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

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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

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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.

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,
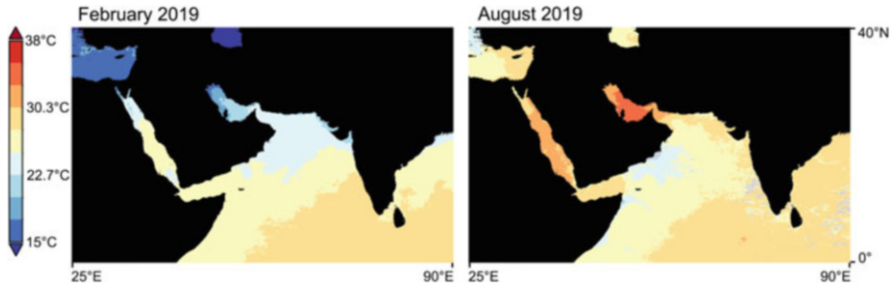
Fig. 1 The Gulf experiences some of the hottest water temperatures in the world in the summer, as well as major seasonal fluctuations in temperatures. In the winter (e.g. February 2019), water temperatures can fall down to 16 °C and less, and in the summer (e.g. August 2019), water temperatures reach 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
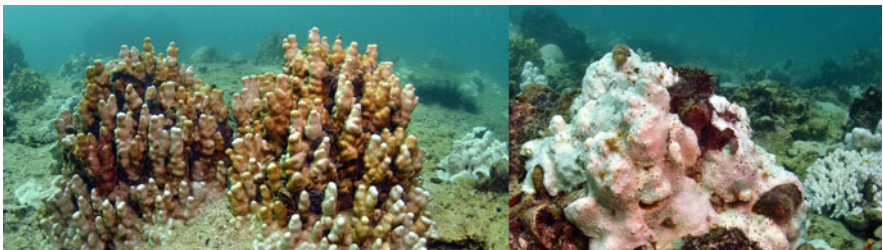
Fig. 2 Coral bleaching occurs regularly in the Gulf when summer temperatures are higher than usual for extended periods, although bleaching thresholds are some of the highest of the world. Left: bleached colony of *Porites harrisoni* showing partial mortality and partial algal overgrowth. Right: bleached 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
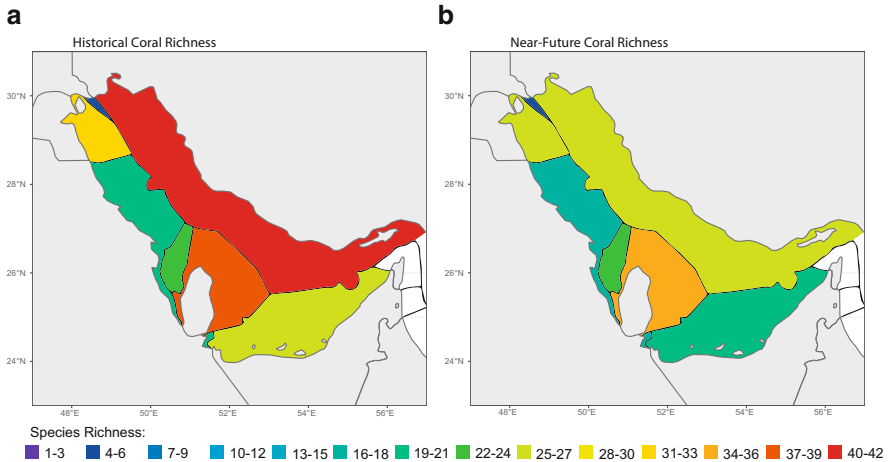
Fig. 3 Spatial patterns in coral richness in the Gulf. The colours are representative of the number of species found in each country bordering the Gulf. (**a**) Historical coral richness, which includes every verified coral species recorded in each country. (**b**) The near-future richness does not include 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).
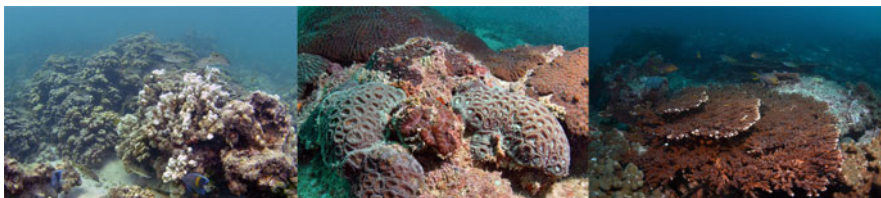
Fig. 4 Examples of coral framework in the Gulf. Left: shallow reef dominated by colonies of *Porites harrisoni*. Centre: coral carpets in deeper (18 m depth) waters, dominated by merulinids. Right: *Acropora downingi* populations have survived in deep coral assemblages exposed to less thermal stress. 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
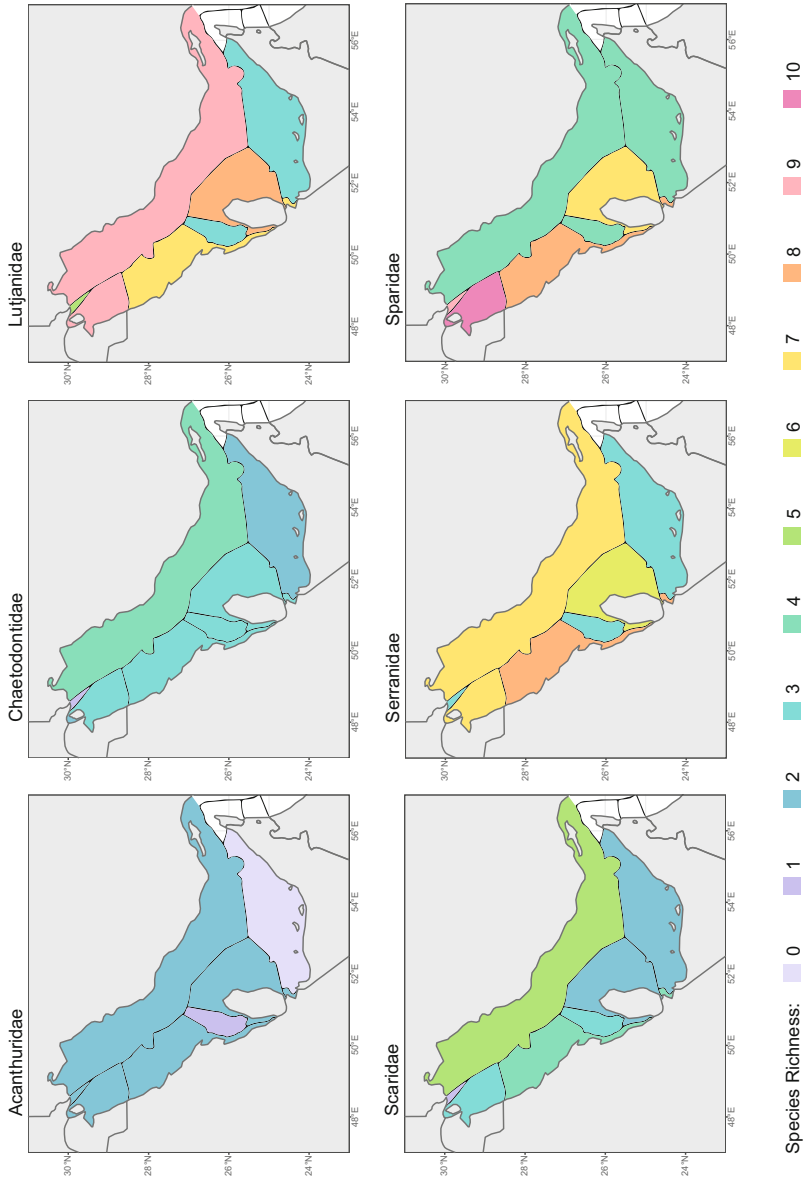
Fig. 5 Spatial patterns in fish richness in the Gulf. The colours are representative of the number of species found in each country bordering the Gulf. The families represented are the surgeonfishes (Acanthuridae), butterflyfishes (Chaetodontidae), snappers (Lutjanidae), parrotfishes (Scaridae), groupers (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.

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