Coral and Reef Fish Communities in the Thermally Extreme Persian/Arabian Gulf: Insights into Potential Climate Change Effects

Chapter · February 2021

DOI: 10.1007/978-3-030-57054-5_3

6 authors, including:

Jess Bouwmeester
Smithsonian Institution
85 PUBLICATIONS **1,301** CITATIONS

Rodrigo Riera
Universidad de Las Palmas de Gran Canaria
291 PUBLICATIONS **2,030** CITATIONS

Pedro Range
Qatar University
89 PUBLICATIONS **1,621** CITATIONS

Radhouan Ben-Hamadou
Qatar University
136 PUBLICATIONS **2,385** CITATIONS

Coral and Reef Fish Communities in the Thermally Extreme Persian/Arabian Gulf: Insights into Potential Climate Change Effects

J. Bouwmeester, R. Riera, P. Range, R. Ben-Hamadou, K. Samimi-Namin, and J. A. Burt

Abstract Coral reefs are facing global challenges, with climate change causing recurrent coral bleaching events at a faster rate than corals may be able to recover from, and leading to an overall decline of coral cover and shifts in communities across the tropics. Scleractinian corals are ecosystem builders that provide a habitat for numerous marine species, and their loss is disrupting a range of ecosystem functions and services that reefs normally provide. Climate change will continue to warm the world's oceans, leading to thermal conditions similar to those already existing in the Persian/Arabian Gulf (hereafter termed "the Gulf"). Indeed, the Gulf is in the summer the world's hottest sea (SST > 36 °C) and thus represents a "natural laboratory" in which to understand how reefs in other regions might respond under

J. Bouwmeester (✉)
Smithsonian Conservation Biology Institute, Front Royal, VA, USA

Hawai'i Institute of Marine Biology, Kaneohe, HI, USA
e-mail: bouwmeesterj@si.edu

R. Riera
Departamento de Ecología, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Conceptión, Chile

IU-ECOAQUA, Grupo en Biodiversidad y Conservación, Departamento de Biología, Universidad de Las Palmas de Gran Canaria, Las Palmas, Canary Islands, Spain

P. Range
Environmental Science Center, Qatar University, Doha, Qatar

R. Ben-Hamadou
Department of Biological and Environmental Sciences, College of Arts and Sciences, Qatar University, Doha, Qatar

K. Samimi-Namin
Department of Zoology, University of Oxford, Oxford, UK

Taxonomy and Systematics Group, Naturalis Biodiversity Center, Leiden, Netherlands

J. A. Burt
Center for Genomics and Systems Biology, New York University Abu Dhabi, Abu Dhabi, United Arab Emirates

S. Rossi, L. Bramanti (eds.), *Perspectives on the Marine Animal Forests of the World*, https://doi.org/10.1007/978-3-030-57054-5_3

increasing temperatures. Recent research has shown that physiological thresholds of Persian/Arabian Gulf corals are higher than elsewhere, allowing them to survive in the Gulf's extreme temperatures. However, these marginal conditions result in coral communities that are low in diversity and comprised mainly of stress-tolerant species that provide limited three-dimensional structure. This low complexity habitat and the environmental extremes are associated with reef fish communities that have lower diversity, abundance, biomass, and size at maturity compared with conspecifics outside of the Gulf, and these fish communities have been shown to function quite differently. As climate change continues, coral reef ecosystems around the world are expected to gradually shift to thermal conditions similar to the present-day Gulf, and as such today's Gulf can provide insights into ecological patterns and processes we can expect in the tropics in the future. However, while Gulf fauna are adapted to extreme temperatures, they live very near their upper thermal threshold each summer. Recent climate change has resulted in recurrent mass bleaching events that have caused widespread loss of coral and knock-on effects on reef-dependent fishes. Thus, paradoxically, on the world's most robust reefs, we may be witnessing the world's first region-wide extirpation of reef fauna as a result of climate change.

Keywords Arabian Gulf · Climate change · Coral bleaching · Coral reef · Extreme environment · Persian Gulf · Scleractinian corals · Thermotolerance

1 Coral Reefs Around the Globe Are Facing Major Challenges in the Face of Climate Change, with Changing Environmental Conditions Progressively Reshaping Coral Reef Ecosystems

Coral reef ecosystems provide us each year with numerous ecosystem services (Moberg and Folke 1999), valued to 40 billion US dollars annually (Conservation International 2008). However, coral reefs around the world are now rapidly deteriorating from thermal stress, repeatedly exposed to ocean temperatures higher than they are able to handle for extensive periods (Burke et al. 2011). Since the development of the fossil fuel industry in the early nineteenth century, CO_2 levels in the atmosphere have risen from 280 ppm in the 1800s to over 410 ppm in 2019, heating both the atmosphere and the world's oceans (Cao and Caldeira 2008; Gruber et al. 2019). In this period, the highest ocean warming rates occurred in the past two decades, with accumulated heat reaching depths below 2000 m (Gleckler et al. 2016). Shallow tropical waters have also experienced numerous temperature anomalies in the recent decades, repeatedly reaching summer temperatures to which coral reefs are not acclimated (Heron et al. 2016; Lough et al. 2018).

Reef-building corals (order Scleractinia) acquire up to 95% of their metabolic needs from photosynthetic dinoflagellates that live within their host's tissue (Muscatine et al. 1983; Muscatine et al. 1984). In periods of thermal stress, the symbiosis between corals and their symbiotic dinoflagellates (family Symbiodiniaceae) is disrupted, and the symbionts are expelled, changing the colour of the coral host to a bright white colour (Weis 2008; Wooldridge 2013). Without symbionts to provide the food and energy it requires for survival, the bleached coral relies on stored reserves for recovery and survival and can die from starvation if new symbionts are not re-acquired in time (Rodrigues and Grottoli 2007).

Coral bleaching has now been reported in every region of the world that hosts coral reefs, and with the rapid recurrence of bleaching events, reefs are struggling to recover, leading to an overall decline in reef-building corals (Pandolfi et al. 2003; Heron et al. 2016; Hughes et al. 2018b). With species-specific susceptibility and resilience from coral bleaching, coral reef assemblages are also changing, shifting to coral assemblages with reduced three-dimensional structure, therefore decreasing the habitat of reef-associated fishes and other reef inhabitants (Hughes et al. 2018a; Darling et al. 2019; Fontoura et al. 2020). Further losses in coral cover and reef complexity will strongly affect ecosystem services that humanity currently benefits from. Recent estimates show that without reefs, annual flood damages would double and annual damage from storms would triple (Beck et al. 2018). With climate change, storms are expected to be stronger and more frequent, likely increasing annual coastal damage and potentially affecting a number of other ecosystem services (Beck et al. 2018; Woodhead et al. 2019). Additionally, the continuous loss and decline in the physical structure of reefs habitats will strongly affect coral reef fisheries (Pratchett et al. 2014), with an estimated loss of 5.4–8.4 billion US dollars per year by 2100, under a high-emission scenario (Speers et al. 2016). This economic loss from reef fishes is likely to have devastating consequences for the estimated billion people whose lives and livelihood rely on reef fish harvests (Speers et al. 2016).

The future of coral reefs is uncertain, but in some already warm regions—such as the Persian/Arabian Gulf (thereafter named "The Gulf")—corals seem to be naturally adapted to higher temperatures, giving us insights into the processes and potential responses that are likely to occur in many other coral reefs around the globe in the coming decades (Burt et al. 2020).

2 The Gulf Is the World's Hottest Sea Each Summer and Is, Thus, a Natural Laboratory to Understand How Climate Change Might Affect Reefs Elsewhere in the Future

The Gulf is a relatively young sea that was formed between 12,000 and 9000 years BP when the basin slowly flooded with rising sea levels after the Holocene glacial retreat (Purkis and Riegl 2012). However, its current sea level was only reached between 3000 and 6000 years BP, forming the modern Gulf and its current coastlines (Purkis and Riegl 2012). The Gulf is also relatively shallow, averaging 35 m depth, with a maximum depth of 100 m near its entrance at the Straits of Hormuz (Purser and Seibold 1973). It is characterised by some of the highest temperature, salinity,

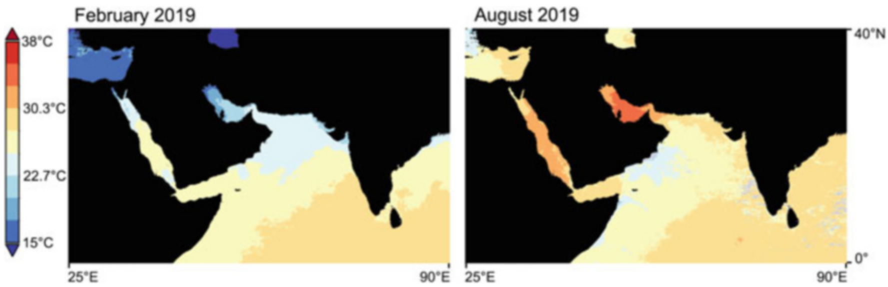

Fig. 1 The Gulf experiences some of the hottest water temperatures in the world in the summer, as well as major seasonal fluctuations in temperatures. In the winter (e.g. February 2019), water temperatures can fall down to 16 °C and less, and in the summer (e.g. August 2019), water temperatures reach 35 °C nearly every year, with shallow water bodies often warming further. The temperatures shown in the map are NASA Aqua/MODIS average monthly sea surface temperatures at 11 microns (Night). The map was produced with the Giovanni online data system, developed and maintained by the NASA GES DISC (available at giovanni.gsfc.nasa.gov)

and nutrient fluctuations encountered in marine ecosystems and represents one of the most extreme environments that scleractinian corals survive in (Riegl and Purkis 2012; Vaughan et al. 2019). Most of the shallow waters of the western and southern Gulf drop down to 16.5 °C in the winter and reach 35 °C in the summer (Fig. 1), with maxima found up to 40 °C in lagoons (Purser and Seibold 1973; John et al. 1990; Foster et al. 2012).

With summer temperatures reaching in excess of 35 °C every summer (Foster et al. 2012), coral bleaching thresholds in the Gulf are among the highest in the world, demonstrating how much corals have the capacity to acclimatise in a warming world (Riegl et al. 2012b). Studies in the SE Gulf have shown that even the more sensitive corals are able to withstand 35 °C temperatures for an average of 22 days before bleaching (Fig. 2) and an average of 27 days before dying (Riegl et al. 2012b). Gulf corals have acclimated to the region's extreme temperatures by adjusting both sides of the partnership: the coral host and the symbiotic dinoflagellates. Indeed, experiments on the brain coral *Platygyra daedalea* revealed that coral larvae from

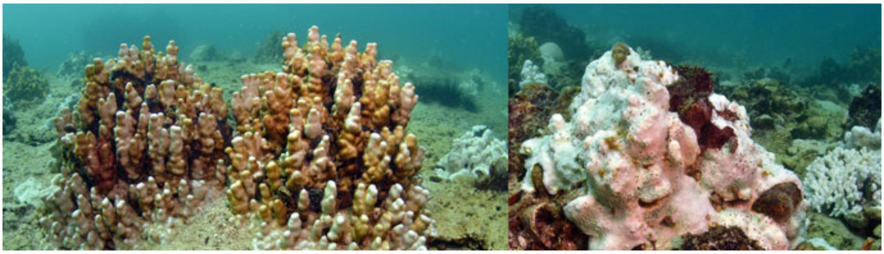

Fig. 2 Coral bleaching occurs regularly in the Gulf when summer temperatures are higher than usual for extended periods, although bleaching thresholds are some of the highest of the world. Left: bleached colony of *Porites harrisoni* showing partial mortality and partial algal overgrowth. Right: bleached colony of *Cyphastrea microphthalma*. Photos: J. Bouwmeester

the Gulf (which have not yet acquired their photosynthetic symbionts) have a higher tolerance to thermal stress than their counterparts outside of the Gulf and have shown to counteract thermal stress by increasing their antioxidant production (Howells et al. 2016a). Thermal tolerance heritability is indeed high for these larvae, which benefit from heat-tolerant gene sequences and gene expression that they acquired through their parental colonies (Kirk et al. 2018; Liew et al. 2020). Similarly, both *in situ* and extracted symbionts showed higher tolerance to thermal stress in populations from the Gulf, in comparison with populations outside the Gulf (Howells et al. 2016a). Recent research has also shown epigenetic changes related to thermal tolerance in the genome of these corals and that these epigenetic modifications are inherited from adults to sperm to larval offspring, providing a potentially much faster means for corals to acclimatise to increasing temperatures than through genetic changes alone (Liew et al. 2020). The symbiont community composition is an equally important factor in thermal tolerance, and studies have shown that most coral species in the environmentally extreme southern Gulf associate with the symbiont *Cladocopium thermophilum*, a species that is unusually tolerant of high temperatures and high salinities and that is prevalent across corals in the southern Gulf (Hume et al. 2013, 2015; D'Angelo et al. 2015; Smith et al. 2017; Howells et al. 2020b).

While Gulf corals exhibit considerable thermal tolerance, they are not immune to coral beaching (Fig. 2). The Gulf has experienced a number of temperature anomalies in recent decades, leading to major bleaching events that have strongly affected coral cover throughout the Gulf. Two back-to-back bleaching events in 1996 and 1998 wiped out large proportions of coral communities in the Gulf (Riegl 1999; Wilson et al. 2002; Rezai et al. 2004), following which recovery was slow in many areas as a result of add-on impacts from major coastal development projects in the region (Sale et al. 2011), although strong recovery was observed in some areas (e.g. Burt et al. 2008). Minor bleaching events returned in 2002 and 2007, followed by three consecutive years of bleaching in 2010, 2011, and 2012 (Riegl and Purkis 2015; Riegl et al. 2018; Burt et al. 2019). The last recorded bleaching event to date was in 2017, which was caused by one of the hottest summers recorded in the history of the region (Burt et al. 2019). In the UAE, corals spent nearly 2 months above bleaching thresholds and were exposed to temperatures above mortality thresholds for nearly 2 weeks, resulting in an overall loss of nearly three-quarters of the coral that year (Burt et al. 2019). Coral reefs often undergo a shift in coral communities following bleaching events (Furby et al. 2013; Hughes et al. 2018a). In the southern Gulf, the biggest shift in coral community occurred following the 1996 and 1998 bleaching events, when *Acropora* assemblages were wiped out at most shallow locations (Sheppard and Loughland 2002), with minimal recovery even 20 years later across much of the southern Gulf (Burt et al. 2011a, 2013a, 2016). While coral diversity was retained in deeper or offshore waters (Burt et al. 2016; Mateos-Molina et al. 2020), the shallow waters of the southern Gulf remain dominated by a low diversity assemblage of robust species, notably poritids and merulinids, which today characterise most southern Gulf coral assemblages (Riegl et al. 2018; Burt et al. 2019).

The Gulf represents one of the most extreme environments in the world where scleractinian corals exist, regularly reaching temperatures that would kill corals in other parts of the world. This acclimation to extreme thermal temperatures and high salinity occurred over a period of 9000–12,000 years, after the Gulf basin was last flooded following the last glaciations. The latest IPCC report predicts that ocean heatwaves are likely to increase 20-fold in frequency at 2 °C warming above pre-industrial levels and could reach a 50-fold increase in frequency if emissions continue to climb (Pörtner et al. 2019). While these changes risk happening at a much faster rate than corals are able to adapt, the Gulf is proof that adaptation is possible, albeit over thousands of years. While the possibility of the effects of climate change slowing down in the near future is highly unlikely, the Gulf offers an insight on how coral communities are likely to be shaped in the future and that thermal thresholds can increase with time under selective pressure. Overall, the Gulf is a unique "natural laboratory" for understanding how climate change might affect reefs elsewhere in the future.

3 The Cost of Surviving in an Extreme Environment Is Low Diversity and Limited Three-Dimensional Structure of Corals

The extreme environmental conditions encountered in the Gulf are selective for corals adapted to these extremes, with Gulf corals surviving in temperatures that would normally cause mortality in other areas (Coles 2003; Burt et al. 2008). As a result, out of the 401 scleractinian coral species that are present in waters surrounding the Arabian Peninsula, only 66 have been recorded in the Gulf (Riegl et al. 2012a; DiBattista et al. 2016; Berumen et al. 2019) although there is still some uncertainty regarding the validity of a few of these records (see Riegl et al. 2012a). However, many shallow coral assemblages in the Gulf have now shifted to a more stress-tolerant assemblage following repetitive bleaching events, with current assemblages mostly composed of sturdy poritids and merulinids (Burt et al. 2011a).

While comprehensive coral checklists exist for the Gulf (e.g. Riegl et al. 2012a; Berumen et al. 2019), they are not readily available for each country. Therefore, to be able to examine spatial patterns in scleractinian coral richness across the Gulf, records from the published literature were compiled for Iraq (Pohl et al. 2014), Kuwait (Downing and Roberts 1993; Hodgson and Carpenter 1995; Benzoni 2006; Benzoni et al. 2007; Riegl et al. 2012a), Saudi Arabia (Coles and Fadlallah 1991; Downing and Roberts 1993; Fadlallah 1996; Riegl et al. 2012a), Bahrain (Burt et al. 2013a), Qatar (Riegl et al. 2012a; Burt et al. 2016; Hoeksema et al. 2018), the UAE (Gulf only) (Riegl et al. 2012a), and Iran (Mostafavi et al. 2007; Samimi-Namin et al. 2009; Shahhosseiny et al. 2011; Riegl et al. 2012a; Rahmani and Rahimian 2013; Ghasemi et al. 2015; Mashini et al. 2015) and were supplemented with recent observations (2016–2018) from the authors in Qatar.

Historical coral richness, which includes every coral record published since the 1980s, varied between 5 species in Iraq and 42 species in Iran (Fig. 3a, Table 1). Qatar followed Iran closely with 38 species. Kuwait, Saudi Arabia, Bahrain, and the

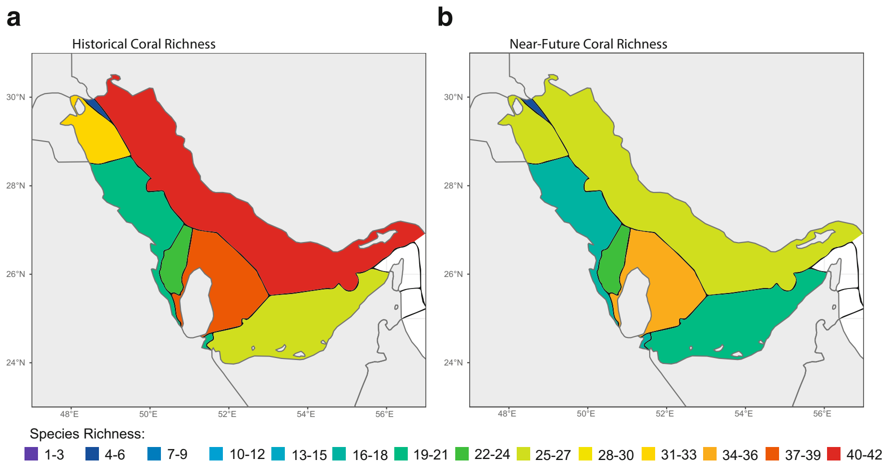

Fig. 3 Spatial patterns in coral richness in the Gulf. The colours are representative of the number of species found in each country bordering the Gulf. (**a**) Historical coral richness, which includes every verified coral species recorded in each country. (**b**) The near-future richness does not include species that have been extirpated from large areas of the Gulf in recent decades and are highly vulnerable to near-future climate change in their remaining Gulf distribution (see species marked with a star* in Table 1) and represents numbers closer to current or near-future coral richness in the Gulf

UAE had a species richness between 21 and 31 species. With a coral richness comparable to the one found in Iran, Qatar likely heavily benefits from natural larval dispersal from Iranian coral communities. Indeed, recent work revealed the presence of wind-driven large-scale eddies that are likely to carry coral larvae from the healthier and more speciose Iranian corals to the more degraded coral assemblages of Qatar and the UAE (Cavalcante et al. 2016). Nonetheless, some species have not recently been recorded in waters from Kuwait, Saudi Arabia, Bahrain, Qatar, and the UAE. These species are mostly branching Acroporidae and Pocilloporidae. Shallow populations of these more sensitive species may have been wiped out following the 1996 and 1998 bleaching events (Sheppard and Loughland 2002) or following the most recent bleaching in 2017 (Burt et al. 2019), potentially leaving the only surviving populations in deeper waters (Mateos-Molina et al. 2020). With populations that may now be restricted to locations further from the shore and potentially less regularly surveyed, current populations of sensitive species are mostly unknown in the western Gulf. Nonetheless, for these species to recover and thrive again throughout the Gulf, fresh larval supply is required. However, studies in the SE Gulf have shown that coral settlement numbers are low (Bento et al. 2017; Burt et al. 2019), with juvenile corals from the Acroporidae and Pocilloporidae families mostly absent, limiting options for the recovery of these populations (Pratchett et al. 2017; Burt and Bauman 2019). Therefore, a second coral richness map was made, excluding those species that are sensitive to thermal stress and that may disappear in the near future in many areas around the Gulf. In the second coral

Table 1 Checklist of zooxanthellate scleractinian corals, in each country that borders the Gulf

Species	Iraq	Kuwait	Saudi Arabia	Bahrain	Qatar	UAE	Iran
Dendrophylliidae							
Turbinara reniformis		X			x	x	
Turbinaria cf. *patula*					x		
Turbinaria peltata		X	X		x	x	
Turbinaria reniformis		X	X	X	x		x
Poritidae							
Goniopora lobata		X			x		x
Porites harrisoni	x	X	X	X	x	x	x
Porites lobata				X		x	x
Porites lutea		X	X	X	x	x	
Porites cf. *nodifera*						x	
Acroporidae							
*Acropora arabensis**		X	X			x	x
*Acropora clathrata**		X	X	X		x	x
*Acropora downingi**		X	X		x	x	x
Acropora cf. *gemmifera**							x
*Acropora horrida**							x
*Acropora mossambica**							x
*Acropora muricata**							x
*Acropora nasuta**							x
*Acropora pharaonis**						x	x
*Acropora tortuosa**					x		x
Acropora cf. *valida**							x
Alveopora tizardi					x		
*Montipora aequituberculata**		X			x		x
*Montipora danae**							x
*Montipora informis**							x
*Montipora spongiosa**							x
Agariciidae							
Pavona cf. *explanulata*		X			x		
Pavona decussata		X		X	x	x	x
Pavona varians			X				
Siderastreidae							
Siderastrea savignyana		X		X	x	x	x
Pocilloporidae							
Madracis kirbyi		X		X			
*Pocillopora damicornis**			X				x
*Stylophora pistillata**		X	X			x	x
Coscinareidae							
Anomastraea irregularis		X	X	X	x		x
Coscinaraea monile	x	X	X		x	x	x
Fungiidae							
Cycloseris costulata					x		

(continued)

Table 1 (continued)

Species	Iraq	Kuwait	Saudi Arabia	Bahrain	Qatar	UAE	Iran
Cycloseris curvata		X			x		x
Cycloseris fragilis					x		
Psammocoridae							
Psammocora albopicta		X	X		x		
Psammocora profundacella					x		x
Psammocora stellata		x	X	X	x	x	x
Incertae sedis							
Leptastrea purpurea	x			X	x	x	
Leptastrea transversa		x	X	X	x		x
Plesiastreidae							
Plesiastrea versipora		x		X	x	x	
Merulinidae							
Cyphastrea microphthalma		x	X	X	x	x	x
Cyphastrea serailia		x		X	x		x
Dipsastraea favus	x		X	X	x	x	x
Dipsastraea pallida		x	X	X	x	x	x
Dipsastraea speciosa			X	X	x	x	x
Echinopora hirsutissima							x
Favites abdita				X			
Favites acuticolis	x	x		X	x		
Favites pentagona		x	X	X	x		x
Hydnophora pilosa		x			x		x
Platygyra daedalea		x	X	X	x	x	x
Platygyra lamellina				X	x	x	
Lobophylliidae							
Echinophyllia aspera					x		x
Sclerophyllia maxima		x			x	x	x
Symphyllia radians							x
Acanthastrea echinata		x		X	x	x	x

The species listed abovereflects recent taxonomic changes. Species marked with an * represent corals that are highly sensitive to bleaching and have disappeared from large areas of the Gulf following recent bleaching events, or are likely to do so in the near future

richness map (Fig. 3b), patterns have changed with numbers likely closer to ones that exist today in the southern Gulf and that might exist soon in the remaining Gulf. In this latter scenario, a drop in species is most noticeable in Iran and in Kuwait. Therefore, coral communities in these regions, which still harbour high richness, need to be monitored and regularly assessed, which is frequently not the case (e.g., Kuwait, Alhazeem et al. 2017). Without regular quantitative surveys and bleaching assessments, it is not possible to accurately determine which populations are healthy and which are threatened.

Extreme temperatures clearly play a major role in shaping Gulf coral populations through mortality, but other life-history processes are affected as well. The recurrent bleaching events have been implicated in the reduction in lifespans of corals, preventing many species from reaching the large colony size that they would if left undisturbed (Bauman et al. 2013). Additionally, corals grow slower in the Gulf compared with their counterparts in less extreme environments (Bauman et al. 2013), but contrasting growth trends are found across species. Indeed, in the southern Gulf, calcification in *Cyphastrea microphthalma* is constrained by high temperature maxima and low light, while calcification in *Platygyra daedalea* is limited by low temperature minima (Howells et al. 2018). They are also subject to high prevalence of disease, which is tied to extreme summer temperatures and proximity to population-related pressures (Aeby et al. 2020; Howells et al. 2020a). Finally, the maintenance and post-disturbance recovery of coral populations are highly dependent on a regular supply of coral recruits, produced locally (self-recruitment) or acquired through larval dispersal from further populations (connectivity) (Jones et al. 2009). Corals spawn in April–May in the southern and western Gulf, in May–June in the NW Gulf, and in June and August in Iran, close to the Straits of Hormuz (Howells et al. 2014). In the southern Gulf, their reproductive output is lower than their counterparts outside the Gulf, in at least two species (Howells et al. 2016b), and settlement numbers are drastically lower than in other regions of the world, revealing limited larval supply (Bauman et al. 2014; Bento et al. 2017; Burt and Bauman 2019).

With restricted larval supply, limited coral growth, coral bleaching, and mass mortality being recurrent processes in the Gulf, coral populations in the Gulf have limited opportunities to form the intricate three-dimensional reef framework that can be found in other regions of the world, particularly in the more environmentally extreme southern Gulf. Furthermore, the already low rates of reef accretion may be further diminished by the high bioerosion rates found in some parts of the Gulf (Al-Mansoori et al. 2019). As a result, the Gulf has few true reef frameworks, with coral assemblages often forming coral carpets instead (Fig. 4) (Riegl 1999; Sale et al. 2011), although true reefs exist in the fossil records (Bruthans et al. 2006; Samimi-Namin and Riegl 2012).

Fig. 4 Examples of coral framework in the Gulf. Left: shallow reef dominated by colonies of *Porites harrisoni*. Centre: coral carpets in deeper (18 m depth) waters, dominated by merulinids. Right: *Acropora downingi* populations have survived in deep coral assemblages exposed to less thermal stress. Photos: J. Bouwmeester

4 With a Limited Reef Framework Comes Low Diversity, Abundance, Biomass, Size at Maturity of Fishes, and Different Functional Roles

Fishes of the Gulf are adapted to the region's extreme environment and are capable of withstanding the stress of osmotic and temperature extremes (Coles and Tarr 1990). In addition to environmental pressures, fish communities are restricted by the natural lack of reef complexity in the Gulf and the high turnover in coral communities following regular bleaching events (Paparella et al. 2019). Around 53% of known fish species in the Gulf are coral-associated, and 5% are coral-dependent (Buchanan et al. 2016); therefore, fish communities in the Gulf are impacted by coral mortality events, together with human-driven perturbations such as fishing, pollution, and coastal development (Burt 2014; Buchanan et al. 2016). After two heavy coral mortality events in the southern Gulf in 1996 and 1988, overall fish richness decreased, and there was a functional shift towards more herbivores, reflecting the change of substrate from coral to algae-dominated (Riegl 2002). In fact, an unusual dominance by herbivores is a common feature of reef fish communities in the southern Gulf, suggesting that recurrent disturbance and extreme conditions are having community-wide influence on fishes (Feary et al. 2010; Burt et al. 2011b). In comparison with other regions of the Indo-Pacific, the Gulf is relatively depauperate in fish species due to the Gulf's extreme environmental constraints on adult fishes and the larval supply (Coles 2003; Feary et al. 2010). Fishes in the Gulf add up to a total of 744 recorded species (Eagderi et al. 2019), representing 43% of the total fishes found throughout the Arabian Peninsula (DiBattista et al. 2016). In coral habitats, total fish richness is highest in offshore coral assemblages, but coral-dependent fish richness is highest on inshore coral reefs which are typically more widespread (Coles and Tarr 1990; Buchanan et al. 2016). However, due to the extensive loss of reefs in coastal areas of the Gulf, particularly in the southwest (i.e. Bahrain, Qatar, and the UAE), an impoverishment of fish assemblages on coastal coral assemblages has been recently observed, with concerns for their conservation (Buchanan et al. 2019). The pervasive extreme environmental stress of the southern Gulf has also been shown to reduce the diversity and productivity of cryptic reef fish species, which has important knock-on implications for the wider fish community as cryptic fish species serve as a primary food source for many larger species on reefs (Brandl et al. 2020).

Comprehensive species lists at the country level are not available for all countries surrounding the Gulf. Therefore, to examine spatial patterns in fish richness across the region, six ecologically important fish families that were more likely to have observation records in the literature than other groups were selected, for which we compiled a species list from the published literature, supplemented with recent observations (2016–2018) from the authors in Qatar. We chose two reef-dependent herbivore families, surgeonfishes (Acanthuridae) and parrotfishes (Scaridae); one corallivore family, butterflyfishes (Chaetodontidae); and three predator families, snappers (Lutjanidae), sea breams (Sparidae), and groupers (Serranidae), and compiled species data from Iraq (Hussain et al. 1988; Jawad et al. 2018; Mhaisen et al. 2018), Kuwait (Downing 1985; Bishop 2003), Saudi Arabia (Krupp and Almarri 1996), Bahrain (Smith and Saleh 1987), Qatar (Sivasubramaniam and Ibrahim 1982; Al-Ansi et al. 2002), the UAE (Gulf only) (Burt et al. 2009; Feary et al. 2010; Burt et al. 2011b, 2013b; Grandcourt et al. 2011), and Iran (Sahafi 2000; Rezai and Savari 2004; Shokri et al. 2005; Raeisi et al. 2011; Khatami et al. 2014; Esmaeili et al. 2015; Tavakoli-Kolour et al. 2015).

Overall, Kuwait, Saudi Arabia, and Iran had the highest fish richness, when only considering the six families, followed by Qatar, Iraq, Bahrain, and the UAE (Fig. 5, Table 2). The northwestern (Saudi Arabia, Kuwait, Iraq) and northeastern Gulf (Iran) experience less extreme environmental conditions than the southern Gulf (Fig. 1, Moradi and Kabiri 2015), which explains why fish richness is higher in these regions, such as within the Lutjanidae and Serranidae families. Saudi Arabian waters also host some of the few complex reef structures that exist in the region (Downing 1985; Coles and Tarr 1990), offering a higher diversity of habitats to fishes and invertebrates. This is here mostly reflected in the snappers (Lutjanidae), groupers (Serranidae), and seabreams (Sparidae), which are some of the larger fishes also commercially targeted by artisanal fisheries (Siddeek et al. 1999). Kuwait showed similar patterns, and Iraq had overall healthy numbers (particularly in the speciose Lutjanidae and Sparidae families) given its smaller surface and given that the presence of coral communities was only recently discovered within its jurisdictional waters (Pohl et al. 2014). Iran showed the highest fish richness for butterflyfishes, parrotfishes, snappers, and groupers, particularly in the latter two families. These fishes are mostly reef-dependent, and their higher richness likely reflects on the higher coral diversity present in Iran, where waters are deeper and cooler than elsewhere in the Gulf (Grandcourt 2012). Bahrain has a lower richness than its neighbour countries in all families, but the country expands over a smaller surface and is mostly surrounded by shallow waters, limiting both coral and fish communities to only the tougher ones that are adapted to the extreme shallow conditions (Smith and Saleh 1987). In contrast, Qatar has access to much deeper waters, where the less extreme conditions leave room for higher diversity (Walton et al. 2018). The UAE, in the southern Gulf, likely has some of the most challenging conditions for corals and fishes, which is reflected in its low fish richness in all families (Finucci et al. 2019).

A particular characteristic of Gulf fishes that is not found elsewhere is the strong seasonal fluctuation in species richness and abundance (Coles and Tarr 1990; Burt et al. 2009). In the southern Gulf, for example, total commercial fish biomass is the highest in the mid-winter and lowest in the hot mid-summer months, although different patterns emerge when considering individual species (Grandcourt 2012). Indeed, while most species are overall more abundant in the winter, a small group of fishes show the opposite pattern with the highest abundance in the summer, and some fishes show no seasonal change (Grandcourt 2012). While no direct evidence exists from tagging studies, it is assumed that the seasonal fluctuations in abundance result from movement of fishes between shallower and deeper waters (Coles and Tarr 1990; Grandcourt 2012). In addition to seasonal movements, some fishes have

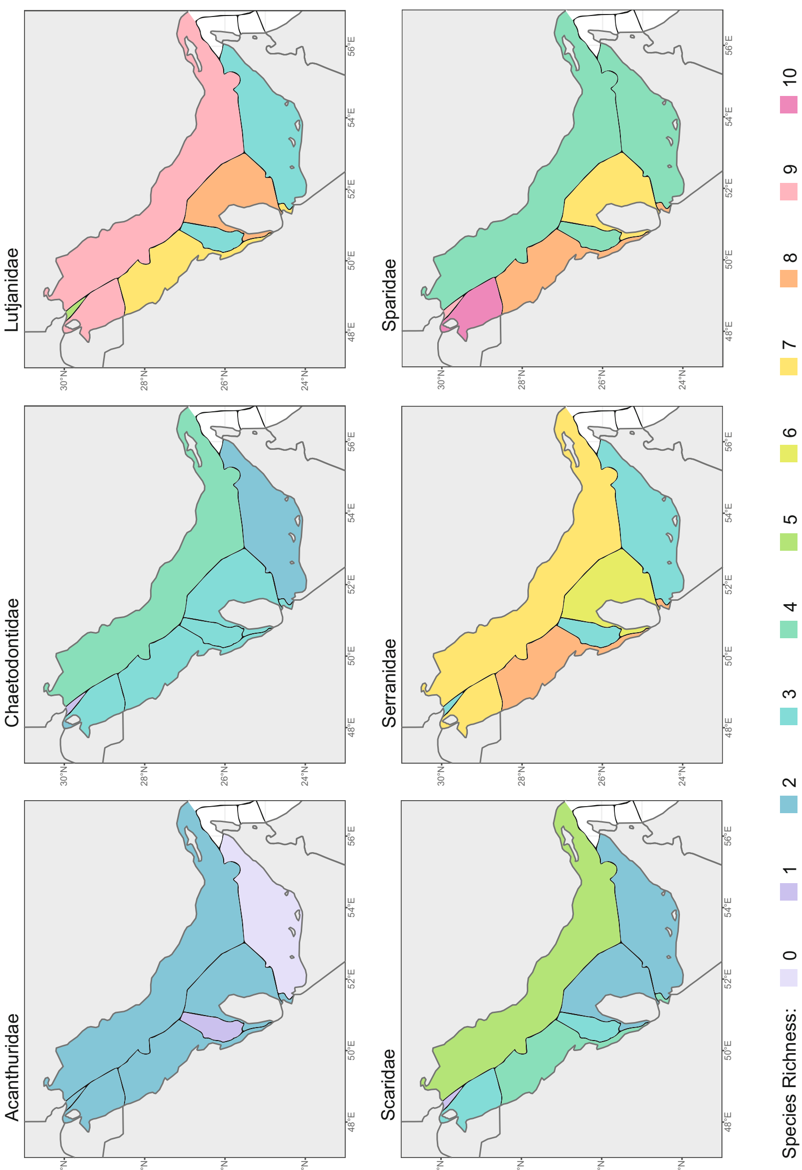

Fig. 5 Spatial patterns in fish richness in the Gulf. The colours are representative of the number of species found in each country bordering the Gulf. The families represented are the surgeonfishes (Acanthuridae), butterflyfishes (Chaetodontidae), snappers (Lutjanidae), parrotfishes (Scaridae), groupers (Serranidae), and seabreams (Sparidae)

Table 2 Species checklist for each of the six families studied, in each country that borders the Gulf

Species	Iraq	Kuwait	Saudi Arabia	Bahrain	Qatar	UAE	Iran
Acanthuridae							
Acanthurus sohal	x	x	x		x		x
Zebrasoma xanthurum	x	x	x	x	x		x
Chaetodontidae							
Chaetodon melapterus		x	x	x	x	x	x
Chaetodon nigropunctatus		x	x	x	x	x	x
Chaetodon vagabundus							x
Heniochus acuminatus	x	x	x	x	x		x
Lutjanidae							
Lutjanus argentimaculatus		x	x	x		x	x
Lutjanus ehrenbergii		x	x	x	x	x	x
Lutjanus fulviflamma	x	x	x	x	x	x	x
Lutjanus johnii	x	x			x		x
Lutjanus kasmira					x		
Lutjanus lutjanus		x	x				x
Lutjanus malabaricus		x			x		x
Lutjanus quinquelineatus		x	x				x
Lutjanus rivulatus	x						
Lutjanus russellii	x	x	x		x		x
Lutjanus sanguineus					x		
Pinjalo pinjalo	x	x	x		x		x
Scaridae							
Chlorurus sordidus		x	x	x			x
Scarus ferrugineus			x				x
Scarus ghobban	x	x	x	x	x	x	x
Scarus persicus		x	x	x	x	x	x
Scarus psittacus							x
Serranidae							
Aethaloperca rogaa			x		x		
Cephalopholis formosa							x
Cephalopholis hemistiktos		x	x	x	x	x	x
Epinephelus areolatus	x	x	x		x		x
Epinephelus bleekeri	x		x				x
Epinephelus coeruleopunctatus		x	x	x			
Epinephelus chlorostigma					x		x
Epinephelus coioides	x	x	x	x	x	x	x
Epinephelus latifasciatus		x					
Epinephelus multinotatus		x	x				
Epinephelus polylepis		x					
Epinephelus stoliczkae					x	x	x
Pseudanthias townsendi			x				

(continued)

Table 2 (continued)

Species	Iraq	Kuwait	Saudi Arabia	Bahrain	Qatar	UAE	Iran
Sparidae							
Acanthopagrus arabicus	x	x			x	x	x
Acanthopagrus berda	x	x	x	x			
Acanthopagrus bifasciatus	x	x	x	x	x	x	x
Argyrops spinifer	x	x	x		x		x
Cheimerius nufar		x	x				
Crenidens crenidens	x	x	x		x		
Diplodus kotschyi	x	x	x	x	x	x	x
Pagellus affinis					x		
Rhabdosargus haffara	x	x	x				
Rhabdosargus sarba	x	x			x	x	
Sparidentex hasta	x	x	x	x			

The species names listed above reflect recent taxonomic changes

adapted to the Gulf's extreme environmental conditions by altering their diets. Indeed, in a seasonal study conducted in the SE Gulf, three fish species, which outside of the Gulf feed predominantly on algae, sponges, or plankton, were found to have coral-dominated diets, with diets even more dominated by coral in the hotter summer months, potentially to meet their energy budgets when thermal stress is at its highest (Shraim et al. 2017). These observations are supported by a recent field and lab study which showed susbtantial changes in feeding behavior of the damselfish P*omacentrus trichrourus* across seasons, with feeding capacity apparently constrained by both extreme heat and cold across seasons (D'Agostino et al. 2020).

The pervasive loss of coastal coral assemblages in the Gulf has triggered a shift in coral-associated fish assemblages (Feary et al. 2013). Hence, with the absence of true reef frameworks throughout the Gulf, submerged artificial structures play an important ecological role in the region, potentially serving as stepping stones between natural habitats (Burt et al. 2009, 2012). They have inadvertently become major artificial reefs, attracting fishes through the complex three-dimensional framework that they offer (Burt et al. 2012). Many of these structures are extensively spread throughout the Gulf, mainly in coastal areas (e.g. breakwaters, groynes, jetties, and seawalls) (Burt et al. 2012), but also offshore, with almost 900 oil and gas platforms and related-submerged infrastructures (Sheppard et al. 2010). The platforms are each surrounded by a strict 500 m no-entrance policy, and permits are required to approach platforms within 5 km. Therefore, fishing activities are exceptionally well-controlled in these areas, which act as protected areas for corals and associated communities such as fishes. In Qatari jurisdictional waters, the largest concentration of oil and gas platforms is located in the Al Shaheen Oil Field, *ca*. 100 km offshore. A high fish diversity (83 species) was reported around surveyed platforms (Torquato et al. 2017), including large aggregations of the whale shark *Rhincodon typus* (Fig. 6) found to feed on high amounts of nutritious food, i.e. mackerel tuna

Fig. 6 Offshore oil and gas platforms are natural preserves for Gulf fishes, including the whale shark *Rhincodon typus*. Photographs: J. Bouwmeester

(*Euthynnus affinis*) eggs, in that area (Robinson et al. 2013). Further work still needs to be conducted since these offshore assemblages are understudied and their role as potential stepping stones among natural reefs is still poorly understood.

Despite the rapid growth of reef science in the Arabian region in the past decade (Burt 2013; Vaughan and Burt 2016), substantial baseline knowledge gaps remain in the region (Feary et al. 2013). Annotated fish checklists have not been conducted in every country, and limited fish surveys are available to compare abundance and biomass patterns across the Gulf (Eagderi et al. 2019). Additionally, coral research is limited in Iran due to restricted access and remote sites, limiting research opportunities in the country that has the longest coastline in the Gulf. Nevertheless, the Gulf is showing that many fishes are capable of adapting to its extreme conditions, at the cost of limited diversity, abundance, biomass, and functional roles. Modelling environmental scenarios is crucial to describe plausible trajectories of the different aspects of the future of the Gulf in general and the fish assemblages in particular.

5 Today's Gulf Coral Communities Can Offer Insights into What Other Reefs Around the Globe May Look Like in the Future

Coral reefs around the world are deteriorating because of climate change (Hughes et al. 2017). Warming waters are affecting the partnership between corals and their symbiotic algae resulting in bleaching events that are now happening at a faster rate than coral communities are able to recover from. Coral assemblages around the world will change, and the Gulf can offer strong insights into how reef fauna will cope with and respond to increasing temperatures (Burt et al. 2020). A loss of diversity, coral cover, and reef complexity are expected, which will have important consequences on reef-dependent fauna, while those corals that acclimate or adapt will need to undergo major physiological changes. Gulf corals provide an opportunity to understand and study adaptations to climate change at the physiological, genetic, and ecological level. Research from the Gulf may help identify corals that are likely to adapt and help direct research and conservation efforts towards those species.

Nonetheless, the Gulf is facing challenges in the future with water temperatures starting to rise above the corals' already high thresholds of bleaching and mortality. While the Gulf's coral communities and associated fish fauna represent a valuable asset for climate science (Burt et al. 2014), even these hardy fauna are under threat. While these are the most thermally tolerant reef species on the planet, they live within a degree of their upper thermal limits each summer. Therefore, as climate change ramps up ocean temperatures globally, the Gulf is likely to be among the first to experience the push across their upper thermal threshold. The increasing magnitude and frequency of bleaching events in the Gulf in recent years suggest that this process may occur sooner rather than later and that the region is at real risk of losing one of its most economically important and biodiverse ecosystems in the coming decades.

References

Al-Ansi M, Abdel-Moati M, Al-Ansari I (2002) Causes of fish mortality along the Qatari waters (Arabian Gulf). Int J Environ Stud 59:59–71

Alhazeem S, Burt J, Alsaffar A, Chen W, Al-Kandari M (2017) Long-term coral community stability in a disturbed marginal reef in Kuwait. J Water Res Ocean Sci 6:85–89. https://doi.org/10.11648/j.wros.20170606.12

Aeby GS, Howells E, Work T, Abrego D, Williams GJ, Wedding LM, Caldwell JM, Moritsch M, Burt JA (2020) Localized outbreaks of coral disease on Arabian reefs are linked to extreme temperatures and environmental stressors. Coral Reefs 39:829–846. https://doi.org/10.1007/s00338-020-01928-4

Aeby GS, Howells E, Work T, Abrego D, Williams GJ, Wedding LM, Caldwell JM, Moritsch M, Burt JA (2020) Localized outbreaks of coral disease on Arabian reefs are linked to extreme temperatures and environmental stressors. Coral Reefs 39:829-846 https://doi.org/10.1007/s00338-020-01928-4

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

Bauman AG, Baird AH, Burt JA, Pratchett MS, Feary DA (2014) Patterns of coral settlement in an extreme environment: the southern Persian Gulf (Dubai, United Arab Emirates). Mar Ecol Prog Ser 499:115–126

Beck MW, Losada IJ, Menéndez P, Reguero BG, Díaz-Simal P, Fernández F (2018) The global flood protection savings provided by coral reefs. Nat Commun 9:2186

Bento R, Feary DA, Hoey AS, Burt JA (2017) Settlement patterns of corals and other benthos on reefs with divergent environments and disturbances histories around the northeastern Arabian peninsula. Front Mar Sci 4:305

Benzoni F (2006) *Psammocora albopicta* sp. nov., a new species of Scleractinian coral from the Indo-West Pacific (Scleractinia; Siderastreidae). Zootaxa 1358:49–57

Benzoni F, Stefani F, Stolarski J, Pichon M, Mitta G, Galli P (2007) Debating phylogenetic relationships of the scleractinian Psammocora: molecular and morphological evidences. Contrib Zool 76:35–54

Berumen ML, Arrigoni R, Bouwmeester J, Terraneo TI, Benzoni F (2019) Corals of the Red Sea. In: Voolstra CR, Berumen ML (eds) Coral reefs of the Red Sea. Springer, Cham, pp 123–155

Bishop J (2003) History and current checklist of Kuwait's ichthyofauna. J Arid Environ 54:237–256

Brandl SJ, Johansen JL, Casey JM, Tornabene L, Morais RA, Burt JA (2020) Extreme environmental conditions reduce coral reef fish biodiversity and productivity. Nat Commun 11:3832. https://doi.org/10.1038/s41467-020-17731-2

Bruthans J, Filippi M, Geršl M, Zare M, Melková J, Pazdur A, Bosák P (2006) Holocene marine terraces on two salt diapirs in the Persian Gulf, Iran: age, depositional history and uplift rates. J Quat Sci 21:843–857

Buchanan JR, Krupp F, Burt JA, Feary DA, Ralph GM, Carpenter KE (2016) Living on the edge: vulnerability of coral-dependent fishes in the Gulf. Mar Pollut Bull 105:480–488

Buchanan JR, Ralph GM, Krupp F, Harwell H, Abdallah M, Abdulqader E, Al-Husaini M, Bishop JM, Burt JA, Choat JH (2019) Regional extinction risks for marine bony fishes occurring in the Persian/Arabian Gulf. Biol Conserv 230:10–19

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

Burt JA (2014) The environmental costs of coastal urbanization in the Arabian Gulf. City 18:760–770

Burt JA, Bauman AG (2019) Suppressed coral settlement following mass bleaching in the southern Persian/Arabian Gulf. Aquat Ecosyst Health Manage. https://doi.org/10.1080/14634988.2019.1676024

Burt JA, 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 JA, Bartholomew A, Usseglio P, Bauman A, Sale P (2009) Are artificial reefs surrogates of natural habitats for corals and fish in Dubai, United Arab Emirates? Coral Reefs 28:663–675

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

Burt JA, Bartholomew A, Feary DA (2012) Man-made structures as artificial reefs in the Gulf coral reefs of the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp 171–186

Burt J (2013) The growth of coral reef science in the Gulf: a historical perspective. Mar Pollut Bull 72:289–301. https://doi.org/10.1016/j.marpolbul.2013.05.016

Burt JA, Al-Khalifa K, Khalaf E, AlShuwaikh B, Abdulwahab A (2013a) The continuing decline of coral reefs in Bahrain. Mar Pollut Bull 72:357–363

Burt JA, Feary DA, Cavalcante G, Bauman AG, Usseglio P (2013b) Urban breakwaters as reef fish habitat in the Persian Gulf. Mar Pollut Bull 72:342–350

Burt JA, van Lavieren H, Feary D (2014) Persian Gulf reefs: an important asset for climate science in urgent need of protection. Ocean Challenge 20:49–56

Burt JA, Smith EG, Warren C, Dupont J (2016) An assessment of Qatar's coral communities in a regional context. Mar Pollut Bull 105:473–479

Burt JA, Paparella F, Al-Mansoori N, Al-Mansoori A, Al-Jailani H (2019) Causes and consequences of the 2017 coral bleaching event in the southern Persian/Arabian Gulf. Coral Reefs 38:567–589

Burt JA, Camp EF, Enochs IC, Johansen JL, Morgan KM, Riegl B, Hoey AS (2020) Insights from extreme coral reefs in a changing world. Coral Reefs 39:495–507. https://doi.org/10.1007/s00338-020-01966-y

Cao L, Caldeira K (2008) Atmospheric CO_2 stabilization and ocean acidification. Geophys Res Lett 35:L19609

Cavalcante GH, Feary DA, Burt JA (2016) The influence of extreme winds on coastal oceanography and its implications for coral population connectivity in the southern Arabian Gulf. Mar Pollut Bull 105:489–497

Coles SL (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

Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. Coral Reefs 9:231–237

Coles SL, Tarr BA (1990) Reef fish assemblages in the western Arabian Gulf: a geographically isolated population in an extreme environment. Bull Mar Sci 47:696–720

Conservation International (2008) Economic values of coral reefs, mangroves, and seagrasses: a global compilation. Center for Applied Biodiversity Science, Arlington

D'Angelo C, Hume BCC, Burt J, Smith EG, Achterberg EP, Wiedenmann J (2015) Local adaptation constrains the distribution potential of heat-tolerant *Symbiodinium* from the Persian/Arabian Gulf. ISME J 9:2551

D'Agostino D, Burt JA, Reader T, Vaughan GO, Chapman BB, Santinelli V, Cavalcante GH, Feary DA (2020) The influence of thermal extremes on coral reef fish behaviour in the Arabian/Persian Gulf. Coral Reefs 39:733–744. https://doi.org/10.1007/s00338-019-01847-z

Darling ES, McClanahan TR, Maina J, Gurney GG, Graham NAJ, Januchowski-Hartley F, Cinner JE, Mora C, Hicks CC, Maire E, Puotinen M, Skirving WJ, Adjeroud M, Ahmadia G, Arthur R, Bauman AG, Beger M, Berumen ML, Bigot L, Bouwmeester J, Brenier A, Bridge TCL, Brown E, Campbell SJ, Cannon S, Cauvin B, Chen CA, Claudet J, Denis V, Donner S, Estradivari FN, Feary DA, Fenner D, Fox H, Franklin EC, Friedlander A, Gilmour J, Goiran C, Guest J, Hobbs J-PA, Hoey AS, Houk P, Johnson S, Jupiter SD, Kayal M, C-y K, Lamb J, Lee MAC, Low J, Muthiga N, Muttaqin E, Nand Y, Nash KL, Nedlic O, Pandolfi JM, Pardede S, Patankar V, Penin L, Ribas-Deulofeu L, Richards Z, Roberts TE, Rodgers KS, Safuan CDM, Sala E, Shedrawi G, Sin TM, Smallhorn-West P, Smith JE, Sommer B, Steinberg PD, Sutthacheep M, Tan CHJ, Williams GJ, Wilson S, Yeemin T, Bruno JF, Fortin M-J, Krkosek M, Mouillot D (2019) Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. Nat Ecol Evol 3:1341–1350

DiBattista JD, Roberts MB, Bouwmeester J, Bowen BW, Coker DJ, Lozano-Cortés DF, Howard Choat J, Gaither MR, Hobbs J-PA, Khalil MT, Kochzius M, Myers RF, Paulay G, Robitzch VSN, Saenz-Agudelo P, Salas E, Sinclair-Taylor TH, Toonen RJ, Westneat MW, Williams ST, Berumen ML (2016) A review of contemporary patterns of endemism for shallow water reef fauna in the Red Sea. J Biogeogr 43:423–439

Downing N (1985) Coral reef communities in an extreme environment: the northwestern Arabian Gulf. In: Proceedings of 5th international coral reef congress, vol 6, pp 343–348

Downing N, Roberts C (1993) Has the Gulf War affected coral reefs of the northwestern Gulf? Mar Pollut Bull 27:149–156

Eagderi S, Fricke R, Esmaeili HR, Jalili P (2019) Annotated checklist of the fishes of the Persian Gulf: diversity and conservation status. Iran J Ichthyol 6:1–171

Esmaeili HR, Masoudi M, Mehraban HR (2015) Assignment of Acanthopagrus populations in the Persian Gulf drainage system of Iran to *Acanthopagrus arabicus* Iwatsuki, 2013 (Perciformes: Sparidae). Iran J Ichthyol 1:23–28

Fadlallah YH (1996) Synchronous spawning of *Acropora clathrata* coral colonies from the western Arabian Gulf (Saudi Arabia). Bull Mar Sci 59:209–216

Feary D, Burt J, Bauman A, Usseglio P, Sale P, Cavalcante G (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

Feary DA, Burt JA, Bauman AG, Al Hazeem S, Abdel-Moati MA, Al-Khalifa KA, Anderson DM, Amos C, Baker A, Bartholomew A (2013) Critical research needs for identifying future changes in Gulf coral reef ecosystems. Mar Pollut Bull 72:406–416

Finucci B, Hurst R, Bagley N, Al Dhaheri S, Grandcourt E (2019) Diversity, abundance, behaviour, and catchability of fishes from trap catch and underwater video in the Arabian Gulf. Fish Res 220:105342

Fontoura L, Zawada KJ, D'agata S, Álvarez-Noriega M, Baird AH, Boutros N, Dornelas M, Luiz OJ, Madin JS, Maina JM (2020) Climate-driven shift in coral morphological structure predicts decline of juvenile reef fishes. Glob Chang Biol 26:557–567

Foster K, Foster G, Al-Cibahy AS, Al-Harthi S, Purkis SJ, Riegl BM (2012) Environmental setting and temporal trends in southeastern Gulf coral communities. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp 51–70

Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of Central Red Sea corals during a major bleaching event. Coral Reefs 32:505–513

Ghasemi S, Mola N, Hoseinpour M, Hosseini-Tayefeh F, Naji A, Pakravan J (2015) Coral diversity of Hengam Island, Persian Gulf, Iran. J Appl Environ Biol Sci 5:43–52

Gleckler PJ, Durack PJ, Stouffer RJ, Johnson GC, Forest CE (2016) Industrial-era global ocean heat uptake doubles in recent decades. Nat Clim Chang 6:394–398

Grandcourt E (2012) Reef fish and fisheries in the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp 127–161

Grandcourt E, Al Abdessalaam T, Francis F, Al Shamsi A (2011) Demographic parameters and status assessments of *Lutjanus ehrenbergii*, *Lethrinus lentjan*, *Plectorhinchus sordidus* and *Rhabdosargus sarba* in the southern Arabian Gulf. J Appl Ichthyol 27:1203–1211

Gruber N, Clement D, Carter BR, Feely RA, Van Heuven S, Hoppema M, Ishii M, Key RM, Kozyr A, Lauvset SK (2019) The oceanic sink for anthropogenic CO_2 from 1994 to 2007. Science 363:1193–1199

Heron SF, Maynard JA, Van Hooidonk R, Eakin CM (2016) Warming trends and bleaching stress of the world's coral reefs 1985–2012. Sci Rep 6:38402

Hodgson G, Carpenter KE (1995) Scleractinian corals of Kuwait. Pac Sci 49:227–246

Hoeksema BW, Bouwmeester J, Range P, Ben-Hamadou R (2018) A large aggregation of self-fragmenting mushroom corals in the Arabian/Persian Gulf. Ecology 99:1236–1238

Howells E, Abrego D, Vaughan G, Burt J (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

Howells EJ, Abrego D, Meyer E, Kirk NL, Burt JA (2016a) Host adaptation and unexpected symbiont partners enable reef-building corals to tolerate extreme temperatures. Glob Chang Biol 22:2702–2714

Howells EJ, Ketchum RN, Bauman AG, Mustafa Y, Watkins KD, Burt JA (2016b) Species-specific trends in the reproductive output of corals across environmental gradients and bleaching histories. Mar Pollut Bull 105:532–539

Howells EJ, Dunshea G, McParland D, Vaughan GO, Heron SF, Pratchett MS, Burt JA, Bauman AG (2018) Species-specific coral calcification responses to the extreme environment of the southern Persian Gulf. Front Mar Sci 5:56

Howells E, Vaughan G, Work T, Burt J, Abrego D (2020a) Annual outbreaks of coral disease coincide with extreme seasonal warming. Coral Reefs 39:771–781. https://doi.org/10.1007/s00338-020-01946-2

Howells EJ, Bauman AG, Vaughan GO, Hume BCC, Voolstra CR, Burt JA (2020b) Corals in the hottest reefs in the world exhibit symbiont fidelity not flexibility. Mol Ecol 29:899. https://doi.org/10.1111/mec.15372

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R (2017) Global warming and recurrent mass bleaching of corals. Nature 543:373–377

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G (2018a) Global warming transforms coral reef assemblages. Nature 556:492–496

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC (2018b) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Hume B, D'angelo C, Burt J, Baker AC, Riegl B, Wiedenmann J (2013) Corals from the Persian/Arabian Gulf as models for thermotolerant reef-builders: prevalence of clade C3 *Symbiodinium*, host fluorescence and ex situ temperature tolerance. Mar Pollut Bull 72:313–322

Hume BC, D'Angelo C, Smith EG, Stevens JR, Burt J, Wiedenmann J (2015) *Symbiodinium thermophilum* sp. nov., a thermotolerant symbiotic alga prevalent in corals of the world's hottest sea, the Persian/Arabian Gulf. Sci Rep 5:8562

Hussain N, Naiama A, Al-Hassan L (1988) Annotated check list of the fish fauna of Khor Al-Zubair, north west of the Arabian Gulf, Iraq. Acta Ichthyol Piscat 8:17–24

Jawad LA, Faddagh Ziyadi M, Näslund J, Pohl T, Al-Mukhtar MA (2018) Checklist of the fishes of the newly discovered coral reef in Iraq, north-west Arabian Gulf, with 10 new records to the Arabian Gulf. Aqua, J Ichthyol Aquat Biol 24:89–138

John V, Coles S, Abozed A (1990) Seasonal cycles of temperature, salinity and water masses of the western Arabian Gulf. Oceanol Acta 13:273–281

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs 28:307–325

Khatami S, Valinassab T, Tavakoli-Kolour P (2014) Identification and assess anthropogenic impacts on species richness of coral reef fishes in Larak Island, Persian Gulf. Int J Mar Sci 4:1–5

Kirk NL, Howells EJ, Abrego D, Burt JA, Meyer E (2018) Genomic and transcriptomic signals of thermal tolerance in heat-tolerant corals (*Platygyra daedalea*) of the Arabian/Persian Gulf. Mol Ecol 27:5180–5194

Krupp F, Almarri MA (1996) Fishes and fish assemblages of the Jubail Marine Wildlife Sanctuary. In: Krupp F, Abuzinada AH, Nader LA (eds) A Marine Wildlife Sanctuary for the Arabian Gulf environmental research and conservation following the 1991 Gulf War oil spill NCWCD. Riyadh and Senckenberg Research Institute, Frankfurt a.M., pp 339–350

Liew YJ, Howells EJ, Wang X, Michell CT, Burt JA, Idaghdour Y, Aranda M (2020) Intergenerational epigenetic inheritance in reef-building corals. Nat Clim Chang 10:254. https://doi.org/10.1038/s41558-019-0687-2

Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs: 1871–2017. Sci Rep 8:6079

Mashini AG, Parsa S, Mostafavi PG (2015) Comparison of *Symbiodinium* populations in corals from subtidal region and tidal pools of northern coasts of Hengam Island, Iran. J Exp Mar Biol Ecol 473:202–206

Mateos-Molina D, Antonopoulou M, Baldwin R, Bejarano I, Burt JA, Garcia-Charton JA, Al-Ghais SM, Walgamage J, Taylor OJS (2020) Applying an integrated approach to coastal marine habitat mapping in the north-western United Arab Emirates. Mar Environ Res 161:105095. https://doi.org/10.1016/j.marenvres.2020.105095

Mhaisen FT, Ali AH, Khamees NR (2018) Marine fish parasitology of Iraq: a review and checklists. Biol Appl Environ Res 2:231–297

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

Moradi M, Kabiri K (2015) Spatio-temporal variability of SST and chlorophyll-a from MODIS data in the Persian Gulf. Mar Pollut Bull 98:14–25

Mostafavi PG, Fatemi SMR, Shahhosseiny MH, Hoegh-Guldberg O, Loh WKW (2007) Predominance of clade D Symbiodinium in shallow-water reef-building corals off Kish and Larak Islands (Persian Gulf, Iran). Mar Biol 153:25–34

Muscatine L, Falkowski P, Dubinsky Z (1983) Carbon budgets in symbiotic associations. In: Schwemmler W, Schenk H (eds) Endocytobiology II. Walter de Gruyter, Berlin, pp 649–658

Muscatine L, Falkowski P, Porter J, Dubinsky Z (1984) Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. Proc R Soc Lond Ser B Biol Sci 222:181–202

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJ, Paredes G (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958

Paparella F, Xu C, Vaughan GO, Burt JA (2019) Coral bleaching in the Persian/Arabian Gulf is modulated by summer winds. Front Mar Sci 6:205

Pohl T, Al-Muqdadi SW, Ali MH, Fawzi NA-M, Ehrlich H, Merkel B (2014) Discovery of a living coral reef in the coastal waters of Iraq. Sci Rep 4:4250

Pörtner H, Roberts D, Masson-Delmotte V, Zhai P, Tignor M, Poloczanska E, Mintenbeck K, Nicolai M, Okem A, Petzold J (2019) IPCC special report on the ocean and cryosphere in a changing climate. IPCC Intergovernmental Panel on Climate Change, Geneva

Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Curr Opin Environ Sustain 7:37–43

Pratchett MS, Baird AH, Bauman AG, Burt JA (2017) Abundance and composition of juvenile corals reveals divergent trajectories for coral assemblages across the United Arab Emirates. Mar Pollut Bull 114:1031–1035

Purkis SJ, Riegl BM (2012) Geomorphology and reef building in the SE Gulf coral reefs of the Gulf. Springer, Dordrecht, pp 33–50

Purser B, Seibold E (1973) The principal environmental factors influencing Holocene sedimentation and diagenesis in the Persian Gulf. In: Purser BH (ed) The Persian Gulf. Springer, Heidelberg, pp 1–9

Raeisi H, Daliri M, Paighambari SY, Shabani MJ, Bibak M, Davoodi R (2011) Length-weight relationships, condition factors and relative weight of five fish species of Bushehr waters, Northern Persian Gulf. Afr J Biotechnol 10:19181–19186

Rahmani M, Rahimian H (2013) Preliminary study on *Acropora* (Scleractinia: Astrocoeniina: Acroporidae) of the Persian Gulf, with emphasis on the north and northeastern areas. Turk J Zool 37:308–320

Rezai H, Savari A (2004) Observation on reef fishes in the coastal waters off some Iranian Islands in the Persian Gulf. Zool Middle East 31:67–76

Rezai H, Wilson S, Claereboudt M, Riegl B (2004) Coral reef status in the ROPME sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea. In: Wilkinson C (ed) Status of coral reefs of the world, vol 1. Australian Institute of Marine Science, Townsville, pp 155–170

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 (2002) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). Mar Biol 140:29–40

Riegl BM, Purkis SJ (2012) Environmental constraints for reef building in the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf. Springer, New York, pp5–32

Riegl B, Purkis S (2015) Coral population dynamics across consecutive mass mortality events. Glob Chang Biol 21:3995–4005

Riegl BM, Benzoni F, Samimi-Namin K, Sheppard C (2012a) The Hermatypic Scleractinian (hard) coral fauna of the Gulf. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp187–224

Riegl BM, Purkis SJ, Al-Cibahy AS, Al-Harthi S, Grandcourt E, Al-Sulaiti K, Baldwin J, Abdel-Moati AM (2012b) Coral bleaching and mortality thresholds in the SE Gulf: highest in the world. In: Riegl BM, Purkis SJ (eds) Coral reefs of the Gulf: adaptation to climatic extremes. Springer, Dordrecht, pp95–105

Riegl B, Johnston M, Purkis S, Howells E, Burt J, Steiner SC, Sheppard CR, Bauman A (2018) Population collapse dynamics in Acropora downingi, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. Glob Chang Biol 24:2447–2462

Robinson DP, Jaidah MY, Jabado RW, Lee-Brooks K, El-Din NMN, Malki AAA, Elmeer K, McCormick PA, Henderson AC, Pierce SJ (2013) Whale sharks, *Rhincodon typus*, aggregate around offshore platforms in Qatari waters of the Arabian Gulf to feed on fish spawn. PLoS One 8:e58255

Rodrigues LJ, Grottoli AG (2007) Energy reserves and metabolism as indicators of coral recovery from bleaching. Limnol Oceanogr 52:1874–1882

Sahafi HH (2000) Identification of marine ornamental fishes in northern part of the Persian Gulf, Iran. Iran J Fish Sci 2:21–36

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

Samimi-Namin K, Riegl B (2012) Raised reef on Larak suggests *Acropora* dominance on the Persian Gulf coral reefs since the Pleistocene. Coral Reefs 31:763–763

Samimi-Namin K, Rezai H, Kabiri K, Zohari Z (2009) Unique coral community in the Persian Gulf. Coral Reefs 28:27–27

Shahhosseiny MH, Mostafavi PG, Fatemi SMR, Karimi E (2011) Clade identification of symbiotic zooxanthellae of dominant sclerectinian coral species of intertidal pools in Hengam Island. Afr J Biotechnol 10:1502–1506

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

Sheppard C, Al-Husiani M, Al-Jamali F, Al-Yamani F, Baldwin R, Bishop J, Benzoni F, Dutrieux E, Dulvy NK, Durvasula SRV, Jones DA, Loughland R, Medio D, Nithyanandan M, Pilling GM, Polikarpov I, Price ARG, Purkis S, Riegl B, Saburova M, Samimi-Namin K, Taylor O, Wilson S, Zainal K (2010) The Gulf: a young sea in decline. Mar Pollut Bull 60:13–38

Shokri MR, Fatemi SMR, Crosby MP (2005) The status of butterflyfishes (Chaetodontidae) in the northern Persian Gulf, IR Iran. Aquat Conserv Mar Freshwat Ecosyst 15:S91–S99

Shraim R, Dieng MM, Vinu M, Vaughan G, McParland D, Idaghdour Y, Burt JA (2017) Environmental extremes are associated with dietary patterns in Arabian Gulf reef fishes. Front Mar Sci 4:285

Siddeek M, Fouda M, Hermosa G Jr (1999) Demersal fisheries of the Arabian Sea, the Gulf of Oman and the Arabian Gulf. Estuar Coast Shelf Sci 49:87–97

Sivasubramaniam K, Ibrahim MA (1982) Demersal fish resources around Qatar. Qatar Univ Sci Bull 2:305–351

Smith GB, Saleh MA (1987) Abundance and bathymetric distribution of Bahrain (Arabian Gulf) reef ichthyofaunas. Estuar Coast Shelf Sci 24:425–431

Smith EG, Hume BC, Delaney P, Wiedenmann J, Burt JA (2017) Genetic structure of coral-*Symbiodinium* symbioses on the world's warmest reefs. PLoS One 12:e0180169

Speers AE, Besedin EY, Palardy JE, Moore C (2016) Impacts of climate change and ocean acidification on coral reef fisheries: an integrated ecological–economic model. Ecol Econ 128:33–43

Tavakoli-Kolour P, Khatami S, Barkhordari A, Farhadi A (2015) Short communication first record of *Cephalopholis formosa* (Shaw, 1812) (Perciformes: Serranidae) in the Persian Gulf. J Appl Ichthyol 31:197–198

Torquato F, Jensen HM, Range P, Bach SS, Ben-Hamadou R, Sigsgaard EE, Thomsen PF, Møller PR, Riera R (2017) Vertical zonation and functional diversity of fish assemblages revealed by ROV videos at oil platforms in the Gulf. J Fish Biol 91:947–967

Vaughan GO, Burt JA (2016) The changing dynamics of coral reef science in Arabia. Mar Pollut Bull 105:441–458. https://doi.org/10.1016/j.marpolbul.2015.10.052

Vaughan G, Al-Mansoori N, Burt J (2019) The Arabian Gulf. In: Sheppard C (ed) World seas: an environmental evaluation, 2nd edn. Elsevier Science, Amsterdam, NL, pp 1–23

Walton ME, Hayes J, Al-Ansi M, Abdallah M, Al Maslamani I, Al-Mohannadi M, Al-Shaikh I, D'Urban Jackson T, Szostek C, Egerton J (2018) Towards spatial management of fisheries in the Gulf: benthic diversity, habitat and fish distributions from Qatari waters. ICES J Mar Sci 75:178–189

Weis VM (2008) Cellular mechanisms of cnidarian bleaching: stress causes the collapse of symbiosis. J Exp Biol 211:3059–3066

Wilson S, Fatemi SMR, Shokri MR, Claereboudt M (2002) Status of coral reefs of the Persian/Arabian Gulf and Arabian Sea region. In: Wilkinson CR (ed) Status of coral reefs of the world, pp 53–62

Woodhead AJ, Hicks CC, Norström AV, Williams GJ, Graham NA (2019) Coral reef ecosystem services in the Anthropocene. Funct Ecol 33:1023–1034

Wooldridge SA (2013) Breakdown of the coral-algae symbiosis: towards formalising a linkage between warm-water bleaching thresholds and the growth rate of the intracellular zooxanthellae. Biogeosciences 10:1647–1658