

## The status of coral reef ecology research in the Red Sea

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## **Abstract**

The Red Sea has long been recognized as a region of high biodiversity and endemism. Despite this diversity and early history of scientific work, our understanding of the ecology of coral reefs in the Red Sea has lagged behind that of other large coral reef systems. We carried out a quantitative assessment of ISI-listed research published from the Red Sea in eight specific topics (apex predators, connectivity, coral bleaching, coral reproductive biology, herbivory, marine protected areas, non-coral invertebrates and reef associated bacteria) and compared the amount of research conducted in the Red Sea to that of the Australia's Great Barrier Reef (GBR) and the Caribbean. On average, for these eight topics, the Red Sea had 1/6<sup>th</sup> the amount of research compared to the GBR and about 1/8<sup>th</sup> the amount of the Caribbean. Further, more than 50% of the published research from the Red Sea originated from the Gulf of Aqaba, a small area (< 2% of the area of the Red Sea) in the far northern Red Sea. We summarize the general state of knowledge in these eight topics and highlight areas of future research priorities for the Red Sea region. Notably, data that could inform science-based management approaches is badly lacking in most Red Sea countries. The Red Sea, as a geologically "young" sea located in one of the warmest regions of the world, has the potential to provide insight to pressing topics such as speciation processes as well as the capacity of reef systems and organisms to adapt to global climate change. As one of the world's most biodiverse coral reef regions, the Red Sea may yet have a significant role to play in our understanding of coral reef ecology at a global scale.

## **Introduction**

The Red Sea has long been recognized as a region of high biodiversity (Stehli and Wells 1971) and endemism (Ormond and Edwards 1987), home to well over 1000 species of fishes and over 50 genera of hermatypic corals. The Red Sea coral reefs were some of the first to be examined by early European taxonomists (e.g., Forsskåll, Ehrenberg, Ruppell, Klunzinger), but have become relatively inaccessible to Western scientists in recent decades due to complicated visa and permitting regulations, coupled with a lack of marine research infrastructure. Despite the size of the Red Sea and diversity of its reef-associated inhabitants, it remains a poorly studied system compared to other large coral reef systems around the world (e.g., the Great Barrier Reef or the Caribbean). The Red Sea, however, is of increasing interest to scientists working on climate change due to its relatively high and variable water temperatures (from 20°C in spring to 35°C in summer) and high salinity (c. 40.0 psu in the northern Red Sea; Edwards 1987). Consequently, the Red Sea is an ideal model system for understanding how reefs may fare under predicted scenarios of global climate change. It is arguably the world's warmest and most saline habitat in which extensive reef formation occurs.

Despite this biodiversity, early history of scientific work, and potential importance for understanding the ability of reefs to adapt and/or acclimate to changing environmental conditions there is a current lack of understanding of the ecology of Red Sea coral reefs. Researchers wishing to access information about the ecology of the Red Sea via modern channels (e.g., ISI or Google Scholar searches) will find relatively little information, particularly in recent years. Further, the vast majority of the accessible published research originates from a ~6km stretch of coastline in the far northern Red Sea, within the Gulf of Eilat / Aqaba (hereafter Gulf of Aqaba). We estimate that over

half of the recent research in the Red Sea originates from this region yet it represents less than 2% of the Red Sea area. There are many reasons to suspect that the processes in this relatively small and isolated region may not be representative of the broader Red Sea “proper” (sensu Head 1987).

This review seeks to quantify the number of ecological studies conducted in the Red Sea and compare this to the number of studies conducted in two other large coral reef systems, the Great Barrier Reef of Australia and the Caribbean. Specifically the objective of this review is to highlight the lack of research in the Red Sea by examining eight topics of current ecological interest in other coral reef systems, and comparing the current state of knowledge in these topics among three distinct biogeographic regions; the Red Sea, the Caribbean, and the Great Barrier Reef (GBR). The coral reef area within the Red Sea (c. 8,890 km<sup>2</sup>) is broadly comparable to that of the Caribbean (c. 10,530 km<sup>2</sup>). Although the reef area is only approximately half that of the GBR (c. 17,400 km<sup>2</sup>), these two reef systems are of similar length (Red Sea: c. 2,000 km; GBR: c. 2,300 km) making the Red Sea one of the longest coral reef system in the world.

We present below assessments of various disciplines falling broadly under the heading of “coral reef ecology”. We do not seek to comprehensively review details of all relevant research in these various disciplines, but rather to quantify the relative magnitude of work in the Red Sea as compared to other regions. Where appropriate, brief summaries of the primary focus of the work within each topic highlight areas where the Red Sea knowledge base is particularly weak. A number of Middle East countries are making a push to invest heavily in education and research institutions in the region (e.g., Mervis 2009), creating an opportunity for renewed and expanded research on coral reefs in the wider Red Sea. It is our hope that this review can highlight some areas in which these research efforts could quickly address important gaps in our knowledge.

## **General Methodology**

To quantify and compare the status of globally accessible research in the Red Sea, we identified eight areas of research focus of current interest to coral reef scientists (hereafter we will refer to these as “topics”), namely apex predators, connectivity, coral bleaching, coral reproduction, herbivory, marine protected areas, non-coral invertebrates (primarily sponges), and reef-associated bacteria. We then quantified the number of published studies in each of these topics using Thomson Reuter’s Web of Knowledge (WoK) and used various regional restrictors to compare the number of studies conducted within the Red Sea to that of the Great Barrier Reef and the Caribbean (Table 1; and see Electronic Supplementary Material for details).

## **Status of Ecological Research in the Red Sea**

### ***Apex Predators***

It is well documented that top predators are the most heavily exploited of marine organisms (Myers et al. 2007; Collette et al. 2011). The collapse of fisheries targeting large-bodied, long-lived, predatory teleosts and sharks, however suggests that it is unlikely that many of these species can be sustainably harvested at a commercially viable level without strict management (Walker 1998; Hilborn, 2007). Effective management can only be achieved through a thorough understanding of the ecology and population biology of these species. Unfortunately, for most Red Sea fisheries-targeted species, this information is completely lacking.

Our WoK search revealed only 39 Red Sea studies (> 60% of which were from the Gulf of Aqaba), compared to 85 from the Great Barrier Reef and 206 from the Caribbean (Table 1, ESM 1). An analysis of the few studies available on Red Sea top

predators showed that their objectives, with very few exceptions (e.g., Shpigel and Fishelson 1991; Belmaker et al. 2005; Clarke et al. 2011), focused on the physiology of a very limited number of species (e.g., Fishelson and Baranes 1997; Karpestam et al. 2007). In some cases, the principal focus was on other species, such as ospreys (Fisher et al. 2001), sponges (Burns and Ilan 2003), humans (Randall and Levy 1976), or parasites (Ivanov and Lipshitz 2006) and only relate peripherally to top predators. Interestingly, this is the only topic of the eight examined for which the Red Sea actually had more published research than the GBR up until the late 1990s, but has subsequently fallen behind (Fig. 1a).

There is a current lack of data on the population ecology, reproductive biology, resource partitioning, and migration patterns of apex predators in the Red Sea. This lack of management-relevant data poses a major obstacle for successful conservation planning. The GBR, which is also lacking essential data about the population status of its top predators, is nonetheless one of the most intensely managed reef systems in the world (McCook et al. 2010). While declines of top predator populations are more likely to be noticed in this type of well-managed system (Robbins et al. 2006), they would most likely go unnoticed in the Red Sea. In the Caribbean, the ecology of many predatory species has received considerable attention (e.g., Lutcavage et al. 1997; Pikitch et al. 2005) and many marine reserves have been established (Bond et al. 2012). In addition, apex predators are of high value to Caribbean and Australian tourism industries and are valued socially and culturally. This does not appear to be the case in any of the Red Sea countries.

If Red Sea marine ecosystems, and the goods and services that humans derive from them, are to be sustained, future work will have to focus on diversity, abundance, and life histories of top predator species within the Red Sea. Research priorities should

include species verification and areas of origin of all species taken directly or as by-catch in fisheries. There is a clear need to identify spatially and temporally sensitive areas, such as nurseries or seasons of high by-catch. Some of the larger, more mobile apex predators almost certainly cross national borders on a regular basis and potentially even have connections with Indian Ocean populations. Any attempts at management for these species will have to secure multinational cooperation – a nontrivial undertaking in this region of the world.

### *Connectivity*

Connectivity is a broad term that in the marine realm usually refers to “the demographic linking of local populations through the dispersal of individuals among them as larvae, juveniles or adults” (Sale et al. 2005). Coral reefs are naturally fragmented, discontinuous habitats and the extent to which reef associated species exchange individuals among spatially discrete populations has implications for their persistence, resilience and recovery (Jones et al. 2009). Connectivity is now recognized as an important parameter informing conservation and management decisions (e.g., Sale et al. 2005, Almany et al. 2009, McCook et al. 2009). Studies dealing with connectivity in coral reefs have dramatically proliferated in the last decade (Jones et al. 2009), and have been fuelled by the development of new genetic techniques (Lowe and Allendorf 2010). Yet the number of studies on connectivity within the Red Sea is minimal compared to the research that has been published from the GBR or the Caribbean (Fig 1b).

Our WoK search revealed only 77 Red Sea studies, compared to 471 from the Great Barrier Reef and 670 from the Caribbean (Table 1, ESM 2). We were primarily seeking research that clearly studied connectivity or population genetics, and explicitly

excluded studies only focusing on community structure. While many studies utilized genetic approaches for taxonomic purposes (especially for microbes), studies related to population connectivity and population genetics were rare. Of the 77 Red Sea connectivity studies, only 13 papers measured gene flow among populations within the Red Sea or between the Red Sea and adjacent regions. The majority of genetic studies were mostly phylogenies that included a few samples from the Red Sea as part of the phylogenetic trees but that did not actually measure gene flow or connectivity within this region.

Our search revealed only eight studies on fishes in the Red Sea. Among these eight studies, two used otolith chemistry to estimate connectivity among habitats while the remaining six studies used genetic markers to discern population structure. Fish are perhaps one of the best-studied groups in coral reefs in terms of phylogeography and population connectivity (Jones et al. 2009). Yet, in the Red Sea this field of study remains poorly addressed.

The unique geologic history of the Red Sea and the high number of endemic species that it harbors, make it an ideal system to study gene flow and speciation. In particular, there is an opportunity to investigate how biophysical gradients (from south to north), distance and historical fluctuations of the sea level have shaped the genetic diversity and species distribution in this region (DiBattista et al. 2013). There are likely to be some hidden genetic breaks throughout its length, and in general, connectivity studies will definitely help to reveal some insight to the processes and mechanisms at the origin of such high endemism rates that are present today in the Red Sea.

Connectivity studies are essential if effective spatial management is to be achieved in a region (McCook et al. 2009). Given a lack of such management in most of the Red Sea, future connectivity research should focus on elucidating general patterns of



larval dispersal, gene flow among populations, and linkages among the many types of coastal habitats found in the Red Sea (e.g., snapper migration corridors from coastal wetlands to reefs further offshore; McMahon et al. 2012). Such data would be essential to inform the design of marine protected areas, should there be a move to develop them within this region.

### *Coral bleaching*

Red Sea reefs thrive in the warmest and most saline waters of any extensive coral reef system in the world, due largely to the limited freshwater inflow and restricted water exchange with the Indian Ocean, (Sheppard et al. 1992). For this reason, Red Sea reefs have been assumed to be highly thermo-tolerant, and thus, predicted to be among the last reefs to bleach as seawater temperatures increase (Grimsditch and Salm 2006). However, recent observations of severe bleaching on inshore reefs in the central Red Sea (Furby et al. 2013) indicate that this prediction may be inaccurate, and raises questions as to whether bleaching events have been occurring in the Red Sea but were overlooked or not reported due to limited observer effort.

Our WoK search yielded only 12 relevant coral bleaching papers from the Red Sea compared with 339 from the GBR and 167 from the Caribbean (Table 1, ESM 3). More than half (7 out of 12) of the relevant Red Sea publications were conducted within the Gulf of Aqaba, showing both a general lack of information on the topic of coral bleaching in the Red Sea as a whole, as well as a very strong regional bias in the little information that is available.

Of the 12 ISI-listed publications found from the Red Sea, only one mentioned the actual occurrence of bleaching events in the Red Sea, recalling three major events all of which occurred in the 1990s in the central and southern Red Sea (Turak et al. 2007). The

description of these bleaching events was based largely on qualitative observations and contained very limited quantitative data. Of the remaining publications, four examined the effects of thermal stress or ultra-violet radiation on zooxanthellae and coral regulatory pathways (Winters et al. 2006, 2009; Zeevi-Ben-Yosef and Benayahu 2008; Kvitt et al. 2011), two discussed oceanographic aspects of thermal stress (Veal et al. 2010; Davis et al. 2011), and one used coral cores to quantify the deleterious effects of ocean warming on coral growth rates (Cantin et al. 2010). Other relevant papers investigated the possibility of Red Sea corals acting as refugia of biodiversity in scenarios of severe global environmental stress (Riegl and Piller 2003), included the Red Sea in a comparative review of global trajectories of the state of coral reefs (Pandolfi et al. 2003), or discussed the relationship between coral disease and bleaching (Rosenberg and Ben-Haim 2002; Danovaro et al. 2008).

It is readily apparent that research relating to coral bleaching in the Red Sea has lagged well behind that of the GBR and Caribbean. Studies quantifying the extent and severity of bleaching events in the Red Sea, the effect of bleaching on reef biodiversity and community structure, patterns of recovery, and predictions for the future are either lacking or are published in grey literature that is difficult to access (e.g., PERSGA/GEF, 2010). Although we do not know what tolerance thresholds Red Sea corals have, functional genomics work could make large advances in this field by addressing questions regarding the mechanisms for tolerance to the local environmental conditions. This is an obvious area in which Red Sea research could make significant contributions to global coral reef ecology.

In contrast, research from both the Caribbean and the GBR covers a more diverse variety of bleaching-related topics with a considerable number of publications concerned with each topic (Fig. 1c). Such topics include: detailed, quantitative, reports on bleaching

events (e.g., Baird and Marshall 1998; Jimenez 2001); investigations of potential causes of bleaching events (Gleason and Wellington 1993; Shinn et al. 2000); the effect of bleaching on different groups of organisms and various aspects of reef community structure and ecological processes (e.g., Meesters and Bak 1993; Mumby 1999; Baird and Marshall 2002); the tolerance thresholds of different coral taxa and clades of zooxanthellae to thermal stress (e.g., Marshall and Baird 2000; Lasker 2003); recovery patterns, long term considerations, and future predictions (e.g., Hughes 2003; Baker et al. 2008); and many other subtopics.

### ***Coral reproductive biology***

Over the past three decades considerable research has focused on the reproductive strategies (timing and mode of reproduction) of scleractinian corals (Baird et al. 2009). Early research focused on brooding taxa that employ internal fertilization and release fully-developed planulae (Harrison 2011), and led to the general misconception that brooding was the main form of larval development of reef corals. However, the discovery of mass spawning events in the mid-1980's on the Great Barrier Reef (Harrison et al. 1984; Babcock et al. 1986) challenged this view and established that hermaphroditic broadcast spawning is the predominate reproductive strategy among scleractinian corals. This reproductive strategy has since been the focus of most studies in coral reproductive biology. Currently, information on the sexual reproductive biology of scleractinian corals is available for over 444 species worldwide (Harrison 2011).

Our WoK search returned 11 articles on coral reproductive biology in the Red Sea (nine of which were from the Gulf of Aqaba). In comparison, 197 articles were found from the Great Barrier Reef and 108 from the Caribbean, which together represent over 50% of the total number of articles in this field (Table 1, ESM 4). Of the two articles

from the Red Sea basin that were not from the Gulf of Aqaba, one study described the synchrony of reproductive condition of *Acropora* species (Hanafy et al. 2010) and the other one found limited larval dispersal of a brooding coral after studying the gene flow between 2 locations in the Gulf of Aqaba and a third location in the main Red Sea basin located over 500 km away (Maier et al. 2005).

Interestingly, among the studies from the Gulf of Aqaba, one study revealed that spawning in this particular region of the Red Sea is asynchronous, with different species releasing gametes at different times throughout the year (Shlesinger et al. 1998). This seems to be in stark contrast with observations from the Great Barrier Reef where synchronous coral spawning seems to be a general trend (e.g., Shlesinger et al. 1998). However, two independent studies conducted in the main Red Sea basin have reported both the presence of synchronous spawning of *Acropora* species in the central Red Sea (Bouwmeester et al. 2011), and a strong synchrony in the gametogenesis of *Acropora* corals (Hanafy et al. 2010), suggesting that reproduction patterns differ between the Gulf of Aqaba and the central Red Sea. The generality of these patterns, however, needs to be investigated further.

To date, our knowledge of patterns of reproduction of corals in the main Red Sea (i.e., excluding the Gulf of Aqaba) are limited to a few species of *Acropora* (Hanafy et al. 2010), and our understanding of recruitment patterns is limited to a single study in the Gulf of Aqaba (Glassom et al. 2004). There is a clear need for future studies to document the reproductive modes of Red Sea corals, quantify the timing of spawning events and how they vary among species and locations, identify environmental cues that are associated with spawning events, and quantify pelagic larval durations and larval competency to better understand reproductive connectivity within the Red Sea.

## ***Herbivory***

Herbivory is widely accepted as a key process structuring benthic communities on coral reefs, and consequently is one of the most thoroughly studied aspects of coral reef ecology (e.g., Hay 1984; Hughes 1994). The importance of herbivory has long been recognised in coral reefs ecosystems worldwide (e.g., GBR: Stephenson and Searles 1960; Caribbean: Randall 1965; Red Sea: Vine 1974), however the majority of these early studies were largely descriptive. The increasing prevalence of anthropogenic and climate-induced disturbance and subsequent collapse of several reef systems from coral- to macroalgal-dominance highlighted the critical importance of herbivory, and brought this research area to the fore (Hughes 1994; McClanahan et al. 2001; Bellwood et al. 2004). This renewed emphasis led to marked increases in herbivory-focused research on the GBR and Caribbean reefs, but there was no corresponding increase in such research in the Red Sea (Fig. 1h). As a consequence, our current understanding of herbivory in the Red Sea is limited, and is based largely on inference from other regions.

Despite the considerable attention herbivory has attracted, our WoK search revealed that only 34 of the 1,066 herbivory papers (3.2%) were conducted within the Red Sea (Table 1, ESM 5). In marked contrast, herbivory has attracted much greater attention on the Great Barrier Reef (322 papers) and in the Caribbean (255 papers), accounting for 30% and 24% of herbivory studies, respectively.

Within Indo-Pacific and Caribbean reef systems a wealth of studies have documented large variation in the abundance and community structure of herbivores across a range of spatial scales (e.g., latitude: Floeter et al. 2005; shelf position: Hoey and Bellwood 2008; habitat: Hay 1981) and related this to variation in algal communities across similar scales (e.g., Wismer et al. 2009). These correlative relationships have been supported by experiments that have demonstrated the exclusion of herbivores leads to a

proliferation of algal biomass and a shift toward larger erect macroalgae (e.g., Hughes et al. 2007) and direct estimates of herbivory using macrophyte assays (e.g., McCook 1996). While this body of work clearly demonstrates the importance of herbivory per se, another suite of studies have focused on understanding the functional importance of individual taxa, the level of redundancy within functional groups, and the influence of habitat characteristics on foraging activities of herbivores (e.g., Bellwood et al. 2006; Mumby 2006; Burkepile and Hay 2006; Hoey and Bellwood 2011; Rasher et al. 2013). Collectively, these studies identified a functional dichotomy between those species that have the capacity to prevent (i.e., grazers) or potentially reverse (i.e., browsers) shifts to macroalgal-dominance on coral reefs.

In marked contrast, studies examining herbivory within the Red Sea have been largely restricted to descriptions of among-habitat variation in herbivore assemblages (e.g., Bouchon-Navaro and Harmelin-Vivien 1981; Brokovich et al. 2010). Apart from a couple of recent papers that have quantified variation in the role of parrotfishes on Red Sea reefs (Alwany et al. 2009; Afeworki et al. 2011) there is a lack of quantitative information on the role of herbivores in this region. The Red Sea contains many endemics for which basic dietary data is completely lacking. Future research should firstly focus on identifying the trophic and functional affinities of individual taxa, and quantifying large-scale variation (i.e., cross-shelf and latitudinal) in herbivore communities and functions. The limited rainfall and freshwater input into the Red Sea makes it an ideal system to examine the effects of herbivory in the absence of land-based eutrophication. For example, cross-shelf variation in benthic communities on the GBR, in particular the high macroalgal cover on inshore reefs, has been suggested to be related to increased nutrient input from terrestrial activities (Wismer et al. 2009). However, Saudi Arabian reefs in the central Red Sea display similar cross-shelf variation in benthic

communities (Hoey and Berumen, pers obs). Finally, comparisons of rates and agents of herbivory between the Red Sea and species-rich regions such as the GBR (the Red Sea has approximately one-third of the herbivore species richness of the GBR; Bellwood and Wainwright 2002) presents a unique opportunity to examine how herbivore diversity influences ecosystem process on coral reefs.

### *Marine protected areas*

Marine protected areas (MPAs) are increasingly popular tools for management of coral reef systems (Mora et al. 2006; Almany et al. 2009). Very few MPAs, unfortunately, have the luxury of having the full spectrum of scientific data available to ensure optimal reserve design (McCook et al. 2009). However, as MPAs become more prevalent, scientific attention is likewise growing in attempts model local characteristics to optimize reserve designs and to assess the effectiveness of existing MPAs.

As with other topics, our WoK search revealed only 17 Red Sea studies, compared to 220 from the Great Barrier Reef and 152 from the Caribbean (Table 1, ESM 6). Within the Red Sea Egypt has the largest number and greatest area of reefs within MPA's. Accordingly, the majority of the results from our WoK search were conducted in the Egyptian Red Sea (ESM 6). Of the studies conducted in Egyptian waters most investigated the effectiveness of established MPAs (Galal et al. 2002; Ashworth et al. 2006; Kochzius 2007; Marshall et al. 2010; Hannak et al. 2011; Samy et al. 2011). The concentration of this research on Egyptian reefs meant that of the eight topics reviewed, this topic had the lowest proportion of studies conducted within the Gulf of Aqaba.

Although very few quantitative data are available, it appears that many of the Red Sea reefs experience heavy fishing pressure (Jin et al. 2012) with little or no effective management. With the exception of perhaps Egypt, the need for management strategies

and implementation is readily apparent. There have been several, and relatively ambitious, plans for MPAs in some regions of the Red Sea. For example, in 1988 the IUCN/UNEP (1988) proposed 40 MPAs along the Saudi Arabian coast of the Red Sea. Most of these recommendations, however, have not been implemented and are generally hidden in grey literature. As several endemic species are targeted in the fisheries (e.g., DesRosiers 2011; Jin et al. 2012), and the region's largest oil producer (Saudi Aramco) has recently begun extraction operations in the Saudi Arabian Red Sea, there are compelling conservation motivations for creating a plan to sustainably harvest the natural resources of the Red Sea.

### ***Non-coral invertebrates (represented by sponges)***

Non-coral invertebrates provide the greatest biodiversity to coral reef environments, but are probably the least studied (Bouchet et al. 2002; Appeltans et al. 2012). The sheer number of invertebrate species inhabiting coral reefs prevented us from reviewing them collectively. Among all non-coral invertebrates associated to reef systems, sponges are an important structural and functional component of coral reefs (Diaz and Tzler 2001) and are among the most commonly studied non-coral invertebrates in reef systems. As such, they were selected as an “indicator” group to observe the trends and current state of research of invertebrates in the Red Sea relative to the GBR and the Caribbean.

Our WoK search revealed 23 studies on sponges from the Red Sea (18 from the Gulf of Aqaba), compared to 88 from the Great Barrier Reef and 170 from the Caribbean (Table 1, ESM 7). These 23 studies from the Red Sea do not seem to show any unifying theme. In fact, they span a broad spectrum of topics – from taxonomy to reproduction and anti-predatory defenses (e.g., Burns et al. 2003; Gugel et al. 2011). Further, several of the papers were not specific to sponges, instead focused more generally on benthic fauna



with only peripheral attention to sponges. Several articles detail the taxonomic identification of new species of sponges; these primarily originate from the Gulf of Aqaba (ESM 7). Of the five studies conducted outside the Gulf of Aqaba, two examined the community structure of sponges using genetic techniques (Wörheide 2006; Wörheide et al. 2008), while the remaining three papers examined symbiotic relationships with sponges and other organisms (Wilkinson and Fay 1979; Ilan et al. 1999; Magnino et al. 1999). As genetic tools and methods continue to be developed, sponges together with other non-coral invertebrates could prove to be ideal model organisms to address numerous evolutionary and ecological questions.

Non-coral invertebrates are understudied worldwide, and the lack of research on this group appears to be accentuated within the Red Sea. Future research should prioritize describing the diversity and distribution of non-coral invertebrates on Red Sea reefs. At the same time, new species may be screened for biomedical applications. Sponges and the vast array of bioactive compounds they harbor have long been of commercial interest for their potential pharmacological value. Given that intensive taxonomic efforts have lapsed since the earliest European naturalists visited, the Red Sea likely holds many exciting new discoveries. Given the number of endemic corals and fishes within the Red Sea, it is likely that a particularly long list of new species of non-coral invertebrates awaits description by modern taxonomy (with increasingly combined morphological and molecular approaches) in the Red Sea.

### ***Reef-associated bacteria***

Recent advances in meta-“omic” approaches have opened up entirely new fields of work related to coral- and reef-associated microbial communities (Rohwer and Youle 2010). Although the ecological role of most of these associated microbial communities remains

enigmatic in most cases, this is an emerging field of work that will inform research in coral disease, coral health and resilience, and likely even thermal tolerances. Our WoK search was restricted to “bacteria” as “microbiology” proved to be far too broad. We acknowledge that while our search may not capture all aspects of microbiology, it does provide a useful comparison of research efforts in this field among the three geographic regions.

Our WoK search revealed 41 Red Sea studies, compared to 342 from the Great Barrier Reef and 166 from the Caribbean (Table 1, ESM 8). Of all the topics we investigated, reef associated bacteria is among the most poorly studied outside of the Gulf of Aqaba. More than 80% of the papers our search returned were from the Gulf of Aqaba (33 out of 41 papers), with the vast majority of the Red Sea very poorly covered. Of the 41 papers from the Red Sea (ESM 8), six focused on the relationships between coral disease and certain bacteria (e.g., Arotsker et al. 2009; Zvuloni et al. 2009). Several publications focused on bacteria isolated from sponges (e.g., Kelman et al. 2001; Bergman et al. 2011) and from coral mucus (e.g., Kooperman et al. 2007; Shnit-Orland and Kushmaro 2009). Perhaps the most unusual studies are those regarding the giant bacterium *Epulopiscium fishelsoni*, an intestinal tract symbiont of some Red Sea surgeonfishes (e.g., Clements and Bullivant 1991; Angert et al. 1993). This enigmatic bacterium was originally discovered in the Red Sea and the paper that identified them as bacteria (as opposed to eukaryotic protists) is amongst one of the most highly cited papers from the region (Angert et al. 1993).

Globally, coral reef-associated microbial research is focusing on relationships between microbes and coral disease and more recently coral bleaching (e.g., Aronson and Precht 2001; Rosenberg et al. 2007). Notably, many studies now recognize the importance of identifying microbiota associated with corals, sponges, and other benthic

organisms under normal, “healthy” conditions (e.g., Rohwer et al. 2002; Taylor et al. 2007). In fact, most microbes are likely non-infectious and many play key roles in nutrient recycling of the reef ecosystem (Moriarty et al. 1985). Understanding the role of these microbial communities will no doubt add to our understanding of many interesting ecological phenomena. Microbial research on reefs in the Red Sea should continue to describe distribution, community composition, and function of reef-associated microbes to establish baseline data. The environmental conditions of the Red Sea, however, provide a unique opportunity to examine the role of microbes under elevated seawater temperatures and salinity. This may provide critical insights into the potential role of microbes on reefs worldwide under continued climate change.

## **GENERAL DISCUSSION**

Despite the extent of coral reefs in the Red Sea, the biodiversity and endemism these reefs contain, and the seminal work of early natural historians in the Red Sea, this region is sorely under-studied. On average across the topics we investigated, Australia’s Great Barrier Reef and the Caribbean have 6 and 8 times the number of published studies, respectively, than the Red Sea. The lack of available information represents, in many cases, a significant hurdle for conservation and management in the region. We hope that, by highlighting gaps and areas of most urgent need for research attention, we can spur work in these areas.

We do not intend to diminish the value of the work that has been done in the Red Sea region. Work from the Red Sea has undeniably been influential in coral reef ecology, as shown by the large number of results that arise due to the KeyWords Plus feature in WoK searches when using the term “Red Sea”. Specifically, this is an indication that many studies from other parts of the world cite heavily work based in the Red Sea.

Nonetheless, the current state of knowledge of coral reef ecology in the Red Sea is generally far behind that of comparable regions around the world. In light of forecast climate change, the Red Sea may serve as an important natural laboratory to help understand the near future for coral reefs elsewhere in the world. The increasing attention to research in the Red Sea can thus have broader impact than simple acquisition of region-specific knowledge.

While conducting this review, we have come across numerous relevant references that would traditionally be considered “grey” literature. Many Red Sea studies are published in conference proceedings or journals of local institutions that may be difficult for researchers outside of the region to discover. Of course, grey literature also exists for the other regions to which we compare the Red Sea results, but the relative importance of this body of knowledge is not clear. A substantial language barrier may exist for many researchers working in Red Sea countries, and in many cases these researchers may not submit their work to WoK-listed journals. In the Caribbean and Great Barrier Reef, however, it could be argued that a higher proportion of the authors are native English speakers, and many of these authors target WoK-listed journals. In these two regions, some hold a perception that grey literature represents work of insufficient quality to have been accepted in WoK-listed journals. On the other hand, many Red Sea researchers may view grey literature as a primary option for publication. A related observation is that the first authors for the vast majority of the WoK papers from the Red Sea are not natives of a Red Sea country. In other words, it appears that most of these papers are written by scientists visiting the region. This may be indicative of a fundamental difference in publication strategy between the Red Sea and the other two regions we assessed. Simply increasing the amount of research funding (or number of institutions) in the region would not likely address this fundamental challenge. Therefore, in parallel to increased capacity

and financial support, efforts for regional improvement should also focus on creative solutions to support local scientists to make a transition from targeting regional “grey” outlets to internationally recognized journals.

While we acknowledge that our WoK searches do not fully capture all possible known information about these areas of research, we maintain that these numbers reflect what is readily accessible to most colleagues who might take an interest in regional work. Although some databases do exist for “grey” Red Sea work (e.g., PERSGA 2010), in many cases some prior knowledge of these databases must exist in order to locate the articles. Therefore, a standardized WoK search likely reveals the actual relative state of internationally accessible knowledge available for each region. Again, our purpose in this review is not to definitively assess all available information from the Red Sea for each of our topics but rather to highlight the knowledge gap.

The Red Sea has the potential to once again have an important influence on coral reef ecology worldwide. As reefs face increasing pressure from global climate change, many authors have suggested that corals in the Red Sea may provide insight to mechanisms of adaptation or tolerance to elevated temperatures. Given the relatively young age of the Red Sea and high endemism of its fauna, the system may help us to understand speciation processes and other processes creating and maintaining biodiversity on coral reefs. Given general consensus that we are experiencing a global biodiversity crisis, coupled with limited resources for conservation, understanding these processes is more important than ever. The Red Sea represents a largely untapped scientific resource with great potential, and it is our hope that future work will strategically address many of these important gaps in our knowledge.

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## REFERENCES

- Afeworki Y, Bruggemann JH, Videler JJ (2011) Limited flexibility in resource use in a coral reef grazer foraging on seasonally changing algal communities. *Coral Reefs* 30: 109-122
- Almany G, Connolly S, Heath D, Hogan J, Jones G, McCook L, Mills M, Pressey R, Williamson D (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. *Coral Reefs* 28:339-351
- Alwany MA, Thaler E, Stachowitsch M (2009) Parrotfish bioerosion on Egyptian Red Sea reefs. *J Exp Mar Biol Ecol* 371: 170-176
- Angert ER, Clements KD, Pace NR (1993) The largest bacterium. *Nature* 362:239-241
- Appeltans W, Ahyong ST, Anderson G, Angel MV, Artois T, Bailly N, Bamber R, Barber A, Bartsch I, Berta A, Blazewicz-Paszkowycz M, Bock P, Boxshall G, Boyko CB, Brandão SN, Bray RA, Bruce NL, Cairns SD, Chan T-Y, Cheng L, Collins AG, Cribb T, Curini-Galletti M, Dahdouh-Guebas F, Davie PJF, Dawson MN, De Clerck O, Decock W, De Grave S, de Voogd NJ, Domning DP, Emig CC, Erséus C, Eschmeyer W, Fauchald K, Fautin DG, Feist SW, Franses CHJM, Furuya H, Garcia-Alvarez O, Gerken S, Gibson D, Gittenberger A, Gofas S, Gómez-Daglio L, Gordon DP, Guiry MD, Hernandez F, Hoeksema BW, Hopcroft RR, Jaume D, Kirk P, Koedam N, Koenemann S, Kolb JrB, Kristensen RM, Kroh A, Lambert G, Lazarus DB, Lemaitre R, Longshaw M, Lowry J, Macpherson E, Madin LP, Mah C, Mapstone G, McLaughlin PA, Mees J, Meland K, Messing CG, Mills CE, Molodtsova TN, Mooi R, Neuhaus B, Ng PKL, Nielsen C, Norenburg J, Opresko DM, Osawa M, Paulay G, Perrin W, Pilger JF, Poore GCB, Pugh P, Read GB, Reimer JD, Rius M, Rocha RM, Saiz-Salinas JI, Scarabino V, Schierwater B, Schmidt-Rhaesa A, Schnabel KE, Schotte M, Schuchert P, Schwabe E, Segers H, Self-Sullivan C, Shenkar N, Siegel V, Sterrer W, Stohr S, Swalla B, Tasker ML, Thuesen EV, Timm T, Todaro MA, Turon X, Tyler S, Uetz P, van der Land J, Vanhoorne B, van Ofwegen LP, van Soest RWM, Vanaverbeke J, Walker-Smith G, Walter TC, Warren A, Williams GC, Wilson SP, Costello MJ (2012) The magnitude of global marine species diversity. *Curr Biol* 22:2189-2202
- Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25-38
- Arotsker L, Siboni N, Ben-Dov E, Kramarsky-Winter E, Loya Y, Kushmaro A (2009) *Vibrio* sp as a potentially important member of the Black Band Disease (BBD) consortium in *Favia* sp corals. *Fems Microbiol Ecol* 70:515-524
- Ashworth JS, Bruce OE, El Hellw M (2006) Fish assemblages of Red Sea backreef biotopes. *Aquat Conserv: Mar Freshw Ecosyst* 16:593-609
- Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. *Mar Biol* 90:379-394
- Baird AH, Marshall PA (1998) Mass bleaching of corals on the Great Barrier Reef. *Coral Reefs* 17:376-376
- Baird AH, Marshall PA (2002) Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. *Mar Ecol Prog Ser* 237:133-141
- Baird AH, Guest JR, Willis BL (2009) Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution and Systematics* 40:551-571

- Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar Coast Shelf Sci* 80:435-471
- Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (ed) *Coral reef fishes: Dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, pp 5-32
- Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping functional group drives coral reef recovery. *Curr Biol* 16: 2434-2439
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429: 827-833
- Belmaker J, Shashar N, Ziv Y (2005) Effects of small-scale isolation and predation on fish diversity on experimental reefs. *Mar Ecol Prog Ser* 289:273-283
- Bergman O, Haber M, Mayzel B, Anderson MA, Shpigel M, Hill RT, Ilan M (2011) Marine-based cultivation of *Diacarnus* sponges and the bacterial community composition of wild and maricultured sponges and their larvae. *Mar Biotechnol* 13:1169-1182
- Bond ME, Babcock EA, Pikitch EK, Abercrombie DL, Lamb NF, Chapman DD (2012) Reef sharks exhibit site-fidelity and higher relative abundance in marine reserves on the mesoamerican barrier reef. *PloS ONE* 7:e32983
- Bouchet P, Lozouet P, Maestrati P, Heros V (2002) Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a New Caledonia site. *Biol J Linn Soc* 75:421-436
- Bouchon-Navaro Y, Harmelin-Vivien ML (1981) Quantitative distribution of herbivorous reef fishes in the Gulf of Aqaba (Red Sea). *Mar Biol* 63: 79-86
- Bouwmeester J, Khalil MT, De La Torre P, Berumen ML (2011) Synchronous spawning of *Acropora* in the Red Sea. *Coral Reefs* 30:1011
- Brokovich E, Ayalon I, Einbinder S, Segev N, Shaked Y, Genin A, Kark S, Kiflawi M (2010) Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. *Mar Ecol Prog Ser* 399: 69-80
- Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* 87: 3128-3139
- Burns E, Ilan M (2003) Comparison of anti-predatory defenses of Red Sea and Caribbean sponges. II. Physical defense. *Mar Ecol Prog Ser* 252:115-123
- Burns E, Ifrach I, Carmeli S, Pawlik JR, Ilan M (2003). Comparison of anti-predatory defenses of Red Sea and Caribbean sponges . I . Chemical defense, *Mar Ecol Prog Ser* 252: 105–114.
- Cantin NE, Cohen AL, Karnauskas KB, Tarrant AM, McCorkle DC (2010) Ocean warming slows coral growth in the Central Red Sea. *Science* 329:322-325
- Clarke C, Lea J, Ormond R (2011) Reef-use and residency patterns of a baited population of silky sharks, *Carcharhinus falciformis*, in the Red Sea. *Mar Freshw Res* 62: 668-675
- Clements KD, Bullivant S (1991) An unusual symbiont from the gut Of surgeonfishes may be the largest known prokaryote. *J Bacteriol* 173:5359-5362
- Collette BB, Carpenter KE, Polidoro BA, Juan-Jorda MJ, Boustany A, Die DJ, Elfes C, Fox W, Graves J, Harrison LR, McManus R, Minte-Vera CV, Nelson R, Restrepo V, Schratwieser J, Sun CL, Amorim A, Brick Peres M, Canales C, Cardenas G, Chang SK, Chiang WC, de Oliveira Leite N, Jr., Harwell H, Lessa R, Fredou FL, Oxenford HA, Serra R, Shao KT, Sumaila R, Wang SP, Watson R, Yanez E



- (2011) High value and long life-Double jeopardy for tunas and billfishes. *Science* 333:291-292
- Danovaro R, Bongiorno L, Corinaldesi C, Giovannelli D, Damiani E, Astolfi P, Greci L, Pusceddu A (2008) Sunscreens cause coral bleaching by promoting viral infections. *Environ Health Perspect* 116:441-447
- Davis KA, Lentz SJ, Pineda J, Farrar JT, Starczak VR, Churchill JH (2011) Observations of the thermal environment on Red Sea platform reefs: a heat budget analysis. *Coral Reefs* 30:25-36
- DesRosiers N (2011) Growth and maturation of *Plectropomus* spp. in the Saudi Arabian Red Sea. MSc thesis, King Abdullah University of Science and Technology, p69
- Diaz MC, Tzler K (2001) Sponges: An essential component of Caribbean coral reefs. *Bull Mar Sci* 69:535-546
- DiBattista JD, Berumen ML, Gaither MR, Rocha LA, Eble JA, Choat JH, Craig MT, Skillings DJ, Bowen BW (in press) After continents divide: comparative phylogeography of reef fishes from the Red Sea and Indian Ocean. *J Biogeogr*
- Edwards FJ (1987) Climate and oceanography. In: Edwards AJ, Head S (eds) *Key environments: Red Sea*. Pergamon Press, Oxford, pp45-68
- Fishelson L, Baranes A (1997) Ontogenesis and cytomorphology of the nasal olfactory organs in the Oman Shark, *Iago omanensis* (Triakidae), in the Gulf of Aqaba, Red Sea. *Anat Rec* 209:409-421
- Fisher PR, Newton SF, Tatwany HMA, Goldspink CR (2001) Variation in the diet of Ospreys *Pandion haliaetus*, Farasan Islands, southern Red Sea-preliminary observations. *Vogelwelt* 122:205-218
- Floeter SR, Behrens MD, Ferreira CEL, Paddock MJ, Horn MH (2005) Geographical gradients of marine herbivorous fishes: Patterns and processes. *Mar Biol* 147: 1435-1447
- Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of central Red Sea corals during a major bleaching event. *Coral Reefs* 22: 505-513
- Galal N, Ormond R, Hassan O (2002) Effect of a network of no-take reserves in increasing catch per unit effort and stocks of exploited reef fish at Nabq, South Sinai, Egypt. *Mar Freshw Res* 53:199
- Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea. *Mar Biol* 144:641-651
- Gleason DF, Wellington GM (1993) Ultraviolet radiation and coral bleaching. *Nature* 365:836-838
- Grimsditch GD, Salm RV (2006) Coral reef resilience and resistance to bleaching. IUCN, Gland, Switzerland, p 52
- Gugel J, Wagler M, Bruemmer F (2011) Porifera, one new species *Suberea purpureaflava* n. sp. (Demospongiae, Verongida, Aplysinellidae) from northern Red Sea coral reefs, with short descriptions of Red Sea *Verongida* and known *Suberea* species. *Zootaxa* 2994: 60-68.
- Hanafy MH, Aamer MA, Habib M, Roupahel AB, Baird AH (2010) Synchronous reproduction of corals in the Red Sea. *Coral Reefs* 29:119-124
- Hannak JS, Kompatscher S, Stachowitsch M, Herler J (2011) Snorkelling and trampling in shallow-water fringing reefs: Risk assessment and proposed management strategy. *J Environ Manage* 92:2723-2733
- Harrison PL (2011) Sexual reproduction of scleractinian corals. In: Dubinsky Z, Stambler N (eds) *Coral reefs: An ecosystem in transition*. Springer, Netherlands, pp59-85

- Harrison PL, Babcock RC, Bull GD, Oliver JK, Wallace CC, Willis BL (1984) Mass spawning in tropical reef corals. *Science* 223:1186-1189
- Hay ME (1981) Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquat Bot* 11: 97-109
- Hay ME (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* 65: 446-454
- Head SM (1987) Introduction. In: Edwards AJ, Head SM (eds) *Key environments: Red Sea*. Pergamon Press, Oxford, UK, pp1-21
- Hilborn R (2007) Moving to sustainability by learning from successful fisheries. *AMBIO* 36:0044-7447
- Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27: 37-47
- Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: a critical feedback on coral reefs? *Ecol Lett* 14: 267-273
- Hughes L (2003) Climate change and Australia: Trends, projections and impacts. *Austral Ecol* 28:423-443
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj M, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17: 360-365
- IUCN/UNEP (1988) *Coral reefs of the world: Volume 2: Indian Ocea, Red Sea and Gulf*. UNEP/IUCN, Gland, Switzerland and Cambridge UK/UNEP, Nairobi, Kenya
- Ilan M, Loya Y, Kolbasov GA, Brickner I (1999) Sponge-inhabiting barnacles on Red Sea coral reefs. *Mar Biol* 133: 709-716
- Ivanov VA, Lipshitz A (2006) Description of a new diphyllidean parasite of triakid sharks from the deep Red Sea. *J Parasitol* 94:841:846
- Jimenez C (2001) Bleaching and mortality of reef organisms during a warming event in 1995 on the Caribbean coast of Costa Rica. *Rev Biol Trop* 49:233-238
- Jin D, Kite-Powell HL, Hoagland P, Solow AR (2012) A bioeconomic analysis of traditional fisheries in the Red Sea off the coast of the Kingdom of Saudi Arabia. *Mar Res Econ* 27:137-148
- Jones GP, Russ GR, Sale PF, Steneck RS (2009) Theme section on “Larval connectivity, resilience and the future of coral reefs” *Coral Reefs* 28:303-305
- Karpestam B, Gustafsson J, Shashar N, Katzir G, Krüger RHH (2007) Multifocal lenses in coral reef fishes. *J Exp Biol* 210:2923-2931
- Kelman D, Kashman Y, Rosenberg E, Ilan M, Ifrach I, Loya Y (2001) Antimicrobial activity of the reef sponge *Amphimedon viridis* from the Red Sea: evidence for selective toxicity. *Aquat Microb Ecol* 24:9-16
- Kochzius M (2007) Community structure of coral reef fishes in El quadim bay (El quseir, Egyptian red sea coast). *Zool Middle East* 42:89-98
- Kooperman N, Ben-Dov E, Kramarsky-Winter E, Barak Z, Kushmaro A (2007) Coral mucus-associated bacterial communities from natural and aquarium environments. *FEMS Microbiol Lett* 276:106-113
- Kvitt H, Rosenfeld H, Zandbank K, Tchernov D (2011) Regulation of apoptotic pathways by *Stylophora pistillata* (Anthozoa, Pocilloporidae) to survive thermal stress and bleaching. *PLoS ONE* 6: e28665

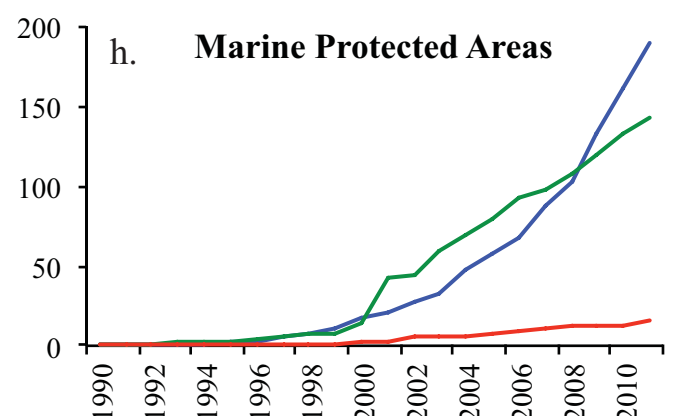
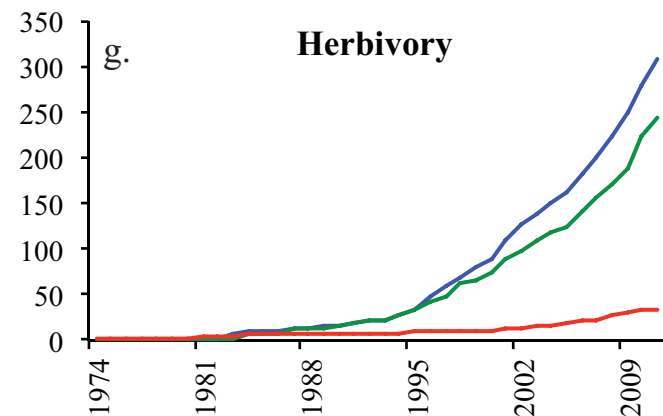
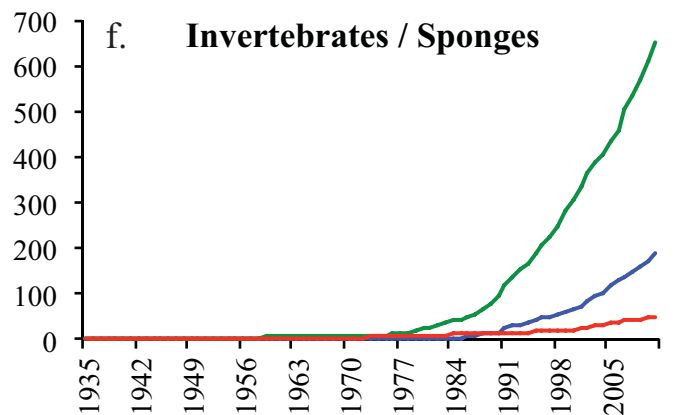
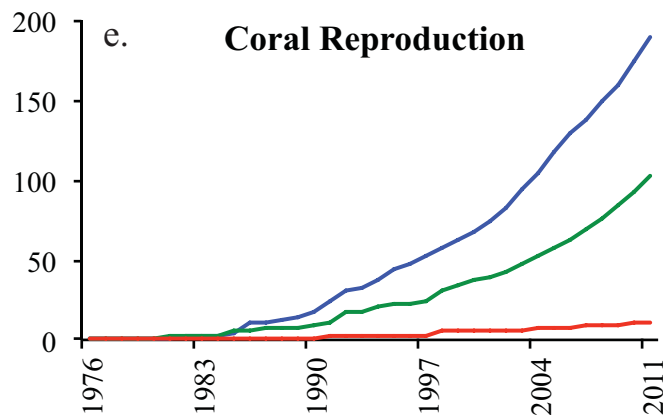
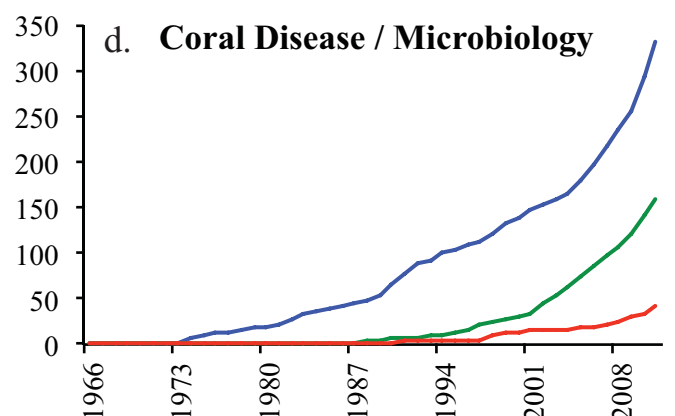
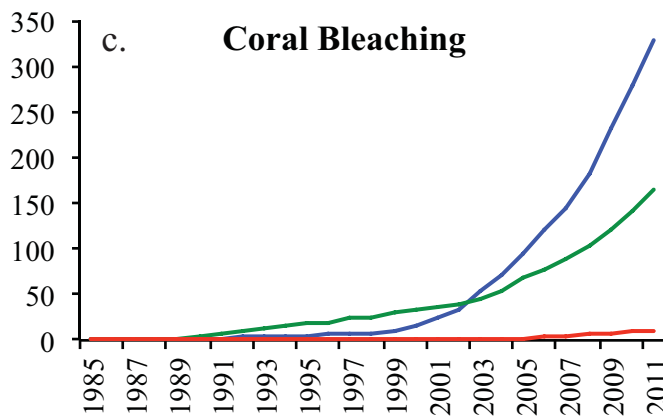
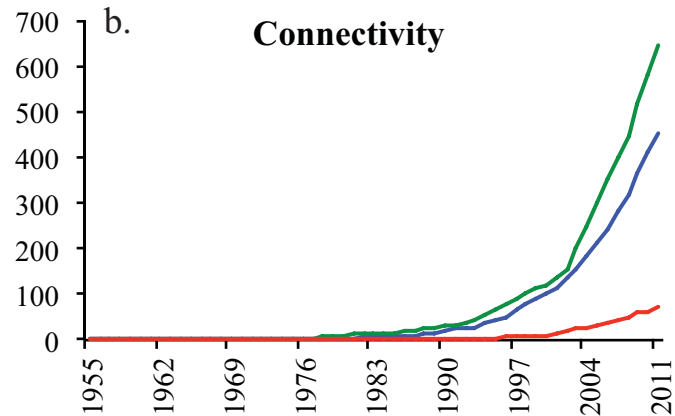
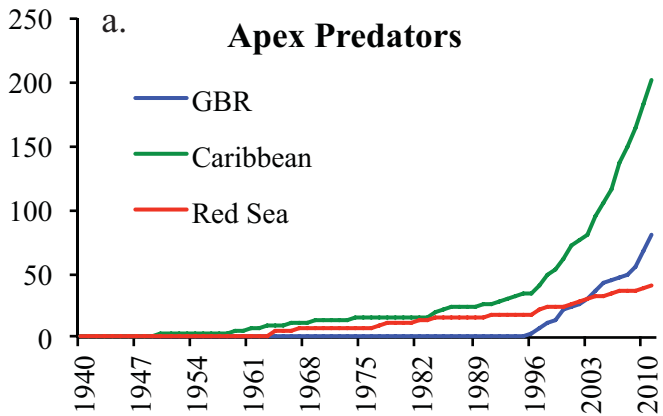
- Lasker HR (2003) Zooxanthella densities within a Caribbean octocoral during bleaching and non-bleaching years. *Coral Reefs* 22:23-26
- Lowe WH, Allendorf FW (2010) What can genetics tell us about population connectivity? *Mol Ecol* 19:3038-3051
- Lutcavage M, Kraus S, Hoggard W (1997) Aerial survey of giant bluefin tuna, *Thunnus thynnus*, in the great Bahama Bank, Straits of Florida, 1995. *Fish Bull* 95:300-310
- Maier E, Tollrian R, Rinkevich B, Nürnberger B (2005) Isolation by distance in the scleractinian coral *Seriatopora hystrix* from the Red Sea. *Mar Biol* 147:1109-1120
- Magnino G, Sarà A, Lancioni T, Gaino E (1999) Endobionts of the coral reef sponge *Theonella swinhoei* (Porifera, Demospongiae). *Invertebr Biol* 118: 213-220
- Marshall NA, Marshall PA, Abdulla A, Roupheal T (2010) The links between resource dependency and attitude of commercial fishers to coral reef conservation in the Red Sea. *Ambio* 39:305-313
- Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs* 19:155-163
- McClanahan TR, Muthiga NA, Mangi S (2001) Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19: 380-391
- McCook LJ (1996) Effects of herbivores and water quality on *Sargassum* distribution on the central Great Barrier Reef: cross-shelf transplants. *Mar Ecol Prog Ser* 139: 179-192
- McCook LJ, Almany GR, Berumen ML, Day JC, Green AL, Jones GP, Leis JM, Planes S, Russ GR, Sale PF, Thorrold SR (2009) Management under uncertainty: guidelines for incorporating connectivity into the protection of coral reefs. *Coral Reefs* 28:353-366
- McCook LJ, Ayling T, Cappo M, Choat JH, Evans RD, De Freitas DM, Heupel M, Hughes TP, Jones GP, Mapstone B (2010) Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves. *Proc Natl Acad Sci USA* 107:18278-18285
- McMahon KW, Berumen ML, Thorrold SR (2012) Linking habitat mosaics and connectivity in a coral reef seascape. *Proc Natl Acad Sci USA* 109:15372-15376
- Meesters EH, Bak RPM (1993) Effects of coral bleaching on tissue regeneration potential and colony survival. *Mar Ecol Prog Ser* 96:189-198
- Mervis J (2009) The big gamble in the Saudi desert. *Science* 326: 354-357
- Mora C, Andrefouet S, Costello MJ, Kranenburg C, Rollo A, Veron J, Gaston KJ, Myers RA (2006) Coral reefs and the global network of marine protected areas. *Science* 312:1750-1751
- Moriarty DJW, Pollard PC, Hunt WG (1985) Temporal and spatial variation in bacterial production in the water column over a coral reef. *Mar Biol* 85:285-292
- Mumby PJ (1999) Bleaching and hurricane disturbances to populations of coral recruits in Belize. *Mar Ecol Prog Ser* 190:27-35
- Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol Appl* 16: 747-769
- Myers R, Baum J, Shepherd T, Powers S, Peterson C (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315:1846-1850
- Ormond RFG, Edwards AJ (1987) Red Sea Fishes. In: Edwards AJ, Head SM (eds) *Red Sea: Key environments*. IUCN/Pergamon Press, Oxford, 251-287
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenahan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003)

- Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955-958
- PERSGA/GEF (2010) The Status of Coral reefs in the Red Sea and Gulf of Aden: 2009 PERSGA Technical Series Number 16. PERSGA, Jeddah
- Pikitch EK, Chapman DD, Babcock EA, Shivji MS (2005) Habitat use and demographic population structure of elasmobranchs at a Caribbean atoll (Glover's Reef, Belize). *Mar Ecol Prog Ser* 302:187-197
- Randall JE (1965) Grazing effects on sea greases by herbivorous reef fishes in the West Indies. *Ecology* 46: 255-260
- Randall JE, Levy MF (1976) A near-fatal shark attack by a mako in the northern Red Sea. *Isr J Zool* 25:61-70
- Rasher DB, Hoey AS, Hay ME (2013) Consumer diversity interacts with prey defences to drive ecosystem function. *Ecology* (doi:10.1890/12-0389.1)
- Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. *Int J Earth Sci* 92:520-531
- Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral-reef shark populations. *Curr Biol* 16:2314-2319
- Rohwer F, Youle M (2010) Coral reefs in the microbial seas. Plaid Press
- Rohwer F, Seguritan V, Azam F, Knowlton N (2002) Diversity and distribution of coral-associated bacteria. *Mar Ecol-Prog Ser* 243:1-10
- Rosenberg E, Ben-Haim Y (2002) Microbial diseases of corals and global warming. *Environ Microbiol* 4:318-326
- Rosenberg E, Koren O, Reshef L, Efrony R, Zilber-Rosenberg I (2007) The role of microorganisms in coral health, disease and evolution. *Nature Reviews Microbiology* 5:355-362
- Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS (2005) Critical science gaps impede use of no-take fishery reserves. *Trend Ecol Evol* 20:74-80
- Samy M, Sanchez Lizaso JL, Forcada A (2011) Status of marine protected areas in Egypt. *Anim Biodivers Conserv* 34:165-177
- Sheppard C, Price A, Roberts C (1992) Marine ecology of the Arabian region. Academic Press, London, p 359
- Shinn EA, Smith GW, Prospero JM, Betzer P, Hayes ML, Garrison V, Barber RT (2000) African dust and the demise of Caribbean coral reefs. *Geophys Res Lett* 27:3029-3032
- Shlesinger Y, Goulet T, Loya Y (1998) Reproductive patterns of scleractinian corals in the northern Red Sea. *Mar Biol* 132:691-701
- Shnit-Orland M, Kushmaro A (2009) Coral mucus-associated bacteria: a possible first line of defense. *FEMS Microbiol Ecol* 67:371-380
- Shpigel M, Fishelson L (1991) Experimental removal of piscivorous groupers of the genus *Cephalopholis* (Serranidae) from coral habitats in the Gulf of Aqaba (Red-Sea). *Environ Biol Fish* 31:0378-1909
- Stehli FG, Wells JW (1971) Diversity and age patterns in hermatypic corals. *Syst Biol* 20: 115-126
- Stephenson W, Searles RB (1960) Experimental studies on the ecology of intertidal environments at Heron Island. *Aust J Mar Freshw Res* 11:241-267
- Taylor MW, Radax R, Steger D, Wagner M (2007) Sponge-associated microorganisms: Evolution, ecology, and biotechnological potential. *Microbiol Mol Biol R* 71:295-347

- Turak E, Brodie J, DeVantier L (2007) Reef-building corals and coral communities of the Yemen Red Sea. *Fauna of Arabia* 23:1-40
- Veal CJ, Carmi M, Dishon G, Sharon Y, Michael K, Tchernov D, Hoegh-Guldberg O, Fine M (2010) Shallow-water wave lensing in coral reefs: a physical and biological case study. *J Exp Biol* 213:4304-4312
- Vine PJ (1974) Effects of algal grazing and aggressive behavior of the fishes *Pomacentrus lividus* and *Acanthurus sohal* on coral-reef ecology. *Mar Biol* 24: 131-136
- Walker TI (1998) Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Mar Freshw Res* 49:1448-6059
- Wilkinson CR, Fay P (1979) Nitrogen fixation in coral reef sponges with symbiotic cyanobacteria. *Nature* 279: 527-529
- Winters G, Beer S, Ben Zvi B, Brickner I, Loya Y (2009) Spatial and temporal photoacclimation of *Stylophora pistillata*: zooxanthella size, pigmentation, location and clade. *Mar Ecol Prog Ser* 384:107-119
- Winters G, Loya Y, Beer S (2006) In situ measured seasonal variations in F-v/F-m of two common Red Sea corals. *Coral Reefs* 25:593-598
- Wismer S, Hoey AS, Bellwood DR (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. *Mar Ecol Prog Ser* 376: 45-54
- Wörheide G (2006) Low variation in partial cytochrome oxidase subunit I (COI) mitochondrial sequences in the coralline demosponge *Astrosclera willeyana* across the Indo-Pacific. *Mar Biol* 148:907-912
- Wörheide G, Epp LS, Macis L (2008). Deep genetic divergences among Indo-Pacific populations of the coral reef sponge *Leucetta chagosensis* (Leucettidae): founder effects, vicariance, or both? *BMC Evol Biol* 8, 24
- Zeevi-Ben-Yosef D, Benayahu Y (2008) Synergistic effects of UVR and temperature on the survival of azooxanthellate and zooxanthellate early developmental stages of soft corals. *Bull Mar Sci* 83:401-414
- Zvuloni A, Artzy-Randrup Y, Stone L, Kramarsky-Winter E, Barkan R, Loya Y (2009) Spatio-temporal transmission patterns of Black-Band disease in a coral community. *PloS ONE* 4:e4993

**Figure 1:** Cumulative number of Web of Knowledge listed publications through time for various topics in coral reef ecology from three regions: Red Sea (red line), Australia's Great Barrier Reef (blue line), Caribbean (green line). Topics were searched on [apps.webofknowledge.com](https://apps.webofknowledge.com) using specific search terms (see Table 1) and refined by the respective region.

Number of publications in Web of Knowledge



**Table 1:** Summary results of the number of publications found using Web of Knowledge search engine for various topics and filtered for specific comparative regions of interest. Red Sea results are separated into all relevant Red Sea results and results exclusive of studies conducted only in the Gulf of Aqaba / Gulf of Eilat. Full details of the records for each search are included online as Electronic Supplementary Material (ESM) with the respective ESM file number indicated in the table.

Topic	Red Sea		Great Barrier Reef	Caribbean	All	ESM	Search Terms
	all	excluding Eilat/Aqaba					
Apex Predators	40	15	85	206	2014	1	"predatory fish*" OR shark*
Connectivity	77	41	471	670	26840	2	((structure or connectivity) and (genetic* or population*) marine) or (phyloge*) and (marine) not "community structure"
Coral Bleaching	12	5	339	167	1182	3	("coral bleaching" or "bleaching event")
Coral Reproduction	11	2	197	108	603	4	scleractinia* reproducti*
Herbivory	34	19	322	255	1066	5	(Herbiv* AND coral-reef OR Graz* AND coral-reef)
Marine Protected Areas	17	10	220	152	2247	6	("marine reserve*" or "marine protected area*" or "no take zone*" or "no entry zone*") and ("fisheries*" or "spillover*" or "catch*" or "fishing*")
Porifera	23	5	88	170	18570	7	Sponge* OR porifer* AND "coral reef"
Reef-Associated Bacteria	41	8	342	166	1555	8	reef bacteria*