 72, 302–312.

Bauman, A.G., Baird, A.H., Burt, J.A., Pratchett, M.S., Feary, D.A., 2014. Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates). Mar. Ecol. Prog. Ser. 499, 115–126.

Bellwood, D.R., Hughes, T.P., Folke, C., Nystrom, M., 2004. Confronting the coral reef crisis. Nature 429, 827–833.

Berumen, M.L., Pratchett, M.S., 2006. Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea. Coral Reefs 25, 647–653.

Böhm, E., Morrison, J.M., Manghnani, V., Kim, H.-S., Flagg, C.N., 1999. The Ras al Hadd Jet: remotely sensed and acoustic Doppler current profiler observations in 1994–1995. Deep-Sea Res. II Top. Stud. Oceanogr. 46, 1531–1549.

Brown, B., 1997. Adaptations of reef corals to physical environmental stress. Adv. Mar. Biol. 31, 221–299.

Burt, J., 2014. The environmental costs of coastal urbanization in the Arabian Gulf. City 18, 760–770.

Burt, J., Bartholomew, A., Usseglio, P., 2008. Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates. Mar. Biol. 154, 27–36.

Burt, J., Al-Harthi, S., Al-Cibahy, A., 2011a. Long-term impacts of coral bleaching events on the world's warmest reefs. Mar. Environ. Res. 72, 225–229.

Burt, J.A., Feary, D.A., Bauman, A.G., Usseglio, P., Cavalcante, G.H., Sale, P.F., 2011b. Biogeographic patterns of reef fish community structure in the northeastern Arabian Peninsula. ICES J. Mar. Sci. 68, 1875–1883.

Caldeira, K., Wickett, M.E., 2003. Anthropogenic carbon and ocean pH. Nature 425, 365.

Carpenter, K.E., Abrar, M., Aeby, G., Aronson, R.B., Banks, S., Bruckner, A., Chiriboga, A., Cortés, J., Delbeek, J.C., DeVantier, L., Edgar, G.J., Edwards, A.J., Fenner, D., Guzmán, H.M., Hoeksema, B.W., Hodgson, G., Johan, O., Licuanan, W.Y., Livingstone, S.R., Lovell, E.R., Moore, J.A., Obura, D.O., Ochavillo, D., Polidoro, B.A., Precht, W.F., Quibilan, M.C., Reboton, C., Richards, Z.T., Rogers, A.D., Sanciangco, J., Sheppard, A., Sheppard, C., Smith, J., Stuart, S., Turak, E., Veron, J.E.N., Wallace, C., Weil, E., Wood, E., 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 321 (5888), 560–563.

Ceccarelli, D.M., Richards, Z.T., Pratchett, M.S., Cvitanovic, C., 2011. Rapid increase in coral cover on an isolated coral reef, the Ashmore Reef National Nature Reserve, northwestern Australia. Mar. Freshw. Res. 62, 1214–1220.

Coles, S.L., 1997. Reef corals occurring in a highly fluctuating temperature environment at Fahal Island, Gulf of Oman (Indian Ocean). Coral Reefs 16, 269–272.

Coles, S.L., 2003. Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific Region. National Museum of Natural History, Smithsonian Institution.

Coles, S.L., Riegl, B.M., 2013. Thermal tolerances of reef corals in the Gulf: a review of the potential for increasing coral survival and adaptation to climate change through assisted translocation. Mar. Pollut. Bull. 72, 323–332.

Coles, S., Looker, E., Burt, J., 2015. Twenty-year changes in coral near Muscat, Oman estimated from manta board tow observations. Mar. Environ. Res. 103, 66–73.

Darling, E.S., McClanahan, T.R., Cote, I.M., 2013. Life histories predict coral community disassembly under multiple stressors. Glob. Chang. Biol. 19, 1930–1940.

De'ath, G., Fabricius, K.E., Sweatman, H., Puotinen, M., 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc. Natl. Acad. Sci. U. S. A. 109, 17995–17999.

Donner, S.D., 2009. Coping with commitment: projected thermal stress on coral reefs under different future scenarios. PLoS ONE 4, e5712.

Donner, S.D., Skirving, W.J., Little, C.M., Oppenheimer, M., Hoegh-Guldberg, O., 2005. Global assessment of coral bleaching and required rates of adaptation under climate change. Glob. Chang. Biol. 11, 251–2265.

Feary, D.A., Burt, J.A., Bauman, A.G., Usseglio, P., Sale, P.F., Cavalcante, G.H., 2010. Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future? J. Fish Biol. 77, 1931–1947.

Fishelson, L., 1973. Ecological and biological phenomena influencing coral-species composition on the reef tables at Eilat (Gulf of Aqaba, Red Sea). Mar. Biol. 19, 183–196.

Foster, K.A., Foster, G., Tourenq, C., Shuriqi, M.K., 2011. Shifts in coral community structures following cyclone and red tide disturbances within the Gulf of Oman (United Arab Emirates). Mar. Biol. 158, 955–968.

Foster, K., Foster, G., Al-Cibahy, A.S., Al-Harthi, S., Purkis, S.J., Riegl, B.M., 2012. Environmental setting and temporal trends in Southeastern Gulf Coral Communities. In: Riegl, B.M., Purkis, S.J. (Eds.), Coral Reefs of the Gulf: Adaptation to Climatic Extremes. Springer, Dordrecht, pp. 51–70.

Fritz, H.M., Blount, C.D., Albusaidi, F.B., Al-Harthy, A.H.M., 2010. Cyclone Gonu storm surge in Oman. Estuar. Coast. Shelf Sci. 86, 102–106.

Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A., Watkinson, A.R., 2003. Long-term region-wide declines in Caribbean corals. Science 301, 958–960.

George, J.D., John, D.M., 1999. High sea temperatures along the coast of Abu Dhabi (UAE), Arabian Gulf—their impact upon corals and macroalgae. Reef Encounter 25, 21–23.

Gilmour, J.P., Smith, L.D., Heyward, A.J., Baird, A.H., Pratchett, M.S., 2013. Recovery of an isolated coral reef system following severe disturbance. Science 340, 69–71.

Glynn, P.W., 1996. Coral reef bleaching: facts, hypotheses and implications. Glob. Chang. Biol. 2, 495–509.

Graham, N.A.J., Cinner, J.E., Norström, A.V., Nyström, M., 2014. Coral reefs as novel ecosystems: embracing new futures. Curr. Opin. Environ. Sustain. 7, 9–14.

Guest, J.R., Baird, A.H., Maynard, J.A., Muttaqin, E., Edwards, A.J., Campbell, S.J., Yewdall, K., Affendi, Y.A., Chou, L.M., 2012. Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. PLoS ONE 7, e33353.

Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's coral reefs. Mar. Freshw. Res. 50, 839–866.

Hoegh-Guldberg, O., 2005. Low coral cover in a high-CO_2 world. J. Geophys. Res. 110, C9.

Hoegh-Guldberg, O., Mumby, P.J., Hooten, A.J., Steneck, R.S., Greenfield, P., Gomez, E., Harvell, C.D., Sale, P.F., Edwards, A.J., Caldeira, K., Knowlton, N., Eakin, C.M., Iglesias-Prieto, R., Muthiga, N., Bradbury, R.H., Dubi, A., Hatziolos, M.E., 2007. Coral reefs under rapid climate change and ocean acidification. Science 318, 1737–1742.

Hoey, A.S., Pratchett, M.S., Cvitanovic, C., 2011. High macroalgal cover and low coral recruitment undermines the potential resilience of the world's southernmost coral reef assemblages. PLoS ONE 6 (10), e25824.

Howells, E.J., Ketchum, R.N., Bauman, A.G., Mustafa, Y., Watkins, K.D., Burt, J.A., 2016. Species-specific trends in the reproductive output of corals across environmental gradients and bleaching histories. Mar. Pollut. Bull. 105, 532–539.

Hughes, T.P., 1989. Community structure and diversity of coral reefs: the role of history. Ecology 70, 275.

Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschaniwskyj, N.A., Pratchett, M.S., Tanner, J.E., Willis, B.L., 1999. Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397, 59–63.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B., Kleypas, J., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933.

Kohler, K.E., Gill, S.M., 2006. Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. Comput. Geosci. 32, 1259–1269.

Kuo, C.-Y., Yuen, Y.S., Meng, P.-J., Ho, P.-H., Wang, J.-T., Liu, P.-J., Chang, Y.-C., Dai, C.-F., Fan, T.-Y., Lin, H.-J., Baird, A.H., Chen, C.A., 2012. Recurrent disturbances and the degradation of hard coral communities in Taiwan. PLoS ONE 7 (8), e44364.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., van Woesik, R., 2001. Coral bleaching: the winners and the losers. Ecol. Lett. 4, 122–131.

Madin, J.S., Connolly, S.R., 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. Nature 444, 477–480.

Maina, J., McClanahan, T.R., Venus, V., Ateweberhan, M., Madin, J., 2011. Global gradients of coral exposure to environmental stresses and implications for local management. PLoS ONE 6, e23064.

McClanahan, T.R., Graham, N.A.J., 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. Mar. Ecol. Prog. Ser. 294, 241–248.

McClanahan, T.R., Ateweberhan, M., Graham, N.A.J., Wilson, S.K., Sebastián, C.R., Guillaume, M.M.M., Bruggemann, J.H., 2007. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. Mar. Ecol. Prog. Ser. 337, 1–13.

Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233.

Orr, J.C., Fabry, V.J., Aumont, O., Bopp, L., Doney, S.C., Feely, R.A., Gnanadesikan, A., Gruber, N., Ishida, A., Joos, F., Key, R.M., Lindsay, K., Maier-Reimer, E., Matear, R., Monfray, P., Mouchet, A., Najjar, R.G., Plattner, G.K., Rodgers, K.B., Sabine, C.L., Sarmiento, J.L., Schlitzer, R., Slater, R.D., Totterdell, I.J., Weirig, M.F., Yamanaka, Y., Yool, A., 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. Nature 437, 681–686.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G., McArdle, D., McClenachan, L., Newman, M.J., Paredes, G., Warner, R.R., Jackson, J.B., 2003. Global trajectories of the long-term decline of coral reef ecosystems. Science 301, 955–958.

Penin, L., Michonneau, F., Baird, A.H., Connolly, S.R., Pratchett, M.S., Kayal, M., Adjeroud, M., 2010. Early post-settlement mortality and the structure of coral assemblages. Mar. Ecol. Prog. Ser. 408, 55–64.

Pratchett, M.S., Trapon, M., Berumen, M.L., Chong-Seng, K., 2011. Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. Coral Reefs 30, 183–193.

Pratchett, M.S., Hoey, A.S., Wilson, S.K., 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Curr. Opin. Environ. Sustain. 7, 37–43.

Richlen, M.L., Morton, S.L., Jamali, E.A., Rajan, A., Anderson, D.M., 2010. The catastrophic 2008–2009 red tide in the Arabian gulf region, with observations on the identification and phylogeny of the fish-killing dinoflagellate *Cochlodinium polykrikoides*. Harmful Algae 9, 163–172.

Riegl, B., 1999. Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): fauna and community structure in response to recurring mass mortality. Coral Reefs 18, 63–73.

Riegl, B., 2003. Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). Coral Reefs 22, 433–446.

Riegl, B.M., Purkis, S.J., 2009. Model of coral population response to accelerated bleaching and mass mortality in a changing climate. Ecol. Model. 220, 192–208.

Riegl, B.M., Purkis, S.J., 2012a. Dynamics of gulf coral communities: observations and models from the world's hottest coral sea. In: Riegl, B.M., Purkis, S.J. (Eds.), Coral Reefs of the Gulf: Adaptation to Climatic Extremes. Springer, Dordrecht, pp. 71–93.

Riegl, B.M., Purkis, S.J., 2012b. Environmental constraints for reef building in the Gulf. In: Riegl, B.M., Purkis, S.J. (Eds.), Coral Reefs of the Gulf: Adaptation to Climatic Extremes. Springer, Dordrecht, pp. 5–32.

Riegl, B., Bruckner, A., Coles, S.L., Renaud, P., Dodge, R.E., 2009. Coral reefs: threats and conservation in an era of global change. Ann. N. Y. Acad. Sci. 1162, 136–186.

Riegl, B.M., Purkis, S.J., Al-Cibahy, A.S., Abdel-Moati, M.A., Hoegh-Guldberg, O., 2011. Present limits to heat-adaptability in corals and population-level responses to climate extremes. PLoS ONE 6, e24802.

Riegl, B., Purkis, S., Al-Cibahy, A., Al-Harthi, S., Grandcourt, E., Al-Sulaiti, K., Baldwin, J., Abdel-Moati, A.M., 2012a. In: Riegl, B.M., Purkis, S.J. (Eds.), Coral bleaching and mortality thresholds in the SE Gulf: highest in the world. Coral Reefs of the Gulf. Adaptation to Climatic Extremes. Springer, Dordrecht, pp. 95–106.

Riegl, B.M., Benzoni, F., Samimi-Namin, K., Sheppard, C., 2012b. The hermatypic scleractinian (hard) coral fauna of the Gulf. In: Riegl, B.M., Purkis, S.J. (Eds.), Coral Reefs of the Gulf: Adaptation to Climatic Extremes. Springer, Dordrecht, pp. 187–224.

Riegl, B.M., Bruckner, A.W., Samimi-Namin, K., Purkis, S.J., 2012c. Diseases, harmful algae blooms (HABs) and their effects on Gulf coral populations and communities. In: Riegl, B.M., Purkis, S.J. (Eds.), Coral Reefs of the Gulf: Adaptation to Climatic Extremes. Springer, Dordrecht, pp. 107–125.

Rowan, R., 2004. Coral bleaching: thermal adaptation in reef coral symbionts. Nature 430, 742.

Sale, P.F., Feary, D., Burt, J.A., Bauman, A., Cavalcante, G., Drouillard, K., 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.

Sheppard, C.R.C., 2003. Predicted recurrences of mass coral mortality in the Indian Ocean. Nature 425, 294–297.

Sheppard, C.R.C., Loughland, R., 2002. Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. Aquat. Ecosyst. Health Manag. 5, 395–402.

Sheppard, C., Price, A., Roberts, C., 1992. Marine ecology of the Arabian Region: patterns and processes in extreme tropical environments. Academic Press, Toronto.

Sheppard, C.R.C., Davy, S.K., Pilling, G.M., 2009. The biology of coral reefs. Oxford University Press.

Sheppard, C., Al-Husiani, M., Al-Jamali, F., Al-Yamani, F., Baldwin, R., Bishop, J., Benzoni, F., Dutrieux, E., Dulvy, N.K., Durvasula, S.R.V., Jones, D.A., Loughland, R., Medio, D., Nithyanandan, M., Pilling, G.M., Polikarpov, I., Price, A.R.G., Purkis, S.J., Riegl, B.M., Saburova, M., Samimi-Namin, K., Taylor, O., Wilson, S., Zainal, K., 2012. Environmental concerns for the future of Gulf coral reefs, In: coral reefs of the Gulf: adaptations to climatic extremes. In: Riegl, B.M., Purkis, S.J. (Eds.), Springer, Dordrecht, pp. 349–368.

Shinn, E.A., 1976. Coral reef recovery in Florida and the Persian Gulf. Environ. Geol. 1, 241–254.

Speed, C.W., Babcock, R.C., Bancroft, K.P., Beckley, L.E., Bellchambers, L.M., Depczynski, M., Field, S.N., Friedman, K.J., Gilmour, J.P., Hobbs, J.P., Kobryn, H.T., Moore, J.A., Nutt, C.D., Shedrawi, G., Thomson, D.P., Wilson, S.K., 2013. Dynamic stability of coral reefs on the west Australian coast. PLoS ONE 8, e69863.

Veron, J.E.N., 2000. Corals of the world. AIMS, Townsville.

Veron, J.E., Hoegh-Guldberg, O., Lenton, T.M., Lough, J.M., Obura, D.O., Pearce-Kelly, P., Sheppard, C.R., Spalding, M., Stafford-Smith, M.G., Rogers, A.D., 2009. The coral reef crisis: the critical importance of <350 ppm CO_2. Mar. Pollut. Bull. 58, 1428–1436.

Walker, B., Holling, C.S., Carpennter, S.R., Kinzig, A., 2004. Resilience, adaptability and transformability in social–ecological systems. Ecol. Soc. 9, 5.

Supplementary Material

Table S2.1 Summary of MANOVA and ANOVA's comparing the cover of benthic categories among regions (Persian Gulf, Musandam, Gulf of Oman), years (2008, 2011) and sites around the Arabian Peninsula

Source of variation	Wilks λ	F	p	Coral		Algae		CCA		Other		Dead		Rock		Sand and Rubble	
				F	p	F	p	F	p	F	p	F	p	F	p	F	p
Region	0.050	26.69	< 0.001	45.128	< 0.001	1.662	0.198	13.472	< 0.001	62.446	< 0.001	0.931	0.400	82.802	< 0.001	29.465	< 0.001
Year	0.202	30.47	< 0.001	7.984	0.006	0.070	0.792	155.690	< 0.001	38.131	< 0.001	6.743	0.012	0.269	0.606	2.458	0.122
Site(Region)	0.133	7.56	< 0.001	12.053	< 0.001	10.014	< 0.001	8.073	< 0.001	7.250	< 0.001	4.209	0.009	5.171	0.003	11.222	< 0.001
Region x Year	0.103	16.35	< 0.001	7.813	0.001	3.428	0.039	16.755	< 0.001	46.944	< 0.001	2.697	0.076	12.694	< 0.001	17.774	< 0.001
Site(Reg) x Year	0.093	9.54	< 0.001	6.230	0.001	2.004	0.123	5.882	0.001	23.357	< 0.001	18.172	< 0.001	20.928	< 0.001	14.640	< 0.001

Table S2.2 Summary of MANOVA and ANOVA's comparing the cover of the four dominant coral families among regions (Persian Gulf, Musandam, Gulf of Oman), years (2008, 2011) and sites around the Arabian Peninsula

Source of variation	Wilks λ	F	p	Acroporidae		Pocilloporidae		Faviidae		Poritidae	
				F	p	F	p	F	p	F	p
Region	0.050	49.785	<0.001	33.198	<0.001	17.079	<0.001	81.671	<0.001	29.304	<0.001
Year	0.749	4.777	0.002	1.050	0.310	0.144	0.706	2.091	0.153	5.977	0.017
Site(Region)	0.121	15.373	<0.001	5.353	0.002	16.928	<0.001	19.694	<0.001	12.082	<0.001
Region x Year	0.548	4.996	<0.001	5.283	0.008	4.766	0.012	11.956	<0.001	1.490	0.234
Site(Reg) x Year	0.677	2.003	0.028	2.432	0.074	1.463	0.234	2.504	0.068	2.652	0.057

Table S2.2 Percent cover of (a) benthic categories, and (b) coral at the three study locations (Persian Gulf, Musandam and Sea of Oman) in 2008 and 2011. Values given are means ± 1SE

	Persian Gulf		Musandam		Sea of Oman	
A) Benthic categories	2008	2011	2008	2011	2008	2011
Live Coral	31.7±3.9	56.1±1.9	46.9±4.0	58.5±6.9	24.2±8.2	14.3±2.2
Turf and fleshy algae	5.0±1.4	7.7±0.6	6.5±1.7	4.3±1.1	8.6±2.5	6.6±0.8
Coralline algae	2.8±0.5	0.5±0.1	12.0±1.8	0.3±0..1	6.8±1.4	1.8±0.9
Other Live	1.0±0.2	3.0±0.5	4.4±0.8	2.3±0.7	3.5±0.6	14.5±2.4
Dead Framework	7.8±0.9	3.1±0.5	5.3±1.0	3.3±0.5	5.1±1.7	7.3±3.2
Rock/Rubble/Sand	51.7±4.0	29.7±2.1	23.7±2.0	31.3±6.7	51.6±7.5	55.5±4.3
B) Coral families						
Acroporidae	0.2±0.1	0.3±0.2	4.9±1.6	16.4±6.0	1.1±0.3	0.5±0.4
Agariciidae	0	0	0.4±0.3	0.02±0.02	0.02±0.02	0
Astrocoeniidae	0	0	0.01±0.01	0	0	0
Dendrophylliidae	0.7±0.2	0.8±0.3	0.02±0.02	0	0.06±0.06	0
Faviidae	15.2±2.3	28.4±4.4	15.0±1.9	9.9±2.5	1.7±0.6	3.2±1.0
Merulinidae	0	0	0.5±0.2	0	0	0
Mussidae	0.5±0.2	0.05±0.03	1.7±0.6	0.1±0.1	0.2±0.1	0.2±0.2
Pectiniidae	0	0	0.4±0.3	0	0.02±0.02	0
Pocilloporidae	0	0	4.9±1.5	11.7±3.4	18.5±8.8	3.6±1.2
Poritidae	14.9±4.3	25.8±5.1	18.3±3.3	20.3±4.6	2.3±1.1	6.8±2.2
Siderastreidae	0.3±0.1	0.8±0.5	0.2±0.1	0.02±0.02	0.1±0.05	0.1±0.05

Table S2.4 Percent cover of (a) benthic categories, and (b) families at the six study sites (Saadiyat and Ras Ghanada [Abu Dhabi], Al Harf and Coral Garden [Musandam], Dibba and Al Aqa [Fujairah] in 2008 and 2011. Values given are means ± 1SE

	Saadiyat		Ras Ghanada		Al Harf		Coral Garden		Dibba		Al Aqa	
A) Benthic categories	2008	2011	2008	2011	2008	2011	2008	2011	2008	2011	2008	2011
Live Coral	34.6±7.0	58.9±3.2	28.9±4.0	53.2±1.3	35.7±2.8	37.5±2.8	58.0±3.7	79.5±4.3	40.8±13.5	10.4±1.5	7.5±1.0	18.2±3.6
Turf and fleshy algae	1.6±0.3	7.9±0.4	8.3±2.0	7.5±1.2	10.6±2.3	7.2±1.1	2.4±0.5	1.3±0.9	7.5±4.6	5.9±1.4	9.7±2.4	7.2±0.8
Coralline algae	1.6±0.4	0.4±0.2	4.0±0.7	0.6±0.2	16.3±2.0	0.1±0.04	7.6±1.6	0.6±0.2	4.0±0.9	0.4±0.1	9.7±2.2	3.2±1.6
Other Live	1.4±0.2	4.3±0.4	0.5±0.1	1.7±0.3	6.1±1.1	0.8±0.2	2.8±0.4	3.8±1.0	2.2±0.7	21.1±2.2	4.8±0.7	8.0±1.6
Dead Framework	8.4±1.2	2.8±0.5	7.3±1.5	3.3±0.9	2.8±1.0	2.8±0.6	7.9±0.9	3.8±0.9	8.7±2.7	0.2±0.1	1.6±0.5	14.4±5.0
Rock/Rubble/Sand	52.4±7.7	25.7±3.4	51.1±3.4	33.6±1.5	26.4±2.0	51.6±4.0	20.9±3.1	11.0±4.1	36.7±11.8	62.0±2.5	66.6±4.3	49.0±7.6
B) Coral families												
Acroporidae	0.1±0.1	0.4±0.4	0.2±0.2	0.1±0.1	3.3±1.3	4.3±1.4	6.6±2.9	28.6±10.0	0.9±0.4	0.9±0.7	1.4±0.5	0
Agariciidae	0	0	0	0	0	0	0.9±0.5	0.03±0.03	0	0	0.03±0.03	0
Astrocoeniidae	0	0	0	0	0.03±0.03	0	0	0	0	0	0	0
Dendrophylliidae	0.3±0.1	0.4±0.2	1.1±04	1.1±0.5	0.03±0.03	0	0	0	0	0	0.1±0.1	0
Faviidae	9.6±1.4	14.3±1.5	20.9±2.9	42.6±1.9	12.0±1.7	11.4±3.6	18.1±3.2	8.5±3.6	0.1±0.1	0.4±0.2	3.2±0.9	6.0±1.0
Merulinidae	0	0	0	0	0.9±0.4	0	0	0	0	0	0	0
Mussidae	0.1±0.1	0	0.8±0.4	0.1±0.1	2.9±0.9	0	0.5±0.4	0.2±0.2	0	0	0.3±0.1	0.4±0.3
Pectiniidae	0	0	0	0	0.8±0.5	0	0	0	0	0	0.03±0.03	0
Pocilloporidae	0	0	0	0	1.4±0.8	3.4±1.5	8.3±2.1	20.0±4.7	36.7±14.5	7.2±1.3	0.3±0.1	0
Poritidae	24.1±6.8	42.4±2.0	5.7±1.0	9.2±1.1	13.4±2.4	18.3±3.4	23.2±5.6	22.2±8.9	3.2±2.1	1.9±1.3	1.4±0.8	11.7±3.3
Siderastreidae	0.3±0.2	1.4±0.9	0.2±0.1	0.2±0.1	0.2±0.1	0.03±0.03	0.2±0.1	0	0	0	0.2±0.1	0.2±0.1

Chapter 3 "Settlement Patterns of Corals and other Benthos on Reefs with Divergent Environments and Disturbances Histories around the Northeastern Arabian Peninsula"

Preface

The recovery of reefs after disturbances depends on the supply of new colonists and which ones will settle in the open spaces created. The different taxa that settle will determine if reefs return to a pre-disturbance assemblage or if they will undergo a long-term shift. The purpose in this second publication was to analyze spatial and seasonal variability in the settlement of benthic organisms on reefs from the three regions (Gulf, Musandam and the Sea of Oman), providing insights into peak settlement periods and recovery dynamics.

Highlights

- Settlement of corals was extremely low compared to those reported for other regions.

- Low rates of coral settlement suggest that these marginal reefs are likely to recover slowly from disturbances.

- Spatial differences in composition of new colonists were more important than temporal differences

- Strong spatial variation in composition of new colonists among regions, driven by: coralline algae in the Gulf, colonial ascidians on the Musandam Peninsula and barnacles in the Sea of Oman.

Settlement Patterns of Corals and other Benthos on Reefs with Divergent Environments and Disturbances Histories around the Northeastern Arabian Peninsula

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Larval supply is a principal factor determining the establishment, structure, and diversity of sessile benthic assemblages on coral reefs. Benthic reef communities in north-eastern Arabia have been subject to recurrent disturbances in recent years, and subsequent recovery will be, in part, driven by variation in the supply of available colonists. Using settlement tiles deployed seasonally over 1 year at eight sites encompassing three environmentally divergent regions (southern Arabian Gulf, the Musandam Peninsula in the Strait of Hormuz, and the Sea of Oman) we assessed spatial and seasonal variability in settlement of benthic reef organisms. There was strong spatial variation in composition of new colonists among regions, mainly driven by the high abundance of coralline algae in the Arabian Gulf, colonial ascidians on the Musandam Peninsula and barnacles in the Sea of Oman. Seasonal differences in composition of new colonists were less important than regional differences, with seasonal variation in settlement not consistent among regions. The number of corals settling to the tiles was low compared to those reported for other regions, with mean densities ranging from 0 corals m^{-2} year^{-1} in the Sea of Oman to 30 ($\pm$ 0.6 SE) and 38 ($\pm$ 0.5 SE) in Musandam and the Arabian Gulf, respectively. Peak coral settlement abundance in the Gulf occurred in summer and autumn and in Musandam in spring (averaging 82 and 70 settlers m^{-2} year^{-1}, respectively, during the peak settlement season). This work provides the first record of large-scale spatial and seasonal patterns of settlement in north-eastern Arabia and provides valuable information on the supply of settlers available to recolonize heavily disturbed reefs in this region. The extremely low rates of coral settlement suggest that these marginal reefs are likely to be extremely slow to recover from on-going and future disturbances.

Keywords: Arabian Peninsula, benthic communities, coral recruits, settlement tiles, seasonality, sessile invertebrates

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INTRODUCTION

Coral reefs provide a variety of significant socio-economic benefits to coastal communities (Ferrario et al., 2014; Guannel et al., 2016), however, climate change and increasing local pressures are jeopardizing the future of reefs (Ateweberhan et al., 2013; Bruno, 2013; Spalding and Brown, 2015). Over the past several decades, reefs have been increasingly degraded by overfishing, pollution, sedimentation, disease and coral predator outbreaks (Maina et al., 2013; Riegl et al., 2013; Pollock et al., 2014; Wear and Thurber, 2015; Mumby, 2016). These stressors have resulted in an estimated loss of up to 50% of coral cover from many reefs in the past several decades (De'ath et al., 2012; Hughes et al., 2017), with a third of reef-building coral species now considered at risk of extinction (Carpenter et al., 2008).

Disturbances such as bleaching, cyclones and crown of thorns outbreaks that cause large-scale coral mortality are becoming increasingly common (Spalding and Brown, 2015). Whether reefs can recover from these disturbances will depend, in part, on the supply of colonists available to settle to newly opened space that appears on reefs following a disturbance (Gilmour et al., 2013). Both stochastic processes which affect the supply of potential colonists and deterministic processes such as habitat availability, larval preferences, and interactions with existing community members, can influence settlement patterns (Lillis et al., 2016). Post-settlement processes then further shape subsequent community development (Caley et al., 1996). As a result, the trajectory of community recovery following disturbance is highly dynamic, with some studies reporting a relatively rapid return to pre-disturbance assemblage structure (Halford et al., 2004; Adjeroud et al., 2009), while others have observed dramatic and long-term shifts (Roff et al., 2015; Guest et al., 2016).

Historically, studies of the role of supply in recovery dynamics have focused on coral recruitment, and have largely overlooked settlement by other members of the benthic community (Zhang et al., 2014). However, algae, sponges, ascidians, and various other sessile members of the benthos are also abundant and integral members of reef communities that support diverse functional roles (Mallela, 2007; Bell, 2008; Glynn and Enochs, 2011; De Goeij et al., 2013; Enochs and Glynn, 2017), although the role that these organisms play in recovery dynamics is not well understood. Non-coral benthos are typically far more abundant than coral spat in early settlement communities (Dunstan and Johnson, 1998; Díaz-Castañeda and Almeda-Jauregui, 1999; Glassom et al., 2004; Mangubhai et al., 2007; Stubler et al., 2016), and initial colonization patterns by these organisms can strongly influence the trajectory of subsequent community development (Stubler et al., 2016). Non-coral settlement patterns may translate into long-term shifts in reef community structure, as variation in the early recruitment rates of non-coral benthos can considerably influence adult abundance of these organisms (Jackson, 1984; Caley et al., 1996; Cowen and Sponaugle, 2009; Zabin, 2015). Further, many non-coral settlers can alternately inhibit or facilitate subsequent colonization by corals (Dunstan and Johnson, 1998; Mangubhai et al., 2007; Birrell et al., 2008; Arnold et al., 2010; Diaz-Pulido et al., 2010). Thus, developing an understanding of the settlement of non-coral benthos can provide valuable insights into the role that recruitment across the wider benthic community may play in affecting the trajectory of initial community development on reefs following disturbance.
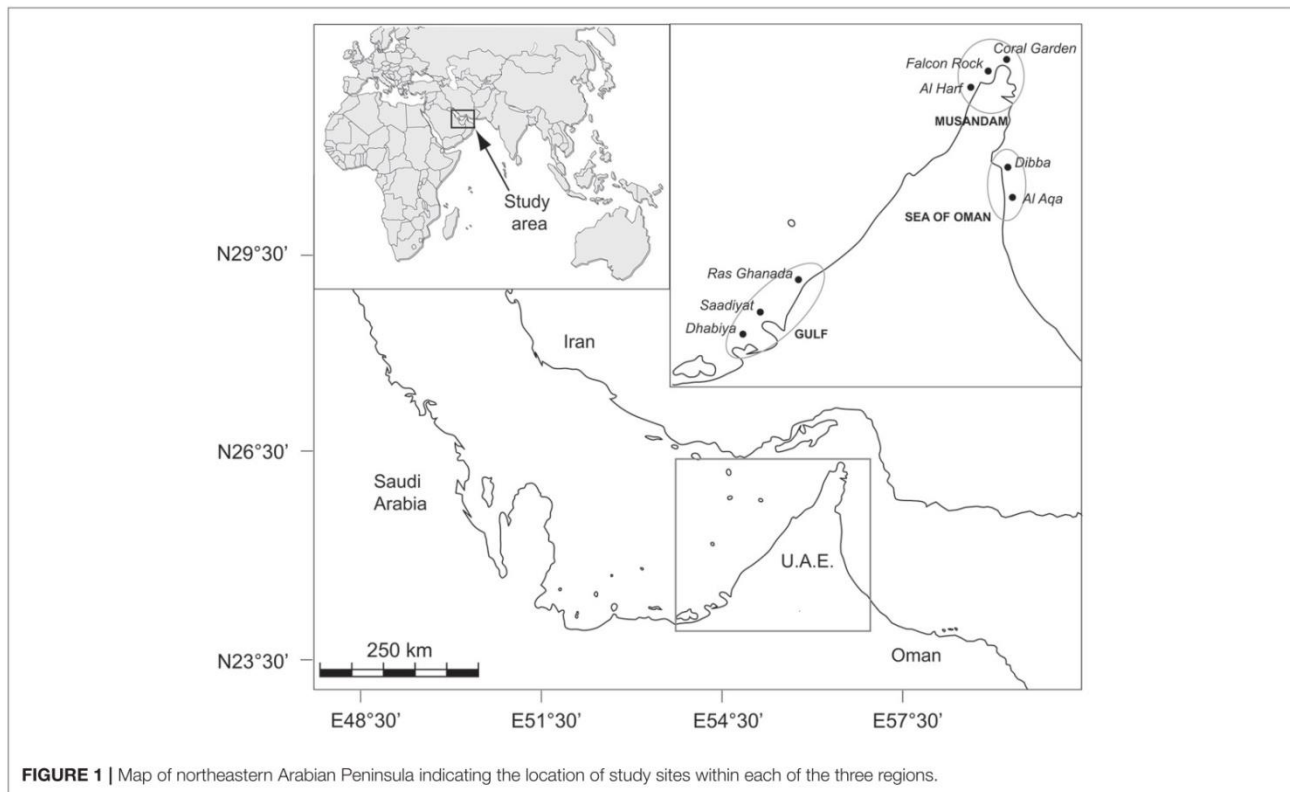
Coral reefs in north-eastern Arabia have been subject to widespread and substantial disturbances in recent years. Recurrent bleaching events and disease outbreaks have heavily affected reefs in the southern Persian/Arabian Gulf (hereafter 'the Gulf') while reefs in the adjacent Sea of Oman have been impacted by a super-cyclone and a large-scale harmful algal bloom (Bauman et al., 2010; Riegl and Purkis, 2015; Burt et al., 2016). All of these disturbances have caused substantial declines in coral cover and shifts in the composition of the wider benthic community (Bento et al., 2016). Recovery of reef communities in subsequent years has been variable, with a return toward pre-disturbance assemblages observed in some locations but not others (Burt et al., 2008, 2011; Bento et al., 2016). Several studies have suggested that this divergence in recovery patterns can largely be attributed to variation in the abundance and composition of juvenile corals that have recruited to these reefs (Burt et al., 2008; Pratchett et al., 2017). However, it is unclear whether these patterns in juvenile corals (up to 5 cm diameter) were primarily shaped by larval supply or post-settlement processes.

The purpose of this study was to investigate spatial and seasonal variability in settlement of benthic organisms on reefs spanning > 750 km of coastline in the north-eastern Arabian Peninsula. Terra-cotta settlement tiles were deployed seasonally over 1 year on reefs in the highly disturbed Gulf and Sea of Oman, and on relatively undisturbed reefs in the Musandam Peninsula. Comparison of seasonal dynamics provides insights into peak settlement periods for sessile benthic invertebrates, while large-scale spatial comparisons provide insights into regional scale disturbance and recovery dynamics.

MATERIALS AND METHODS

This study was performed across eight sites in three regions spanning >750 km of coastline in the north-eastern Arabian Peninsula: three sites in the southern Arabian Gulf (Saadiyat, Dhabiya, and Ras Ghanada), three sites along the Musandam Peninsula (Al Harf, Falcon Rock, and Coral Garden) and two sites in the Sea of Oman (Dibba and Al Aqa) (**Figure 1**). All sites were fringing reefs at comparable depths (2–8 m) with coral cover varying between ca. 20–60% among reefs. Communities were generally dominated by faviids and poritids in all regions, with other subdominant families differing in relative abundance among sites. A full description of the benthos in each region is provided in Bento et al. (2016).

Settlement of benthic organisms was quantified at all sites using unglazed terracotta settlement tiles (10 × 10 × 1.5 cm) following methods adapted from Mundy (2000). At each site, 30 tiles were attached to the substratum at ca. 5 m depth and spaced 1–3 m apart. Each tile was secured to the reef using a stainless steel stud that was epoxied into the substratum and

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FIGURE 1 | Map of northeastern Arabian Peninsula indicating the location of study sites within each of the three regions.

passed through a 1 cm hole in the center of each tile. A 2 cm plastic washer was placed over each stud to position the tile 2 cm above the reef substratum. The textured (i.e., corrugated) surface of each tile was always positioned facing the substratum, as previous studies have shown that settlement primarily occurs on the underside of tiles and that textured materials generally have higher settlement than smooth surfaces (Burt et al., 2009). To assess seasonal variation in settlement, tiles were deployed and replaced every 3 months over 1 year. Each deployment represented a specific season: (summer: July–September 2012, autumn: October–December 2012, winter: January–March 2013, and spring: April–June 2013), with all tiles deployed/collected across all sites within ca. 7–10 days at the beginning/end of each season. These four seasons were selected based on the periods of highest (summer) and lowest (winter) sea surface temperatures, as well as the transitional spring and autumn periods that are known to be important discrete spawning and/or settlement seasons for a variety of marine fauna in this region (e.g., Bauman et al., 2011; John, 2012; Howells et al., 2014).

Upon retrieval, the bottom of each tile was photographed with a 10 megapixel Nikon D-80 digital camera fitted with a macro lens. Only the bottom surfaces of tiles were analyzed as virtually all settlement in this region occurs on the bottoms of tiles (Burt et al., 2009; Bauman et al., 2014). Percent cover of various benthos on each tile was calculated by image analyses using the software CPC with Excel extension (Kohler and Gill, 2006), with coverage tabulated from 50 random point intercepts per tile.

Substratum and benthic community type was categorized into 15 broad groups and several sub-groups: bare tile, coralline algae, coral, ascidiacea (subgroups: colonial ascidian, solitary ascidian), sponge, cnidaria (subgroups: anemone, hydrozoa, zoanthid), arthropoda (subgroup: barnacle), mollusca (subgroups: bivalve, chiton, gastropoda), annelid (subgroup: polychaeta), bryozoa, other live (subgroups: mobile invertebrate, urchin, other), algae (subgroups: algae, turf algae), sand/silt, non-benthos (subgroups: gap, tape, shadow), and unknown taxa. Due to the small size of coral recruits (age: ≤3 mo) and their relatively limited coverage, density of coral juveniles was tabulated separately. Following photography for community analysis, tiles were cleaned of living tissue in bleach for 24 h, rinsed and air dried before tabulating the number of coral recruits on each tile using an Olympus DP-70 stereo-microscope (40X magnification).

Data Analyses

Before statistical analyses, percent cover for the various benthic groups was standardized as a proportion of the total living benthos (i.e., relative abundance), and an arcsine-square root transformation was applied to normalize the data, as recommended by Zar (2010). Coral densities were $\log(x + 1)$ transformed. Prior to multivariate analyses, benthic categories occurring in <5% of samples were excluded from analyses to avoid the influence of outliers (McCune et al., 2002).

To explore the overall spatial and seasonal structure of settlement assemblages, and to identify which components of

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the benthos were driving any settlement differences, multivariate analyses were performed using Primer, v6 (Clarke and Gorley, 2006). Non-metric multi-dimensional scaling (nMDS) analyses based on Bray-Curtis distance matrices were used to illustrate the influence of regions and seasons on benthic community composition, with taxa strongly driving divergence along nMDS axes identified using Pearson rank-correlations ($r \geq \pm 0.5$ for either axis). To ease interpretation, each season was manually shaded in the resulting nMDS and the vector plot overlaid. Spatial and seasonal differences in settlement community structure were tested with a partially-nested permutational multivariate analysis of variance (PERMANOVA) on the main effects of seasons and regions with sites nested within regions. A similarity percentages analysis (SIMPER) was used to assess which benthic components contributed most to the observed variation in settlement community structure (Clarke and Gorley, 2006). Spatial and seasonal differences in settlement community structure were tested with a partially-nested permutational multivariate analysis of variance (PERMANOVA) on the main effects of seasons and regions with sites nested within regions based on our a priori hypotheses. Key benthic groups and sub-groups identified by our multivariate analyses and coral settlement densities were then then tested with univariate PERMANOVAs to identify significant settlement differences.

A multiple regression was also employed to determine whether the density of coral spat was associated with percent cover of any other components of the settlement community (including each live benthos category plus bare tile). Before regression analyses, the normality of the residuals and homogeneity of variances were confirmed by plotting residuals against fitted values and using QQ plots (Zuur et al., 2007).

RESULTS

Multivariate ordination of the overall settlement community observed in this study indicated strong differences in community structure between regions, with individual sites clustering as region-specific groups across all seasons with no overlap among regions (**Figure 2**). Vector plots indicated regional differences were primarily driven by variation in the relative abundance of three benthic groups: coralline algae, colonial ascidians, and barnacles (**Figure 2**), although other benthos also made strong contributions (Supplementary Table 1). SIMPER analyses showed that settlement communities in the Gulf were primarily characterized by the presence of coralline algae, polychaetes, and bryozoans, which together contributed >80% to similarity in tile assemblage structure in this region (**Table 1**). In the Musandam region, over half of the similarity in settlement communities was driven by strong contributions from both colonial ascidians and bryozoans, with polychaetes and turf algae making more modest contributions (**Table 1**). Bryozoans were also the most common component of Sea of Oman settlement communities, where they contributed over a third of the similarity in community structure, followed by barnacles and turf algae also playing important roles. The SIMPER analysis showed higher abundances of
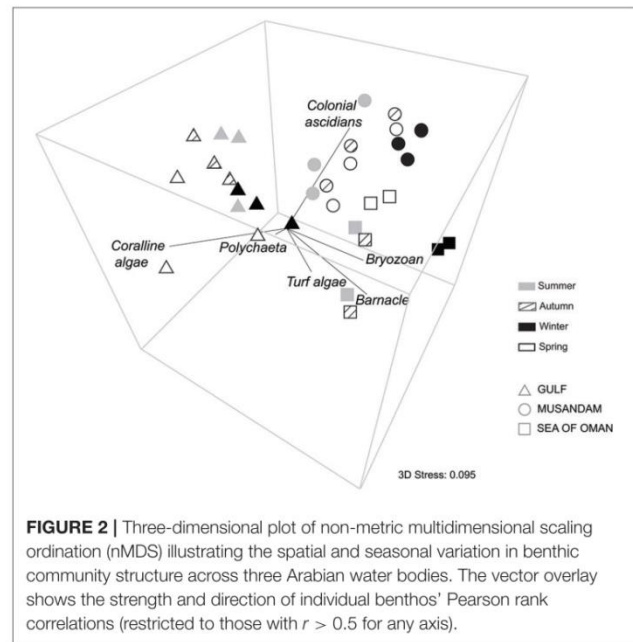
FIGURE 2 | Three-dimensional plot of non-metric multidimensional scaling ordination (nMDS) illustrating the spatial and seasonal variation in benthic community structure across three Arabian water bodies. The vector overlay shows the strength and direction of individual benthos' Pearson rank correlations (restricted to those with $r > 0.5$ for any axis).

coralline algae in the Gulf was the main driver of differences between both Musandam and Sea of Oman communities, where colonial ascidians, bryozoans, and turf algae were more abundant (**Table 1**). Differences between Musandam and the Sea of Oman settlement communities were largely driven by higher cover of colonial ascidians in the Musandam vs. cover of bryozoans, barnacles, polychaetes and turf algae in Sea of Oman sites (**Table 1**).

While assemblage structure primarily grouped regionally, there were also modest seasonal changes in the settlement community within each region (**Figure 2**), although these changes were not consistent within regions as shown by a significant interaction between seasons and regions in PERMANOVA (**Table 2**). In the Gulf the settlement community showed considerable overlap in structure across summer, autumn, and winter, indicating a good degree of similarity across these seasons, with divergence in the remaining season (spring) being primarily due to higher abundances of coralline algae settling into a single site (Ras Ghanada; **Figure 2**) within this season. In the Musandam the settlement community composition was more similar to Gulf communities during the warm summer season but diverged in the cooler autumn and spring seasons, with the greatest divergence from the Gulf occurring in the cold winter season, when all three Musandam sites had highly convergent community structure, with higher settlement of colonial ascidians (**Figure 2**). The settlement community in the Sea of Oman varied spatio-temporally. The community at Dibba was fairly consistent across summer, autumn, and spring, while the community at Al Aqa was comparable to that found within Dibba in spring, but diverged markedly in the summer and autumn (**Figure 2**). In the winter there were dramatic shifts in the settlement community at both of the Sea of Oman sites, with the assemblages at the two sites

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TABLE 1 | Benthic groups responsible for >90% of within-regions similarities and >70% of among-regions dissimilarities based on SIMPER analysis.

Gulf			Gulf vs. Musandam				
Within group similarity: 46.3%	Cont. (%)	Cum. (%)	*Between-group dissimilarity: 62.2%*	Gulf % cover	Musandam % cover	Cont. (%)	Cum. (%)
Coralline algae	33.7	33.7	Coralline algae	28.2	1.2	18.1	18.1
Polychaeta	25.2	58.9	Colonial ascidian	12.5	30.7	17.4	35.5
Bryozoan	24.5	83.4	Bryozoan	20.7	25.3	13.5	49.0
Colonial ascidian	7.1	90.5	Polychaeta	19.2	15.4	11.8	60.9
			Turf algae	5.6	9.5	10.0	70.9
Musandam			**Gulf vs. Sea of Oman**				
Within group similarity: 50.9%			*Between-group dissimilarity: 67.5%*	Gulf % cover	Sea of Oman % cover		
Bryozoan	27.6	27.6	Coralline algae	28.2	3.3	16.2	16.2
Colonial ascidian	27.4	55.0	Bryozoan	20.7	32.2	14.6	30.8
Polychaeta	19.1	74.0	Barnacle	0.2	22.2	14.4	45.3
Turf algae	12.3	86.3	Polychaeta	19.2	7.8	12.4	57.6
Barnacle	5.4	91.7	Turf algae	5.6	14.3	11.2	68.8
			Colonial ascidian	12.5	8.6	10.7	79.5
Oman			**Musandam vs. Sea of Oman**				
Within group similarity: 42.7%			*Between-group dissimilarity: 59.3%*	Musandam % cover	Sea of Oman % cover		
Bryozoan	36.2	36.2	Colonial ascidian	30.7	8.6	18.8	18.8
Barnacle	23.0	59.2	Bryozoan	25.3	32.2	15.7	34.4
Turf algae	18.2	77.4	Barnacle	5.1	22.2	14.5	48.9
Polychaeta	9.0	86.4	Polychaeta	15.4	7.8	12.2	61.1
Colonial ascidian	4.4	90.9	Turf algae	9.5	14.3	11.5	72.5

Mean relative abundance (as % of live cover) in each region and individual (Cont.) and cumulative (Cum.) contribution to dissimilarity are shown.

TABLE 2 | Results of the three factor partially nested PERMANOVA analyses assessing differences between regions, seasons and sites (within regions) in benthic community composition.

Source	Df	SS	MS	Pseudo-F	P(perm)
Region	2	3.09E5	1.54E5	7.83	0.0035
Season	3	84334	28111	4.70	0.0001
Site (Region)	5	99698	19940	17.97	0.0001
Region × Season	6	1.5E5	25599	4.26	0.0001
Site (Region) × Season	15	90840	6056	5.46	0.0001

converging with each other but diverging from the communities observed in all other seasons in this region, due to the settlement of barnacles in both sites. SIMPER analyses (**Table 3**) showed that the major taxa driving seasonal changes largely reflected the same groups that were associated with regional differences (above; **Figure 2**), indicating that fluctuations in the relative abundance of these key regional taxa was the primary driver of seasonal shifts in settlement communities.

SIMPER analyses were further used to examine the main benthos driving seasonal differences within regional settlement communities (**Table 3**). The only benthic group that showed wide seasonal variation in all three regions were the bryozoans; all other benthos that were key drivers of seasonal change were important in just one or two regions. In addition to bryozoans, seasonal differences in the Gulf were mainly attributable to variation in the amount of coralline algae, colonial ascidians, and polychaetes, in the Musandam to colonial ascidians, and in the Sea of Oman to barnacles. These seasonal drivers largely reflected the same benthos associated with regional community differences (above; **Figure 2**).

There was a significant interaction between the main effects of season, region and sites (within region) in structuring settlement of each major benthos (**Figure 3**), indicating that patterns of change were not consistent among the main effects for any of these benthic groups (PERMANOVA Pseudo- $F_{(15, 824)}$: bryozoans = 11.0, polychaetes = 7.2, turf algae = 5.0, coralline algae = 3.9, barnacles = 7.4, colonial ascidian = 2.7; $p < 0.001$ for each]. Bryozoans showed strong but inconsistent seasonal fluctuations in all regions, with highest cover in the winter in the Gulf and Musandam (**Figures 3A,B**), while densities peaked in the autumn in the Sea of Oman when cover was nearly 50% higher than peak densities in the other regions (**Figure 3C**). While coralline algae cover was negligible in other regions, it

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TABLE 3 | Benthic taxa identified as important seasonal drivers of divergence in community structure in SIMPER.

Region	Season comparison	δ	Percent contribution to dissimilarity					
			Coralline algae	Colonial ascidian	Bryozoan	Polychaetes	Turf algae	Barnacle
Gulf	Spring vs. Summer	51.1	15.1	17.0				
	Spring vs. Autumn	53.1	16.2	14.8	15.2	16.8		
	Summer vs. Autumn	51.9		17.0		15.0		
	Spring vs. Winter	56.6	20.9		17.6	15.5		
	Summer vs. Winter	59.8	16.7	15.2	16.8			
	Autumn vs. Winter	56.4	16.9		18.8	16.2		
Musandam	Spring vs. Summer	46.9		19.4				
	Spring vs. Autumn	49.1		19.1	15.6			
	Summer vs. Autumn	50.3		18.6				
	Spring vs. Winter	47.6		21.2	17.7			
	Summer vs. Winter	50.5		19.2	19.1			
	Autumn vs. Winter	55.4		18.5	19.0	15.2		
Sea of Oman	Spring vs. Summer	56.2			15.4			15.1
	Spring vs. Autumn	65.4			22.0		19.1	
	Summer vs. Autumn	59.7			20.4			15.8
	Spring vs. Winter	61.2					18.3	24.7
	Summer vs. Winter	54.8			16.6			20.0
	Autumn vs. Winter	69.2			23.4			26.3

Only benthic groups strongly contributing to the dissimilarity (δ >15%) in each pairwise comparison are shown.

was the most abundant benthic component on tiles in the Gulf, and it doubled in cover from winter to summer (mean cover: 16.3% ± 2.2 SE to 31.6% ± 2.7 SE respectively; **Figure 3A**). Colonial ascidians were considerably more abundant in the Musandam than other regions, explaining its identification as a major distinguishing taxa for tiles in this region in earlier SIMPER analyses, and cover was generally comparable across seasons for this group (**Figure 3B**). In the Sea of Oman barnacles heavily dominated settlement in winter, when they comprised over half of the benthos at each site and were substantially more widespread than in other seasons; barnacles were uncommon in Musandam and nearly non-existent in the Gulf.

Coral Recruits

In total, 216 coral recruits were observed on the 845 tiles deployed across the 8 sites throughout the study. No coral settlers were observed across the entire study in the Gulf of Oman, and there was inconsistent and high variation in coral settlement among sites and seasons within the Gulf and Musandam (**Figure 4**; **Table 4**). In the Gulf, mean settlement was highest in autumn but this was mainly due to a large pulse at Saadiyat reef (90% of spat this season); a second peak in settlement also occurred in summer, with a small number of spat recorded in spring as well. In the Musandam, coral settlement mainly occurred in the spring, although spat were observed in low densities in all seasons in at least one site.

Multiple regression revealed that coral density was unrelated to cover of other benthic components [including bare tile space; $R^2 = 0.27$; $F_{(10, 96)} = 0.736$, $p = 0.69$], reflecting the considerable

variability and low incidence of coral settlement observed in this study.

DISCUSSION

Coral reef communities in north-eastern Arabia have been subject to various large-scale disturbances in recent years. To date, there had been limited knowledge of the spatial and seasonal patterns of settlement of coral and non-coral benthos, limiting our understanding of the important role that supply may play following disturbance. The results of this study show that settlement of corals was extremely low and that non-coral benthic settlement was highly variable between regions and across sites within regions.

The most striking result of this study was the strong regionally structured patterns of non-coral settlement, with regional differences persisting across seasons throughout the study. These large-scale differences in non-coral settlement mirror the divergence of benthic community structure on reefs across these regions (Bauman et al., 2013; Bento et al., 2016), and is likely driven by the highly divergent environmental conditions among these seas, which have also been subject to varying degrees of disturbance.

The southern Gulf represents one of the most extreme coral reef environments on earth, with sea surface temperatures ranging >25°C annually, daily mean maxima >34°C for several months during summer, and salinities that consistently exceed 44 PSU (Sheppard et al., 1992; Coles, 2003; Foster et al., 2012). In addition, these reefs have experienced numerous large-scale

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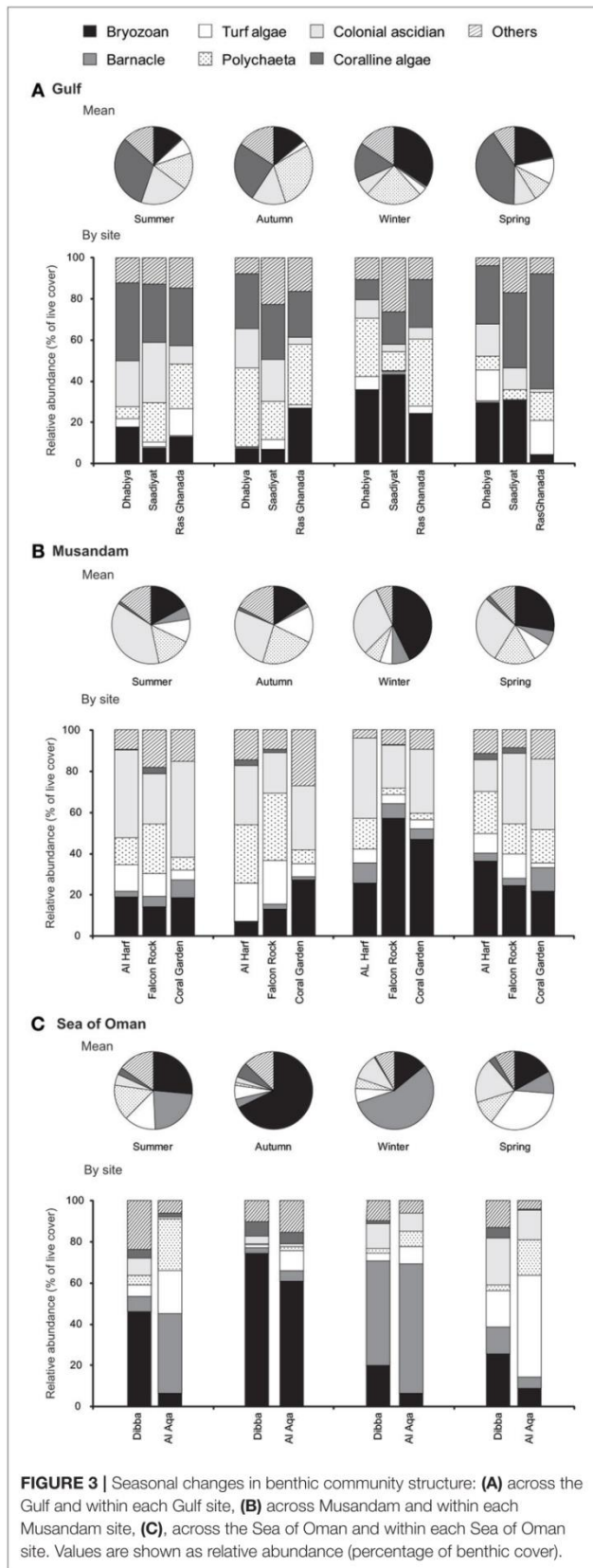
FIGURE 3 | Seasonal changes in benthic community structure: **(A)** across the Gulf and within each Gulf site, **(B)** across Musandam and within each Musandam site, **(C)**, across the Sea of Oman and within each Sea of Oman site. Values are shown as relative abundance (percentage of benthic cover).

bleaching events over the past two decades (Riegl and Purkis, 2015), resulting in widespread shifts in benthic community structure from which there has been only limited recovery (George and John, 2000; Sheppard and Loughland, 2002; Burt et al., 2008, 2011). In the wake of earlier mass bleaching events, coralline algae dramatically increased in abundance on southern Gulf reefs (George and John, 2000, 2002). In the current study, coralline algae dominated the settlement community on southern Gulf reefs (covering 28% of tile surfaces, on average), and it was the primary differentiator in settlement community structure from the other regions (where it covered <3.5% of tile surfaces in both areas). Thus, the presence of coralline algae as a major component of the settlement community in the southern Gulf appears to be a persistent, long-term characteristic of this highly disturbed, extreme environment.

In contrast to the Gulf, the Sea of Oman has environmental conditions that are more benign. Due to its greater depth and exchange with the wider Indian Ocean, SSTs in the Gulf of Oman are less extreme (mean summer maxima <32°C, range 10°C annually) and salinity is comparable to oceanic conditions (37 PSU) (Foster et al., 2012; Howells et al., 2014). Its waters are also highly productive compared with the Gulf and Musandam as a result of monsoon-induced upwelling (Sheppard et al., 1992). Although reefs in the Sea of Oman have experienced widespread disturbance in the past decade as a result of cyclone storm damage and a hypoxic event associated with an algal bloom (Bauman et al., 2010; Burt et al., 2016), the frequency of impacts to coral reefs here has not been as severe as in the Gulf and there are indications that recovery of reef communities is underway (Bento et al., 2016; Pratchett et al., 2017). Barnacles were one of the primary drivers of the divergence of Sea of Oman reefs from the other regions, with barnacles here covering nearly a quarter of settlement tiles (22%) on average, compared with low abundance in the Musandam (5% cover) and a near absence in the Gulf (0.2% cover). Barnacles are reported to be among the most abundant members of settlement communities in Oman (Wallström et al., 2011; Dobretsov et al., 2013; Polman et al., 2013; Dobretsov, 2015), likely a reflection of their success as filter-feeders in this high-productivity environment (Sheppard et al., 1992), suggesting that the high barnacle abundance we observed is a result of long-term supply dominance in the Sea of Oman.

The Musandam Peninsula sits at the interface between the Arabian Gulf and the Sea of Oman at the Strait of Hormuz. Environmental conditions in the Musandam are generally comparable to the Sea of Oman, although productivity is lower due to a lack of monsoonal upwelling in this area (Sheppard and Salm, 1988; Sheppard et al., 1992; Reynolds, 1993). In addition to having relatively benign environmental conditions, Musandam reefs have also escaped the various large-scale disturbances that affected reefs in the adjacent seas, and reef communities here have among the highest coral cover and diversity in northeastern Arabia and are considered among the most pristine in the region (Sheppard et al., 2010; Bento et al., 2016; Burt et al., 2016). Colonial ascidians were the primary driver of divergence of Musandam reefs from those in the other regions, with these organisms covering nearly a third of Musandam tiles (30.7% cover), nearly triple the coverage in the other regions

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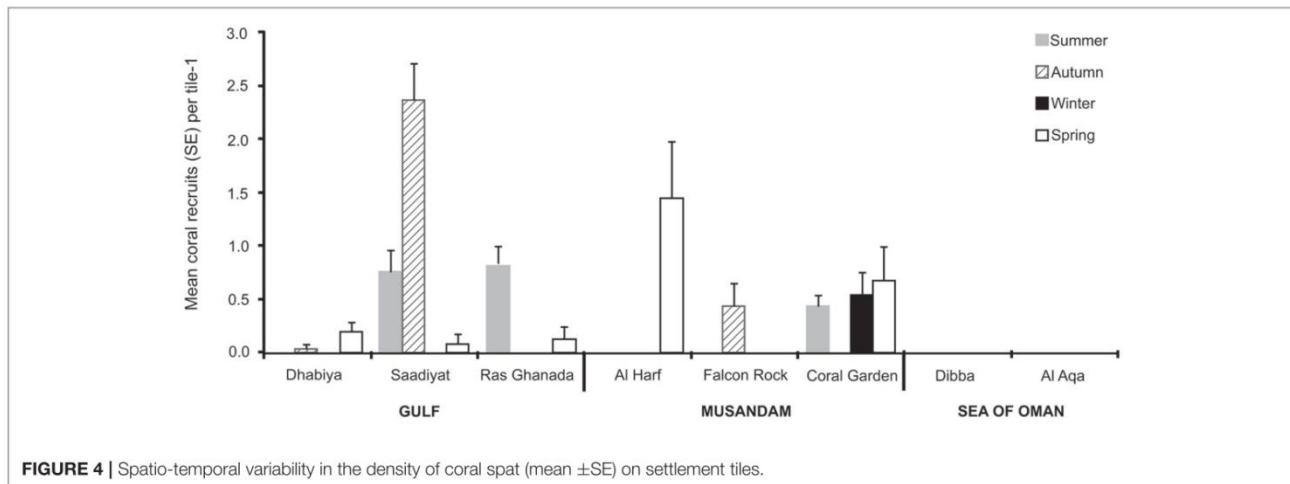
FIGURE 4 | Spatio-temporal variability in the density of coral spat (mean ±SE) on settlement tiles.

TABLE 4 | Results from PERMANOVA tests comparing mean coral recruits densities among regions, sites and seasons.

Source	df	MS	Pseudo-F	p-value
Region	2	2.0454	0.68978	0.5171
Season	3	0.54429	0.20592	0.8917
Site (Region)	4	3.0654	24.549	**0.0001**
Region * Season	6	1.4905	0.55661	0.7421
Site (Region) * Season	12	2.7596	22.1	**0.0001**
Total	747			

Values in bold are significant (p < 0.05).

(8.6–12.5% cover). Ascidians are relatively common members of the benthic community on reefs in the Musandam (R. Bento, unpubl. data), particularly compared to reefs in the southern Gulf or Sea of Oman where they are virtually undetected in benthic surveys (Burt et al., 2011; Grizzle et al., 2016). Given their short pelagic duration and limited larval swimming ability, ascidians generally have a relatively localized dispersal (Shanks et al., 2003; Weersing and Toonen, 2009), suggesting that the high abundance of colonial ascidians observed on Musandam settlement plates likely relates to their high abundance in the wider reef community.

While regional differences primarily structured settlement communities, there were also modest within-region shifts in settlement communities over the course of the year. Much of these within-region shifts were related to fluctuations in the abundance of bryozoans, a dominant member of the community across all regions, as well as to fluctuations in the relative abundance of those same key benthic categories that drove between-region differences. In all three regions the period of peak bryozoan settlement coincided with a reciprocal decline in the abundance of the region-specific key taxa; peak bryozoan abundance in the winter coincided with the lowest annual mean cover of coralline algae in the Gulf and colonial ascidians in the Musandam, while peak bryozoan settlement in the autumn in the Sea of Oman and coincided with a decline of barnacle cover on tiles. In all cases, peak coverage of bryozoans occurred

in the season with maximum chlorophyll-a concentrations for every region (Nezlin et al., 2010; Piontkovski et al., 2011; Moradi and Kabiri, 2015), suggesting that while bryozoans settle year round, their success in these particular seasons may be related to enhanced post-settlement growth due to higher planktonic food availability. Together, these observations suggest that while there are distinct regional settlement signatures, seasonality in bryozoan settlement is largely responsible for modulating within-region temporal dynamics. It should be noted, however, that these results represent seasonal settlement data from a single year. While this is useful information given the lack of data available previously, benthic recruitment is highly variable from year to year and it is unknown whether the results of this study are representative of longer-term patterns. A multi-year year settlement study to assess the role of recruitment in sessile benthic population dynamics is warranted.

Coral Settlement Patterns

Coral settlement was low across all three regions in this study. Across the full year of study, coral densities were minimal in the Gulf and Musandam (mean: 38 and 30 coral settlers m^{-2} $year^{-1}$, respectively, across the year, and averaging 82 and 70 settlers m^{-2} $year^{-1}$ even when considering only the peak settlement season), and corals were entirely absent from settlement tiles in the Sea of Oman throughout the study. The observed densities were substantially lower than has commonly been reported in tropical reef environments (Seychelles: 595 spat m^{-2} $year^{-1}$, Chong-Seng et al., 2014; Indonesia: 286–705 m^{-2} $year^{-1}$, Sawall et al., 2013; Kenya: 101–908 m^{-2} $year^{-1}$, Mangubhai et al., 2007), and less than half of densities reported for comparable high latitude marginal reefs (Eilat: 190 m^2 $year^{-1}$, Glassom and Chadwick, 2006; Solitary Islands: 132 spat m^{-2} $year^{-1}$, Harriott and Banks, 1995; Taiwan: 111 spat m^{-2} $year^{-1}$, Soong et al., 2003). The observed densities are also low compared with a recent study of coral settlement in Dubai in the southern Gulf where densities of 121 coral settlers m^{-2} $year^{-1}$ were reported (Bauman et al., 2014), although those data were mainly collected on breakwaters that have been suggested to entrain eggs, potentially enhancing

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settlement compared with what would occur on natural reefs (Burt et al., 2009). Overall, the low densities noted in this region are similar to that seen in heavily degraded, highly disturbed reef environments (Singapore: 55 m^{-2} year^{-1}, Bauman et al., 2015; Florida: 38 m^{-2} year^{-1}, Van Woesik et al., 2014). Together, the low densities observed in the Gulf and Musandam and the complete absence of coral settlement in the Sea of Oman suggest that there is cause for concern for the regeneration of degraded coral reef communities within the Arabian Peninsula.

The low abundance of coral spat observed here is unlikely to be due to interactions with other members of the settlement community. The abundance of coral recruits was unrelated to cover of any other benthos in our analyses, and bare space was relatively common (ranging from 55% in the Gulf to 20% in the Sea of Oman), suggesting ample availability of habitat for coral settlement. Instead, the low coral settlement likely reflects a limited supply of coral larvae. Low coral settlement has been reported earlier in the southern Gulf (Bauman et al., 2014), and is likely the result of depressed fecundity of corals being exposed to recurrent bleaching events and extreme environmental conditions (Riegl and Purkis, 2015; Howells et al., 2016). Although coral cover is high in the Musandam (Bento et al., 2016; Burt et al., 2016), we observed low levels of coral settlement. This suggests that low coral recruitment is characteristic of reefs in northeastern Arabia, and the high coral cover in the Musandam is likely the result of the relatively low levels of disturbance in this area rather than high larval supply. The implication is that the relatively pristine reefs in the Musandam may be highly vulnerable to any future disturbances that may occur, as any recovery would be potentially limited by low recruitment levels. The absence of coral settlement to tiles in the Sea of Oman was surprising. Reproductive studies occurring near these sites have shown that common coral species were spawning during this study in April 2013 (Howells et al., 2014), and fecundity was substantially higher than conspecifics in the southern Gulf (Howells et al., 2016). Additionally, juvenile surveys on these sites in 2012 showed that corals were recruiting to these reefs, although densities were half of that observed in the southern Gulf (Pratchett et al., 2017), suggesting that recruitment is impaired here. Reefs in the Sea of Oman sites have low coral cover (18%) relative to the southern Gulf and the Musandam (56 and 58%, respectively, Bento et al., 2016), mainly as a result of a algal bloom in 2009 when 50–90% of corals were lost from reefs (Bauman et al., 2010; Foster et al., 2011). As a result, while individual corals here are fecund, reef-wide reproductive output for a variety of dominant coral species is low as a consequence of the limited number of fecund adults in the community (Howells et al., 2016), potentially explaining the absence of coral settlers on tiles and the relatively low overall juvenile recruitment rates observed by Pratchett et al. (2017). It should be noted, however, that recovery on highly disturbed reefs typically takes 10–15 years (Purkis and Riegl, 2005; Burt et al., 2008; Ateweberhan et al., 2011), even in areas where larval supply remains depressed for up to 6 years (Gilmour et al., 2013). As the current study was performed 8 years after the catastrophic HAB event, this suggests that there is hope that recovery may occur in the near future. It is unclear whether the absence of coral settlement observed here

extends to other parts of the Sea of Oman. A recent survey of coral reefs 400 km southwest around Muscat, Oman, suggested that many coral reefs there continue to have high coral cover despite showing indications of localized decline in some areas over the past two decades, with available evidence suggesting that declines were primarily due to a recent cyclone rather than the dramic HAB induced loss that impacted the coral communities on reefs studied here (Coles et al., 2015). An assessment of the reproductive capacity and settlement patterns of corals on reefs elsewhere in the Sea of Oman is highly warranted.

Coral reefs around the world are becoming increasingly degraded as a result of climate change and localized anthropogenic impacts (Hughes et al., 2010; Pandolfi et al., 2011) with widespread shifts toward a dominance of non-coral benthos (Colvard and Edmunds, 2011; Kelmo et al., 2013, 2014). While many studies have focused efforts on understanding the dynamics of coral settlement following disturbance (Glassom et al., 2004; Abelson et al., 2005; Green and Edmunds, 2011; Sawall et al., 2013; Bauman et al., 2014), few studies have explored the role that non-coral benthos may play in affecting early recovery dynamics on reefs (Colvard and Edmunds, 2011; Luter et al., 2016). Non-coral benthos are among the first colonists to settle on substrates opened by disturbance, and typically reach an abundance and coverage that greatly exceeds that of coral spat (Dunstan and Johnson, 1998; Díaz-Castañeda and Almeda-Jauregui, 1999; Glassom et al., 2004; Mangubhai et al., 2007; Stubler et al., 2016). Given that many of these non-coral benthos can alternatively facilitate or inhibit subsequent coral recruitment in the space opened by disturbance, their presence could dramatically impact the trajectory of subsequent recovery on disturbed reefs. Our results showed that the initial settlement community was highly region-specific, with non-coral benthos being the primary members of the settlement community in all areas. In some regions, these initial communities were dominated by taxa known to facilitate settlement of coral larvae (for example, over a quarter of Gulf tile space was covered by crustose coralline algae, a well-known inducer of larval coral settlement (Ritson-Williams et al., 2014; Tebben et al., 2015), suggesting conditions favorable to coral colonization following disturbance. In others, however, early settlement communities were dominated by fauna known to inhibit coral larval settlement (e.g., ascidians covered a third of tiles in the Musandam, and various ascidians are known to produce allelochemicals that can inhibit coral settlement (Chadwick and Morrow, 2011). Our knowledge of the types of benthic organisms and the mechanisms that they use to interact with coral larvae is relatively under-developed (Ritson-Williams et al., 2009), but our results here suggest that such information is essential if we are to understand how the initial settlement community may affect the trajectory of early community development. Initial settlement communities will, of course, be shaped by post-settlement processes that will likely lead to mature assemblages that are markedly different in their structure. But because this first stage of development provides the foundation open which all post-settlement processes can act, it represents a critical bottleneck that has important implications for whether or not a disturbed reef has the capacity to recover.

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AUTHOR CONTRIBUTIONS

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fmars. 2017.00305/full#supplementary-material

REFERENCES

Abelson, A., Olinky, R., and Gaines, S. (2005). Coral recruitment to the reefs of Eilat, Red Sea: temporal and spatial variation, and possible effects of anthropogenic disturbances. *Mar. Pollut. Bull.* 50, 576–582. doi: 10.1016/j.marpolbul.2005.02.021

Adjeroud, M., Michonneau, F., Edmunds, P. J., Chancerelle, Y., De Loma, T. L., Penin, L., et al. (2009). Recurrent disturbances, recovery trajectories, and resilience of coral assemblages on a South Central Pacific reef. *Coral Reefs* 28, 775–780. doi: 10.1007/s00338-009-0515-7

Arnold, S. N., Steneck, R., and Mumby, P. J. (2010). Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Mar. Ecol.* 414, 91. doi: 10.3354/meps08724

Ateweberhan, M., Feary, D. A., Keshavmurthy, S., Chen, A., Schleyer, M. H., and Sheppard, C. R. (2013). Climate change impacts on coral reefs: synergies with local effects, possibilities for acclimation, and management implications. *Mar. Pollut. Bull.* 74, 526–539. doi: 10.1016/j.marpolbul.2013.06.011

Ateweberhan, M., McClanahan, T. R., Graham, N. A. J., and Sheppard, C. R. C. (2011). Episodic heterogeneous decline and recovery of coral cover in the Indian Ocean. *Coral Reefs* 30:739. doi: 10.1007/s00338-011-0775-x

Bauman, A. G., Baird, A. H., Burt, J. A., Pratchett, M. S., and Feary, D. A. (2014). Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates). *Mar. Ecol. Prog. Ser.* 499, 115–126. doi: 10.3354/meps10662

Bauman, A. G., Burt, J. A., Feary, D. A., Marquis, E., and Usseglio, P. (2010). Tropical harmful algal blooms: an emerging threat to coral reef communities? *Mar. Pollut. Bull.* 60, 2117–2122. doi: 10.1016/j.marpolbul.2010.08.015

Bauman, A. G., Feary, D. A., Heron, S. F., Pratchett, M. S., and Burt, J. A. (2013). Multiple environmental factors influence the spatial distribution and structure of reef communities in the northeastern *Arabian Peninsula. Mar. Pollut. Bull.* 72, 302–312. doi: 10.1016/j.marpolbul.2012.10.013

Bauman, A. G., Guest, J. R., Dunshea, G., Low, J., Todd, P. A., and Steinberg, P. D. (2015). Coral settlement on a highly disturbed equatorial reef system. *PLoS ONE* 10:e0127874. doi: 10.1371/journal.pone.0127874

Bauman, A., Baird, A., and Cavalcante, G. (2011). Coral reproduction in the world's warmest reefs: southern Persian Gulf (Dubai, United Arab Emirates). *Coral Reefs* 30, 405–413. doi: 10.1007/s00338-010-0711-5

Bell, J. J. (2008). The functional roles of marine sponges. *Estuar. Coast. Shelf Sci.* 79, 341–353. doi: 10.1016/j.ecss.2008.05.002

Bento, R., Hoey, A. S., Bauman, A. G., Feary, D. A., and Burt, J. A. (2016). The implications of recurrent disturbances within the world's hottest coral reef. *Mar. Pollut. Bull.* 105, 466–472. doi: 10.1016/j.marpolbul.2015. 10.006

Birrell, C., Mccook, L., Willis, B., and Diaz-Pulido, G. (2008). Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. *Oceanogr. Mar. Biol.* 46, 25–63. doi: 10.1201/9781420065756.ch2

Bruno, J. F. (2013). Coral reefs: building a better crystal ball. *Curr. Biol.* 23, R473–R475. doi: 10.1016/j.cub.2013.04.042

Burt, J. A., Coles, S., Van Lavieren, H., Taylor, O., Looker, E., and Samimi-Namin, K. (2016). Oman's coral reefs: a unique ecosystem challenged by natural and man-related stresses and in need of conservation. *Mar. Pollut. Bull.* 105, 498–506. doi: 10.1016/j.marpolbul.2015.11.010

Burt, J., Al-Harthi, S., and Al-Cibahy, A. (2011). Long-term impacts of coral bleaching events on the world's warmest reefs. *Mar. Environ. Res.* 72, 225–229. doi: 10.1016/j.marenvres.2011.08.005

Burt, J., Bartholomew, A., and Usseglio, P. (2008). Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates. *Mar. Biol.* 154, 27–36. doi: 10.1007/s00227-007-0892-9

Burt, J., Bartholomew, A., Bauman, A., Saif, A., and Sale, P. F. (2009). Coral recruitment and early benthic community development on several materials used in the construction of artificial reefs and breakwaters. *J. Exp. Mar. Biol. Ecol.* 373, 72–78. doi: 10.1016/j.jembe.2009.03.009

Caley, M. J., Carr, M. H., Hixon, M. A., Hughes, T. P., Jones, G. P., and Menge, B. A. (1996). Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* 27, 477–500. doi: 10.1146/annurev.ecolsys.27.1.477

Carpenter, K. E., Abrar, M., Aeby, G., Aronson, R. B., Banks, S., Bruckner, A., et al. (2008). One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321, 560–563. doi: 10.1126/science.1159196

Chadwick, N. E., and Morrow, K. M. (2011). "Competition among sessile organisms on coral reefs," in *Coral Reefs: An Ecosystem in Transition,* eds Z. Dubinsky and N. Stambler (Dordrecht: Springer), 347–371. doi: 10.1007/978-94-007-0114-4_20

Chong-Seng, K., Graham, N., and Pratchett, M. (2014). Bottlenecks to coral recovery in the Seychelles. *Coral Reefs* 33, 449–461. doi: 10.1007/s00338-014-1137-2

Clarke, K. R., and Gorley, R. N. (2006). *PRIMER V6: User Manual-Tutorial.* Plymouth, UK: Plymouth Marine Laboratory.

Coles, S. L. (2003). Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific Region. *Atoll Res. Bull.* 507, 1–19. doi: 10.5479/si.00775630.507.1

Coles, S., Looker, E., and Burt, J. (2015). Twenty-year changes in coral near Muscat, Oman estimated from manta board tow observations. *Mar. Environ. Res.* 103, 66–73. doi: 10.1016/j.marenvres.2014.11.006

Colvard, N. B., and Edmunds, P. J. (2011). Decadal-scale changes in abundance of non-scleractinian invertebrates on a Caribbean coral reef. *J. Exp. Mar. Biol. Ecol.* 397, 153–160. doi: 10.1016/j.jembe.2010.11.015

Cowen, R. K., and Sponaugle, S. (2009). Larval dispersal and marine population connectivity. *Ann. Rev. Mar. Sci.* 1, 443–466. doi: 10.1146/annurev.marine.010908.163757

De Goeij, J. M., Van Oevelen, D., Vermeij, M. J., Osinga, R., Middelburg, J. J., De Goeij, A. F., et al. (2013). Surviving in a marine desert: the sponge loop retains resources within coral reefs. *Science* 342, 108–110. doi: 10.1126/science.1241981

De'ath, G., Fabricius, K. E., Sweatman, H., and Puotinen, M. (2012). The 27-year decline of coral cover on the great barrier reef and its causes. *Proc. Natl. Acad. Sci. U.S.A.* 109, 17995–17999. doi: 10.1073/pnas.1208909109

Díaz-Castañeda, V., and Almeda-Jauregui, C. (1999). Early benthic organism colonization on a Caribbean coral reef (Barbados, West Indies): a plate experimental approach. *Mar. Ecol.* 20, 197–220.

Diaz-Pulido, G., Harii, S., Mccook, L., and Hoegh-Guldberg, O. (2010). The impact of benthic algae on the settlement of a reef-building coral. *Coral Reefs* 29, 203–208. doi: 10.1007/s00338-009-0573-x

Dobretsov, S. (2015). Biofouling on artificial substrata in Muscat waters. *J. Agric. Mar. Sci.* 19, 24–29. doi: 10.24200/jams.vol20iss0pp24-29

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Dobretsov, S., Abed, R. M., and Voolstra, C. R. (2013). The effect of surface colour on the formation of marine micro and macrofouling communities. *Biofouling* 29, 617–627. doi: 10.1080/08927014.2013.784279

Dunstan, P. K., and Johnson, C. R. (1998). Spatio-temporal variation in coral recruitment at different scales on heron reef, southern great barrier reef. *Coral Reefs* 17, 71—81. doi: 10.1007/s003380050098

Enochs, I. C., and Glynn, P. W. (2017). "Trophodynamics of eastern pacific coral reefs," in *Coral Reefs of the Eastern Tropical Pacific*, eds P. Glynn, D. Manzello, and I. Enochs (Dordrecht: Springer Science + Business Media, B. V.), 291–314.

Ferrario, F., Beck, M. W., Storlazzi, C. D., Micheli, F., Shepard, C. C., and Airoldi, L. (2014). The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nat. Commun.* 5:3794. doi: 10.1038/ncomms4794

Foster, K. A., Foster, G., Tourenq, C., and Shuriqi, M. K. (2011). Shifts in coral community structures following cyclone and red tide disturbances within the gulf of oman (United Arab Emirates). *Mar. Biol.* 158, 955–968. doi: 10.1007/s00227-010-1622-2

Foster, K., Foster, G., Al-Cibahy, A. S., Al-Harthi, S., Purkis, S. J., and Riegl, B. M. (2012). Environmental setting and temporal trends in southeastern gulf coral communities. *Coral Reefs Gulf* 3, 51–70. doi: 10.1007/978-94-007-3008-3_4

George, D., and John, D. (2000). "The status of coral reefs and associated macroalgae in Abu Dhabi (UAE) after recent coral bleaching events," in *Proceedings of the International Symposium on the Extent and Impact of Coral Bleaching in the Arabian Region* (Riyadh).

George, J., and John, D. (2002). "Is it Curtains for Coral Reefs in the Southern Arabian Gulf," in *Proccesdings of International Society of Reef Studies in European Meeting* (Cambridge).

Gilmour, J. P., Smith, L. D., Heyward, A. J., Baird, A. H., and Pratchett, M. S. (2013). Recovery of an isolated coral reef system following severe disturbance. *Science* 340, 69–71. doi: 10.1126/science.1232310

Glassom, D., and Chadwick, N. (2006). Recruitment, growth and mortality of juvenile corals at Eilat, northern Red Sea. *Mar. Ecol. Prog. Ser.* 318, 111–122. doi: 10.3354/meps318111

Glassom, D., Zakai, D., and Chadwick-Furman, N. E. (2004). Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Mar. Biol.* 144, 641–651. doi: 10.1007/s00227-003-1243-0

Glynn, P. W., and Enochs, I. C. (2011). "Invertebrates and their roles in coral reef ecosystems," in *Coral Reefs: An Ecosystem in Transition*, eds Z. Dubinsky and N. Stambler (Dordrecht: Springer), 273–325. doi: 10.1007/978-94-007-0114-4_18

Green, D. H., and Edmunds, P. J. (2011). Spatio-temporal variability of coral recruitment on shallow reefs in St. John, US Virgin Islands. *J. Exp. Mar. Biol. Ecol.* 397, 220–229. doi: 10.1016/j.jembe.2010.12.004

Grizzle, R. E., Ward, K. M., Alshihi, R. M., and Burt, J. A. (2016). Current status of coral reefs in the United Arab Emirates: distribution, extent, and community structure with implications for management. *Mar. Pollut. Bull.* 105, 515–523. doi: 10.1016/j.marpolbul.2015.10.005

Guannel, G., Arkema, K., Ruggiero, P., and Verutes, G. (2016). The Power of three: coral reefs, seagrasses and mangroves protect coastal regions and increase their resilience. *PLoS ONE* 11:e0158094. doi: 10.1371/journal.pone.0158094

Guest, J. R., Tun, K., Low, J., Verges, A., Marzinelli, E. M., Campbell, A. H., et al. (2016). 27 years of benthic and coral community dynamics on turbid, highly urbanised reefs off Singapore. *Sci. Rep.* 6:36260. doi: 10.1038/srep36260

Halford, A., Cheal, A. J., Ryan, D., and Williams, D. M. B. (2004). Resilience to large-scale disturbance in coral and fish assemblages on the great barrier reef. *Ecology* 85, 1892–1905. doi: 10.1890/03-4017

Harriott, V. J., and Banks, S. A. (1995). Recruitment of scleractinian corals in the solitary islands marine reserve, a high latitude coral-dominated community in Eastern Australia. *Mar. Ecol. Prog. Ser.* 123, 155–161. doi: 10.3354/meps123155

Howells, E. J., Abrego, D., Vaughan, G. O., and Burt, J. A. (2014). Coral spawning in the Gulf of Oman and relationship to latitudinal variation in spawning season in the northwest Indian Ocean. *Sci. Rep.* 4:7484. doi: 10.1038/srep07484

Howells, E. J., Ketchum, R. N., Bauman, A. G., Mustafa, Y., Watkins, K. D., and Burt, J. A. (2016). Species-specific trends in the reproductive output of corals across environmental gradients and bleaching histories. *Mar. Pollut. Bull.* 105, 532–539. doi: 10.1016/j.marpolbul.2015.11.034

Hughes, T. P., Graham, N. A., Jackson, J. B., Mumby, P. J., and Steneck, R. S. (2010). Rising to the challenge of sustaining coral reef resilience. *Trends Ecol. Evol.* 25, 633–642. doi: 10.1016/j.tree.2010.07.011

Hughes, T. P., Kerry, J. T., Álvarez-Noriega, M., Álvarez-Romero, J. G., Anderson, K. D., Baird, A. H., et al. (2017). Global warming and recurrent mass bleaching of corals. *Nature* 543, 373–377. doi: 10.1038/nature21707

Jackson, J. (1984). Ecology of cryptic coral reef communities. III. Abundance and aggregation of encrusting organisms with particular reference to cheilostome Bryozoa. *J. Exp. Mar. Biol. Ecol.* 75, 37–57. doi: 10.1016/0022-0981(84)90022-4

John, D. (2012). "Marine algae (seaweeds) associated with coral reefs in the Gulf," in *Coral reefs of the Gulf: adaptation to climatic extremes Vol. Coral Reefs of the World 3*, eds B. Riegl and S. Purkis (Dordrecht: Springer Science+Business Media, B. V.), 309–335.

Kelmo, F., Bell, J. J., and Attrill, M. J. (2013). Tolerance of sponge assemblages to temperature anomalies: resilience and proliferation of sponges following the 1997-8 El-Nino southern oscillation. *PLoS ONE* 8:e76441. doi: 10.1371/journal.pone.0076441

Kelmo, F., Bell, J. J., Moraes, S. S., Gomes Rda, C., Mariano-Neto, E., and Attrill, M. J. (2014). Differential responses of emergent intertidal coral reef fauna to a large-scale El-Nino southern oscillation event: sponge and coral resilience. *PLoS ONE* 9:e93209. doi: 10.1371/journal.pone.0093209

Kohler, K. E., and Gill, S. M. (2006). Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput. Geosci.* 32, 1259–1269. doi: 10.1016/j.cageo.2005.11.009

Lillis, A., Bohnenstiehl, D., Peters, J. W., and Eggleston, D. (2016). Variation in habitat soundscape characteristics influences settlement of a reef-building coral. *Peer J.* 4:e2557. doi: 10.7717/peerj.2557

Luter, H. M., Duckworth, A. R., Wolff, C. W., Evans-Illidge, E., and Whalan, S. (2016). Recruitment variability of coral reef sessile communities of the far north great barrier reef. *PLoS ONE* 11:e0153184. doi: 10.1371/journal.pone.0153184

Maina, J., De Moel, H., Zinke, J., Madin, J., Mcclanahan, T., and Vermaat, J. E. (2013). Human deforestation outweighs future climate change impacts of sedimentation on coral reefs. *Nat. Commun.* 4:1986. doi: 10.1038/ncomms2986

Mallela, J. (2007). Coral reef encruster communities and carbonate production in cryptic and exposed coral reef habitats along a gradient of terrestrial disturbance. *Coral Reefs* 26, 775–785. doi: 10.1007/s00338-007-0260-8

Mangubhai, S., Harrison, P. L., and Obura, D. O. (2007). Patterns of coral larval settlement on lagoon reefs in the mombasa marine national park and reserve, kenya. *Mar. Ecol. Prog. Ser.* 348, 149–159. doi: 10.3354/meps07090

McCune, B., Grace, J. B., and Urban, D. L. (2002). *Analysis of Ecological Communities*. Gleneden Beach, OR: MjM Software Design.

Moradi, M., and Kabiri, K. (2015). Spatio-temporal variability of SST and Chlorophyll-a from MODIS data in the Persian Gulf. *Mar. Pollut. Bull.* 98, 14–25. doi: 10.1016/j.marpolbul.2015.07.018

Mumby, P. J. (2016). Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs. *Fish Fish.* 17, 266–278. doi: 10.1111/faf.12078

Mundy, C. N. (2000). An appraisal of methods used in coral recruitment studies. *Coral Reefs* 19, 124–131. doi: 10.1007/s003380000081

Nezlin, N. P., Polikarpov, I. G., Al-Yamani, F. Y., Subba Rao, D. V., and Ignatov, A. M. (2010). Satellite monitoring of climatic factors regulating phytoplankton variability in the Arabian (Persian) Gulf. *J. Mar. Sys.* 82, 47–60. doi: 10.1016/j.jmarsys.2010.03.003

Pandolfi, J. M., Connolly, S. R., Marshall, D. J., and Cohen, A. L. (2011). Projecting coral reef futures under global warming and ocean acidification. *Science* 333, 418–422. doi: 10.1126/science.1204794

Piontkovski, S., Al-Azri, A., and Al-Hashmi, K. (2011). Seasonal and interannual variability of chlorophyll-a in the Gulf of Oman compared to the open Arabian Sea regions. *Int. J. Remote Sens.* 32, 7703–7715. doi: 10.1080/01431161.2010.527393

Pollock, F. J., Lamb, J. B., Field, S. N., Heron, S. F., Schaffelke, B., Shedrawi, G., et al. (2014). Sediment and turbidity associated with offshore dredging increase coral disease prevalence on nearby reefs. *PLoS ONE* 9:e102498. doi: 10.1371/journal.pone.0102498

Polman, H., Verhaart, F., and Bruijs, M. (2013). Impact of biofouling in intake pipes on the hydraulics and efficiency of pumping capacity. *Desalinat. Water Treat.* 51, 997–1003. doi: 10.1080/19443994.2012.707371

Pratchett, M. S., Baird, A. H., Bauman, A. G., and Burt, J. A. (2017). Abundance and composition of juvenile corals reveals divergent trajectories

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for coral assemblages across the United Arab Emirates. *Mar. Pollut. Bull.* 114, 1031–1035. doi: 10.1016/j.marpolbul.2016.11.036

Purkis, S., and Riegl, B. (2005). Spatial and temporal dynamics of Arabian Gulf coral assemblages quantified from remote-sensing and in situ monitoring data. *Mar. Ecol.* 287, 99–113. doi: 10.3354/meps287099

Reynolds, R. M. (1993). Physical oceanography of the Gulf, Strait of Hormuz, and the Gulf of Oman–Results from the Mt Mitchell expedition. *Mar. Pollut. Bull.* 27, 35–59. doi: 10.1016/0025-326X(93)90007-7

Riegl, B., and Purkis, S. (2015). Coral population dynamics across consecutive mass mortality events. *Glob. Chang. Biol.* 21, 3995–4005. doi: 10.1111/gcb.13014

Riegl, B., Berumen, M., and Bruckner, A. (2013). Coral population trajectories, increased disturbance and management intervention: a sensitivity analysis. *Ecol. Evol.* 3, 1050–1064. doi: 10.1002/ece3.519

Ritson-Williams, R., Arnold, S. N., Fogarty, N. D., Steneck, R. S., Vermeij, M. J., and Paul, V. J. (2009). New perspectives on ecological mechanisms affecting coral recruitment on reefs. *Smithson. Contrib. Mar. Sci.* 38, 437–457. doi: 10.5479/si.01960768.38.437

Ritson-Williams, R., Arnold, S., Paul, V., and Steneck, R. (2014). Larval settlement preferences of Acropora palmata and Montastraea faveolata in response to diverse red algae. *Coral Reefs* 33, 59–66. doi: 10.1007/s00338-013-1113-2

Roff, G., Doropoulos, C., Zupan, M., Rogers, A., Steneck, R. S., Golbuu, Y., et al. (2015). Phase shift facilitation following cyclone disturbance on coral reefs. *Oecologia* 178, 1193–1203. doi: 10.1007/s00442-015-3282-x

Sawall, Y., Jompa, J., Litaay, M., Maddusila, A., and Richter, C. (2013). Coral recruitment and potential recovery of eutrophied and blast fishing impacted reefs in Spermonde Archipelago, Indonesia. *Mar. Pollut. Bull.* 74, 374–382. doi: 10.1016/j.marpolbul.2013.06.022

Shanks, A. L., Grantham, B. A., and Carr, M. H. (2003). Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. App.* S159–S169. doi: 10.1890/1051-0761(2003)013[0159:PDDATS]2.0.CO;2

Sheppard, C. R. C., and Loughland, R. (2002). Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. *Aqua. Ecossys. Health Manage.* 5, 395–402. doi: 10.1080/14634980290002020

Sheppard, C. R. C., and Salm, R. V. (1988). Reef and coral communities of Oman, with a description of a new coral species (Order Scleractinia, genusAcanthastrea). *J. Nat. Hist.* 22, 263–279. doi: 10.1080/00222938800770201

Sheppard, C., Al-Husiani, M., Al-Jamali, F., Al-Yamani, F., Baldwin, R., Bishop, J., et al. (2010). The Gulf: a young sea in decline. *Mar. Pollut. Bull.* 60, 13–38. doi: 10.1016/j.marpolbul.2009.10.017

Sheppard, C., Price, A., and Roberts, C. (1992). *Marine Ecology of the Arabian Region: Patterns and Processes in Extreme Tropical Environments*. Toronto, ON: Academic Press.

Soong, K., Chen, M.-H., Chen, C.-L., Dai, C.-F., Fan, T.-Y., Li, J.-J., et al. (2003). Spatial and temporal variation of coral recruitment in Taiwan. *Coral Reefs* 22, 224–228. doi: 10.1007/s00338-003-0311-8

Spalding, M. D., and Brown, B. E. (2015). Warm-water coral reefs and climate change. *Science* 350, 769–771. doi: 10.1126/science.aad0349

Stubler, A. D., Stevens, A. K., and Peterson, B. J. (2016). Using community-wide recruitment and succession patterns to assess sediment stress on Jamaican coral reefs. *J. Exp. Mar. Biol. Ecol.* 474, 29–38. doi: 10.1016/j.jembe.2015.09.018

Tebben, J., Motti, C. A., Siboni, N., Tapiolas, D. M., Negri, A. P., Schupp, P. J., et al. (2015). Chemical mediation of coral larval settlement by crustose coralline algae. *Sci. Rep.* 5:10803. doi: 10.1038/srep10803

Van Woesik, R., Scott, W. J., and Aronson, R. B. (2014). Lost opportunities: coral recruitment does not translate to reef recovery in the Florida Keys. *Mar. Pollut. Bull.* 88, 110–117. doi: 10.1016/j.marpolbul.2014.09.017

Wallström, E., Jespersen, H. T., and Schaumburg, K. (2011). A new concept for anti-fouling paint for Yachts. *Prog. Org. Coat.* 72, 109–114. doi: 10.1016/j.porgcoat.2011.03.001

Wear, S. L., and Thurber, R. V. (2015). Sewage pollution: mitigation is key for coral reef stewardship. *Ann. N.Y. Acad. Sci.* 1355, 15–30. doi: 10.1111/nyas.12785

Weersing, K., and Toonen, R. J. (2009). Population genetics, larval dispersal, and connectivity in marine systems. *Mar. Ecol. Progr. Ser.* 393, 1–12. doi: 10.3354/meps08287

Zabin, C. J. (2015). Patterns of adult abundance vary with recruitment of an invasive barnacle species on Oahu, Hawaii. *J. Exp. Mar. Biol. Ecol.* 464, 44–51. doi: 10.1016/j.jembe.2014.12.009

Zar, J. H. (2010). *Biostatistical Analysis*. New York, NY: Prentice Hall.

Zhang, S. Y., Speare, K. E., Long, Z. T., Mckeever, K. A., Gyoerkoe, M., Ramus, A. P., et al. (2014). Is coral richness related to community resistance to and recovery from disturbance? *PeerJ* 2:e308. doi: 10.7717/peerj.308

Zuur, A., Ieno, E. N., and Smith, G. M. (2007). *Analyzing Ecological Data*. New York, NY: Springer Science & Business Media.

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Supplementary Material

Supplementary Table 1. Pearson r-values of benthic groups strongly associated with each axis of the MDS. Only benthos with r>[0.5] are included.

Axis	Benthic group	r-values
MDS1	Coralline algae	r = 0.75
	Barnacle	r = -0.57
MDS2	Polychaeta	r = 0.77
	Turf algae	r = 0.57
	Bryozoans	r = -0.73
MDS3	Colonial ascidians	r = -0.68

Chapter 4 "Seasonal changes in community structure of small-bodied, site-attached reef fishes in the Northeastern Arabian Peninsula"

Preface

Changes in the reef benthic community, as well as existing extreme environmental conditions, are known to impact fish communities, affecting their density, richness and biomass. While pelagic, and non reef-dependent fish, can migrate under extreme conditions or after disturbances, small-bodied site-attached reef fish, might have different responses due to their limited spatial range, flexible responses to environmental changes and short life-spans. This study examines how seasonal variation in different environmental factors affects the density, biomass, size structure, and functional composition of small site-attached reef fish communities.

Highlights

- Lower density and biomass of small site-attached reef fish communities in the Gulf than both Musandam and the Sea of Oman;

- In the Gulf, fish densites doubled in cooler months than warmer months, while the opposite was observed in Musandam and the Sea of Oman;

- Territorial herbivores were characteristic of the Gulf while diurnal planktivores of Musandam and the Sea of Oman;

- Regional differences in fish communities explained by salinity and wind speed

Seasonal changes in community structure of small-bodied, site-attached reef fishes in the north-eastern Arabian Peninsula

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Abstract

Reef fish communities are affected by climate change, particularly small abundant residents that are site-attached. Changes in the abundance and community composition of these fishes can give valuable information on the conditions of the reef system. The density, biomass and size-class structure of small-bodied, site-attached reef fish in three environmentally distinct marine regions of the northeastern Arabian Peninsula were quantified over a two-year period to explore spatial and seasonal variation. Comparing between the southern Arabian Gulf where seas are characterized by extreme temperatures and salinity, and the Musandam Peninsula and northern Sea of Oman, two areas with more benign oceanographic conditions, revealed dramatic differences in community density, biomass and structure. Although damselfishes (F. Pomacentridae) numerically dominated communities in all areas, dominant species differed between regions with *Pomacentrus aquilus* and *Pomacentrus trichrourus* more common in Arabian Gulf communities, and *Chromis xanthopterygia, Neopomacentrus cyanomos,* and *Pomacentrus leptus* dominating Musandam and Sea of Oman communities. Marked differences in seasonal dynamics between regions were observed with a doubling of density in winter compared with warmer seasons for the southern Arabian Gulf, while the opposite was observed in Musandam Peninsula and Sea of Oman. Lastly, at the functional level ~90% of the total small-bodied fish community in the Musandam Peninsula and Sea of Oman consisted of omnivorous and diurnal planktivores, whereas Arabian Gulf communities were dominated by territorial herbivores and omnivorous planktivores. Salinity and wind speed were the main environmental factors explaining

regional differences in the structure of fish communities between southern Arabian Gulf and both Musandam and Sea of Oman, while minimum temperature was an important factor explaining seasonal differences within the Gulf.

Keywords: seasonality; community structure; Arabian Peninsula; site-attached; salinity; Pomacentridae

Introduction

Escalating anthropogenic disturbances together with global increases in sea-surface temperature (SST) caused by climate change have led to reductions in the species composition and three-dimensional complexity of coral communities globally (Hughes et al., 2003; Hughes et al., 2017). Such changes to coral reefs have substantialy impacted resource availability (e.g., food, shelter) for the associated fauna, resulting in reductions in the abundance, diversity and size structure of reef fish populations (Wilson et al., 2006; Pratchett et al., 2008; Bonin et al., 2011; Rogers et al., 2014). Small, site-attached fish species are likely to be among the most heavily affected by changes in reef complexity, as they are closely associated with the reef matrix and reliant on fine-scale habitat structure (Munday and Jones, 1998; Ferreira et al., 2001). As these fishes constitute a substantial proportion of reef fish community abundance and diversity, losses as a result of habitat degradation are likely to have important implications for the functional and structural attributes of reef-associated fish communities (Munday and Jones, 1998; Ackerman and Bellwood, 2000; Floeter et al., 2004; Munday et al., 2008). While the response of the wider coral reef fish assemblage to physical extremes is well studied (Munday et al., 2008; Nilsson et al., 2009), the impacts of these environmental changes on the community structure of small site-attached reef fish communities is less well known.

Reef fish communities around the Arabian peninsula have become increasingly studied in the past decade as seas surrounding the area are biogeographically linked but are characterized by widely divergent environmental conditions, making it a 'natural laboratory' to study the influence of thermal stress on fishes (Feary et al., 2010; Burt et al., 2011b; Feary et al., 2012; Shraim et al., 2017). The northeastern Arabian Peninsula is bounded by the southern Arabian/Persian Gulf (hereafter called 'the Gulf'), the Strait of Hormuz adjacent to the Musandam peninsula, as well as the Sea of Oman, and these seas have an environmental regime largely structured by

seasonal variation in a range of environmental factors (Sheppard et al., 1992; Burt et al., 2011b; Feary et al., 2012). For example, as a result of its shallow depth, restricted water exchange and surrounding arid environment, the southern Gulf is characterized by extreme SSTs ranging from winter lows of <12°C to summer highs of >36°C (Sheppard et al., 1992; Sheppard, 1993), and hyper-saline conditions (>44 PSU) that occur year-round (Reynolds, 1993). In contrast, the adjacent Musandam and Sea of Oman water bodies both have deeper waters that are well mixed with those of the Indian Ocean, resulting in much milder seasonal changes in SSTs, from 22°C in the winter to 34°C in the summer (Kleypas et al., 1999; Schils and Wilson, 2006), and salinity that is comparable to normal oceanic conditions (35–37 PSU) (Schils and Wilson, 2006; Foster et al., 2012) .

Studies in the region have shown that the more extreme environmental conditions of the Gulf substantially impacts reef fish communities, resulting in a lower abundance, diversity, biomass and functional diversity of assemblages when compared with the more environmentally benign Musandam and Oman seas (Feary et al., 2010; Burt et al., 2011b). However, these studies focused on broader reef fish communities, potentially obscuring patterns and dynamics that may differ for small, site-attached reef fish species. Small-bodied fish, such as pomacentrids, are extremely flexible in their behavioral responses to environmental changes (Fricke, 1977), and adaptation to changes in local water temperature also occur more rapidly in small-bodied, short-lived species than larger species (Feary et al., 2014). Nevertheless, this adaptation might have downsides, as a reduction in swimming performance in smaller fishes makes them more vulnerable to predation (Coker et al., 2009; Johansen and Jones, 2011b). Thus regional differences in environmental conditions may play out differently for small-bodied reef fish than has been recognized previously. In addition, those earlier region-wide comparative studies have largely been based on one-time snap-shot surveys, ignoring the strong temporal variability that occurs in this sub-tropical region. There is increasing evidence that regional reef fish abundance and composition fluctuate with seasonal changes in temperature, and the influence appears to vary spatially around the region as a result of differences in the range of thermal conditions (Coles and Tarr, 1990; Burt et al., 2009; Grandcourt, 2012). Thus there is a need to develop a better understanding of the spatial and temporal

dynamics of the small, site-attached reef fish species that serve important functional roles on the reefs of north-eastern Arabia.

This study examined the role of seasonal variation in environmental factors in structuring the density, biomass, size structure, and functional composition of small site-attached reef fish communities (<20cm adult TL, reef-associated and cryptobenthic species) throughout the southern Gulf, Musandam, and Sea of Oman regions. In the north-eastern Arabian Peninsula small, site-attached reef fishes can make up 5% of the coral associated fish community richness (representing 52% of the coral-dependent fish community), and contain a range of species that are at an elevated risk of extinction (Buchanan et al., 2016). We hypothesise that the physical extremes of the Gulf negatively affect the small-site attached reef fish community, with the dramatic seasonal changes in environment conditions more negatively affecting density, biomass and functional composition of these assemblages compared with the more benign environments experienced in the adjacent seas.

Methods

Sampling design and study area

To examine the role of seasonal environmental variability in structuring the density, biomass and functional composition of small bodied (<20cm TL), site-attached reef fish assemblages in north-eastern Arabia, we performed visual surveys across eight sites spanning three regional seas: the Gulf (Dhabiya, Saadiyat, Ras Ghanada), Musandam (Al Harf, Falcon Rock, Coral Garden) and Sea of Oman (Dibba, Al Aqa) (Figure 4.1). All sites were characterized by fringing and patch reefs at similar depth (c. 2–8 m) and general habitat conditions, with sites separated by 13–33 km within regions. Surveys were performed every three months (i.e. quarterly) at each site over two years (April 2011 – April 2013), encompassing four seasons each year (winter: January-March, spring: April-June, summer: July-September and autumn: October-December). Within each season the surveys were performed within ca. 10 days across all sites to ensure consistency of seasonal sampling.
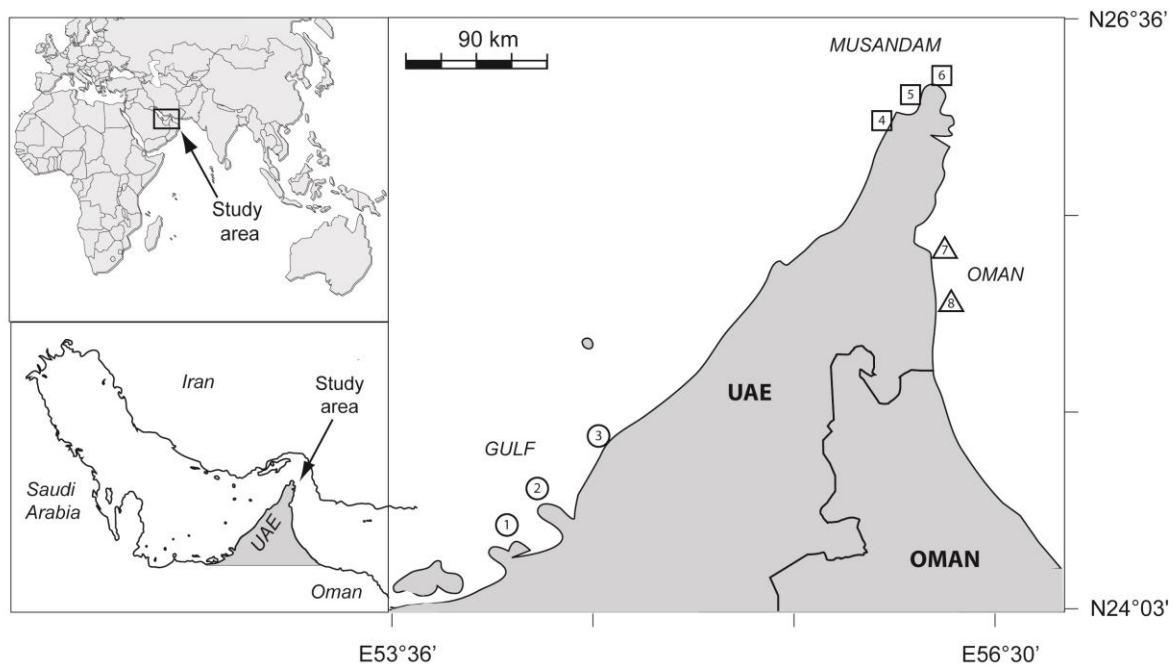
Figure 4.1
Study area in the Arabian Peninsula showing the location of the 8 sites among the three regions: Gulf sites in circles (1: Dhabiya, 2: Saadiyat, 3: Ras Ghanada), Musandam sites in squares (4: Al Harf, 5: Falcon Rock, 6: Coral Garden) and Sea of Oman sites in triangles (7: Dibba, 8: Al Aqa).

During each survey period, visual censuses of small-bodied, site-attached reef fish communities were performed on six replicate belt-transects (30 m x 1 m) space ca. 3 m apart. One metre wide transects were used as these are the most appropriate for surveying small reef-dependent species (Adam et al., 2011; Bozec et al., 2011), and are particularly appropriate in areas with reduced visibility such as the southern Gulf or the Sea of Oman where visibility is often <5 m (Burt et al., 2009; Feary et al., 2010). Within each transect, all species for which maximum adult body size <20 cm TL (following Froese and Pauly, 2017) were identified and categorized into 5 cm interval size classes. Care was taken not to re-census fishes that left and re-entered the transect area. Estimated total lengths of each individual were converted to biomass based on species-specific growth coefficients (Froese and Pauly, 2017). When a species-specific coefficient was not available, a coefficient from a species with similar morphology (from the same genus) was used. Species were classified at broad and fine functional groupings (i.e., herbivore [territorial farmer], omnivore [benthic omnivore, diurnal planktivore, omnivorous planktivore], and carnivore [generalist carnivore, micro-invertivore, ectoparasite feeder, nocturnal planktivore]) (Froese and Pauly, 2017) to explore functional differences in fish communities.

Environmental data

To explore spatio-temporal relationships between environmental parameters and fish community composition, the sea-surface temperature (SST), surface salinity, dominant current speed and dominant wind speed were gathered from model outputs and satellite observations for each site at each sampling period. SST, salinity and current data (all data in daily average intervals) were obtained from the 1/12° Global Hybrid Coordinate Ocean Model (HYCOM) (Metzger et al., 2010). Wind data was derived from the National Center for Atmospheric Research, Research Data Archive (rda.ucar.edu). All wind data was a 6-hour average of the effective neutral wind at a height of 10 metres and within grid spacing of 0.205-deg x 0.204-deg in E-O and N-S directions, respectively. All parameters were acquired for the period 01 April 2011 – 30 April 2013. Each environmental parameter was averaged across daily readings (SST, salinity, current, and wind) for each site during each quarterly survey period. Minimum, maximum and variance of SST and salinity for each season were also calculated.

Data analysis

Univariate and permutational multivariate analyses of variance were performed to compare and contrast community density (individuals $100m^{-2}$), biomass (kg ha^{-1}), size-class structure (cm TL), taxonomic composition and functional composition (broad and fine functional classification) among regions (Gulf, Musandam, and Sea of Oman), among seasons (winter, spring, summer and autumn), and years (year 1 and year 2). All analyses were performed in SPSS (IBM Corporation, 2016) and PRIMER 6.0 software (Clarke and Gorley, 2006), including the PERMANOVA add-on package (Anderson, 2001). Data were first tested for normality and unequal variance using the Shapiro-Wilk W and Levene's tests. Fish density and biomass did not meet these assumptions, and therefore both were log(x+1) transformed prior to statistical analyses (Zar, 1999). To assess seasonal differences in density and biomass of small site-attached fishes between regions, a nonparametric permutation-based analysis of variance test (PERMANOVA, 9999 permutations) on the Euclidian distance matrix was performed (Anderson and Braak, 2003). Variability was analysed between regions (fixed factor with 3 levels), sites (random factor with 8 levels nested in 'Region'), years (random factor with 2 levels), and seasons (fixed factor with 4

levels). When mean square estimates of interaction terms were negative, the interaction terms for subsequent PERMANOVA analyses were pooled with the residual (following Fletcher and Underwood (2002); Anderson et al. (2008)). Where significant differences between factors were detected ($p < 0.05$), pairwise comparisons were performed using Monte Carlo adjusted p-values to determine which means differed significantly.

Seasonal differences in regional fishes density and biomass were analyzed using a partially nested 4-way PERMANOVA based on Bray-Curtis distance matrix (9999 permutations) (Anderson, 2001). To visualize multivariate patterns, non-metric multidimensional scaling (nMDS) ordinations of Bray-Curtis dissimilarity matrices, calculated from log(x+1) transformed data, were used. Spearman rank correlation was used to identify species strongly driving divergence along the nMDS axes ($r \geq 0.8$ for either axis). Similarity percentage (SIMPER) analyses were performed to determine which species, functional group and/or size class characterised each season and region, and which factor contributed mostly to dissimilarity between groups (Clarke and Warwick, 2001). Density of species, functional groups, and size classes of fishes that were identified by SIMPER as being important spatio-temporal drivers of community difference were analysed using PERMANOVA (Anderson, 2001) based on a Euclidean distance measure (Terlizzi et al., 2007). Before multivariate analyses, all species occurring in less than 5% of samples were removed to reduce the influence of outliers (McCune et al., 2002).

To determine environmental variables that may influence the spatio-temporal variation in community structure across seasons and regions, distance-based linear modeling (DistLM) with Bray-Curtis distance measures and 9999 permutations was used. The best-fit model, based on corrected Akaike Information Criterion for finite samples (AICc), was then visualized with distance-based redundancy ordination analysis (dbRDA) (Anderson et al., 2008). Ordinations were optimized with vector overlays to graphically illustrate environmental variables driving differences in fish communities. Before analyses, all environmental parameters that had non-skewed distributions were log(x+0.1) transformed to normalize the data (Clarke and Gorley, 2006). Following this, all environmental variables were then standardized to account for differences in scales and units among variables. Multi-collinearity of all environmental variables was checked using draftsman plots, and any variables that

were strongly collinear (Pearson's *r* >0.95 or <-0.95) were reduced to a single representative variable.

Results

A total of 26 species of small bodied site-attached reef fishes (from 8 families) were observed across all sites and seasons, with 13 species (7 families) observed in the Gulf, 24 species (8 families) in Musandam and 17 species (7 families) in the Sea of Oman. Only four species in Musandam and two species in the Gulf were restricted to those water bodies; all other species were shared among two or more regions (Supplementary Table S 4.1). Pomacentridae was the most speciose family across all three regions (nine species in total: four in the Gulf, nine in Musandam, and eight in the Sea of Oman), and was also the most abundant, making up 95.7% of the total abundance of fishes observed in this study.

The small site-attached fish communities showed significant variation in density and biomass across regions, seasons, and years (PERMANOVA, density: Pseudo-F=4.21, p<0.001; biomass: Pseudo-F=2.18, p=0.04; Figure 4.2). In terms of regional differences, both density and biomass were substantially lower in the Gulf than in the Sea of Oman or Musandam, where density and biomass averaged two to six times greater than the Gulf across years, respectively (Figure 4.2). The lower density in the Gulf was significant for every season relative to Musandam across both years, while differences were only significant during autumn and summer in year 1 when compared with the Sea of Oman (p<0.05 for each; Figure 4.2a). The most dramatic difference in density tended to occurred during the summer, when the Sea of Oman and Musandam densities were four- to 12-fold higher than in the Gulf, respectively, although there was some year-to-year variability. In parallel, biomass in the Gulf was also lower than the Musandam or the Sea of Oman in every season (except Year 2 spring), although these differences were not significant due to high variability (Figure 4.2b). Biomass was highly variable among seasons and between years in Musandam and the Sea of Oman, but was largely stable and low within and among years in the Gulf (Figure 4.2b). Seasonal biomass variation in Musandam and the Sea of Oman was largely driven by differences in the abundance of heavier, larger bodied fishes (e.g. *Abudefduf vaigiensis*) (Figure 4.2).
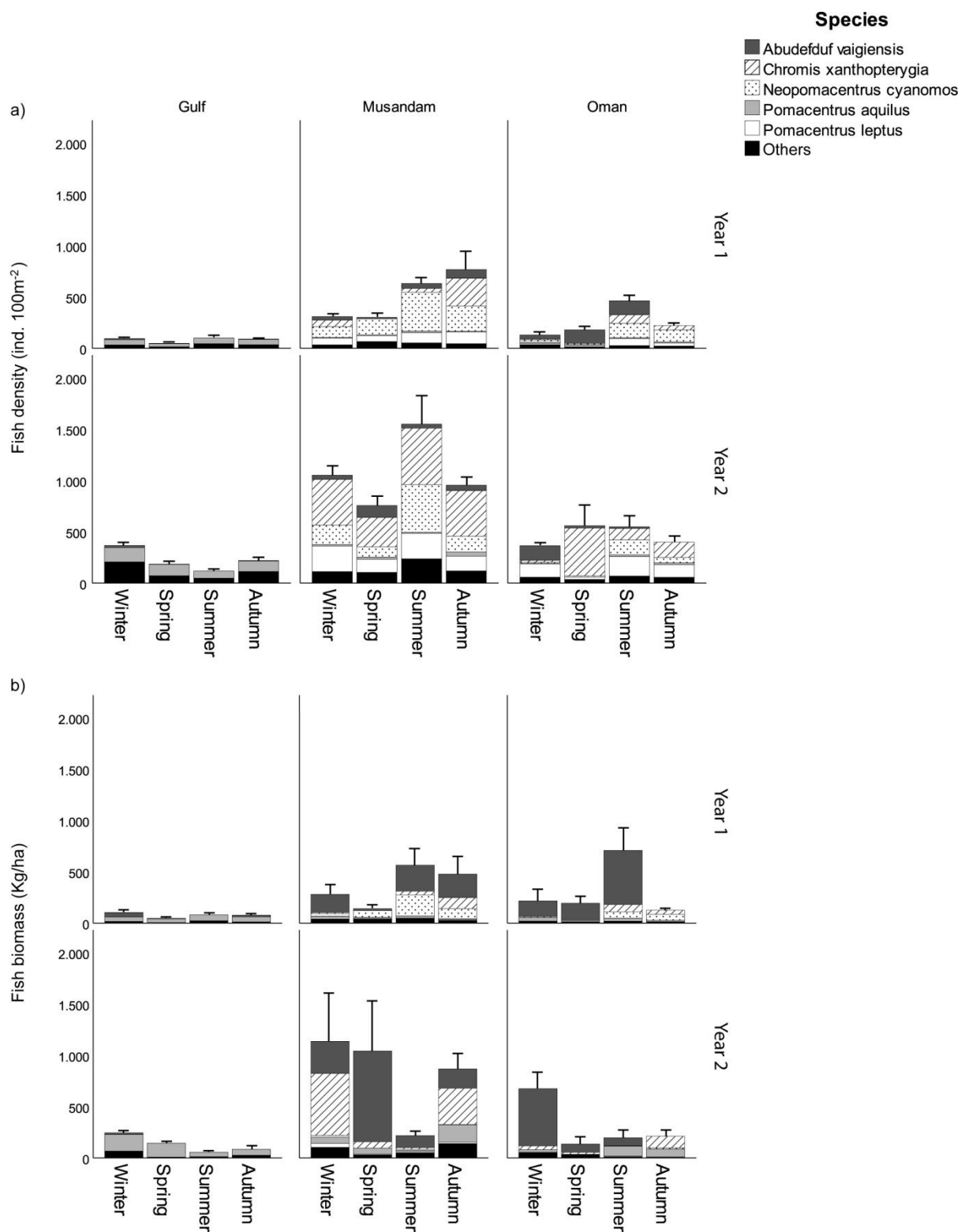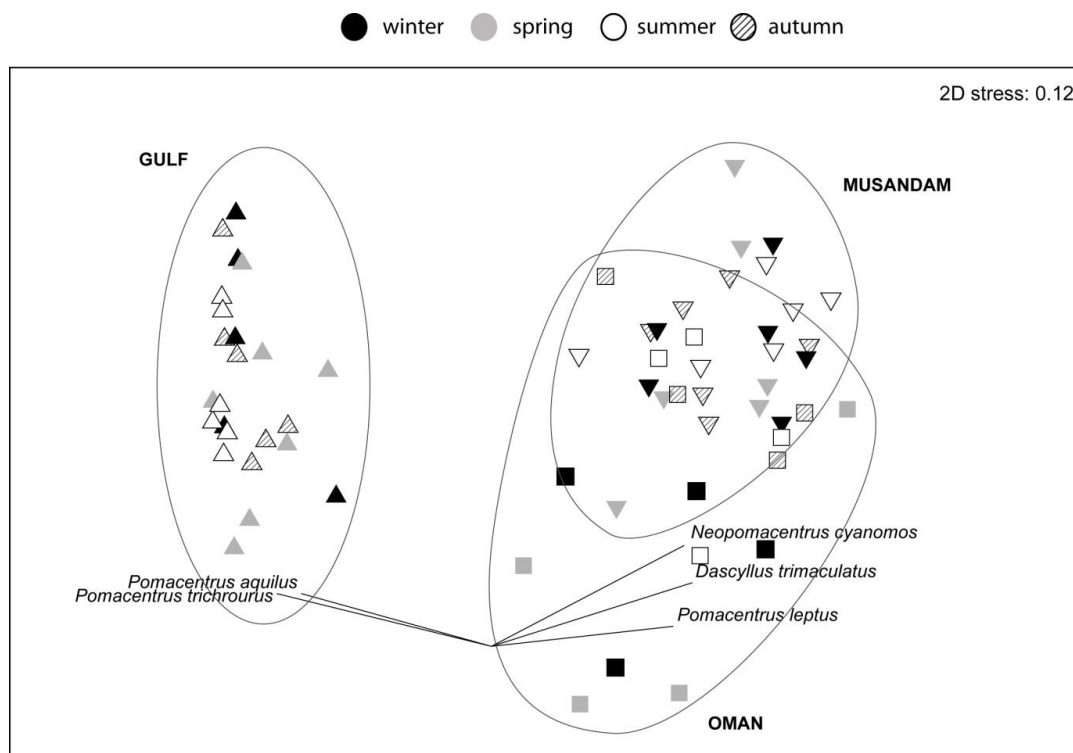
Figure 4.2
Variation in (a) density (ind. 100m^{-2}) and (b) biomass (kg ha^{-1}) of small site-attached species across regions, years and seasons (mean ± SE).

There were substantial changes in density across seasons within each region, but these changes were not consistent between regions. In the Gulf, although densities were low across seasons, a significant 50% decrease in density was observed from winter to spring across both years ($p=0.03$ and $p=0.02$, respectively), with density continuing to decline into summer in year 2 (a 70% decline from winter to summer, $p=0.02$) (Figure 4.2a). There was considerable seasonal variability between years in the Musandam, although like the Gulf the spring season tended to be characterized by low density. Densities were highest during summer and autumn in year 1, when densities more than doubled from winter and spring ($p<005$ each, except between autumn and winter ($p=0.07$)), while in year 2 peak densities were observed only in summer, when densities were a third to twice as high as in other seasons, although these differences were not significant ($p>0.05$). Similarly to Musandam seasonal pattern, densities in the Sea of Oman were also a third to twice as high in the summer across years as well as in spring for year 2, although these differences were not significant ($p>0.05$) (Figure 4.2a). The high inter-seasonal variation in density in Musandam and the Sea of Oman were largely driven by the occurrence of *Chromis xanthopterygia* and *Neopomancentrus cyanomos*, two planktivorous species that tend to form large feeding schools above coral heads. The occurrence of these schools within transects thus resulted in large fluctuations in density from season to season in those seas, but are notably absent from transects in the more seasonally stable Gulf communities. In terms of biomass, while seasonal changes in the Gulf were largely consistent with changes in density in both years, there was broad and inconsistent variation in biomass among seasons and years in Musandam and the Sea of Oman (Figure 4.2b). This substantial variation in seasonal biomass in Musandam and the Sea of Oman was largely due to variation in the relative abundance of larger- versus smaller-bodied reef fish species among seasons (Figure 4.2a,b). Of particular importance to seasonal variation in biomass in these regions was *A. vaigiensis*, which comprised only a modest proportion of the overall density (<15% on average), but contributed anywhere from a third to over three-quarters of seasonal biomass due to its larger body size compared with the more common smaller damselfish species (Figure 4.2b).

Variation in community structure

Multivariate ordination of fish communities, based on density, showed that assemblages in the Gulf were markedly different from the assemblages in the other regions consistently across all seasons, while there was a considerable amount of overlap in community structure in Musandam and the Sea of Oman (Figure 4.3). Differences in community structure were primarily driven by damselfishes, with *Pomacentrus aquilus* and *Pomancentrus trichrourus* being more abundant in the Gulf, while *N. cyanomos*, *Pomancentrus leptus* and *Dascyllus trimaculatus* were more common to the other regions (Figure 4.3). PERMANOVA analysis showed that there was a significant interaction between the main effects of regions, seasons and years, indicating that temporal differences were not consistent across regions (Table 4.1). As such, pair-wise PERMANOVA comparisons were used to assess temporal differences in density within regions.

Figure 4.3
Non-metric multidimensional scaling (NMDS) of small site-attached reef fish communities across three regions in the Arabian Peninsula (Gulf △, Musandam ▽ and Sea of Oman ☐ sites) based on density for year 1 and 2. Ellipses have been added around each regional cluster to aid interpretation. The vectors overlay displays the strength and direction of a species' Spearman rank correlations with either axis (restricted to those with r > 0.8)

Table 4.1
Results of the three-factor analyses of variance assessing differences between regions, seasons and sites (within regions) in small site-attached fish community composition based on density (PERMANOVA, based on Bray-Curtis distance, data log(x+1). Significant probabilities are indicated in bold.

		Fish community composition		
Source	df	MS	Pseudo-F	P
Region	2	2.6074E5	6.3559	**0.0063**
Year	1	49026	6.3454	**0.0135**
Season	3	11054	2.2253	0.0595
Site (Region)	5	21344	2.7625	**0.002**
Region * Year	2	20895	2.7045	**0.0422**
Region * Season	6	8143.3	1.5512	0.099
Year * Season	3	4967.3	1.8059	**0.0228**
Site (Region) * Year	5	7726.2	11.975	**0.0001**
Site (Region) * Season	a			
Region * Year * Season	6	5249.8	1.9086	**0.0016**
Site (Region) * Year * Season	30a	2750.5		
Res	320	645.17		

a) <u>Pooled data</u>: Pooled terms included those that resulted in negative estimators of components of variation

Within each region, there were significant differences in fish community structure among all seasons each year (p<0.05 each), with the exception of winter and both autumn and summer for the Gulf in year 1 (p=0.14 and p=0.08, respectively), and summer and winter for Musandam in year 2 (p=0.11). SIMPER analyses showed that >58% of seasonal variation in the Gulf was primarily driven by two species (*P. aquilus* and *P. trichrourus*), with *A. vaigiensis* also having an important role in the winter differences from other seasons in year 1 (Table S 4.2). Variation among seasons in Musandam was largely driven by two main species (*C. xanthopterigya, N. cyanomos*), which together with *P. leptus* and *Chromis flavaxilla* contributed >50% of divergence between seasons (Table S 4.2). *C. xanthopterigya, N. cyanomos* and *P. leptus* also drove seasonal differences in community structure in the Sea of Oman, which along with *A. vaigiensis* were responsible for >43% of community dissimilarity between seasons (Table S 4.2). The seasonal variation of these particular species

was not consistent between regions (see Figure 4.2a), reflecting the significant PERMANOVA region x season x year interaction effect reported above.

Seasonal differences in the size-class structure of the fish community across regions were also observed. While fish in the two smallest size classes (0-5 cm and 5-10 cm) made up the majority of fishes in all three regions, they made up virtually the entire community (98.4%) in the Gulf, while larger size classes (11-15 cm and 15-20 cm) were better represented in Musandam and the Sea of Oman communities (Figure 4.4). As a result, seasonal variation in density and biomass were relatively consistent in the Gulf where fishes were small, while modest changes in the abundance of larger-bodied fish in Musandam and the Sea of Oman during particular seasons could result in large changes in biomass estimates. For example, in year 2 the lowest density of fishes in the Sea of Oman occurred in winter and autumn (Figure 4.2a), and while in autumn biomass was also lower, in winter occurred the highest fish biomass, mainly due to the presence of the rare but larger-bodied *A. viagiensis* which made up >80% of the community biomass this season (Figure 4.2b). In contrast, the highest fish abundance observed in this study was in Musandam in summer of year 2, when biomass was among the lowest recorded over the two years in that region because the abundance was almost exclusively of the smaller size class (TL <5 cm) of species such as *C. xanthopterygia*, *N. cyanomos*, and *P. leptus* and lower densities of the larger size class of *A. vaigiensis* (TL >10cm) (Figure 4.2; Figure 4.4). The three former small species together made up >73% of fish density in each of these regions across years (Figure 4.2a), but contributed only marginally to overall biomass (Figure 4.2b).

Functional groups

There were marked differences in functional groups contributing to the fish community among regions, reflecting differences in the species composition reported above. In the Gulf, communities were heavily dominated by omnivorous planktivores and territorial farmers, which together made up >95% of the fish community, on average (Figure 4.5). Here, these groups were mainly comprised of *P. trichrourus* and *P. aquilus*, respectively, each making up 91% and 100% of the individuals in their respective functional groups in the Gulf. In contrast, territorial farmers were rare in Musandam and the Sea of Oman, where diurnal planktivores (a group absent in

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the Gulf) and omnivorous planktivores dominated fish communities. Together these two functional groups made up >85% of the fishes within these regions, represented mainly by *N. cyanomos* and *C. xanthopterygia*, respectively. In both the Gulf and Musandam the functional structure of the fish communities was relatively stable across seasons and years, with only modest shifts in the relative proportion of the two dominant groups (Figure 4.5). In contrast, in the Sea of Oman there was large seasonal variation in the abundance of the two dominant functional groups (diurnal planktivores and omnivorous planktivores), and these seasonal changes were not consistent from year to year. This variation in functional groups in the Sea of Oman is largely the result of differences in the abundance of four schooling species (*N. cyanomos* and *C. xanthopterygia* as diurnal planktivores and *A. vaigiensis* and *P. leptus* as omnivorous planktivores; Figure 4.2), which were the dominant species within their respective functional groups and whose presence or absence within transects could result in large changes in abundance as a result of their gregarious behaviour.
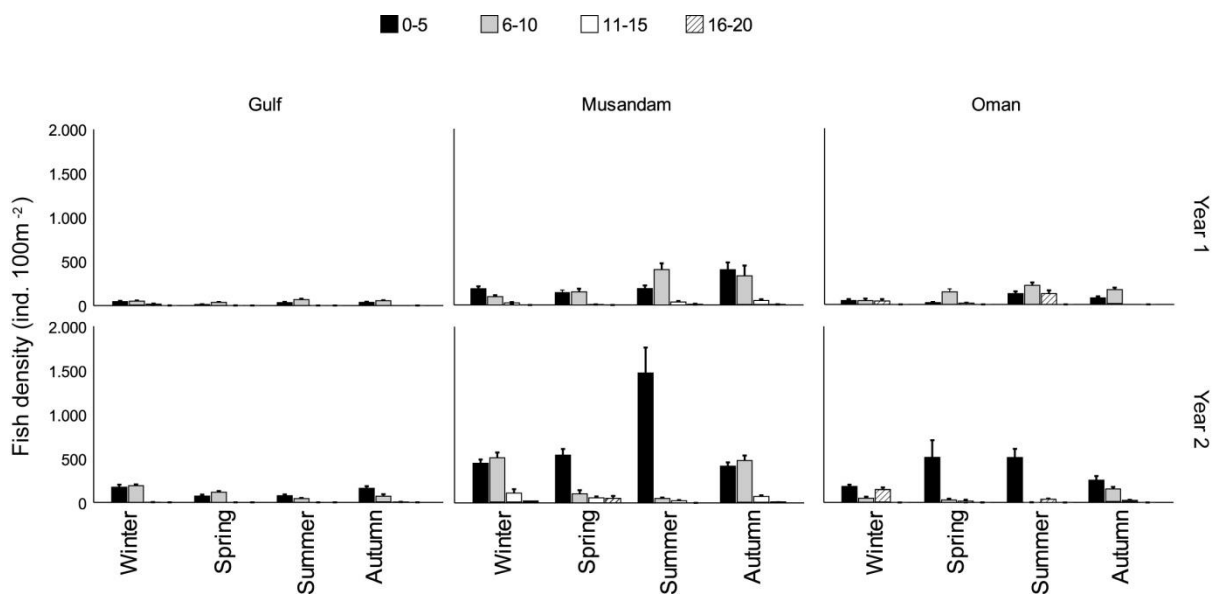
Figure 4.4
Seasonal variation of small site-attached fish density of each size class (cm TL) per region and year. Error bars are +/- 1SE.
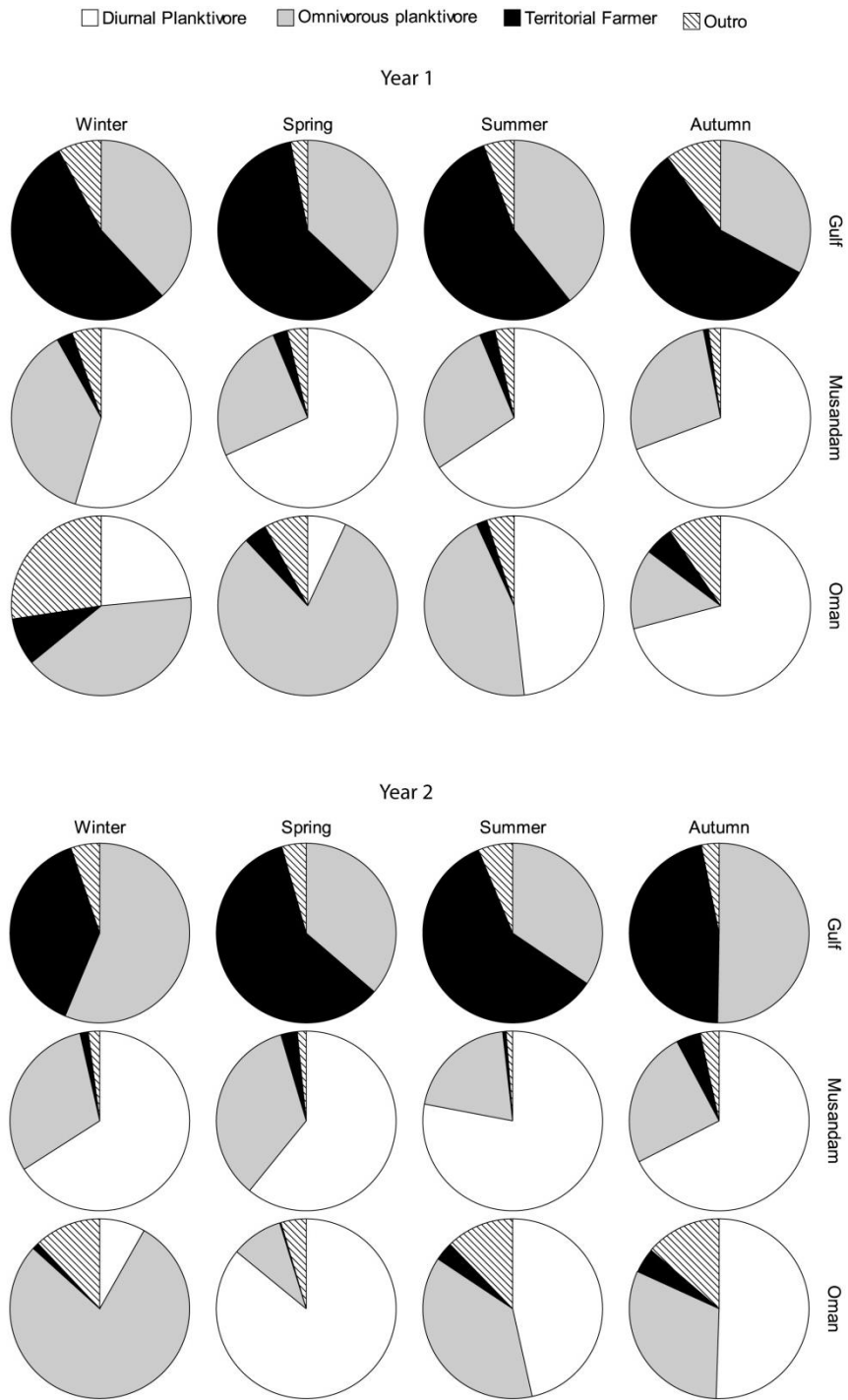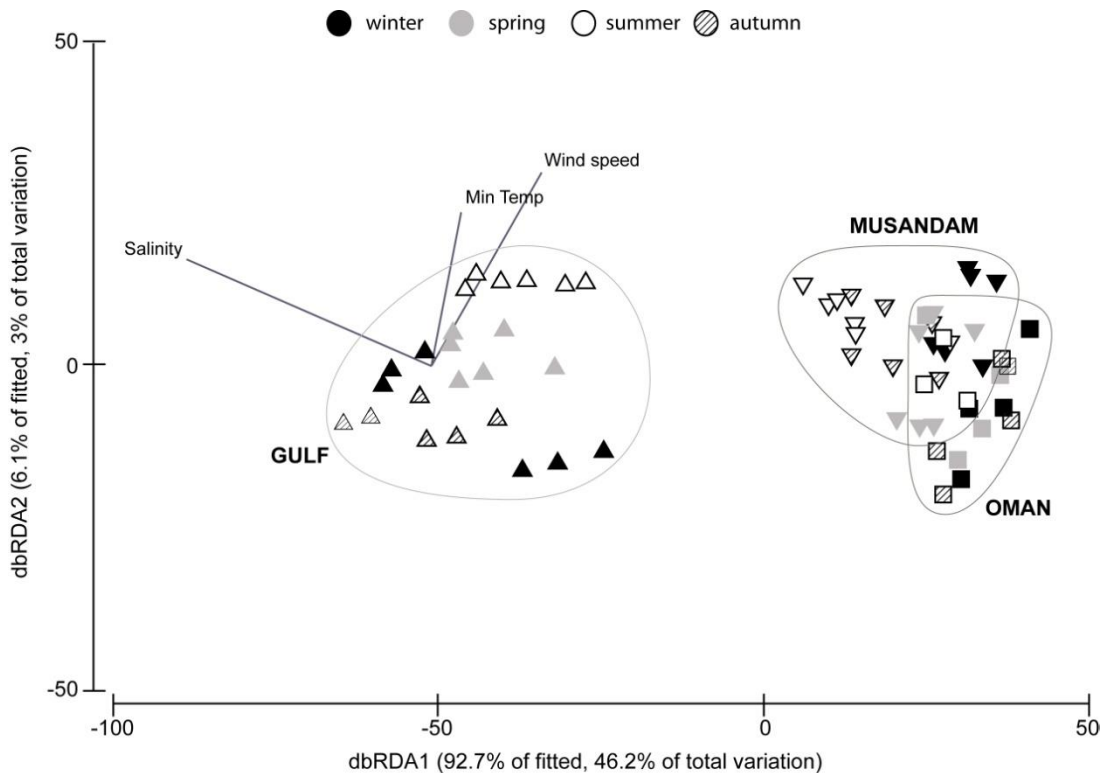
Figure 4.5
Seasonal differences in relative abundance of principal fine functional groups within each region. Fine functional groups divided by: diurnal planktivores, omnivorous planktivores, territorial herbivores and others (benthic omnivores, ectoparasite feeder, generalist carnivores, micro-invertivores, and nocturnal planktivores).

Environmental factors

Three environmental factors together explained 49.8% of the total variation in fish density among regions: salinity, wind speed, and minimum temperature (DistLM, BEST modeling). The distance-based redundancy analysis (dbRDA) plot, illustrating the fish community structure, showed that the environmental factors strongly diverged the Gulf fish community from those of Musandam and the Sea of Oman, where there was considerable similarity indicated by the broad overlap of points (Figure 4.6). The first dbRDA axis accounted for 46.2% of the total variation in fish community structure while the second dbRDA axis accounted for only 3%. Salinity was positively correlated with the first dbRDA axis (r=0.99), while wind speed was negatively correlated (r=-0.66), and both distinguished the Gulf fish communities from Musandam and the Sea of Oman, with communities in the former region being influenced by higher levels of salinity (mean 41psu vs 38 and 37psu, respectively) and the two later by stronger winds (mean 5.1 and 4.4 m/s in Musandam and the Sea of Oman vs 3.8m/s in the Gulf) (Figure 4.6, Figure S 4.1). The second dbRDA axis was better correlated with minimum temperature (r=0.47), and while seasonal differences were clearer within the Gulf, with the summer being visibly separated from the remaining seasons by higher values of minimum temperature (mean minimum temperature values of 32°C in the summer compared with 19°C in winter), these were not consistent within Musandam and the Sea of Oman (Figure 4.6, Figure S 4.1).

Figure 4.6
Distance-based redundancy analysis (dbRDA) illustrating the relationship between environmental predictors that best explain the variation of fish community in the different regions (Gulf $\triangle$, Musandam ∇ and Sea of Oman $\square$ sites). The dbRDA was constrained by the best-fit explanatory variables, with AICc, from a multivariate multiple regression analysis (DISTLM) and vectors overlays are shown for predictor variables explaining a significant proportion of the variation.

Discussion

Small site-attached reef fish are important and abundant residents on tropical reefs, and constitute a high percentage of the reef-dependent fish community (Bell and Galzin, 1984; Sale, 1991). Although this sub-group of fishes are extremely flexible in their behavioural responses to regular environmental changes (Fricke, 1977), they are still under threat from climate change, being affected not only by extreme environmental fluctuations that lead to physiological alterations (Pörtner and Knust, 2007), but also by modifications in the reef matrix that affect their shelter and nesting areas (Munday and Jones, 1998; Ferreira et al., 2001). As such, changes in their composition and abundance can give valuable information on the condition of reefs (Bell and Galzin, 1984; Komyakova et al., 2013). This study explored the community structure of small-bodied site-attached reef fishes in north-eastern Arabia, one of the

most thermally extreme reef environments on earth, providing insights of future conditions expected to happen in other parts of the world as environmental conditions become more extreme and potentially more variable. Understanding how such fish communities may respond to long-term differences, across such variable and extreme environmental conditions, allow us to understand how they may respond to future climate change. In parallel, our results enable us to understand how seasonal fluctuations might structure fish communities in high-latitude marginal reef environments that are likely to become a refugia for tropical species experiencing range expansion as the warming of the tropics pushes equatorial species further towards the poles (Yamano et al., 2011; Baird et al., 2012).

While small-bodied fish community abundance, biomass and functional composition varied both spatially and temporally, the most dramatic differences in our study occurred at the regional level, with the more seasonally variable Gulf environment having fish communities quite different from Musandam and the Sea of Oman, which were broadly similar to each other. Gulf communities had reduced abundance and biomass, a predominance of herbivores (territorial farmers) and omnivorous planktivore functional groups, and stable community structure across seasons. In comparison, in the more benign oceanic conditions found in Musandam and the Sea of Oman, fish communities exhibited a predominance of diurnal and omnivorous planktivores, and a community structure extremely variable across seasons and years, with variation mainly driven by several gregarious schooling species which dominated communities. Abundance and biomass values in the Gulf were two and six times lower than in the Sea of Oman and Musandam, and these sharp differences could be explained by the environmental differences that exist between these regions, as recurrent periods of physiological stress (as extreme SSTs and high salinities in the Gulf) are known to have a substantial effect on fish communities (Feary et al., 2010). For instances, increases in water temperatures and changes in salinity causes increases in fish metabolic rate (Plaut, 2000; Boeuf and Payan, 2001; Pörtner and Knust, 2007), which force fish to augment food consumption to maintain their growth, or to reduce energy allocated for other activities (Angilletta Jr et al., 2003; Donelson et al., 2010). As a result, fish suffer possible impaired growth, decreases in critical swimming speed and regular activity level, and consequently decreasing their ability to forage for food (Plaut, 2000; Boeuf and Payan, 2001; Hurst, 2007; Johansen and Jones, 2011a). While differences in the wider fish communities

across these regions have been documented in the past (Feary et al., 2010; Burt et al., 2011b; Grandcourt, 2012), they have been biased towards large-bodied species. Both large and small-bodied fish suffer from these previously stated physiological alterations, but small-bodied fishes, as damselfish, are particularly vulnerable to extreme variations in environmental conditions, which have been documented to decline their abundances (Booth and Beretta, 2002; Jones et al., 2004) and change their community structure (Bellwood et al., 2006). As common prey species for piscivores, they also become vulnerable to reductions in swimming performance, enhancing predation risk (Coker et al., 2009). Together these ecophysiological pressures may explain the extreme divergence of Gulf fish communities from those in the biogeographically linked, but more benign, neighboring seas.

Differences in the density and biomass of small-bodied reef fish between regions may also be an indirect response to regional differences in the structure and composition of benthic communities (Ferreira et al., 2001; Wilson et al., 2010). Recurrent bleaching events, for example, have occurred within the Gulf since 1996 (Riegl and Purkis, 2012; Riegl et al., 2018) resulting in substantial loss of live coral and shifts in community composition (Riegl, 1999; 2003; Burt et al., 2008; Burt et al., 2011a). Near complete loss of branching *Acropora* species and a concomitant increase in massive and sub-massive Faviids and Poritids (Riegl, 1999; 2003; Burt et al., 2008; Burt et al., 2011a) have reduced the complexity of the reef matrix and the amount of habitat available for small-bodied reef fishes that are often tightly associated with coral (Buchanan et al., 2016). In addition to the physical environmental stress, such benthic-related changes likely also contribute to the low densities of small-bodied site-attached reef fish species within the Gulf. In parallel, reefs in the Sea of Oman, have experienced wide-range mortality of *Acropora* and *Pocillopora* as a result of a harmful algal bloom in 2008 (Bauman et al., 2010). Concordantly, small-bodied fishes in this region don't subsist under an extreme environment, but the reduction of the complex reef matrix may explain the lower densities in the Sea of Oman compared with the relatively intact and topographically complex reef habitat within Musandam (Burt et al., 2016), albeit still substantially more abundant than in the low-complexity, environmentally extreme Gulf.

While regional differences were the most crucial drivers of community structure for small-bodied reef fish, temporal variation was also apparent, and this was not

consistent among regions. Density and biomass in the Gulf experienced drops of 50-70% from winter to the warmer spring and summer seasons, and while this could be due to the physiological responses of individuals, it could also be due to increased sheltering of small-bodied fish species during summer when predatory snappers and groupers become common on these reefs (Burt et al., 2009; Burt et al., 2013), artificially decreasing observations during visual census. As summer temperature, in the Sea of Oman and Musandam, do not exceed for long periods the maximum temperatures for optimum growth for damselfish (approximately 31°C as shown in Nakano et al. 2004 and Rummer et al. 2014), seasonal density patterns were contrary to the Gulf, with higher densities in the summer. In contrast to the Gulf, overall fish abundance in the Musandam and the Sea of Oman was generally highest in the summer months. The summer sea temperatures are not nearly as extreme in these seas, rarely exceeding the 31 °C maximum temperatures for damselfishes, suggesting that physical thermal stress is likely less important that in the Gulf. In addition, the warmer summer season is also characterized by higher productivity in these areas as a result of monsoon upwelling, which could explain the substantially higher observation of planktivorous damselfish schools driving densities in the warmer seasons in these regions. These species were typically small-bodied in size, explaining the paradoxical observation of low biomass during periods of peak density on reefs in the Musandam and the Sea of Oman.

Although there were broad differences in community structure among all three regions, the damselfishes dominated communities across all study sites. Both *P. aquilus* and *P. trichrourus* are abundant fishes in the Gulf (Burt et al., 2011b; Shraim et al., 2017) and were the primary species responsible for regional difference. In comparison, three species were important in structuring communities in Musandam and the Sea of Oman: *C. xanthopterygia*, *N. cyanomos* and *P. leptus*. We can expect that regional differences in pomacentrids populations are related to the fact that only a few species can tolerate the extreme SST and salinity that characterizes the Gulf, as has been reported for other reef-associated fish species (i.e., Gulf butterflyfish populations, see Pratchett et al., 2013). The relatively high proportion of damselfishes made up by *P. aquilus* and *P. trichrourus* in the Gulf suggest that these hardy species are able to flourish in an environment that is largely absent of direct competitors, and recent research has shown that they have broadened their dietary

habits to make use of resources not typical of these species in other regions (Shraim et al., 2017). Further research on the physiological and ecological constraints structuring the diverse damselfish populations in this region is warranted.

One surprising result from this study was the observation of relatively stable communities in the highly thermally variable Gulf, while the more stable environments of the Musandam and the Sea of Oman were characterized by highly seasonally variable assemblages. These highly dynamic changes in the fish community structure are a result of the differences in species composition between regions, and external influences besides environmental seasonality could be masking existing patterns. Within both Musandam and the Sea of Oman, the primary species influencing seasonal dissimilarities are known schooling species (*N. cyanomos* and *C. xanthopterygia*), and the occurrence of schools in surveys would be affected by a variety of factors in addition to thermal conditions, such as food availability, predation pressure, visibility and others (Pitcher, 1986), making abundance estimates for these gregarious species much more dynamic. In contrast, the dominant species in the Gulf were mainly sedentary territorial farmers (*P. aquilus*) and non-schooling planktivores (*P. trichrourus*), behavioral attributes which would result in more consistent estimates of abundance and function across seasons.

The environmental factors driving differences in fish communities varied regionally. In the Gulf salinity and minimum temperature were important in structuring the fish community, reflecting the more extreme nature of this environment and the general perception of this being a physiologically hostile area for reef fishes (Feary et al., 2010; Pratchett et al., 2013). The limited coral cover but high abundance of algae on reefs in this area likely explain the prevalence of territorial farmers on these reefs (Burt et al., 2008; Burt et al., 2011a), in keeping with observations from earlier studies on the wider reef fish communities (Feary et al., 2010; Burt et al., 2013). In contrast, in Musandam and the Sea of Oman physical factors related to water motion, such as winds, explained most of the difference in community structure. These areas are known to be highly productive, particularly during the summer when monsoon-driven upwelling results in nutrient rich surface waters that support high densities of phytoplankton and herbivorous zooplankton (Sheppard et al., 1992; Wilson et al., 2006), explaining the high abundance of planktivorous fishes observed here. The dominance of planktivores on Sea of Oman reefs had been noted earlier in

association with the monsoon (Burt et al., 2011b), suggesting that differences in productivity are important in controlling community structure in the Sea of Oman and the Musandam.

Fish diversity and abundance is threatened when permanent reef degradation occurs (Jones et al., 2004), and our results suggest that fundamental shifts in small-bodied reef fish community structure are likely to happen as the global climate continues to change. Small-bodied reef fish assemblages will likely respond to environmental changes in their environment, with a few acclimatized species of damselfish persisting (such as *P. aquilus* and *P. trichrourus*) becoming dominant and herbivores becoming more abundant on reefs as coral cover declines and algae become more prevalent. But despite their ability to persist, these species are occurring near their upper thermal limit threshold, which may result in reduced swimming performance, higher vulnerability to predation, and enhanced metabolic demands for maintenance. The low abundance and biomass of fishes in the Gulf suggests that these costs have community-level impacts, and given that reduced body size is linked with fecundity, these costs will extend through generations. Environmental extremes, together with the continuing regional reef degradation, threaten the future of the small-bodied fish communities (Munday et al., 2007). Many of the species discussed in this paper are considered vulnerable to regional extinction within the next century as a result of these threats (Buchanan et al., 2016), and rapid, aggressive management efforts are necessary if there is to be hope that this ecologically important and biologically diverse group of fishes are to hope to persist on reefs in northeastern Arabia.

Acknowledgements

References

Ackerman, J.L., and Bellwood, D.R. (2000). Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series* 206, 227-237.

Adam, T.C., Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Edmunds, P.J., Carpenter, R.C., et al. (2011). Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS ONE* 6(8), e23717.

Anderson, M., and Braak, C.T. (2003). Permutation tests for multi-factorial analysis of variance. *Journal of statistical computation and simulation* 73(2), 85-113.

Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26(1), 32–46.

Anderson, M.J., Gorley, R.N., and Clarke, R.K. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.* Plymouth: PRIMER-E Limited.

Angilletta Jr, M.J., Wilson, R.S., Navas, C.A., and James, R.S. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology & Evolution* 18(5), 234-240.

Baird, A.H., Sommer, B., and Madin, J.S. (2012). Pole-ward range expansion of Acropora spp. along the east coast of Australia. *Coral Reefs* 31(4), 1063–1063.

Bauman, A.G., Burt, J.A., Feary, D.A., Marquis, E., and Usseglio, P. (2010). Tropical harmful algal blooms: an emerging threat to coral reef communities? *Marine Pollution Bulletin* 60(11), 2117-2122.

Bell, J.O., and Galzin, R. (1984). Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series* 15(3), 265-274.

Bellwood, D.R., Hoey, A.S., Ackerman, J.L., and Depczynski, M. (2006). Coral bleaching, reef fish community phase shifts and the resilience of coral reefs. *Global Change Biology* 12(9), 1587-1594.

Boeuf, G., and Payan, P. (2001). How should salinity influence fish growth? *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology* 130(4), 411-423.

Bonin, M.C., Almany, G.R., and Jones, G.P. (2011). Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. *Ecology* 92(7), 1503-1512.

Booth, D.J., and Beretta, G.A. (2002). Changes in a fish assemblage after a coral bleaching event. *Marine Ecology Progress Series* 245, 205-212.

Bozec, Y.M., Kulbicki, M., Laloë, F., Mou-Tham, G., and Gascuel, D. (2011). Factors affecting the detection distances of reef fish: implications for visual counts. *Marine Biology* 158(5), 969-981.

Buchanan, J.R., Krupp, F., Burt, J.A., Feary, D.A., Ralph, G.M., and Carpenter, K.E. (2016). Living on the edge: Vulnerability of coral-dependent fishes in the Gulf. *Marine Pollution Bulletin* 105(2), 480-488.

Burt, J., Al-Harthi, S., and Al-Cibahy, A. (2011a). Long-term impacts of coral bleaching events on the world's warmest reefs. *Marine Environmental Research* 72(4), 225-229.

Burt, J., Bartholomew, A., and Usseglio, P. (2008). Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates. *Marine Biology* 154(1), 27-36.

Burt, J., Bartholomew, A., Usseglio, P., Bauman, A., and Sale, P.F. (2009). Are artificial reefs surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates? *Coral Reefs* 28(3)**,** 663-675.

Burt, J.A., Coles, S., van Lavieren, H., Taylor, O., Looker, E., and Samimi-Namin, K. (2016). Oman's coral reefs: A unique ecosystem challenged by natural and man-related stresses and in need of conservation. *Marine Pollution Bulletin* 105(2)**,** 498-506.

Burt, J.A., Feary, D.A., Bauman, A.G., Usseglio, P., Cavalcante, G.H., and Sale, P.F. (2011b). Biogeographic patterns of reef fish community structure in the northeastern Arabian Peninsula. *ICES Journal of Marine Science* 68(9)**,** 1875-1883.

Burt, J.A., Feary, D.A., Cavalcante, G., Bauman, A.G., and Usseglio, P. (2013). Urban breakwaters as reef fish habitat in the Persian Gulf. *Marine Pollution Bulletin* 72(2)**,** 342-350.

Clarke, K.R., and Gorley, R.N. (2006). *PRIMER V6: User Manual PRIMER-E.* Plymouth, U.K.

Clarke, K.R., and Warwick, R.M. (2001). *Changes in marine communities: an approach to statistical analysis and interpretation.* Plymouth, U.K.: PRIMER-E Ltd.

Coker, D.J., Pratchett, M.S., and Munday, P.L. (2009). Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology* 20(6)**,** 1204-1210.

Coles, S.L., and Tarr, B.A. (1990). Reef fish assemblages in the western Arabian Gulf: a geographically isolated population in an extreme environment. *Bulletin of Marine Science* 47(3)**,** 696-720.

Donelson, J.M., Munday, P.L., McCormick, M.I., Pankhurst, N.W., and Pankhurst, P.M. (2010). Effects of elevated water temperature and food availability on the reproductive performance of a coral reef fish. *Marine Ecology Progress Series* 401**,** 233-243.

Feary, D.A., Burt, J.A., Bauman, A.G., Usseglio, P., Sale, P.F., and Cavalcante, G.H. (2010). Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future? *Journal of Fish Biology* 77(8)**,** 1931-1947.

Feary, D.A., Burt, J.A., Cavalcante, G.H., and Bauman, A.G. (2012). "Extreme physical factors and the structure of Gulf fish and reef communities," in *Coral Reefs of the Gulf,* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 163-170.

Feary, D.A., Pratchett, M.S., J Emslie, M., Fowler, A.M., Figueira, W.F., Luiz, O.J., et al. (2014). Latitudinal shifts in coral reef fishes: why some species do and others do not shift. *Fish and Fisheries* 15(4)**,** 593-615.

Ferreira, C.E., Goncalves, J.E., and Coutinho, R. (2001). Community structure of fishes and habitat complexity on a tropical rocky shore. *Environmental Biology of Fishes* 61(4)**,** 353-369.

Fletcher, D.J., and Underwood, A.J. (2002). How to cope with negative estimates of components of variance in ecological field studies. *Journal of Experimental Marine Biology and Ecology* 273(1)**,** 89-95.

Floeter, S.R., Ferreira, C.E.L., Dominici-Arosemena, A., and Zalmon, I.R. (2004). Latitudinal gradients in Atlantic reef fish communities: trophic structure and spatial use patterns. *Journal of Fish Biology* 64(6)**,** 1680-1699.

Foster, K., Foster, G., Al-Cibahy, A.S., Al-Harthi, S., Purkis, S.J., and Riegl, B.M. (2012). "Environmental setting and temporal trends in southeastern Gulf coral communities," in *Coral Reefs of the Gulf,* eds. B. Riegl & S. Purkis. (Dordrecht: Springer), 51-70.

Fricke, H.W. (1977). Community structure, social organization and ecological requirements of coral reef fish (Pomacentridae). *Helgoländer wissenschaftliche Meeresuntersuchungen* 30(1), 412-426.

Froese, R., and Pauly, D. 2017. FishBase. [Accessed version (10/2017)].

Grandcourt, E. (2012). "Reef fish and fisheries in the Gulf," in *Coral Reefs of the Gulf,* eds. B. Riegl & S. Purkis. (Dordrecht: Springer), 127-161.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., et al. (2003). Climate change, human impacts, and the resilience of coral reefs. *Science* 301(5635), 929-933.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., et al. (2017). Global warming and recurrent mass bleaching of corals. *Nature* 543(7645), 373-377.

Hurst, T.P. (2007). Causes and consequences of winter mortality in fishes. *Journal of Fish Biology* 71(2), 315-345.

IBM Corporation (2016). "IBM SPSS Statistics for Windows". Version 24.0 ed. (Armonk, NY: IBM Corporation).

Johansen, J., and Jones, G. (2011a). Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Global Change Biology* 17(9), 2971-2979.

Johansen, J.L., and Jones, G.P. (2011b). Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Global Change Biology* 17(9), 2971-2979.

Jones, G.P., I., M.M., Srinivasan, M., and Eagle, J.V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences* 101(21), 8251-8253.

Kleypas, J.A., McManus, J.W., and Meñez, L.A. (1999). Environmental limits to coral reef development: where do we draw the line? *American Zoologist* 39(1), 146-159.

Komyakova, V., Munday, P.L., and Jones, G.P. (2013). Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE* 8(12), e83178.

McCune, B., Grace, J.B., and Urban, D.L. (2002). *Analysis of ecological communities.* Gleneden Beach, OR: MjM software design.

Metzger, E.J., Hurlburt, H.E., Xu, X., Shriver, J.F., Gordon, A.L., Sprintall, J., et al. (2010). Simulated and observed circulation in the Indonesian Seas: 1/12 global HYCOM and the INSTANT observations. *Dynamics of Atmospheres and Oceans* 50(2), 275-300.

Munday, P.L., and Jones, G.P. (1998). "The ecological implications of small body size among coral-reef fishes," in *Oceanography and Marine Biology: An Annual Review,* eds. A.D. Ansell, R.N. Gibson & M. Barnes. UCL Press), 373-411.

Munday, P.L., Jones, G.P., Pratchett, M.S., and Williams, A.J. (2008). Climate change and the future for coral reef fishes. *Fish and Fisheries* 9(3), 261-285.

Munday, P.L., Jones, G.P., Sheaves, M., Williams, A.J., and Goby, G. (2007). "Vulnerability of fishes of the Great Barrier Reef to climate change," in *Climate Change and the Great Barrier Reef: A Vulnerability Assessment.,* eds. J.

Johnson & P. Marshall. (Townsville, Australia: Great Barrier Reef Marine Park Authority), 357–392.

Nakano, K., Takemura, A., Nakamura, S., Nakano, Y., and Iwama, G.K. (2004). Changes in the cellular and organismal stress responses of the subtropical fish, the Indo-Pacific sergeant, Abudefduf vaigiensis, due to the 1997–1998 El Nino/Southern Oscillation. *Environmental Biology of Fishes* 70(4)**,** 321-329.

Nilsson, G.E., Crawley, N., Lunde, I.G., and Munday, P.L. (2009). Elevated temperature reduces the respiratory scope of coral reef fishes. *Global Change Biology* 15(6)**,** 1405-1412.

Pitcher, T.J. (1986). "Functions of shoaling behaviour in teleosts," in *The behaviour of teleost fishes.* (Boston, MA: Springer), 294-337.

Plaut, I. (2000). Resting metabolic rate, critical swimming speed, and routine activity of the euryhaline cyprinodontid, Aphanius dispar, acclimated to a wide range of salinities. *Physiological and Biochemical Zoology* 73(5)**,** 590-596.

Pörtner, H.O., and Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315(5808)**,** 95-97.

Pratchett, M.S., Hoey, A.S., Feary, D.A., Bauman, A.G., Burt, J.A., and Riegl, B.M. (2013). Functional composition of Chaetodon butterflyfishes at a peripheral and extreme coral reef location, the Persian Gulf. *Marine Pollution Bulletin* 72(2)**,** 333-341.

Pratchett, M.S., Munday, P.L., Wilson, S.K., Graham, N.A.J., Cinner, J.E., Bellwood, D.R., et al. (2008). Effects of climate-induced coral bleaching on coral-reef fishes - Ecological and economic consequences. *Oceanography and Marine Biology* 46**,** 251-296.

Reynolds, R.M. (1993). Physical oceanography of the Gulf, Strait of Hormuz, and the Gulf of Oman - Results from the Mt Mitchell expedition. *Marine Pollution Bulletin* 27**,** 35-59.

Riegl, B. (1999). Corals in a non-reef setting in the southern Arabian Gulf (Dubai, UAE): fauna and community structure in response to recurring mass mortality. *Coral Reefs* 18(1)**,** 63-73.

Riegl, B. (2003). Climate change and coral reefs: different effects in two high-latitude areas (Arabian Gulf, South Africa). *Coral Reefs* 22(4)**,** 433-446.

Riegl, B., Johnston, M., Purkis, S., Howells, E., Burt, J., Steiner, S.C.C., et al. (2018). Population collapse dynamics in Acropora downingi, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. *Global Change Biology* 24(6)**,** 2447-2462.

Riegl, B.M., and Purkis, S.J. (2012). "Coral reefs of the Gulf: adaptation to climatic extremes in the world's hottest sea," in *Coral Reefs of the Gulf* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 1-4.

Rogers, A., Blanchard, J.L., and Mumby, P.J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology* 24(9)**,** 1000-1005.

Rummer, J.L., Couturier, C.S., Stecyk, J.A., Gardiner, N.M., Kinch, J.P., Nilsson, G.E., et al. (2014). Life on the edge: thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. *Global Change biology* 20(4)**,** 1055-1066.

Sale, P.F. (1991). *The ecology of fishes on coral reefs.* San Diego Academic Press.

Schils, T., and Wilson, S.C. (2006). Temperature threshold as a biogeographic barrier in northern Indian Ocean macroalgae. *Journal of Phycology* 42(4)**,** 749-756.

Sheppard, C., Price, A., and Roberts, C. (1992). *Marine ecology of the Arabian Region: patterns and processes in extreme tropical environments.* Toronto: Academic Press.

Sheppard, C.R. (1993). Physical environment of the Gulf relevant to marine pollution: an overview. *Marine Pollution Bulletin* 27**,** 3-8.

Shraim, R., Dieng, M.M., Vinu, M., Vaughan, G., McParland, D., Idaghdour, Y., et al. (2017). Environmental extremes are associated with dietary patterns in Arabian Gulf reef fishes. *Frontiers in Marine Science* 4**,** 285.

Terlizzi, A., Anderson, M.J., Fraschetti, S., and Benedetti-Cecchi, L. (2007). Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. *Marine Ecology Progress Series* 332**,** 25-39.

Wilson, S.K., Fisher, R., Pratchett, M.S., Graham, N.A., Dulvy, N.K., Turner, R.A., et al. (2010). Habitat degradation and fishing effects on the size structure of coral reef fish communities. *Ecological Applications* 20(2)**,** 442-451.

Wilson, S.K., Graham, N.A., Pratchett, M.S., Jones, G.P., and Polunin, N.V. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? *Global Change Biology* 12(11)**,** 2220-2234.

Yamano, H., Sugihara, K., and Nomura, K. (2011). Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophysical Research Letters* 38(4)**,** L04601.

Zar, J.H. (1999). *Biostatistical analysis.* Englewood Cliffs, NJ.: Prentice Hall.

Supplements

Table S 4.1

Mean density (individual 100 m^{-2} ± SE) of small site-attached reef fish species that were observed within each region, with respective family and fine functional group, averaged across all seasons.

Family	Species	Fine functional group	Gulf	Musandam	Oman
Apogonidae	*Apogon aureus*	Generalist carnivore		2.0 ± 0.6	0.03 ± 0.03
	Cheilodipterus novemstriatus	Generalist carnivore	0.1 ± 0.04	0.3 ± 0.2	
	Cheilodipterus persicus	Generalist carnivore	2.0 ± 0.5	2.7 ± 0.9	3.5 ± 1.5
Blenniidae	*Ecsenius pulcher*	Benthic omnivore	0.9 ± 0.2	1.1 ± 0.2	2.5 ± 0.4
Gobiidae	*Amblygobius albimaculatus*	Benthic omnivore	0.4 ± 0.1		
	Cryptocentrus lutheri	Micro-invertivore	0.5 ± 0.1	0.4 ± 0.1	
	Valenciennea persica	Micro-invertivore		0.3 ± 0.1	
	Valenciennea sexguttata	Micro-invertivore		0.02 ± 0.02	
Labridae	*Halichoeres marginatus*	Micro-invertivore		3.3 ± 0.5	24.4 ± 2.8
	Halichoeres stigmaticus	Micro-invertivore	1.4 ± 0.3		
	Labroides dimidiatus	Ectoparasite feeder		3.6 ± 0.4	2.8 ± 0.5
Ostraciidae	*Ostracion cyanurus*	Benthic omnivore		1.4 ± 0.2	1.9 ± 0.3
Pempheridae	*Pempheris vanicolensis*	Nocturnal planktivore		0.5 ± 0.5	0.3 ± 0.3
Pomacentridae	*Abudefduf vaigiensis*	Omnivorous planktivore	5.9 ± 1.3	54.3 ± 7.3	62.2 ± 10.3
	Amphiprion clarkii	Omnivorous planktivore	0.02 ± 0.02	1.2 ± 0.2	0.5 ± 0.2
	Chromis flavaxilla	Diurnal planktivore		54.9 ± 12.0	
	Chromis xanthopterygia	Diurnal planktivore		262.1 ± 31.0	109.9 ± 28.5
	Dascyllus trimaculatus	Omnivorous planktivore		19.4 ± 2.6	3.3 ± 1.0
	Neopomacentrus cyanomos	Diurnal planktivore		224.2 ± 24.5	64.4 ± 10.9
	Pomacentrus aquilus	Territorial farmer	76.3 ± 4.6	16.3 ± 2.4	10.2 ± 1.4
	Pomacentrus leptus	Omnivorous planktivore		137.2 ± 9.4	73.0 ± 8.1
	Pomacentrus trichourus	Omnivorous planktivore	62.5 ± 7.3	2.1 ± 1.0	0.1 ± 0.1
Pseudochromidae	*Pseudochromis aldabraensis*	Generalist carnivore	0.7 ± 0.2	3.0 ± 0.4	0.1 ± 0.05
	Pseudochromis linda	Generalist carnivore		0.1 ± 0.1	
	Pseudochromis nigrovittatus	Generalist carnivore	0.9 ± 0.2	0.02 ± 0.02	0.1 ± 0.1
	Pseudochromis persicus	Generalist carnivore	1.2 ± 0.2	0.2 ± 0.1	

Table S 4.2

Similarity results of small site-attached reef fish species, based on density, calculated by SIMPER analyses. Only species strongly contributing to the dissimilarity (δ >15%) in each seasonal pairwise comparison within regions and years are shown. Season codes: Wi: Winter; Sp: Spring; Su: Summer; Au: Autumn.

Percentage contribution to dissimilarity based on density

Region	Season comparison	δ (2011/2012)	P. aquilus	P. trichrourus	C. xanthopterigya	N. cyanomosos	P. leptus	A. vaigienses	δ (2012/2013)	P. aquilus	P. trichrourus	C. xanthopterigya	N. cyanomosos	P. leptus	A. vaigienses	C. flavaxilla
Gulf	Sp vs. Au	45.97	37.18	34.00					41.43	33.84	47.98					
	Su vs. Au	39.13	29.87	42.55					44.59	34.97	47.47					
	Sp vs. Su	44.98	39.51	41.09					42.21	37.76	43.01					
	Au vs. Wi	40.15	24.22	34.62				18.61	43.27	27.79	47.03					
	Sp vs. Wi	47.29	34.26	30.50				20.47	43.13	22.71	51.33					
	Su vs. Wi	39.91	30.16	37.32				16.63	51.85	27.77	49.59					
Musandam	Sp vs. Au	64.58			20.69	24.20	16.90		42.75			21.05	16.75			
	Su vs. Au	52.71			21.87	24.95	15.75		41.74			20.10	20.15			
	Sp vs. Su	57.20				34.58	17.18		46.41			20.85	21.56			15.50
	Au vs. Wi	54.09			19.88	25.79	16.95		36.28			16.53	17.96			
	Sp vs. Wi	61.90			16.68	25.02	15.54		41.43			19.83	17.91	15.23		
	Su vs. Wi	52.17			17.08	29.92	15.55		36.01			21.28	20.29			17.16
Oman	Sp vs. Au	77.72				29.45		31.37	75.07			33.99			23.30	
	Su vs. Au	58.86			18.26	24.20	15.74	26.30	46.53			29.18	23.79	16.36		
	Sp vs. Su	66.47				29.53	15.28	26.50	80.80			25.39			30.42	
	Au vs. Wi	74.14			15.88	35.73			59.44			24.24			28.42	
	Sp vs. Wi	68.11						43.28	80.92			25.60		25.94	24.10	
	Su vs. Wi	72.88			15.00	29.76		23.38	51.68			17.92	17.17		28.32	

Table S 4.3
Similarity results of small site-attached reef fish species, based on biomass, calculated by SIMPER analyses. Only species strongly contributing to the dissimilarity (δ >15%) in each seasonal pairwise comparison within regions and years are shown. Season codes: Wi: Winter; Sp: Spring; Su: Summer; Au: Autumn.

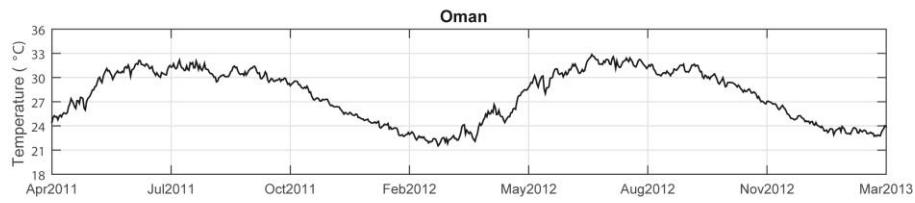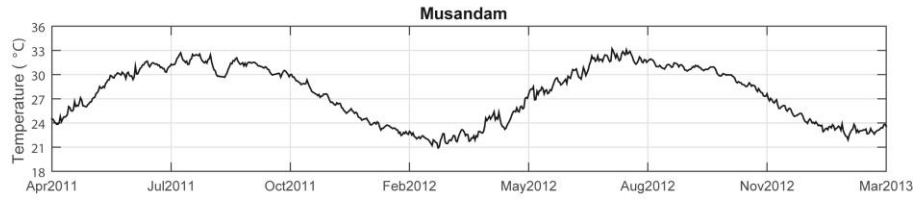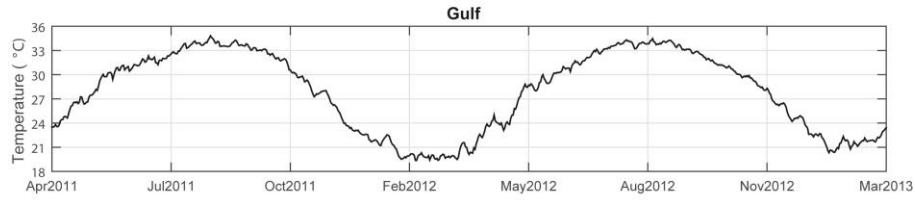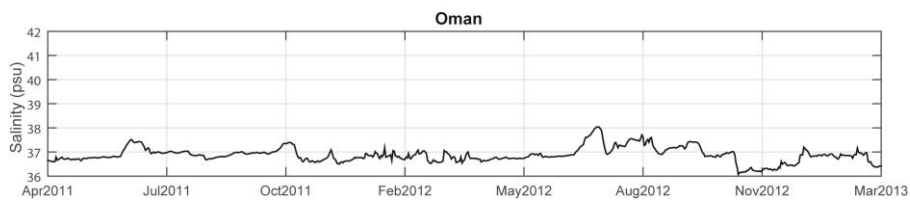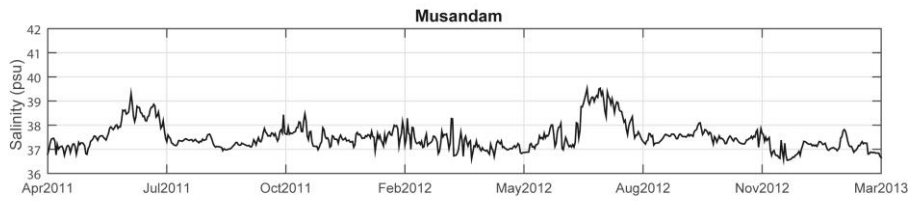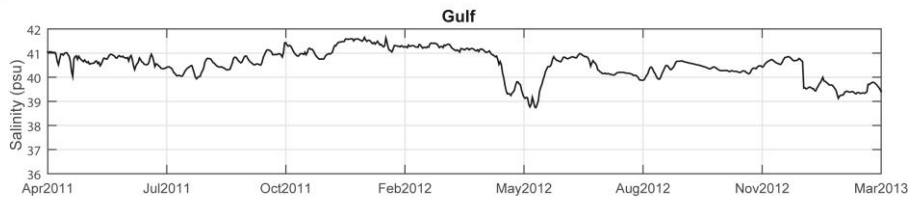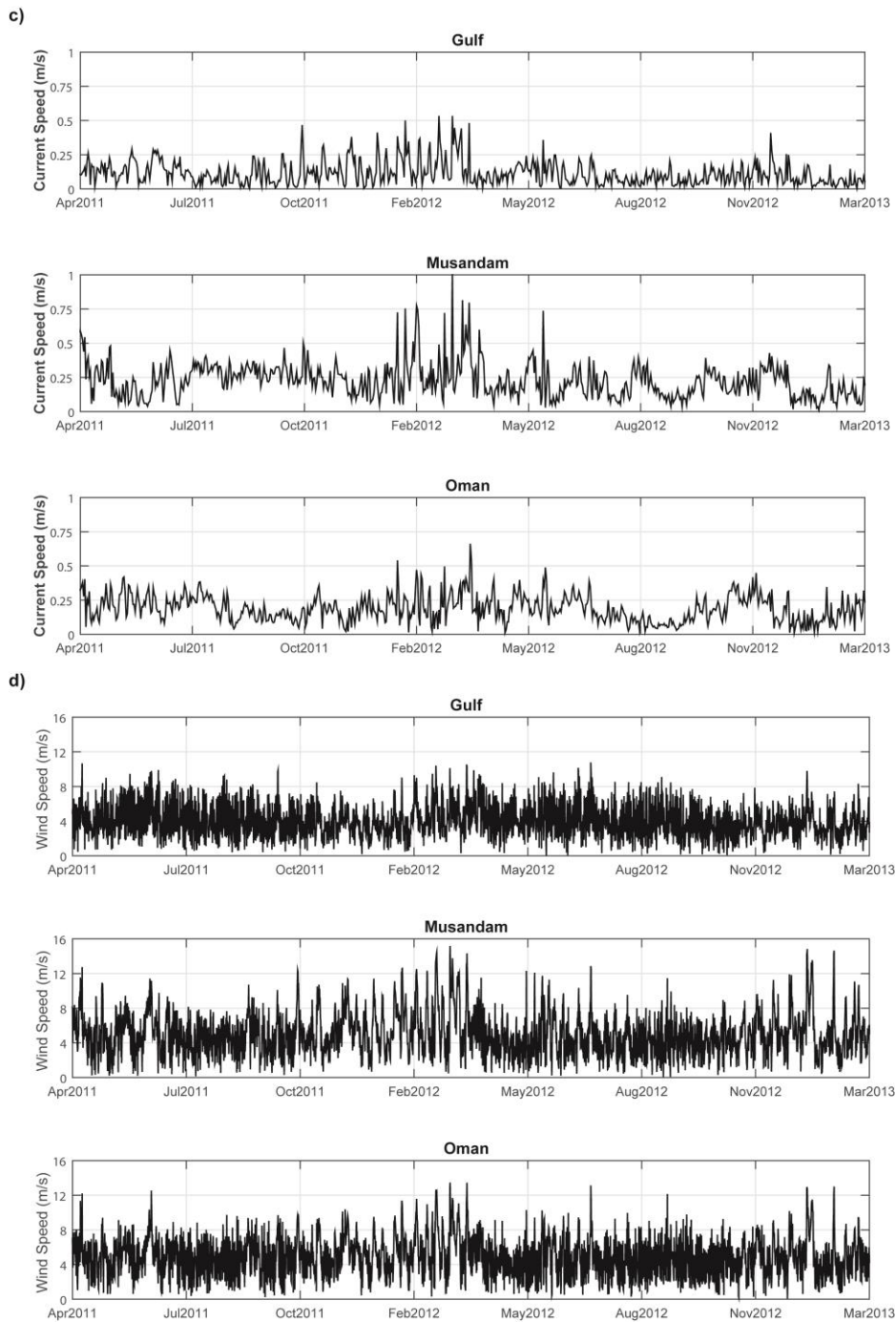Percentage contribution to dissimilarity based on biomass

Region	Seasons	δ (2011/2012)	P. aquilus	P. trichrourus	C. xanthopterigya	N. cyanomosos	A. vaigienses	Pseudochromis persicus	δ (2012/2013)	P. aquilus	P. trichrourus	C. xanthopterigya	N. cyanomosos	A. vaigienses	Pseudochromis persicus	Pseudochromis nigrovittatus	Dascyllus trimaculatus
Gulf	Sp vs. Au	31.15	17.82	32.46			35.87		53.45	44.60	19.52						
	Su vs. Au	32.22		40.95			26.83		50.73	41.98	28.24						
	Sp vs. Su	31.64	18.84	52.40			18.05		35.37	26.99	29.96			17.92	15.13		
	Au vs. Wi	37.97		21.89			34.65	15.17	55.06	33.87	25.69						
	Sp vs. Wi	38.52	16.68	23.22			32.84		37.50		35.64			20.78		15.71	
	Su vs. Wi	38.94		33.44			24.83		43.26	20.37	32.47						15.03
Musandam	Sp vs. Au	67.52					17.36		46.54			17.81		15.90			
	Su vs. Au	54.91				17.40	17.55		50.14		17.97	16.99					
	Sp vs. Su	60.36				18.76	19.81		49.61		15.93			21.91			15.03
	Au vs. Wi	56.36					16.81		42.68		15.94						
	Sp vs. Wi	67.62					16.29		53.41			17.72		16.39			
	Su vs. Wi	55.01				18.75	18.04		52.84					18.75			
Oman	Sp vs. Au	72.90				20.55	26.38		75.49	16.44		22.12		16.43			
	Su vs. Au	57.57					28.53		57.79	19.96		27.13					
	Sp vs. Su	57.16				21.82	17.40		73.18	20.57				18.26			
	Au vs. Wi	69.31	15.04			20.86	19.14		68.72			16.93		31.70			
	Sp vs. Wi	54.31	19.96				29.23		61.78					26.74			
	Su vs. Wi	62.26				18.93	10.57		55.66	17.55				29.60			

a)

Gulf

Musandam

Oman

b)

Gulf

Musandam

Oman

Figure S 4.1
Changes in environmental parameters across the two years of study, within each region: (a) sea-surface temperature (°C), (b) surface salinity (psu), (c) dominant current speed (m/s) and (d) dominant wind speed (m/s). All data gathered from model outputs and satellite observations for each site at each sampling period.

Chapter 5 "Diel variation in grazing activity by fish and macro-invertebrates in an extreme environment: comparison between the Gulf and the Sea of Oman"

Preface

Reef recovery after disturbances is greatly dependent on the grazing action of the herbivorous functional group. Depending on the fish or invertebrates performing this grazing, reefs can recover to a pre-disturbance state or they can suffer a phase-shift and become algal dominated. In this final study we identify rates of herbivory and the primary taxa responsible for algae removal in the extreme environment of the Gulf and compare these with the taxa in the Sea of Oman.

Highlights

- Diurnal herbivory is greater in the Gulf, with a two-fold higher reduction in algal cover than the Sea of Oman;

- Nocturnal herbivory is greater in the Sea of Oman than the Gulf;

- The omnivorous angelfish, *Pomacanthus maculosus*, was the dominant herbivore in the Arabian Gulf;

- Macro-invertebrates (gastropods and *Diadema setosum*) were the dominant herbivores in the Sea of Oman.

Diel variation in grazing activity by fish and macro-invertebrates in an extreme environment: comparison between the Gulf and the Sea of Oman.

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Abstract

Herbivory is a key process on coral reefs, maintaining a healthy balance between corals and benthic algae. While numerous studies have shown that a limited suite of species, the macroalgal browsers, are capable of removing macroalgae, most studies have been conducted on biodiverse, low-latitude reefs. It is unknown how these findings translate to marginal high-latitude coral reef environments. We used tiles with established algal communities to investigate the rates of herbivory, as well as to identify key herbivores species, in two marginal coral reef environments: the southern Arabian Gulf, a naturally extreme environment, and the northern Sea of Oman. Replicate tiles were deployed for 12h at dawn and at dusk at two sites within each region, and stationary video-cameras used to record feeding activity. The experiment was repeated over three days. Diurnal herbivory resulted in two-fold greater reduction in algal cover in the southern Arabian Gulf than the northern Sea of Oman ($36.2 \pm 5.9\%.12h^{-1}$ and $19.2 \pm 5.0\%.12h^{-1}$ (mean ±SE), respectively). The opposite was observed for nocturnal herbivory, with the greatest reduction in algal cover being recorded in the northern Sea of Oman ($28.2 \pm 4.5\%.12h^{-1}$) compared to the southern Arabian Gulf ($11.1 \pm 6.2\%.12h^{-1}$). Analysis of video footage revealed the angelfish *Pomacanthus maculosus* was the dominant herbivore in the Arabian Gulf, accounting for 89.3% of total mass-standardized bites recording during diurnal periods. In contrast, macro-invertebrates (i.e., gastropods and the Black Longspine

urchin [*Diadema setosum*]) were the dominant herbivores in the Sea of Oman. While previous studies in biodiverse reef systems have shown the important functional role of single species of rabbitfish and surgeonfish in algae removal, our results show that the abundant omnivore angelfish, *P. maculosus*, acts as a functionally important herbivore in the Gulf.

Keywords: Video camera; herbivory; coral reef; turf algae; *Diadema setosum*; *Pomacanthus maculosus*

Introduction

Herbivory is widely regarded as one of the most critical processes on coral reefs, maintaining a healthy balance between corals and benthic algae (Mumby et al., 2006; Hughes et al., 2007), and providing space for the settlement of benthic organisms (Bellwood et al., 2012). Grazing activity by herbivores can decrease coral reefs vulnerability to shift to an alternate assemblage that is typically dominated by algae (Bellwood et al., 2004; Hughes et al., 2007). Different species of fish and invertebrates act as key herbivores by removing algae and opening space available for coral to settle (Korzen et al., 2011). Herbivory is becoming increasingly important as threats to reefs around the world augment, resulting in declines in the cover and diversity of corals and concomitant increases in cover and biomass of benthic macroalgae (Hughes et al., 2010; Graham et al., 2011; Graham et al., 2013; Hughes et al., 2018). The ability of reefs to recover from such events will not only depend on the abundance, but importantly the composition, of local herbivore assemblages (Burkepile and Hay, 2008; Bennett et al., 2015).

Macro-herbivores can be divided in two broad functional groups based on their feeding behavior: the browsers and the grazers (including scrapers, excavators, and croppers) (Wilson et al., 2003; Bellwood et al., 2006). Browsers are selective herbivores that feed typically on brown macroalgae (Mantyka and Bellwood, 2007b), and are considered important in reversing phase-shifts of alga-dominated regimes (Bellwood et al., 2006; Hoey and Bellwood, 2009). In contrast, grazers feed more commonly on the epilithic algal matrix (e.g. surgeonfish, parrotfish and rabbitfish), with some species of parrotfish scraping or excavating the underlying substrate as

they feed (Bonaldo et al., 2014), opening space in the substrate for new corals and other benthos to settle (Bellwood et al., 2012), and helping reefs to resist phase-shifts after disturbances (Nyström, 2006). While the primary species responsible for high herbivory rates are commonly comprised of well-known groups, such as parrotfish and rabbitfish (Mantyka and Bellwood, 2007a; Cvitanovic and Bellwood, 2008; Fox and Bellwood, 2008), numerous studies from low latitude reefs have reported that removal of algae is often restricted to a limited suite of species, despite the range of herbivores present (Bellwood et al., 2006; Hoey and Bellwood, 2009; Plass-Johnson et al., 2015). Collectively these studies have shown that the removal of macroalgae is solely performed by one or two species of rabbitfish (Plass-Johnson et al., 2015; Gilby et al., 2017), or surgeonfish (Hoey and Bellwood, 2009). To date, the vast majority of these studies have been conducted on biodiverse low latitude reefs, but how these findings translate to higher latitude reefs in marginal environments is still unknown.

Reefs in the Arabian/Persian Gulf (hereafter called 'the Gulf') exist under a highly variable environment, with wide temperature range and high salinity (Sheppard et al., 1992), making this region ideal to conduct studies on extreme environments. The Gulf, is characterized by extreme SSTs with an annual fluctuations of approximately 24°C, ranging <12°C during the winter to >36°C in the summer (Sheppard et al., 1992; Sheppard, 1993), and year-round hyper-saline conditions (>44 PSU) (Reynolds, 1993). This region is biogeographically connected with the Sea of Oman, that in contrast, is characterized by much moderate annual variation in SSTs, approximately 12°C, ranging from 22°C in the winter to 34°C in the summer (Kleypas et al., 1999; Schils and Wilson, 2006), and with salinity values similar to other tropical reefs (35–37 PSU) (Schils and Wilson, 2006; Foster et al., 2012). Besides differences in environmental conditions, both these disparate regions have suffered different impacts that have compromised and resulted in the loss of live coral cover and coral richness (Bauman et al., 2010; Burt et al., 2011a; Riegl et al., 2012; Riegl and Purkis, 2012; Riegl et al., 2018). This loss of living corals has opened space for the colonization by algae, that is mainly comprised of turf and coralline algae, with reefs in the winter months being dominated by dense beds of foliose brown algae (John, 2012).

In both the Gulf and Sea of Oman, the herbivore community is comprised of both fish and invertebrates, with echinoderms present in high numbers, but with limited species richness (George, 2012; R. Bento, unpubl. data). Reef fish communities in these disparate regions are structurally and functionally distinct, with communities in the Gulf comprising lower richness, abundance and biomass, with a different trophic guild structure than the Sea of Oman (Feary et al., 2010; Burt et al., 2011b; Hoey et al., 2016). Although herbivores constitute the principal functional group in the Gulf, they are mainly comprised by the damselfish territorial farmer, *Pomacentrus aquilus*, while generally more common herbivorous fish groups, such as parrotfish and surgeonfishes, are rare or absent from reefs within the southern Gulf, but frequent within the Sea of Oman (Feary et al., 2010; Burt et al., 2011b; Hoey et al., 2016). This difference in herbivores composition between regions and the lack of what are considered essential herbivores in the Gulf raises the question as to who are the major herbivores in this extreme system.

This study aimed to understand the rates of herbivory, as well as to identify key macro-herbivores species, and how this varies between two distinct marginal environments. We conducted a series of *in situ* experiments to quantify the density and impact of macro-herbivores, and to identify diel variation at two different environments in the Arabian Peninsula: the Gulf and the Sea of Oman.

Methods

Study location

This study was conducted during July 2013 along the west (Arabian Gulf) and east (Sea of Oman) coast of the United Arab Emirates, on the Arabian Peninsula (Figure 5.1). Two sites in the Arabian Gulf (Saadiyat and Emily) and two sites in the Sea of Oman (Dibba and Al Aqa) were selected to examine spatial variation in the rates of herbivory and to identify the fish and invertebrate species responsible for biomass consumption. Experiments were conducted at a similar depth (c.a 2-5m) and in areas of coral cover on each reef.
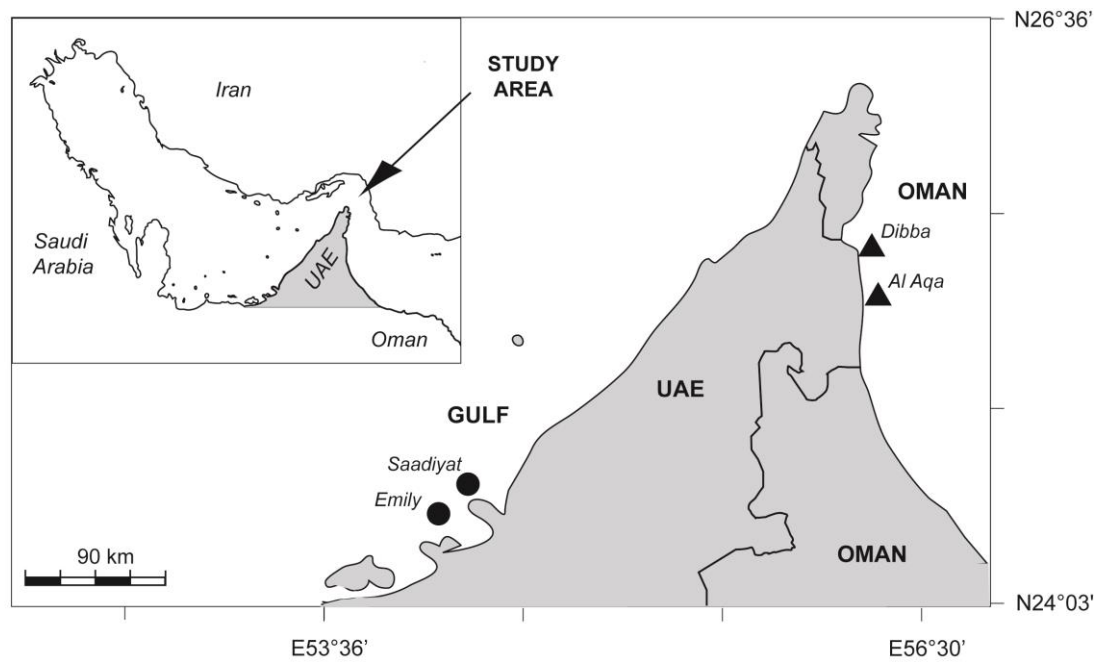
Figure 5.1
Location of the four sites where the manipulative study was conducted on the Arabian Peninsula. Two sites located on the Gulf (circles: Saadiyat and Emily), and two sites located on the Sea of Oman side (triangles: Dibba and Al Aqa).

Experimental tiles

Algal communities were established on 125 unglazed terracotta experimental tiles (10 x 10 x 1.5 cm), with a smooth top and a rough underside, by preconditioning the tiles for three months on Saadiyat reef (Arabian Gulf). Tiles were placed on the reef with the rough surface facing upward at a depth of 5m and enclosed within an exclusion cage (mesh size =5cm) to exclude the action of grazers.

After three months the tiles were collected and sets of five tiles were randomly selected. Each tile was individually identified with numbered cable ties, photographed and deployed on the reef at each site. Photographs were taken using a standardized digital camera setup (10 megapixel Nikon D-18) with a frame to ensure that all photos were taken at the same distance and orientation. Each tile was attached to a small dive weight using a cable tie, and placed in an area free of live coral. Three tiles were left exposed to herbivores, and two tiles were placed within individual exclusion cages (approximately 20 × 20 × 20 cm; 1.5 cm square plastic mesh), to control for losses due to experimental handling and translocation. Tiles were deployed either in the morning (~7:00) or evening (~19:00), and collected after 12h.

Tiles were photographed immediately after collection (as previously described). This entire procedure was repeated for three consecutive days (three diurnal and three nocturnal deployments) at each site.

Analyzing the photographs taken of the tiles, the cover of algae, coralline algae, coral, ascidians, sponges, arthropods (barnacles), mollusks (bivalves, chiton, and gastropods), annelids (polychaetes), bryozoans, 'other living' and sand/silt was determined using CPCe, with 50 random points per tile (Kohler and Gill, 2006). Algae were further identified to the genus level as being *Champia*, *Chondria*, *Cystoseira*, *Padina*, *Peyssonelia*, *Ulva*, turf algae or placed in an 'other macroalgae' category. The mean percentage cover of benthic taxa across tiles before the experiment was 74.3% ± 1.8% SE algae (comprised on average of 93% turf algae), with 16.7% ± 1.4% SE being bare tile. The remaining categories occupied less than 5% cover.

Video observations

To identify the fish and macro-invertebrate species that potentially fed on the experimental tiles, small underwater digital video cameras (GoPro) mounted on a dive weight were positioned approximately 1m from a tile exposed to local herbivore assemblages. To record nocturnal feeding behavior, two red-filtered lights were positioned on either side of the tiles (two lights per tile). Filming commenced and continued without disturbance for 2h at the start of each deployment (i.e., 07:00 and 19:00 hours; total of 4h per tile per day). A total of 36 h of video observations was gathered from 3 sites (3 tiles x 4h = 12h footage site^{-1}). No video recordings were possible at the Emily site in the Gulf due to logistical constraints.

All video footage was viewed, and all fish and macro-invertebrates feeding on the tiles were recorded and identified to either species (fish) or family (invertebrates). The body size of each fish (total length, TL) was estimated using the experimental tile as a size reference. The total number of bites taken per fish species on each tile and size was recorded over the entire time period tiles were videoed. To account for differences in the impact between fish species of individual bites due to variation in body size, mass standardized bite impact (total bites x body mass in kilograms) was calculated for each fish species identified feeding on the tiles (following Bellwood et al. 2006) . Body mass was estimated using published length-weight relationships for each species (Kulbicki et al., 2005; Froese and Pauly, 2017). As individual bites by

macro-invertebrates could not be observed, invertebrate grazing activity was estimated by recording the number of macro-invertebrates on each tile and the total period in which they were present on the tile (following Korzen et al. 2011).

Data analysis

Rates of herbivory

Variation in the reduction in algal cover among regions, sites and diel period was analysed using a generalized linear model (GLM) with a normal response variable and identity link function. In the model used, region and diel period were fixed factors, with site as a random factor nested within region. The analyses were performed on the change in the algal cover over the 12h period. The choice of model was based on the corrected Akaike information criterion (AICc) ranking. Assumptions of homoscedasticity, independence and non-autocorrelation were confirmed using residual plots.

Effects of treatment caging were tested with general linear models, with contrast using the data of percentage cover lost of algae on each caged tile versus exposed tiles. Assumptions of homoscedasticity were checked by Levene's test, and normality assumption was met for this model.

Agents of herbivory

Differences in the assemblages of fishes feeding on the tiles among regions, sites and period were analyzed using a three-way permutational analysis of variance (PERMANOVA), based on Bray-Curtis distance matrix (9999 permutations) (Anderson, 2001). All multivariate statistical analyses were performed using SPSS (IBM Corporation, 2016) and Primer-E v6 software (Clarke and Gorley, 2006) with the PERMANOVA+ add-on package (Anderson et al., 2008).

Results

Herbivory rates

Reduction in algae cover differed between periods (diurnal vs. nocturnal), between regions, and among sites (nested in region) (Table 5.1). Alga cover reduction on tiles was highest during the day in the Gulf (day: 36.2% ± 5.9% SE, night: 15.2% ± 4.2%

SE; p<0.001), with no significant differences observed in the Sea of Oman (p>0.05; Figure 5.2). The reduction in algal cover observed in both regions was due primarily to reductions in the cover of turf algae. Within the Gulf, the cover of turf algae reduced by 22.8 ± 6.5% during the diurnal deployments, and 7.8 ± 5.6% at night. Within Sea of Oman sites reduction of turf cover varied from 26.2 ± 4.8% at night to 5.5 ± 5.4% during the day (Figure 5.3). There was a significant caging treatment effect (GLM, p=0.036), whereby exposed tiles, open to all grazers, had higher algal percentage cover loss than caged tiles that excluded all fish and macro-invertebrates (Figure S 5.1, Supplements).
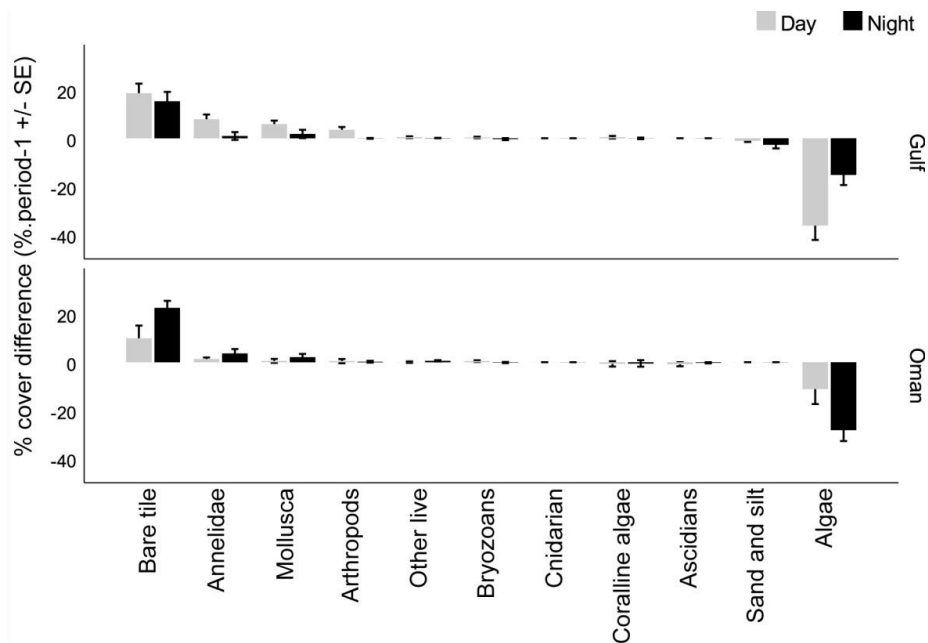
Figure 5.2
Variations in the % cover of the different main categories identified on uncaged tiles across regions, during day and night grazing (12h periods each). The % cover change was calculated as the difference of % cover on tiles before and after grazing. The means are based on 9 uncaged tiles left for 12h (day or night) within each site at each region (total of 3 days).

Table 5.1
Results of the generalized linear model assessing differences between
region, sites and period of the day in percentage cover loss of algae.
Significant values in bold.

Source	Type III χ^2	df	p-value
(Intercept)	122.485	1	**0.000**
Region	0.203	1	0.652
Period	1.787	1	0.181
Region*Period	11.391	1	**0.001**
Site (Region)	3.004	2	0.223
Site*Period (Region)	8.775	2	**0.012**
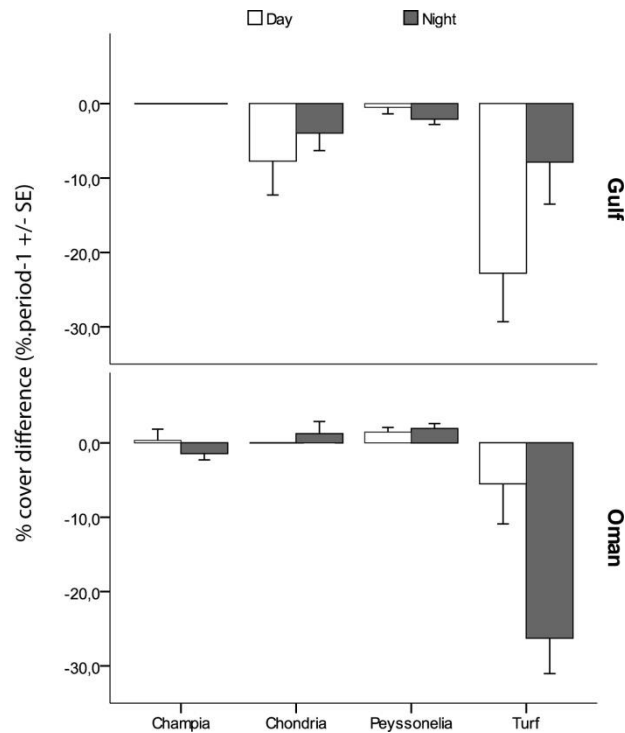
Figure 5.3
Variations in the % cover of the five most abundant algae genera on exposed
tiles across regions, during day and night grazing (12h each). The % cover
change was calculated as the difference of % cover on tiles before and after
grazing. The means are based on 9 exposed tiles left for 12 h (day or night)
within each site at each region (total of 3 days).

Video analysis

A total of 1333 bites from 8 fish species were recorded feeding on the tiles across both regions, with 934 bites in the Gulf (from 5 species) and 399 bites in Sea of Oman (from 4 species). Only one species, *Ecsenius pulcher*, was seen grazing on the tiles across both regions. Video footage revealed that the Arabian anglefish, *Pomacanthus maculosus*, accounted for 92.0% of total mass-standardized bites in the Gulf, while *Scolopsis ghanam* accounted for 94.3% of the total mass-standardized bites in the Sea of Oman sites (Table 5.2, Figure 5.4). Diurnal grazing in the Gulf was dominated by *P. maculosus*, accounting for 89.3% of total diurnal mass-standardized bites, with *P. aquilus* accounting for 10.1% of total diurnal mass-standardized bites (5.9 kg. bites), the remaining species collectively accounted for less than 1% of the diurnal mass-standardised bites. Fish grazing activity was only observed during the day for Sea of Oman, with total removal rates dominated by *S. ghanam* with 2.7 kg.bites (94.3% of the total mass-standardized bites).

Table 5.2
Total standardized bites (Kg x bites) of the main fish species, and respective functional group (FG), observed grazing on the algae tiles in both regions, Gulf and Sea of Oman. Values are based on the 12h of footage per site.

			Total standardized bites			
			Gulf		Oman	
Family	**Species**	**FG**	**Morning**	**Evening**	**Morning**	**Evening**
Blenniidae	*Ecsenius pulcher*	Omnivore	0.03	0	0.1	0
Mullidae	*Parupeneus margaritatus*	Carnivore	0	0	0.03	0
Nemipteridae	*Scolopsis ghanam*	Carnivore	0	0	2.7	0
Pomacanthidae	*Pomacanthus maculosus*	Omnivore	52.1	19.4	0	0
Pomacentridae	*Pomacentrus aquilus*	Herbivore	5.9	0	0	0
	Pomacentrus trichrourus	Omnivore	0.3	0	0	0
	Pomacentrus leptus	Omnivore	0	0	0.02	0
Pseudochromidae	*Pseudochromis nigrovittatus*	Carnivore	0.1	0	0	0
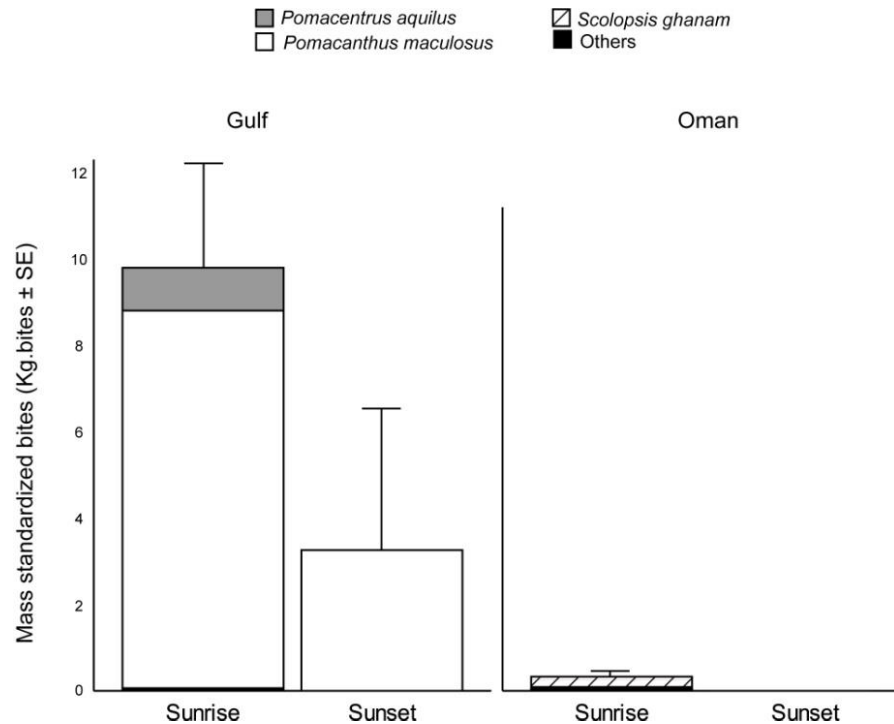
Figure 5.4
Mean number of mass standardized bites taken by fish feeding on tiles per
hour, within each region, at sunrise and sunset. The remaining five species
are grouped as "others" as individually they accounted for < 4% of all bites.

From the total of 12h of night video footage from Sea of Oman a total of 6h08m had
macro-invertebrate activity, where gastropods were observed on tiles for a total of
3h41m (31% of the total video time), while one species of echinoid (*Diadema
setosum*) was found on tiles for a total of 2h27m (20% of the total video time). Night
grazing in the Gulf was solely done by one fish species (*P. maculosus*) with total
removal rates of 19.4 kg. bites (Table 5.2, Figure 5.4). Significant differences
between the fish assemblages that grazed in the different sites within each region
were confirmed with PERMANOVA, as well as the interaction with each site and
period of the day (Table 5.3).

Table 5.3
Results of the three factor permutation analyses of variance (PERMANOVA) assessing differences between regions, sites and period of the day in mass standardised bite impact from the fish community feeding on the tiles (data fourth-root transformed). Significant values in bold.

Source	df	MS	Pseudo-F	P (MC)
Region	1	15383	7.369	0.056
Site (Region)	1	2087.4	3.232	**0.028**
Period	1	23343	11.183	**0.042**
Region*Period	1	9209	4.412	0.102
Site(Region)*Period	1	2087.4	3.232	**0.028**
Residual	30	645.77		

Discussion

Herbivory is widely accepted as a critical process on coral reefs, with parrotfishes, surgeonfishes and rabbitfishes being the dominant herbivores on low latitude Indo-Pacific reefs (Green and Bellwood, 2009; Adam et al., 2011; Steneck et al., 2017). Surprisingly, herbivory in the present study, undertaken in a marginal high-latitude reef environment, revealed that main diurnal grazing activity wasn't accomplished by any of the known teleost herbivores within the region, but by *P. maculosus*. This angelfish was the dominant herbivore, and accounted for the majority (92%) of mass standardized bites. Interestingly, although *P. maculosus* is an abundant reef fish in the Gulf (Shraim et al., 2017), it is generally regarded as an omnivore, feeding predominately on invertebrates and sponges (Randall, 1967; Ferreira et al., 2004; Shraim et al., 2017).

Control of algae cover in reefs have been traditionally linked to the dominant species of herbivores present in each habitat, but recent studies have shown that these assumptions do not translate into reality, with fish known as belonging to other functional groups having important roles in algae removal (Bellwood et al., 2006; Fox and Bellwood, 2008). Although both regions have a good representation of herbivores, particularly damselfish in the Gulf (e.g. *P. aquilus*) and parrotfish in the Sea of Oman (Randall, 1995; Feary et al., 2010; Burt et al., 2011b), neither groups fed extensively on tiles in the present study. This is despite fish communities in the Gulf being mainly comprised of herbivores, with the territorial farmer damselfish comprising up to 99% of the total abundance of communities; the remaining larger herbivores more commonly found on reefs in other areas (e.g., parrotfish, rabbitfish,

surgeonfish) are rare or absent within this region (Feary et al., 2010; Burt et al., 2011b; Hoey et al., 2016). In addition, territorial farmers feed differently than large 'typical' reef herbivores within reefs, predominantly having a low impact on algae loss, while also promoting algal growth in defended territories (Hata and Kato, 2004; Ceccarelli et al., 2005); such a low level of algae loss was also found within the present study (*P. aquilus*: 10.2% of the total diurnal mass standardized bites). Lastly, large-bodied herbivorous fishes were not observed feeding on the experimental tiles, probably because of the reduced numbers of such large herbivores in the Gulf, namely parrotfishes (Feary et al., 2010; Burt et al., 2011b; Hoey et al., 2016). This reduced number of large-bodied herbivorous fishes (e.g., parrotfishes, surgeonfishes and rabbitfishes) is believed to be linked to the extreme environment in the region as well as to the low quality and reduced availability of food (Hoey et al., 2016).

Overall, higher algal cover reduction in the Gulf was observed during the day, with an average decrease of $36\%.12h^{-1}$, while in the Sea of Oman higher algal cover reduction was observed at night ($28\%.12h^{-1}$). While fish diurnal grazing activity was more influential than night grazing in the Gulf, the opposite was observed in the Sea of Oman with nocturnal macro-invertebrate grazing activity playing an essential role in this region. Interestingly, although *P. maculosus* is also present in the Sea of Oman (Randall, 1995), no individuals of this species were observed grazing during the day on the experimental tiles in this region, and in parallel, no macro-invertebrate grazing activity were observed within the Gulf, although echinoids are present in the region (George, 2012; Bauman et al., 2016) and were observed nearby the experimental tiles in this study. These differences in herbivore composition between regions reflect the differences observed in low vs. high-latitude Indo-Pacific reefs, with the later having a reduced abundance of herbivorous fishes (e.g., Southeast Australia: Hoey et al. 2011; Japan: Nakamura et al. 2013) while urchin grazing activity is observed in temperate regions (Ling, 2008). In the Sea of Oman, invertebrates' grazing was divided between one echinoid species (*D. setosum*) and a range of unidentified gastropod species. Although gastropods stayed 20% longer periods grazing on tiles than *D. setosum*, this does not mean that the actual grazing activity was higher, since macro-herbivore invertebrates, such as *D. setosum*, have large foraging ranges and low grazing frequencies, while smaller macro-herbivore invertebrates (small gastropods) have small foraging ranges but high grazing

frequency within those ranges (Carpenter, 1986). Invertebrates grazers are essential in promoting reef resilience and are increasingly important in regions where fish population decline as a result of different impacts, such as overexploitation or habitat degradation (Altman-Kurosaki et al., 2018), but at the same time, intensive grazing by sea-urchins can lower the settlement of new coral spat and have destructive effects due to high rates of bioerosion (Hutchings, 1986; Korzen et al., 2011). Future studies on the echinoids populations of the Sea of Oman are needed to understand the population grazing rates benefits and impacts further.

Our results, showing the importance of a single species (*P. maculosos*) in structuring herbivory within the Gulf, are comparable to previous studies (Australia: batfish, *Platax pinnatus* Bellwood et al., 2006; the Great Barrier Reef: rabbitfish, *Siganus canaliculatus* Fox and Bellwood, 2008, surgeonfish, *Naso unicornis* Hoey and Bellwood, 2009), and in degraded reef systems (Singapore: rabbitfish, *Siganus virgatus* Bauman et al., 2017). To our knowledge *P. maculosus* has not been previously recognized as a key herbivore on reefs and, although we registered high herbivory rates from *P. maculosus* in the Gulf, a study by Shraim et al. (2017) on the diet of common species (including *P. maculosus*), based on gut content analyses, in the Southwest Arabian Gulf, observed that algae was almost absent from these fish diets in the warmer months, the same period that our study was undertaken (July). Herbivory rates tend to increase in the summer months (Lefèvre and Bellwood, 2011), and we propose that *P. maculosus* might be removing algae from the substrate but not ingesting, though further work on understanding the trophic behavior of *P. maculosus* will be necessary to understand their role as important herbivores within the Gulf system. Independently of feeding habits, our results indicate that *P. maculosus* plays an essential functional role in the region, during the summer period, helping to remove algae from the substrate.

Reefs suffering long-term anthropogenic disturbances, under varying levels of reef degradation, can maintain herbivory by a few key species (Plass-Johnson et al., 2015). While the results of the present study suggest that *P. maculosus* may play a crucial functional role in restoring the balance between corals and algae in the Gulf, caution should be used in assuming low functional redundancy in the region. Our study was conducted during the season with higher SSTs and salinity values, and video recordings were comprised of one day only. It is recommended to explore our

results further with multiple-choice algal assays studies (as seen in Mantyka and Bellwood 2007a), as well as increase the hours of video footage to cover more than one day, while also undertake further seasonal studies of herbivory rates to understand how the differences in seasonal extremes might influence herbivory activity in the Gulf. As these regions are marginal reef systems with limited diversity and abundance of herbivorous fishes, it is crucial to identify functionally important herbivores and understand the significance of each fish species' role in macroalgal removal, as these cannot be assumed based on studies from other regions that exhibit species diverse systems in higher latitudes. As reefs around the world are expected to face extreme environments and concomitant recurrent bleaching events from climate change (Hughes et al., 2017), herbivory will be more important than ever, and further investigation is needed to identify functionally essential herbivores that regulate or remove macroalgae within the natural extreme environment of the Gulf.

Acknowledgments

References

Adam, T.C., Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Edmunds, P.J., Carpenter, R.C., et al. (2011). Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS ONE* 6(8), e23717.

Altman-Kurosaki, N.T., Priest, M.A., Golbuu, Y., Mumby, P.J., and Marshell, A. (2018). Microherbivores are significant grazers on Palau's forereefs. *Marine Biology* 165(4), 74.

Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26(1), 32–46.

Anderson, M.J., Gorley, R.N., and Clarke, R.K. (2008). *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods.* Plymouth: PRIMER-E Limited.

Bauman, A.G., Burt, J.A., Feary, D.A., Marquis, E., and Usseglio, P. (2010). Tropical harmful algal blooms: an emerging threat to coral reef communities? *Marine Pollution Bulletin* 60(11), 2117-2122.

Bauman, A.G., Dunshea, G., Feary, D.A., and Hoey, A.S. (2016). Prickly business: abundance of sea urchins on breakwaters and coral reefs in Dubai. *Marine Pollution Bulletin* 105(2), 459-465.

Bauman, A.G., Hoey, A.S., Dunshea, G., Feary, D.A., Low, J., and Todd, P.A. (2017). Macroalgal browsing on a heavily degraded, urbanized equatorial reef system. *Scientific Reports* 7(1), 8352.

Bellwood, D.R., Hoey, A.S., and Hughes, T.P. (2012). Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proceedings of the Royal Society B: Biological Sciences* 279(1733), 1621-1629.

Bellwood, D.R., Hughes, T.P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. *Nature* 429(6994), 827-833.

Bellwood, D.R., Hughes, T.P., and Hoey, A.S. (2006). Sleeping functional group drives coral-reef recovery. *Current Biology* 16(24), 2434-2439.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J., and Saunders, B.J. (2015). Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters* 18(7), 714-723.

Bonaldo, R.M., Hoey, A.S., and Bellwood, D.R. (2014). The ecosystem roles of parrotfishes on tropical reefs. *Oceanography and Marine Biology: An Annual Review* 52, 81-132.

Burkepile, D.E., and Hay, M.E. (2008). Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences* 105(42), 16201-16206.

Burt, J., Al-Harthi, S., and Al-Cibahy, A. (2011a). Long-term impacts of coral bleaching events on the world's warmest reefs. *Marine Environmental Research* 72(4), 225-229.

Burt, J.A., Feary, D.A., Bauman, A.G., Usseglio, P., Cavalcante, G.H., and Sale, P.F. (2011b). Biogeographic patterns of reef fish community structure in the northeastern Arabian Peninsula. *ICES Journal of Marine Science* 68(9), 1875-1883.

Carpenter, R.C. (1986). Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* 56(4), 345-364.

Ceccarelli, D.M., Jones, G.P., and McCook, L.J. (2005). Effects of territorial damselfish on an algal-dominated coastal coral reef. *Coral Reefs* 24(4), 606-620.

Clarke, K.R., and Gorley, R.N. (2006). *PRIMER V6: User Manual PRIMER-E.* Plymouth, U.K.

Cvitanovic, C., and Bellwood, D.R. (2008). Local variation in herbivore feeding activity on an inshore reef of the Great Barrier Reef. *Coral Reefs* 28(1), 127-133.

Feary, D.A., Burt, J.A., Bauman, A.G., Usseglio, P., Sale, P.F., and Cavalcante, G.H. (2010). Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future? *Journal of Fish Biology* 77(8), 1931-1947.

Ferreira, C.E.L., Floeter, S.R., Gasparini, J.L., Ferreira, B.P., and Joyeux, J.C. (2004). Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *Journal of Biogeography* 31(7), 1093-1106.

Foster, K., Foster, G., Al-Cibahy, A.S., Al-Harthi, S., Purkis, S.J., and Riegl, B.M. (2012). "Environmental setting and temporal trends in southeastern Gulf coral communities," in *Coral Reefs of the Gulf,* eds. B. Riegl & S. Purkis. (Dordrecht: Springer), 51-70.

Fox, R.J., and Bellwood, D.R. (2008). Remote video bioassays reveal the potential feeding impact of the rabbitfish Siganus canaliculatus (f: Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs* 27(3), 605-615.

Froese, R., and Pauly, D. 2017. FishBase. [Accessed version (10/2017)].

George, J.D. (2012). "Reef-associated macroinvertebrates of the SE Gulf," in *Coral Reefs of the Gulf,* eds. B. Riegl & S. Purkis. (Dordrecht: Springer), 253-308.

Gilby, B.L., Tibbetts, I.R., and Stevens, T. (2017). Low functional redundancy and high variability in Sargassum browsing fish populations in a subtropical reef system. *Marine and Freshwater Research* 68(2), 331-341.

Graham, N.A.J., Bellwood, D.R., Cinner, J.E., Hughes, T.P., Norström, A.V., and Nyström, M. (2013). Managing resilience to reverse phase shifts in coral reefs. *Frontiers in Ecology and the Environment* 11(10), 541-548.

Graham, N.A.J., Nash, K.L., and Kool, J.T. (2011). Coral reef recovery dynamics in a changing world. *Coral Reefs* 30(2), 283-294.

Green, A.L., and Bellwood, D.R. (2009). *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: a practical guide for coral reef managers in the Asia Pacific Region.* Gland, Switzerland: IUCN.

Hata, H., and Kato, M. (2004). Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. *Journal of Experimental Marine Biology and Ecology* 313(2), 285-296.

Hoey, A.S., and Bellwood, D.R. (2009). Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* 12(8), 1316-1328.

Hoey, A.S., Feary, D.A., Burt, J.A., Vaughan, G., Pratchett, M.S., and Berumen, M.L. (2016). Regional variation in the structure and function of parrotfishes on Arabian reefs. *Marine Pollution Bulletin* 105(2), 524-531.

Hoey, A.S., Pratchett, M.S., and Cvitanovic, C. (2011). High macroalgal cover and low coral recruitment undermines the potential resilience of the world's southernmost coral reef assemblages. *PLoS ONE* 6(10), e25824.

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., et al. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359(6371), 80-83.

Hughes, T.P., Graham, N.A., Jackson, J.B., Mumby, P.J., and Steneck, R.S. (2010). Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution* 25(11)**,** 633-642.

Hughes, T.P., Kerry, J.T., Alvarez-Noriega, M., Alvarez-Romero, J.G., Anderson, K.D., Baird, A.H., et al. (2017). Global warming and recurrent mass bleaching of corals. *Nature* 543(7645)**,** 373-377.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., et al. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17(4)**,** 360-365.

Hutchings, P.A. (1986). Biological destruction of coral reefs. *Coral Reefs* 4(4)**,** 239-252.

IBM Corporation (2016). "IBM SPSS Statistics for Windows". Version 24.0 ed. (Armonk, NY: IBM Corporation).

John, D.M. (2012). "Marine algae (Seaweeds) associated with coral reefs in the Gulf," in *Coral Reefs of the Gulf,* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 309-335.

Kleypas, J.A., McManus, J.W., and Meñez, L.A. (1999). Environmental limits to coral reef development: where do we draw the line? *American Zoologist* 39(1)**,** 146-159.

Kohler, K.E., and Gill, S.M. (2006). Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32(9)**,** 1259-1269.

Korzen, L., Israel, A., and Abelson, A. (2011). Grazing effects of fish versus sea urchins on turf algae and coral recruits: possible implications for coral reef resilience and restoration. *Journal of Marine Biology* 2011**,** 1-8.

Kulbicki, M., Guillemot, N., and Amand, M. (2005). A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybium* 29(3)**,** 235-252.

Lefèvre, C.D., and Bellwood, D.R. (2011). Temporal variation in coral reef ecosystem processes: herbivory of macroalgae by fishes. *Marine Ecology Progress Series* 422**,** 239-251.

Ling, S.D. (2008). Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state. *Oecologia* 156(4)**,** 883-894.

Mantyka, C.S., and Bellwood, D.R. (2007a). Direct evaluation of macroalgal removal by herbivorous coral reef fishes. *Coral Reefs* 26(2)**,** 435-442.

Mantyka, C.S., and Bellwood, D.R. (2007b). Macroalgal grazing selectivity among herbivorous coral reef fishes. *Marine Ecology Progress Series* 352**,** 177-185.

Mumby, P.J., Dahlgren, C.P., Harborne, A.R., Kappel, C.V., Micheli, F., Brumbaugh, D.R., et al. (2006). Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311(5757)**,** 98-101.

Nakamura, Y., Feary, D.A., Kanda, M., and Yamaoka, K. (2013). Tropical fishes dominate temperate reef fish communities within western Japan. *PLoS ONE* 8(12)**,** e81107.

Nyström, M. (2006). Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *AMBIO: A Journal of the Human Environment* 35(1)**,** 30-35.

Plass-Johnson, J.G., Ferse, S.C.A., Jompa, J., Wild, C., and Teichberg, M. (2015). Fish herbivory as key ecological function in a heavily degraded coral reef system. *Limnology and Oceanography* 60(4)**,** 1382-1391.

Randall, J.E. (1967). Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* 5**,** 665-847.

Randall, J.E. (1995). *Coastal Fishes of Oman.* Honolulu: University of Hawaii Press.

Reynolds, R.M. (1993). Physical oceanography of the Gulf, Strait of Hormuz, and the Gulf of Oman - Results from the Mt Mitchell expedition. *Marine Pollution Bulletin* 27**,** 35-59.

Riegl, B., Johnston, M., Purkis, S., Howells, E., Burt, J., Steiner, S.C.C., et al. (2018). Population collapse dynamics in Acropora downingi, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. *Global Change Biology* 24(6)**,** 2447-2462.

Riegl, B.M., Bruckner, A.W., Samimi-Namin, K., and Purkis, S.J. (2012). "Diseases, harmful algae blooms (HABs) and their effects on Gulf coral populations and communities," in *Coral Reefs of the Gulf,* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 107-125.

Riegl, B.M., and Purkis, S.J. (2012). "Dynamics of Gulf coral communities: observations and models from the world's hottest coral sea," in *Coral Reefs of the Gulf,* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 71-93.

Schils, T., and Wilson, S.C. (2006). Temperature threshold as a biogeographic barrier in northern Indian Ocean macroalgae. *Journal of Phycology* 42(4)**,** 749-756.

Sheppard, C., Price, A., and Roberts, C. (1992). *Marine ecology of the Arabian Region: patterns and processes in extreme tropical environments.* Toronto: Academic Press.

Sheppard, C.R. (1993). Physical environment of the Gulf relevant to marine pollution: an overview. *Marine Pollution Bulletin* 27**,** 3-8.

Shraim, R., Dieng, M.M., Vinu, M., Vaughan, G., McParland, D., Idaghdour, Y., et al. (2017). Environmental extremes are associated with dietary patterns in Arabian Gulf reef fishes. *Frontiers in Marine Science* 4**,** 285.

Steneck, R.S., Bellwood, D.R., and Hay, M.E. (2017). Herbivory in the marine realm. *Current Biology* 27(11)**,** R484-R489.

Wilson, S.K., Bellwood, D.R., Choat, J.H., and Furnas, M.J. (2003). Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology* 41**,** 279-310.

Supplements
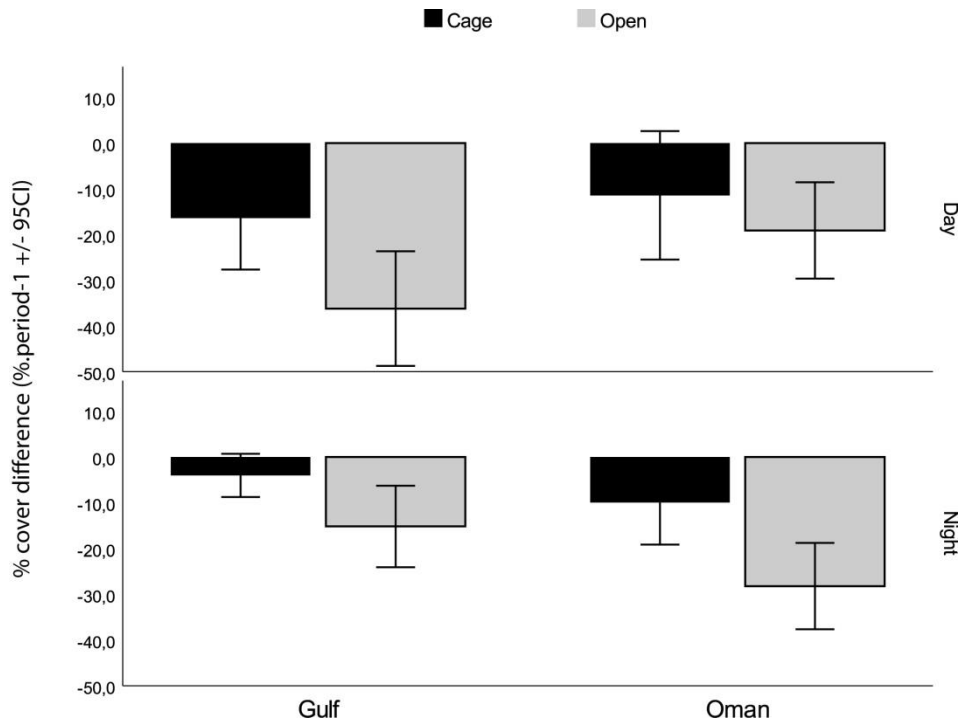
Figure S 5.1

Regional differences in the percentage cover of algae after day and night grazing (12h periods each) on caged and open tiles. The % cover change was calculated as the difference of %cover on the tiles before and after grazing. The means are based on 6 caged tiles and 9 exposed tiles (at each day and night period) within each site at each region (total of 3 days). Whiskers bars are 95% confidence intervals.

Chapter 6 Discussion

Current forecasts indicate great losses in worldwide coral cover from emerging threats associated with climate change, with dire predictions of coral reefs being severely degraded by 2050 (Hoegh-Guldberg, 1999; Silverman et al., 2009; Burke et al., 2011). Recurrent pan-tropical bleaching events have been experienced when environmental parameters are above the reef threshold (Hughes et al., 2017; Hughes et al., 2018a), with studies showing extensive loss of coral cover and richness, accompanied by increasing algae cover and loss of fish species within key functional groups (Hoegh-Guldberg, 1999; Graham et al., 2006; De'ath et al., 2012). Despite the extreme environment that the Gulf exhibit, with high fluctuations in sea surface temperature (SSTs) and salinities above coral reef thresholds (Sheppard et al., 1992; Coles and Riegl, 2013), this study shows that the region supports highly resistant coral (Chapter 2) and small-bodied fish communities (Chapter 4), both limited to a few resilient species. Nevertheless, coral communities exhibited a slow recovery rate (Chapter 3) and herbivory was primarily dependent on one single fish species (Chapter 5), indicating that while the reef community persists in such extreme environment, it might be in their maximum upper threshold and in a different assemblage from what is observed in tropical reefs.

Reef communities under natural extreme environments

Coral communities

In the last half-century, several severe bleaching events have reduced coral cover around the globe, with the most severe cases in 1998, 2010 and recently in 2015/16 (Wilkinson, 2000; Riegl et al., 2011; Riegl and Purkis, 2012a; Hughes et al., 2018a). If post-bleaching phases result in an elevated percentage of coral mortality, the reef suffers a transformation in the assemblage structure and functional diversity of corals. In some cases, reefs suffer almost complete coral loss with no sign of recovery (Hoegh-Guldberg, 1999), while in other cases, highly sensitive branching coral (e.g. Acropora and Pocillopora) die and coral community persist under the dominance of massive resistant species (e.g. Porites and Favites) (e.g., Great Barrier Reef (GBR): Hughes et al. (2018b); French Polynesia: Pratchett et al. (2011); Indian Ocean: Ateweberhan et al. (2011)). This third pattern was observed in the Gulf,

where there was a reduction in the abundance and diversity of species traits, and coral community shifted into a dominance of species with stress-tolerant life-histories and low structural complexity (Porites and faviids) (Burt et al., 2011a; Riegl and Purkis, 2012b; Bauman et al., 2013). The prevalence of these families in the extreme environment of the Gulf is expected, with high reef cover of Porites and faviids commonly found within disturbed reef systems as these two families are considered resistant to a range of stressors (i.e., bleaching, COTs, and storms) (Loya et al., 2001; Baird and Marshall, 2002; Madin and Connolly, 2006; McClanahan et al., 2007; Guest et al., 2012; Baird et al., 2013). But interestingly, this study shows that not only do these corals persist under an extreme environment, they are able to withstand frequent bleaching events (2010 and 2011, see Riegl and Purkis, 2012a). Over the three years of this study (2008-2011) both coral families increased in percentage cover within the Gulf by ~20% (Bento et al., 2016, see Chapter 2), showing that these coral families are extremely resilience and persist even after extreme pressure.

While reefs in the Gulf exhibited a depauperate coral assemblage of a few stress-tolerant species, reefs in the Sea of Oman and Musandam, are characterized by less extreme and less variable environmental conditions with fewer major disturbances in recent years, supporting a higher diversity of coral families, including the stress-sensitive, fast-growing, three-dimensional Acroporidae and Pocilloporidae (Bento et al., 2016, see Chapter 2). These regional differences in community composition, between the Gulf and both Musandam and Sea of Oman, reflect the different environmental regimes and disturbance history between these regions. Identifying the coral species that are sensitive to heat waves and that easily die, and the ones that persist in bleaching events is crucial to understand how climate change impacts biodiversity, species composition and ecosystem function (Hughes et al., 2018b). As suggested in this study results, recent studies have shown that reefs by 2050 will be unrecognizable (Hoegh-Guldberg, 1999; Silverman et al., 2009; Burke et al., 2011), and it appears that they might exist, even though under a different configuration, with the prevalence of thermally-resistant species of corals, Porites and faviids.

Settlement of new benthos after disturbances

Post-disturbance trajectory of reefs is not only dependent on the coral species that are resilient and prevail. Benthos that settle on the open space created after

disturbances can influence the settlement and survival of coral spat, and therefore the possible recovery of reefs post-disturbance. The divergence in coral community structure across the three regions of this study (Bento et al., 2016, see Chapter 2) was mirrored in the regional differences in the settlement of non-coral organisms (Bento et al., 2017, see Chapter 3). While coralline algae, that is known to facilitate settlement of coral larvae (Ritson-Williams et al., 2014; Tebben et al., 2015), characterized non-coral settlement in the Gulf, Sea of Oman open space was substantially covered with barnacles and by colonial ascidians in Musandam, these latter benthic taxa (in comparison to coralline algae), are known to inhibit coral larval settlement (Chadwick and Morrow, 2011). The high level of settlement of barnacles and ascidians within the Sea of Oman and the Musandam respectively, are a reflection of the high taxa abundance of each group within the respective reef community. In addition, increases in coralline algae cover in the Gulf has been previously reported after significant bleaching events (George and John, 2000; George and John, 2002), suggesting that high coralline algae cover is characteristic of the Gulfs highly disturbed environment.

In the current study, coral communities showed a slow rate of recovery, as the number of coral spat settling in open space was much lower than what has been observed in other tropical reefs: there was an average of 38 coral settlers m^{-2} $year^{-1}$ in this study (Bento et al., 2017, see Chapter 3) compared with 100-900 coral settlers m^{-2} $year^{-1}$ in tropical reefs (Kenya: Mangubhai et al., 2007; Indonesia: Sawall et al., 2013; Seychelles: Chong-Seng et al., 2014). Low densities of coral spat were observed in all three regions, Gulf, Musandam and Sea of Oman, suggesting it is a characteristic of the Arabian Peninsula. The higher coral cover observed in Musandam (Bento et al., 2016, see Chapter 2) is then a reflection of this undisturbed environment and presumably not substantially due to high coral recruitment. In parallel, low densities of coral spats, with similar values to what was observed in the region, are typically observed in highly disturbed and degraded reef environments (van Woesik et al., 2014; Bauman et al., 2015). Although high stress-resistant coral Porites and faviids dominate Gulf reefs (Bento et al., 2016, see Chapter 2), these families have slow growth rates, which together with the low densities of coral spat indicates a slow-growing reef rate. Such results increase the concern for the future of the Gulf reefs, as they might not be able to accompany the predicted rising number of

future bleaching events as the intensity of global warming continues to escalate (Hughes et al., 2018a).

Small-bodied fish community

The loss of functionally-diverse corals is a precursor of further shifts in the condition and dynamics of other reef communities. The persisting extreme environment and low reef structure complexity in the Gulf (Bento et al., 2016, Chapter 2) has also influenced the abundance and biomass of small-bodied fish which are two and six times lower than the neighboring regions, the Musandam and Sea of Oman (Chapter 4). Such low abundance and biomass of small-bodied fishes within the Gulf may also be explained by the different environmental regimes experienced across regions, as severe alterations in the environment (high values or variations in SSTs and salinities) also have substantial negative effects on fish metabolic rate (Plaut, 2000; Boeuf and Payan, 2001; Pörtner and Knust, 2007). Different reactions can results from such physiological changes, such as impaired growth and decreased swim speed (Plaut, 2000; Boeuf and Payan, 2001; Hurst, 2007; Johansen and Jones, 2011), which in turn can compromise the fish ability to forage for food and to avoid predators (Coker et al., 2009). While the extreme environment in the Gulf can explain the reduction in biomass and abundances of small-bodied fish in the region, the reduced complexity of the Gulf and Sea of Oman's reef matrix, both exhibiting higher coral cover of *Porites* and faviids (Bento et al., 2016, Chapter 2), can also explain the lower abundances of small-bodied fish in both regions when compared with the relatively intact and topographically more complex Musandam reefs (Burt et al., 2016), as these exhibit increased nesting and shelter area for this fish community.

Small site-attached reef fish community in all three regions was primarily comprised of Pomacentrids, although different species were represented in the Gulf (*Pomacentrus aquilus* and *Pomacentrus trichrourus*) compared with the similar community assemblage in both Musandam and Sea of Oman (*Neopomacentrus cyanomos*, *Chromis xanthopterygia* and *Pomacentrus leptus*) (Chapter 4). These observed differences might be a result of different success of species moving from the Indian Ocean to the Gulf, with only a few species tolerating and persisting in this semi-closed extreme environment, as it has been suggested for the Gulf butterflyfish community (Pratchett et al., 2013). Small-bodied fish assemblages in Musandam and

Sea of Oman were mainly schooling species of diurnal and omnivorous planktivores, which presented a highly variable structure across seasons. The highly productive water in those regions (Kleypas et al., 1999; Schils and Wilson, 2006) and the seasonal variation in local winds (supplemental material Chapter 4) can influence zooplankton availability and as a potential consequence, the differences observed in both regions planktivores communities. On the contrary, the Gulf small-bodied fish community was mainly comprised of sedentary territorial farmers (*P. aquilus*) and non-schooling planktivores (*P. trichrourus*), resulting in a more temporally stable community across seasons. It is clear from this study results that although small site-attached reef fish assemblages might persist in an extreme environment, like the Gulf, it will be under their upper thermal limit threshold, with a few resilient species, lower biomass, slower swimming performance and higher vulnerability to predation.

Recovery and prevention of phase-shifts: the important role of herbivory

The ability of coral reefs to overcome recurrent impacts will depend on the community resilience and the environment in which they exist. While previous studies have shown the importance of herbivores in preventing and reversing phase-shifts (Nyström and Folke, 2001; Bellwood et al., 2004; Hughes et al., 2007; Bennett et al., 2015), it is now clear that this vital role might not be dependent on a group of species but actually single species, resulting in low functional redundancy within the community (Bellwood et al., 2006a; Bellwood et al., 2006b). As reef communities decline around the globe, it is imperative to prevent the elimination of such key species, particularly in a system that already exhibits low fish species richness, as the Gulf (Feary et al., 2010; Burt et al., 2011b). When a system presents a low degree of functional redundancy, with species that are responsible for algae removal not possibly replaced by other species, it is crucial to study and protect the only species that can improve the reef resilience (Nyström, 2006). Although herbivores were the primary functional group of small-bodied fish community (Chapter 4), as well as in the general Gulf fish community (Feary et al., 2010; Burt et al., 2011b), these are represented mainly by the abundant territorial farmer in the Gulf (*Pomacentrus aquilus*), which contribute only ~10% to the diurnal removal of algae from the reef, while surprisingly the omnivorous angelfish, *Pomacanthus maculosus*, is responsible for ~90% of the herbivory activity in the Gulf (Chapter 5). The low impact of the damselfish in algal removal was already expected as these territorial

farmers have a different effect on the reef algae as they promote algal grow on the area they defend (Hata and Kato, 2004; Ceccarelli et al., 2005). With herbivores in the Gulf being represented mainly by the territorial farmer damselfish (~90% of total reef fish community) (Burt et al., 2011b), urchins being available (Bauman et al., 2016) but not observed grazing on settlement tiles in this study (Chapter 5), the role of the Arabian angelfish, *P. maculosus*, is enormous for the prevailing future of the Gulf reef communities. As intensity of global warming continues to escalate, threatening even more the reef community in the Gulf, studies to further identify functionally essential herbivores that regulate or remove macroalgae within the natural extreme environment of the Gulf are mandatory.

Conclusion

The Gulf has experienced bleaching events of increasing frequency and magnitude in recent years and stronger than in other coral provinces (Hughes et al., 2018a), and marine life in this region is projected to face high rates of local extinction by 2090 (Wabnitz et al., 2018). While our results show that the Gulf reef community might persist under a different configuration, it is unclear for how long can this system prevail in such condition as recurrent bleaching events are likely to occur annually in the coming decades (Hughes et al., 2018a). Is this homogenization of coral assemblages, with simpler morphological characteristics and less diverse reef communities, a short stage before complete degradation or a slight hope in the future of the region's reefs? Worldwide species have shown a poleward or deeper water migration as a reaction to increases in SSTs (Yamano et al., 2011). The GBR, for example, over the past 30 thousand years has been dealing with sea-level changes by exhibiting lateral migration and has been able to withstand SSTs fluctuations. Nevertheless, it still faced highly sensitive periods of reduced growth when events outpaced the reef growth (Webster et al., 2018). Similar migration, from the eastern part of the Gulf to the coast of Iraq and Iran, as well as species extinctions, are expected by 2090 in the Gulf with increases in SSTs (Wabnitz et al., 2018). Due to the Gulf's shallow semi-enclosed environment this may be a dead-end for the reef community, with replenishment of lost species dependent on an adequate supply of larvae from sources coming from the narrow entrance in the Strait of Hormuz, the only link with the Indian Ocean (Coles, 2003; Wabnitz et al., 2018). Despite this study results showing that reef communities able to withstand extreme environments, such

as the Gulf, might reorganize into novel, heat-tolerant reef assemblages, they might not be able to accompany the accelerating rate of disturbances in the foreseeable future.

References

Ateweberhan, M., McClanahan, T.R., Graham, N.A.J., and Sheppard, C.R.C. (2011). Episodic heterogeneous decline and recovery of coral cover in the Indian Ocean. *Coral Reefs* 30(3)**,** 739-752.

Baird, A.H., and Marshall, P.A. (2002). Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Marine Ecology Progress Series* 237**,** 133-141.

Baird, A.H., Pratchett, M.S., Hoey, A.S., Herdiana, Y., and Campbell, S.J. (2013). Acanthaster planci is a major cause of coral mortality in Indonesia. *Coral Reefs* 32(3)**,** 803-812.

Bauman, A.G., Dunshea, G., Feary, D.A., and Hoey, A.S. (2016). Prickly business: abundance of sea urchins on breakwaters and coral reefs in Dubai. *Marine Pollution Bulletin* 105(2)**,** 459-465.

Bauman, A.G., Guest, J.R., Dunshea, G., Low, J., Todd, P.A., and Steinberg, P.D. (2015). Coral settlement on a highly disturbed equatorial reef system. *PLoS ONE* 10(5)**,** e0127874.

Bauman, A.G., Pratchett, M.S., Baird, A.H., Riegl, B., Heron, S.F., and Feary, D.A. (2013). Variation in the size structure of corals is related to environmental extremes in the Persian Gulf. *Marine Environmental Research* 84**,** 43-50.

Bellwood, D.R., Hughes, T.P., Folke, C., and Nyström, M. (2004). Confronting the coral reef crisis. *Nature* 429(6994)**,** 827-833.

Bellwood, D.R., Hughes, T.P., and Hoey, A.S. (2006a). Sleeping functional group drives coral-reef recovery. *Current Biology* 16(24)**,** 2434-2439.

Bellwood, D.R., Wainwright, P.C., Fulton, C.J., and Hoey, A.S. (2006b). Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society B: Biological Sciences* 273(1582)**,** 101-107.

Bennett, S., Wernberg, T., Harvey, E.S., Santana-Garcon, J., and Saunders, B.J. (2015). Tropical herbivores provide resilience to a climate-mediated phase shift on temperate reefs. *Ecology Letters* 18(7)**,** 714-723.

Bento, R., Feary, D.A., Hoey, A.S., and Burt, J.A. (2017). Settlement Patterns of Corals and other Benthos on Reefs with Divergent Environments and Disturbances Histories around the Northeastern Arabian Peninsula. *Frontiers in Marine Science* 4**,** 305.

Bento, R., Hoey, A.S., Bauman, A.G., Feary, D.A., and Burt, J.A. (2016). The implications of recurrent disturbances within the world's hottest coral reef. *Marine Pollution Bulletin* 105(2)**,** 466-472.

Boeuf, G., and Payan, P. (2001). How should salinity influence fish growth? *Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology* 130(4)**,** 411-423.

Burke, L., Reytar, K., Spalding, M., and Perry, A. (2011). "Reefs at risk revisited". (Washington, DC: World Resources Institute).

Burt, J., Al-Harthi, S., and Al-Cibahy, A. (2011a). Long-term impacts of coral bleaching events on the world's warmest reefs. *Marine Environmental Research* 72(4)**,** 225-229.

Burt, J.A., Coles, S., van Lavieren, H., Taylor, O., Looker, E., and Samimi-Namin, K. (2016). Oman's coral reefs: A unique ecosystem challenged by natural and man-related stresses and in need of conservation. *Marine Pollution Bulletin* 105(2)**,** 498-506.

Burt, J.A., Feary, D.A., Bauman, A.G., Usseglio, P., Cavalcante, G.H., and Sale, P.F. (2011b). Biogeographic patterns of reef fish community structure in the northeastern Arabian Peninsula. *ICES Journal of Marine Science* 68(9), 1875-1883.

Ceccarelli, D.M., Jones, G.P., and McCook, L.J. (2005). Effects of territorial damselfish on an algal-dominated coastal coral reef. *Coral Reefs* 24(4), 606-620.

Chadwick, N.E., and Morrow, K.M. (2011). "Competition among sessile organisms on coral reefs," in *Coral reefs: An ecosystem in transition*. (Dordrecht: Springer), 347-371.

Chong-Seng, K.M., Graham, N.A.J., and Pratchett, M.S. (2014). Bottlenecks to coral recovery in the Seychelles. *Coral Reefs* 33(2), 449-461.

Coker, D.J., Pratchett, M.S., and Munday, P.L. (2009). Coral bleaching and habitat degradation increase susceptibility to predation for coral-dwelling fishes. *Behavioral Ecology* 20(6), 1204-1210.

Coles, S.L. (2003). Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: a comparison to the Indo-Pacific Region. *Atoll Research Bulletin* 507, 1-19.

Coles, S.L., and Riegl, B.M. (2013). Thermal tolerances of reef corals in the Gulf: a review of the potential for increasing coral survival and adaptation to climate change through assisted translocation. *Marine Pollution Bulletin* 72(2), 323-332.

De'ath, G., Fabricius, K.E., Sweatman, H., and Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences* 109(44), 17995-17999.

Feary, D.A., Burt, J.A., Bauman, A.G., Usseglio, P., Sale, P.F., and Cavalcante, G.H. (2010). Fish communities on the world's warmest reefs: what can they tell us about the effects of climate change in the future? *Journal of Fish Biology* 77(8), 1931-1947.

George, J., and John, D. (Year). "Is it curtains for coral reefs in the southern Arabian Gulf", in: *Proceedings of the International Society for Reef Studies European Meeting*).

George, J.D., and John, D.M. (Year). "The status of coral reefs and associated macroalgae in Abu Dhabi (UAE) after recent coral bleaching events", in: *Proceedings of the International Symposium on the Extent and Impact of Coral Bleaching in the Arabian Region*).

Graham, N.A., Wilson, S.K., Jennings, S., Polunin, N.V., Bijoux, J.P., and Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences* 103(22), 8425-8429.

Guest, J.R., Baird, A.H., Maynard, J.A., Muttaqin, E., Edwards, A.J., Campbell, S.J., et al. (2012). Contrasting patterns of coral bleaching susceptibility in 2010 suggest an adaptive response to thermal stress. *PLoS ONE* 7(3), e33353.

Hata, H., and Kato, M. (2004). Monoculture and mixed-species algal farms on a coral reef are maintained through intensive and extensive management by damselfishes. *Journal of Experimental Marine Biology and Ecology* 313(2), 285-296.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50(8), 839 - 866.

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., et al. (2018a). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359(6371)**,** 80-83.

Hughes, T.P., Kerry, J.T., Alvarez-Noriega, M., Alvarez-Romero, J.G., Anderson, K.D., Baird, A.H., et al. (2017). Global warming and recurrent mass bleaching of corals. *Nature* 543(7645)**,** 373-377.

Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Dietzel, A., Eakin, C.M., et al. (2018b). Global warming transforms coral reef assemblages. *Nature* 556(7702)**,** 492.

Hughes, T.P., Rodrigues, M.J., Bellwood, D.R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., et al. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17(4)**,** 360-365.

Hurst, T.P. (2007). Causes and consequences of winter mortality in fishes. *Journal of Fish Biology* 71(2)**,** 315-345.

Johansen, J.L., and Jones, G.P. (2011). Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Global Change Biology* 17(9)**,** 2971-2979.

Kleypas, J.A., McManus, J.W., and Meñez, L.A. (1999). Environmental limits to coral reef development: where do we draw the line? *American Zoologist* 39(1)**,** 146-159.

Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., and van Woesik, R. (2001). Coral bleaching: the winners and the losers. *Ecology Letters* 4(2)**,** 122-131.

Madin, J.S., and Connolly, S.R. (2006). Ecological consequences of major hydrodynamic disturbances on coral reefs. *Nature* 444(7118)**,** 477-480.

Mangubhai, S., Harrison, P.L., and Obura, D.O. (2007). Patterns of coral larval settlement on lagoon reefs in the Mombasa Marine National Park and Reserve, Kenya. *Marine Ecology Progress Series* 348**,** 149-159.

McClanahan, T.R., Ateweberhan, M., Graham, N.A.J., Wilson, S.K., Sebastián, C.R., Guillaume, M.M.M., et al. (2007). Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series* 337**,** 1-13.

Nyström, M. (2006). Redundancy and response diversity of functional groups: implications for the resilience of coral reefs. *AMBIO: A Journal of the Human Environment* 35(1)**,** 30-35.

Nyström, M., and Folke, C. (2001). Spatial Resilience of Coral Reefs. *Ecosystems* 4(5)**,** 406-417.

Plaut, I. (2000). Resting metabolic rate, critical swimming speed, and routine activity of the euryhaline cyprinodontid, Aphanius dispar, acclimated to a wide range of salinities. *Physiological and Biochemical Zoology* 73(5)**,** 590-596.

Pörtner, H.O., and Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315(5808)**,** 95-97.

Pratchett, M.S., Hoey, A.S., Feary, D.A., Bauman, A.G., Burt, J.A., and Riegl, B.M. (2013). Functional composition of Chaetodon butterflyfishes at a peripheral and extreme coral reef location, the Persian Gulf. *Marine Pollution Bulletin* 72(2)**,** 333-341.

Pratchett, M.S., Trapon, M., Berumen, M.L., and Chong-Seng, K. (2011). Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. *Coral Reefs* 30(1)**,** 183-193.

Riegl, B.M., and Purkis, S.J. (2012a). "Dynamics of Gulf coral communities: observations and models from the world's hottest coral sea," in *Coral Reefs of the Gulf,* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 71-93.

Riegl, B.M., and Purkis, S.J. (2012b). "Environmental constraints for reef building in the Gulf," in *Coral Reefs of the Gulf,* eds. B.M. Riegl & S.J. Purkis. (Dordrecht: Springer), 5-32.

Riegl, B.M., Purkis, S.J., Al-Cibahy, A.S., Abdel-Moati, M.A., and Hoegh-Guldberg, O. (2011). Present limits to heat-adaptability in corals and population-level responses to climate extremes. *PLoS ONE* 6(9), e24802.

Ritson-Williams, R., Arnold, S.N., Paul, V.J., and Steneck, R.S. (2014). Larval settlement preferences of Acropora palmata and Montastraea faveolata in response to diverse red algae. *Coral Reefs* 33(1), 59-66.

Sawall, Y., Jompa, J., Litaay, M., Maddusila, A., and Richter, C. (2013). Coral recruitment and potential recovery of eutrophied and blast fishing impacted reefs in Spermonde Archipelago, Indonesia. *Marine Pollution Bulletin* 74(1), 374-382.

Schils, T., and Wilson, S.C. (2006). Temperature threshold as a biogeographic barrier in northern Indian Ocean macroalgae. *Journal of Phycology* 42(4), 749-756.

Sheppard, C., Price, A., and Roberts, C. (1992). *Marine ecology of the Arabian Region: patterns and processes in extreme tropical environments.* Toronto: Academic Press.

Silverman, J., Lazar, B., Cao, L., Caldeira, K., and Erez, J. (2009). Coral reefs may start dissolving when atmospheric CO2 doubles. *Geophysical Research Letters* 36(5), L05606.

Tebben, J., Motti, C.A., Siboni, N., Tapiolas, D.M., Negri, A.P., Schupp, P.J., et al. (2015). Chemical mediation of coral larval settlement by crustose coralline algae. *Scientific Reports* 5, 10803.

van Woesik, R., Scott, W.J., and Aronson, R.B. (2014). Lost opportunities: coral recruitment does not translate to reef recovery in the Florida Keys. *Marine Pollution Bulletin* 88(1), 110-117.

Wabnitz, C.C., Lam, V.W.Y., Reygondeau, G., Teh, L.C., Al-Abdulrazzak, D., Khalfallah, M., et al. (2018). Climate change impacts on marine biodiversity, fisheries and society in the Arabian Gulf. *PLoS ONE* 13(5), e0194537.

Webster, J.M., Braga, J.C., Humblet, M., Potts, D.C., Iryu, Y., Yokoyama, Y., et al. (2018). Response of the Great Barrier Reef to sea-level and environmental changes over the past 30,000 years. *Nature Geoscience,* 1.

Wilkinson, C. (2000). *Status of Coral Reefs of the World: 2000.* Cape Ferguson, Queensland, and Dampier, Western Australia: Australian Institute of Marine Science.

Yamano, H., Sugihara, K., and Nomura, K. (2011). Rapid poleward range expansion of tropical reef corals in response to rising sea surface temperatures. *Geophysical Research Letters* 38(4), L04601.