



# The Red Sea: Environmental Gradients Shape a Natural Laboratory in a Nascent Ocean

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## Abstract

This chapter introduces the environmental gradients that characterize the broader Red Sea habitat. The Red Sea is formed by an actively spreading rift and notably has only one natural connection to the Indian Ocean – a narrow, shallow opening known as the Strait of Bab al Mandab. The resultant isolation undoubtedly plays a key role in shaping the environmental gradients, species endemism, and distinct evolutionary trajectory observed within the Red Sea. While this young ocean is known to be among the saltiest and warmest seas on Earth, there are important spatial and temporal gradients that likely influence the biological communities residing in its waters.

## Keywords

Red Sea · Physical environment · Ecosystems · Environmental gradients · Coral reefs · Brine pools · Seagrass meadows · Biogeography

## 1.1 Introduction

The Red Sea, a narrow, marginal sea of the Indian Ocean nearly 2000 km long and 200–300 km wide, offers many opportunities as a ‘natural laboratory’ due to the different gradients, often reaching extreme values, that occur within this unique body of water. While the Red Sea is recognized as one of the warmest and saltiest seas on the planet, these traits are not uniform but change strongly along its main

axis, extending from 12.5°N in the south to 30°N at Suez in the north. The lack of freshwater input (very low regional rainfall, no riverine input, etc.) and the warm desert climate of the region lead to high evaporation rates. This contributes to the pattern of salinity increasing with distance from the Bab al Mandab, where inputs of Indian Ocean water from the Gulf of Aden enter the Red Sea, creating an inverse estuarine circulation (Sofianos and Johns 2002). Temperature generally shows an opposite pattern in that the highest sea surface temperature (SST) occurs in the south and decreases northward (Chaidez et al. 2017; Ngugi et al. 2012). Inorganic nutrients also exhibit strong spatial gradients in the upper 200 m of the water column. Dissolved inorganic nitrogen (DIN) concentrations in excess of 15  $\mu\text{mol N L}^{-1}$  occur in the south and at depth, while they approach nanomolar concentrations in the surface layer of the central and northern Red Sea (Churchill et al. 2014; Kürten et al. 2016; Wafar et al. 2016b). Surface chlorophyll concentration inferred from remote sensing techniques generally shows similar spatial variability, declining from south to north, while the southern Red Sea typically exhibits consistently higher values year-round (Kheireddine et al. 2017; Li et al. 2017; Raitzos et al. 2013). A vertical gradient is also present. Water temperature decreases gradually within the upper layers (approximately 400 m), as observed in other oceans. However, uniquely to the Red Sea, temperature stabilizes at depth and does not fall below  $\sim 21$  °C even at depths below 2000 m (Roder et al. 2013). This contrasts with other seas and oceans, where water temperature below the upper layers continues to decrease with increasing depth, typically reaching 2–4 °C at depths of 1000 m and dropping to less than 2 °C in the deep basins. This unique temperature gradient is likely to influence the metabolic requirements of any organisms venturing to or residing at these depths. For example, deep-water corals are usually associated with the cold water typically found at depths below 500–600 m in the ocean, but somehow in the Red Sea they have adapted to the much warmer conditions

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encountered at depth and associated energetic requirements (Roder et al. 2013; Roik et al. 2015b; Röthig et al. 2017; Yum et al. 2017). Other physical gradients and processes that contribute to the uniqueness of the Red Sea include regional wind patterns, surface currents and eddies, and dust inputs (Zarokanellos et al. 2017b).

Notably, most of the aforementioned gradients also show strong seasonal signals, increasing from more tropical regimes in the south to more temperate regimes in the north. For many of these variables, reliable time-series data with sufficient spatial coverage is only recently available (Roik et al. 2016). Contemporary work has focused on understanding the nature of these gradients and explicitly addressing spatial and temporal variability. This provides an important introduction to the environment in which Red Sea coral reefs reside, which are the focus of this book.

These environmental gradients are also expected to influence other largely unknown or under-sampled biological variables such as primary productivity (Qurban et al. 2017), dissolved organic matter, microbial standing stocks/biomass, plankton community metabolism, and the genetic makeup of most of Red Sea species. It remains to be seen if the Red Sea conforms to the same biological rules as other oceans and tropical seas; some of the limitations and drivers in other systems (e.g., nutrient availability, seasonal mixing, stratification and upwelling, etc.) may function quite differently in the Red Sea. The potential flow-on effects could play a role in structuring entire ecosystems present in the Red Sea.

Despite these gradients and the relatively extreme conditions, the Red Sea is host to many diverse ecosystems along its length, including mangroves, seagrass habitats, soft-bottom sediment flats, coral reefs, and more. The roles of the prominent environmental gradients on these ecosystems are not thoroughly studied and warrant further investigation. The recent increase in interest in research institutions in the region (Mervis 2009) has led to growing efforts to examine the interactions of environmental gradients.

The Red Sea exhibits high levels of endemism and has long been recognized as a biodiversity hotspot for tropical marine fauna (DiBattista et al. 2015b). Comparisons of the unique species found in the Red Sea to broad-ranging species that co-occur in the Red Sea and species outside of the Red Sea may offer some insight to the evolutionary history of Red Sea fauna and the adaptations necessary for survival in these conditions. Since the present Red Sea may reflect future conditions in other regions of the world, its communities might provide some forecast as to how reefs and other marine ecosystems in other parts of the world will fare under climate change scenarios, particularly in the context of genetic capacities for adaptation (Aranda et al. 2016; Voolstra et al. 2017). However, it is important to note that the Red Sea is experiencing its own rapidly-changing conditions as a result of global climate change (Chaidez

et al. 2017; Raitzos et al. 2011) and, unfortunately, its coral reef communities are not immune to impacts of these changes (Cantin et al. 2010; Furby et al. 2013; Hughes et al. 2018; Monroe et al. 2018; Osman et al. 2018; Riegl et al. 2012; Roik et al. 2015a).

It is in the background and in the context of these gradients that coral reef ecosystems exist within the Red Sea. In several of the Red Sea countries, the reefs represent a critical component of their respective tourism industries. In other Red Sea countries, a substantial number of people rely on reef-based fisheries (Jin et al. 2012). In some locations, these industries remain under-developed or under-utilized. However, the Kingdom of Saudi Arabia, one of the areas where tourism has remained low, has announced a major eco-tourism area in the northern Red Sea, with the unique premise that ecosystems should receive no impacts from this development, where coral reefs, together with seagrass meadows, are arguably the more vulnerable habitats. Therefore, while the Red Sea provides a window into fascinating scientific questions, there are also important practical applications for understanding the relationship between environmental conditions and the general state of coral reefs in this region.

In this chapter, we seek to address the various gradients of the Red Sea in four broad categories:

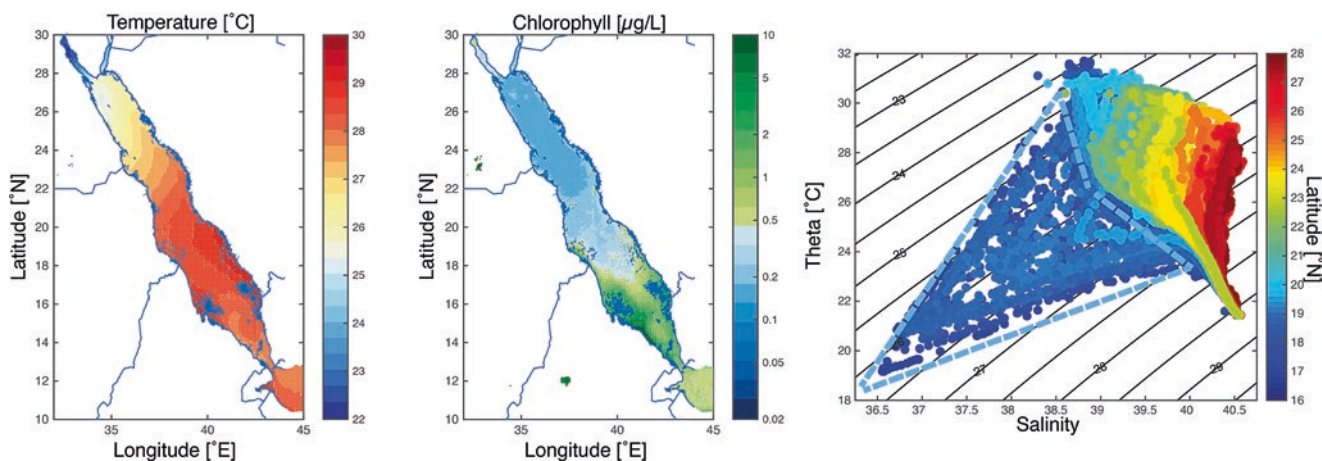
1. The physical environment
2. Nutrients and productivity
3. Gene flow and genetic diversity
4. Biogeography

Although knowledge of some of these remains imperfect, we believe that this overview provides a useful context for subsequent chapters in this volume, where many of the facets mentioned here will be addressed in detail.

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## 1.2 The Physical Environment of the Red Sea

Much of what has been known about the physical environment of the Red Sea is derived from remotely-sensed measurements and simulations of the physical dynamics, with limited *in situ* observations (Acker et al. 2008; Raitzos et al. 2013). Temperature shows a latitudinal gradient in all seasons, with warmest temperatures in the south and cooler temperatures in the north (Fig. 1.1). However, the surface temperature range in the north is greater than in the south. The northern Red Sea can see an average SST seasonal change from a winter low of ~22 °C to a summer high of 29–30 °C. In the southern Red Sea, the SST may range from a winter low of <26 °C to a summer high of >31 °C. Salinity shows an inverse gradient, with higher salinities in the north (>40) and lowest salinities in the south (see Fig. 1.1).



**Fig. 1.1** The left and center panels show the 15-year averages for SST and chlorophyll a from the MODIS Aqua instrument (source NASA’s Giovanni: <http://giovanni.gsfc.nasa.gov/>). The right panel shows a temperature-salinity diagram for a joint KAUST-WHOI hydrographic cruise during September–October 2011. The spatial extent of the temperature-salinity dataset is from 16°N to 28°N within the Saudi

Arabian EEZ and extends vertically through the water column. Latitude in the right panel is indicated by color coding from blue in the south to red in the north. The black lines are the contours of density anomaly [ $\text{kg}/\text{m}^3$ ]. Gulf of Aden intermediate water (sometimes known as Gulf of Aden intrusion water) is outlined with light blue dashed lines

Temperature gradients are dynamic and changing (Chaidez et al. 2017; Raitzos et al. 2011). Red Sea SSTs have increased rapidly in the latter half of 1990–2010, at an average rate of  $0.17 \pm 0.07 \text{ }^\circ\text{C decade}^{-1}$ , exceeding the global rate while the northern Red Sea is warming even faster, at between 0.40 and  $0.45 \text{ }^\circ\text{C decade}^{-1}$ , rendering the northern Red Sea one of the fastest-warming areas in the world (Chaidez et al. 2017).

The along-basin change in salinity results from large annual evaporation of approximately  $2 \text{ m year}^{-1}$  (Patzert 1974; Sofianos and Johns 2002; Tragou et al. 1999). The only significant source of “fresh” water for the Red Sea is Gulf of Aden water, which enters the Red Sea with a salinity of about 36. Thus, the Red Sea functions as an “inverse” estuary where fresher water enters the system and the strong thermohaline circulation resulting from evaporation results in a warm, salty outflow that is traceable throughout much of the Indian Ocean (Beal et al. 2000; Zhai et al. 2015). This unique environmental profile is likely to have major impacts on the biological and ecological functions of the Red Sea environment, as there appear to never have been any permanent riverine inputs to the Red Sea. For example, the Nile River does not appear to have ever emptied into the Red Sea (DiBattista et al. 2015a). Rare rainfall events on the coast may provide local input of freshwater via ephemeral rivers known locally as “wadis”, sometimes in such quantities as to have significant ecological impacts (e.g., freshwater-induced coral bleaching events) (Antonius 1988). Such events are rare, with average rainfall of about  $100 \text{ mm year}^{-1}$ ; rainfall declines from  $100 \text{ mm year}^{-1}$  in the south to about  $50 \text{ mm year}^{-1}$  in the northern Red Sea (Almazroui et al. 2012).

It is well-established that numerous transient eddies characterize the Red Sea. Analysis of sea level anomaly (SLA)

has demonstrated that the central Red Sea is especially characterized by high levels of eddy activity (Zhan et al. 2014). While long term averages from models and SLA have suggested that subregions may be dominated by either cyclonic or anti-cyclonic eddies, in the central Red Sea both types of eddies have been observed and often form in eddy pairs (Zarokanellos et al. 2017b). The duration of these eddies varies, typically ranging from a few weeks to several months. These eddies have been detected by various measurements, including SLA, remotely sensed chlorophyll, SST patterns, and *in-situ* measurements (Kürten et al. 2016; Raitzos et al. 2013; Sofianos Sarantis and Johns William 2007; Zhai and Bower 2013; Zhan et al. 2014); the eddies are also indicated in numerical models of Red Sea circulation (Clifford et al. 1997; Sofianos and Johns 2002; Yao et al. 2014). These eddies play an important role in modulating the depth of the nutricline, and may contribute to nutrient exchange between the open sea and coral reefs. The eddies likely play further important roles in disrupting potential boundary currents along the latitudinal gradient of the Red Sea coastline (Zarokanellos et al. 2017a). The ability of the eddies to facilitate longitudinal connections (i.e., east-west connectivity across the Red Sea) has not often been investigated, but is a potentially important feature (Raitzos et al. 2017).

The evaporation-driven thermohaline circulation results in a northward transport within the upper layer of the basin (Sofianos and Johns 2003). Modeling indicates that this current initiates along the western boundary in the south and crosses over to the eastern coast mid-basin, influenced by topographically-steered winds (Zhai et al. 2015). Observations are fewer, but support the northward transport along the eastern boundary in the northern half of the basin (Bower and

Farrar 2015). Recent hydrographic surveys utilizing ship, gliders, and surface current mapping observations provide additional support for the presence of an eastern boundary current (Zarokanellos et al. 2017b). This northward transport will also contribute to the dispersal of organisms along the axis of the basin but has yet to be carefully investigated.

There are no permanent riverine inputs to the Red Sea. Nonetheless, terrigenous inputs are likely to be a very important component of Red Sea nutrient cycles, delivered via deposition of atmospheric dust. Soils in coastal plains surrounding the Red Sea (Jish Prakash et al. 2016) are calculated to deliver 7.5 Mt of dust suspended in the atmosphere per year, corresponding to 76 Kt of iron oxides and 6 Kt of phosphorus per year, with over 65% of dust emitted from the northern region, much of which is likely to be deposited in the Red Sea (Anisimov et al. 2017). The Red Sea is exposed to ~15–20 dust storms per year (Jish Prakash et al. 2015), with atmospheric dust loads (and likely the subsequent inputs) double over the southern Red Sea compared to the northern Red Sea (Banks et al. 2017), particularly during the summer, when dust loads are highest (Osipov and Stenchikov 2018). In addition to delivering nutrients, dust cools the Red Sea, reduces the surface wind speed, and weakens both the exchange at the Bab al Mandab strait and the overturning circulation, affecting salinity distribution and heat budgets, and thereby circulation of the Red Sea (Osipov and Stenchikov 2018).

The Red Sea, geologically, has been formed by the separation of the Nubian plate from the Arabian plate. These plates continue to separate at a rate of about 16 mm per year. This activity leads to potential influence on the oceanography. At present, the activity seems to be more prominent in the south as opposed to the north (Xu et al. 2015). For example, between 2011–2013, two new islands emerged in the Zubair archipelago (in Yemeni waters) as a result of volcanic activity (Xu et al. 2015). The emergence of these two new islands would otherwise provide a unique opportunity to observe the establishment and succession of benthic communities, but the islands are unfortunately located in an area of intense political unrest. The separation of the two plates that surround the Red Sea determined the formation of deep anoxic brine pools mainly along the central axis of the basin (Backer and Schoell 1972; Pautot et al. 1984). Due to temporary isolation from fresh seawater inputs during the Miocene, the precipitation of thick evaporitic layers occurred in the ancient Red Sea. These evaporites were later dissolved when they were exposed to fresh seawater, similarly to what occurred after the Messinian Salinity Crisis in the Mediterranean Sea (Garcia-Castellanos and Villaseñor 2011; Searle and Ross 2007). The dissolution of the evaporites determined the formation of deep anoxic brine lakes, some of which are extremely sulfuric and others that are influenced by hydrothermal fluids (Schardt 2016; Swift et al. 2012).

The brine pools have a high density that limits the mixing with the overlying seawater and may include different vertically-stratified water bodies (of tens or more m depth) of increasing salinities (Bougouffa et al. 2013). At the transition between the brine and the deep seawater, a very productive water layer occurs along a sharp salinity gradient and chemocline referred to as the brine-seawater interface (Daffonchio et al. 2006). Due to the density barrier, such a chemocline (whose thickness varies between one to tens of m) entraps the organic matter sinking from the overlying water column. The different combinations of redox couples along the chemocline enable the selection of unique groups of microorganisms (Ngugi et al. 2015) that remain stratified along the salinity gradient per the availability of the suitable redox couples for their metabolisms (Borin et al. 2009). The environment surrounding the brine pools hosts complex communities of animals that exploit the carbon and nutrient resources emanating from the pool (Batang et al. 2012; Vestheim and Kaartvedt 2016).

The gradients on the surface of the brine pools represent a further source of microorganism variability in the Red Sea with potential biotechnology applications (Grotzinger et al. 2018).

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### 1.3 Nutrients and Productivity in the Red Sea

The Red Sea, as a whole, is an oligotrophic system. However, the few nutrients that are present in the upper layers do not have an even distribution throughout the basin. This is apparent even in remotely-sensed chlorophyll-a concentrations (Raitso et al. 2013) used as a proxy for the biomass of phytoplankton, the pelagic primary producers. The northern half of the sea typically has less chlorophyll than the southern half. There are seasonal maxima of productivity in coastal habitats (Racault et al. 2015), likely linked to irregular oceanographic features such as eddy circulation (Kürten et al. 2016; Zarokanellos et al. 2017b) or the delivery of nutrient-rich Gulf of Aden intrusion water (Churchill et al. 2014; Wafar et al. 2016a). Based on the strong differences in inorganic nutrient availability, small-sized phytoplankton (*Synechococcus* and *Prochlorococcus* cyanobacteria and picoeukaryotes) are relatively more abundant in the central and northern reaches (Kheireddine et al. 2017), although not in absolute numbers (Kürten et al. 2014). Stronger nitrogen limitation at higher latitudes would be the likely cause for the frequent presence of *Trichodesmium* in the northern reaches, including the Gulf of Aqaba (Post et al. 2002), although no evidence of latitudinal gradients in *Trichodesmium* distribution is available yet (Devassy et al. 2017).

The latitudinal gradient in phytoplankton biomass and productivity translates into other components of pelagic food



webs. Thus, heterotrophic prokaryotes (bacteria and archaea) and zooplankton increase their abundance towards the south (Kürten et al. 2014). Although much less is known about other planktonic groups, the scant evidence points to larger stocks in the richer lower latitude waters, as recently reported for chaetognaths (Al-Aidaros et al. 2017).

While total biodiversity (i.e., species richness) may not be greatly affected (Devassy et al. 2017), changes in species composition of planktonic assemblages do occur along the latitudinal axis. For instance, changes in the species composition of prokaryotic plankton have been described (Ngugi et al. 2012), including the widespread SAR11 clade (Ngugi and Stingl 2012). This pattern accompanies the trend of increasing planktonic biomass towards the south, a pattern that is consistent across the inshore-offshore gradient (Pearman et al. 2016, 2017). However, northern and southern regions did not differ significantly in the ecotype compositions of *Prochlorococcus* (Shibl et al. 2016). More conspicuous changes in functional genes (rather than taxa) have been recently reported in a study of 45 metagenomes obtained in a latitudinal transect along the eastern coast (Thompson et al. 2016). In spite of these geographical differences, the temporal variability, often overlooked in subtropical and tropical waters, seems comparable to the latitudinal one for planktonic microbial communities (Pearman et al. 2017; Silva et al. 2019).

At higher trophic levels, the latitudinal patterns of productivity may be influencing the biology of Red Sea fish populations. The southern half of the Red Sea is the preferred habitat for Red Sea whale sharks (Berumen et al. 2014). Other parts of the Red Sea may not provide sufficient food for these planktivorous sharks. The seasonal fluctuations in productivity may also reflect food availability for reef-dwelling planktivorous fishes. Another study (Robitzsch et al. 2016) linked local variations in food availability to larval growth rates and metabolism in *Dascyllus* damselfishes.

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#### 1.4 Gene Flow and Genetic Diversity in the Red Sea

The presence of such clear environmental gradients within the Red Sea might be expected to lead to a corresponding genetic gradient if populations exhibit local adaptation to the potentially stressful conditions (e.g., high temperature or salinity). Even without the environmental gradients, the physical length of the Red Sea coastline may create genetically distinguishable populations at opposite ends. In terms of coral reef habitats, the Red Sea presents an interesting case with several thousands of kilometers of nearly-continuous reef habitat. It is arguably the longest fringing reef of the world, bordering over 4000 km of the eastern and western shorelines of the Red Sea and the Gulf of Aqaba.

The aforementioned temporal eddies thus introduce the potential for east-west transport of larvae and, thus, genetic connectivity between both sides of the Red Sea (Raitsos et al. 2017).

To date, these topics have been addressed in several fishes and a few coral species but very rarely in other taxa. Various methods and genetic markers have been employed. Notably, not all studies are able to include samples at either extreme of the Red Sea (e.g., the Gulf of Suez or the Gulf of Aqaba in the north, or near the Bab al Mandab in the south).

Studies on benthic invertebrates have indicated very little population differentiation (Giles et al. 2015; Robitzsch et al. 2015) along the Red Sea. Giles et al. (2015) analyzed samples of a reef sponge (*Stylissa carteri*) with high sampling coverage along the Saudi Arabian Red Sea coast, including samples from the Gulf of Aqaba to the Farasan Islands (at the border of Saudi Arabia and Yemen), and one site on the opposite coast (from Sudan). The authors found that the marked environmental difference of the Farasan Islands habitat explained more of the genetic variation in the samples than geographic distance. In other words, the majority of the Red Sea was relatively genetically homogeneous for this common sponge, but the distinct environment of the Farasan Islands was reflected in a genetically distinct population.

Various studies of fish genetics within the Red Sea reached similar conclusions. The majority of the Red Sea appears to be reasonably well-mixed genetically, with some exceptions found in samples from the farthest ends. For example, Froukh and Kochzius (2008) found limited connectivity between the Gulf of Aqaba and central Red Sea sites in the fourline wrasse (*Larabicus quadrilineatus*), but did not have samples from the northern Red Sea (outside of the Gulf of Aqaba). Nanninga et al. (2014) studied the two-band anemonefish (*Amphiprion bicinctus*) using spatial coverage similar to that of Giles et al. (2015) and likewise found that environmental gradients explained more variation than geographic distance. Interestingly, the location of the genetic break in the anemonefish population was not exactly the same as it was for the sponge. There could be a few potential explanations for this, such as differences in larval ecology of the two species or differences in the sensitivity to the environmental conditions. Saenz-Agudelo et al. (2015) analyzed a subset of the anemonefish samples from Nanninga et al. (2014) and added additional samples from outside the Red Sea. Using a next-generation sequencing approach, Saenz-Agudelo et al. (2015) tested explicit theories about potential barriers to connectivity within and outside of the Red Sea, confirming the within-Red Sea patterns previously mentioned. These three brief examples from fishes suggest that each species may have slightly different genetic gradients throughout the Red Sea, but the general pattern holds that populations are well-mixed throughout the majority of the Red Sea.

A recent study used long-term particle dispersion model simulations and satellite-derived biophysical observations to show that physical oceanography largely explains the genetic homogeneity through the Red Sea (Raitsos et al. 2017). The modeling results also suggest that there is a high degree of west-east connectivity, which is driven by frequent occurrences of eddies that transport surface water across the Red Sea. Wilson (2017) examined the west-east connectivity of two *Plectropomus* grouper species and found relatively high levels of gene flow between Sudanese and Saudi Arabian populations, which supports the predictions of the models from Raitsos et al. (2017). For more information about connectivity and fishes please refer to Chap. 8 in this book.

## 1.5 Biogeography of Red Sea Organisms

In some well-studied groups, the Red Sea is well-known for hosting a relatively high proportion of endemic species. This is true, for example, among conspicuous reef fishes and corals, and is also true in other taxonomic groups where sufficient data is available (DiBattista et al. 2015b). This latter caveat is important – there are very few groups for which large-scale, systematic surveys of the faunal communities and their distributions within the Red Sea have been completed. Establishing an organism's status as endemic requires some reasonable confidence that the organism does not occur in neighboring areas. For many of the waters around the Arabian Peninsula and the northwestern Indian Ocean, this is a non-trivial undertaking. The evolutionary history of the Red Sea, combined with its unique environmental properties, has likely played a role in the observed level of endemism. Several case studies, however, reveal that there are multiple scenarios of evolutionary connectivity (DiBattista et al. 2013). Some species are recent invaders (i.e., colonized the Red Sea from the Indian Ocean within the last 20,000–25,000 years) while others seem to have persisted inside the Red Sea with minimal genetic connection to the Indian Ocean for hundreds of thousands of years (DiBattista et al. 2013). There does not appear to be, therefore, a single mechanism responsible for the endemism found in the Red Sea.

A global assessment of marine ecoregions identified two putative ecoregions within the Red Sea, demarcated at approximately 20°N (Spalding et al. 2007). However, biogeographic patterns have been explored in detail only for some of the biological assemblages. Corals and reef communities have probably received the most attention. The coastal, fringing communities show notable gradients along the Saudi Arabian coast (Sheppard and Sheppard 1991), with diversity highest in the northern and central Red Sea, declining in the southern, more turbid region. This is in contrast to surveys of the offshore communities, which found relatively homogenous compositions of fish and benthic assemblages

(Roberts et al. 2016). (It is important to note that the latter study did not include the communities on the extreme north or south ends of the Red Sea.) Similar results were found when surveying offshore coral communities (Sawall et al. 2014). It is worth mentioning that the Sheppard and Sheppard (1991) surveys occurred ~20 years prior to Sawall et al. (2014) and (Roberts et al. 2016), so the assemblages may have experienced changes or homogenization over this time-frame (Riegl et al. 2012).

In overall assessments of the reef fish communities, Roberts et al. (2016) did not find any trends in endemism along the Red Sea's latitudinal gradient. When analyzing the distribution patterns of more specific taxonomic groups (e.g., families), however, some species appear to have restricted ranges within the Red Sea. For example, some species of butterflyfishes occur primarily in the northern and central regions of the Red Sea (Roberts et al. 1992). Each of these cases provides an interesting opportunity to examine factors that might control distribution of a given species, but this remains understudied.

While latitudinal gradients in assemblage composition throughout most of the offshore Red Sea reefs may be difficult to detect, stronger cross-shelf patterns may exist. At a scale of only 10s of km, (Khalil et al. 2017) found differences in both benthic and fish assemblages on reefs in the central Saudi Arabian Red Sea. Such cross-shelf gradients have been documented in other parts of the world (Malcolm et al. 2010), but have rarely been assessed in the Red Sea. Some species appear to be inshore specialists, while others only occur in offshore habitats. It is arguable that there are stronger environmental gradients between offshore and inshore habitats than there are along most of the latitudinal gradient of the Red Sea.

On the near-shore and fringing reef communities, stronger evidence of a latitudinal gradient is present (Sheppard and Sheppard 1991). The strongest community changes in both offshore and nearshore assemblages occur near the Farasan Islands. Unfortunately, the current political situation is a complicating factor restricting access and work in this region (the Farasan Islands complex bridges the border between Saudi Arabia and Yemen). Given the high productivity and turbidity of the Farasan Islands region, it seems likely that this area could contain one of the most unique reef assemblages, but this remains one of the most difficult places to sample.

Fishes are covered in more depth in Chap. 8. This is perhaps the best-studied group and provides several good examples of the challenges of addressing biogeography in an understudied region. These include sampling representative areas to determine with reasonable confidence that something is or is not present (critical to assess endemism), distinguishing widespread species from cryptic species complexes (Priest et al. 2016), anticipating regional variations in habitat

usage, and mis-identifications when relying on literature resources alone (e.g., note the number of corrections in Golani and Bogorodsky (2010)).

Even where (or especially where) the actual coral species or reef communities may not show large changes in species composition, the composition of their symbionts may provide some insight to the environmental conditions the host animals are experiencing (Hume et al. 2016; Sawall et al. 2014, 2015; Ziegler et al. 2017) (discussed in later chapters). The role of holobionts in local adaptations for widespread species is not fully understood, but the current notion is that all animals and plants evolved with microbial partners that contribute to the physiology and adaptation of their host organisms, particularly in extreme environments (Bang et al. 2018; McFall-Ngai et al. 2013). From the Red Sea, there are unique opportunities to examine these patterns, especially with regard to the response of corals (e.g., coral bleaching and coral disease) and other reef-associated organisms to climate change, which will be discussed in detail in later chapters (see also Furby et al. 2013; Monroe et al. 2018; Roik et al. 2015a).

Mangroves, mostly monospecific stands of *Avicennia marina*, occupy an estimated 120 km<sup>2</sup> in the Red Sea (Almahasheer et al. 2016a) along the narrow belt of intertidal zone in the Red Sea. In contrast with global declines in mangrove habitat, the area covered by mangroves on the Red Sea coast expanded by 12% over the 41-year period from 1972 to 2013. Mangroves shift in height from tree heights of about 15 m in the southern Red Sea to about 2 m near their northern limit at 28°N (Almahasheer et al. 2016a; Hickey et al. 2017). Mangroves are highly nutrient-limited in the northern half of the Red Sea, particularly with respect to iron, which, combined with cool winter temperatures, may result in the stunted nature of the trees (Almahasheer et al. 2016b).

Seagrass communities in the Red Sea include numerous mixed communities (dominated by *Thalassia hemprichii*, *Halophila ovalis*, and *Cymodocea rotundata*) prevalent in reef lagoons in the southern half of the Red Sea (Price et al. 1988), where they are heavily grazed by green turtles as well as thalassinidean and alpheid shrimps. Meadows of *Thalassodendrom ciliatum*, *Halophila stipulacea*, and *Enhalus acorodies* often form monospecific stands or patches (the former two more abundant in the north (Price et al. 1988)). Other dominant macrophytes include *Sargassum* and *Turbinaria* brown algae, which are prevalent on some inshore reef flats, and dense *Halimeda* populations in reef lagoons. Macroalgal abundance is highest in the southern Red Sea, where nutrient concentrations are higher. However, a recent study screened 7 species of seagrasses and 10 species of macroalgae measured at 21 locations, spanning 10° of latitude along the Saudi Arabian coast, and found that almost 90% of macrophyte species had iron concentrations indicative of iron deficiency and more than 40% had critically low

iron concentrations, suggesting that iron is a limiting factor of primary production throughout the Red Sea (Anton et al. 2018). However, no latitudinal pattern was detected in any of the performance parameters studied, indicating that, unlike the case for planktonic primary producers, the south to north oligotrophic gradient of the Red Sea is not reflected in iron concentration, chlorophyll-a concentration, or productivity of Red Sea macrophytes (Anton et al. 2018).

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