Incidence of lesions on Fungiidae corals in the eastern Red Sea is related to water temperature and coastal pollution

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ABSTRACT

As sea surface temperatures rise and the global human population increases, large-scale field observations of marine organism health and water quality are increasingly necessary. We investigated the health of corals from the family Fungiidae using visual observations in relation to water quality and microbial biogeochemistry parameters along 1300 km of the Red Sea coast of Saudi Arabia. At large scales, incidence of lesions caused by unidentified etiology showed consistent signs, increasing significantly from the northern to southern coast and positively correlated to annual mean seawater temperatures. Lesion abundance also increased to a maximum of 96% near the populous city of Jeddah. The presence of lesioned corals in the region surrounding Jeddah was

strongly correlated with elevated concentrations of ammonium and changes in microbial communities that are linked to decreased water quality. This study suggests that both high seawater temperatures and nutrient pollution may play an indirect role in the formation of lesions on corals.

Key words: Scleractinia, Saudi Arabia, Microbes, Climate change, Marine ecology, Nutrients

1. Introduction

Corals are essential to the biological productivity of reef environments, but are being lost at increasing rates due to factors related to rising global sea surface temperatures (SST) and anthropogenic pressures (Hoegh-Guldberg 1999, McClanahan et al. 2002, Wilkinson 2008). Disease is particularly problematic for corals because it is often non-recoverable (Goreau et al. 1998, Harvell et al. 1999, Willis et al. 2004). Coral disease can be defined as a deviation from normal structure or function, accompanied by a characteristic set of clinical signs (Work and Aeby 2006). A number of studies have quantified diseased corals, including the presence of lesions or morphologic alterations on the coral, in some cases finding as many as 50% of corals affected on a reef (e.g., Antonius 1984, Edmunds 2002, Peters 1984, Porter et al. 2001, Sato et al. 2009). Understanding the causal factors related to coral disease is complicated, as the holobiont is composed of an assemblage of disparate organisms including the animal host, symbiotic dinoflagellate algae (*Symbiodinium* spp.), bacteria, archaea, fungi and viruses. The degree to which these organisms interact to maintain a healthy, functioning coral is a question of fundamental

49 importance to our understanding of the disease state.

50 On a global scale, climatic warming is expanding the range and increasing the
51 virulence of certain pathogens (Harvell et al. 2002, 2007, Rosenberg and Ben-Haim
52 2002). Anomalously high water temperatures are correlated with outbreaks of coral
53 diseases (Bruno et al. 2007, Harvell et al. 2002, Hayes et al. 2001, Porter et al. 2001,
54 Willis et al. 2004). Understanding the relationship between disease and SST is necessary
55 to predict and mitigate future disease outbreaks in corals and may help pinpoint
56 geographic regions at risk for disease development.

57 Poor water quality from nutrient pollution or sedimentation is also a major factor
58 linked to declines in coral health (e.g., Acosta 2001, Bruno et al. 2003, Pastorok and
59 Bilyard 1985). In particular, moderate increases in nutrient concentrations have been
60 shown to cause a significant increase in severity of coral disease. In experimental field
61 manipulations, the application of fertilizer (>1μM concentration each of nitrate,
62 ammonium and phosphorus) caused an increase in both the spread of disease and host
63 tissue loss (Bruno et al. 2003). High nutrient levels can also negatively impact coral
64 recruitment, coral cover, and community composition (Fabricius 2005). In addition to
65 nutrients, abundances and major types of microorganisms are an important component of
66 water quality. For example, ratios of heterotrophic to autotrophic bacteria can indicate an
67 imbalance in an oligotrophic reef environment (Dinsdale et al. 2008). Understanding the
68 relationships between coral disease and multiple components of water quality and
69 biogeochemistry is important to quantifying the influence of these factors on coral health.

70 Finally, aquaculture may be a source of bacterial pathogens to the marine
71 environment and thus may play a role in the distribution of coral disease. Some strains of

Vibrio spp. have been found to cause disease in aquaculture facilities (Ruangpan and Kitao 1991) and are highly similar to *Vibrio* spp. found associated with Yellow Band Disease in hard and soft corals (Cervino et al. 2004a, 2008, 2012). Aquaculture facilities are expected to proliferate globally over the next twenty years (Brugère and Ridler 2004), and their increased abundance may present threats to corals and other marine organisms. The exact relationship between aquaculture effluent and coral health is unknown, and examining the occurrence of diseased corals in relation to known aquaculture facilities may provide evidence for such a link.

The Red Sea provides an ideal environment for understanding the factors influencing coral health because it experiences a wide gradient of temperatures, little terrestrial runoff or freshwater input, and anthropogenic impacts that are almost exclusively isolated, point-source pollution. The temperature gradient ($\pm$ 4°C mean annual) across the length of the Red Sea allows an opportunity to study reefs residing in substantially warmer versus cooler waters but otherwise with similar properties. In addition, water quality and coral health on individual reefs in close proximity to Jeddah can be studied to assess the impacts of pollution from a highly developed urban coastline. Finally, the waters off the city of Al Lith in the south-central Red Sea region encompass a gradient of distal to proximal reefs subjected to differing amounts of effluent from a large aquaculture facility.

In this study, we characterized the health status of Fungiidae (mushroom corals) in the eastern Red Sea. The Fungiidae family is comprised of scleractinian coral species with free-living and attached life cycles and solitary and colonial morphologies (Hoeksema 1989). Certain fungiids are capable of active movement across substrate, are

95 competitively aggressive, and are able to regenerate and bud asexually in disturbed
96 habitats (Chadwick 1988, Gilmour 2004, Sheppard 1979). Several studies have found
97 them to be tolerant to sedimentation, despite a life cycle that often ends with the adult
98 coral living on sandy substrate on reef edges (Erftemeijer et al. 2012, Hoeksema 1989,
99 Schuhmacher 1977).
100 We surveyed reef sites from the straits of Tiran in the north to the Farasan Banks
101 in the south (approx. 1300 km) over the course of three years, to determine how reef
102 environment affects a family of free-living, reef-building coral (Fungiidae: genera as
103 identified in Veron 2000, *Fungia, Ctenactis, Herpolitha*). These genera were chosen for
104 this study because they were identified during initial surveys as exhibiting consistent
105 patterns of lesions. The lesion patterns were categorized as "Yellow Band Disease-like"
106 due to their visual similarity to lesions described as Yellow Band Disease (YBD) in
107 *Fungia* and *Herpolitha* spp. mushroom corals from Indonesia (Cervino et al. 2008).
108 However, the necessary investigations have not been completed to confirm that this is
109 YBD in the Red Sea. A cultivation-independent microbiological study of *Ctenactis*
110 *crassa* and *Herpolitha limax* does not suggest a clear pathogen assemblage occurring
111 with the lesioned corals (Apprill et al. 2013), and ongoing work is addressing the
112 histopathological and genetic details of this disease system. The aims of this study were
113 to: (1) quantify the distribution of lesions in fungiid corals throughout the eastern Red
114 Sea; and (2) quantify the relationship between lesion incidence and environmental
115 factors, including sea surface temperature, water quality, and proximity to urbanity and
116 aquaculture facilities.
117

2. Materials and Methods

2.1. Coral surveys

Fungiid populations were surveyed at 56 reefs on the outer shelf of the Red Sea along a 1300 km stretch of Saudi Arabia (Fig. 1). This study was completed over the course of 2008 - 2010 using five separate cruises: 11-22 November 2008 (central Red Sea), 9-25 June 2009 (southern Red Sea), 1-14 October 2009 (southern Red Sea; with frequent sampling near the aquaculture facility in Al Lith), 18-30 May 2010 (northern Red Sea), and 1-15 September 2010 (northern Red Sea) (Supplementary Table 1). Three coral genera from the family Fungiidae were included in the investigation: *Fungia, Herpolitha,* and *Ctenactis* (taxonomy according to Vernon 2000). Belt transect surveys of 50 m x 1 m (Hoeksema 2012a,b) were completed at 10 m, the average depth of reefs in the study area using SCUBA, and 2-4 transects were assessed per reef. All fungiids within transects were identified to genus and categorized as healthy, bleached or lesioned.

Healthy fungiids showed no visible signs of stress (Fig. 2A, B). The coral tissue was typically a deep brown color that paled towards the edges of the septal ridges. Bleached fungiids frequently exhibited a white mottled pattern (Fig. 2C) or were uniformly pale (Fig. 2D). When mottled, the bleaching areas appeared haphazardly located on the surface of the coral, with indistinct edges between healthy and bleached areas. Fungiids with a yellow blotch pattern similar to those found by Cervino and colleagues (2008) were classified as ‘lesioned’ (Fig. 2E, F). Macro photos illustrate the margins of the lesions and extent of tissue damage (Fig. 2G, H). Characteristics of fungiid lesions included: central and peripheral location, multifocal to coalescing distribution, lanceolate to irregular shape with distinct edges and smooth margins, and a

pale yellow discoloration. The lesions are two-dimensional and small in size relative to coral (or polyp) size. The number of lesions per coral varied. Symptoms of tissue loss without algal growth, as well as skeletal degradation, were observed occasionally but not quantified in this study.

2.2. Water sampling

Seawater was sampled for measurements of inorganic nutrients and microbial abundances at sites during the 2009 and 2010 cruises (Supplementary Table 1). Seawater was sampled just above the depth of corals, approximately 10 m, using a Masterflex peristaltic pump (Cole Parmer, Vernon Hills, IL, USA). For inorganic nutrients, water was collected from the same depth into 150 ml polypropylene acid-washed bottles and frozen at -20°C. Samples (1 ml) for microbial abundances were fixed in a final concentration of 1% (v:v) paraformaldehyde and stored in cryovials in liquid nitrogen for 3 weeks, followed by storage at -80ºC until analysis.

2.3. Nutrient analysis

Dissolved inorganic nutrient concentrations (ammonium, nitrate + nitrite, phosphate and silicate) were measured using a continuous segmented flow system consisting of a Technicon AutoAnalyzer II (SEAL Analytical, Mequon, WI, USA) and an Alpkem RFA 300 Rapid Flow Analyzer (Alpkem, Clackamas, OR, USA). Phosphate was measured using a modified molybdenum blue method (Bernhart and Wilhelms 1967). Standard methods were utilized to measure nitrate + nitrite (Armstrong et al. 1967). Ammonium was measured using the indophenol blue method (U.S. Environmental

Protection Agency, 1983), and concentrations were verified using the method of Holmes et al. 1999.

2.4. Direct cell counts

Microbial abundances were determined using flow cytometry. In order to enumerate both pigmented and non-pigmented cells, aliquots of the preserved water samples were analyzed in two manners, stained and unstained. Unstained samples were run on an EPICS ALTRA flow cytometer (Beckman Coulter Inc., Brea, CA, USA), and excitation in the visible wavelengths was used to enumerate cyanobacteria (*Prochlorococcus* and *Synechococcus* spp.) and eukaryotic phytoplankton (picoplankton), on the basis of chlorophyll (red fluorescence, 680 nm), phycoerythrin (orange fluorescence, 575 nm), forward scatter, and 90° side scatter signatures. A second aliquot of sample was diluted 1:10 into 30 mM (final) potassium citrate buffer, and stained with Sybr Green I (1:5000 final dilution of initial stock) (Molecular Probes, Eugene, OR, USA) for two hours in the dark at 4°C. Excitation at 488 nm on the same machine was used to enumerate picoplankton on the basis of DNA staining (Sybr Green I green fluorescence, 525 nm), chlorophyll (red fluorescence), phycoerythrin (orange fluorescence), forward scatter, and 90° side scatter signatures, and counts of *Prochlorococcus* spp. cells from unstained samples were subtracted from total prokaryotic cells (as indicated by their DNA signature) to obtain abundances of non-pigmented picoplankton. Data were analyzed off-line using FlowJo software (v. 6.3.3, Tree Star, Inc., Ashland, OR, USA).

187 *2.5. Sea surface temperature*

188 Sea surface temperature (SST) data were obtained from the MODIS (MODerate
189 Resolution Imaging Spectroradiometer) sensors onboard the NASA Aqua platform using
190 mid-infrared (IR) and thermal IR channels (Brown and Minnett 1999; Walton et al.
191 1998). SST data used in this study were produced with the Giovanni online data system,
192 developed and maintained by the NASA GES DISC (Acker and Leptoukh 2007). The
193 SST data were acquired at 9 km spatial resolution, with averages computed over three
194 years, corresponding to the same period as the coral health surveys (October 2007 -
195 2010).

196

197 *2.6. Statistical Analysis*

198 A principal component analysis (PCA) was used to explore relationships between
199 environmental parameters directly measured at each site, as well as latitude and SST.
200 The analysis did not include information about the lesioned corals, and these data were
201 overlaid onto the symbols for each site. The analysis was conducted using PRIMER
202 version 6.1.13.

203 Linear regressions were performed to quantify the relationships between coral
204 lesion incidence and environmental variables including SST, inorganic nutrient
205 concentrations, microbial communities, and distance from point sources including a
206 major urban area (Jeddah) and aquaculture facility (Al Lith). Relationships that did not
207 follow normal distributions were further explored using data transformations, and square
208 root and logarithmic transformations of data were found to minimize non-normal

residuals and therefore the transformed data were presented in the relevant figures. Analyses were conducted using StatPlus version 5.8.0, 2009.

3. Results

3.1. Fungiid health in the Eastern Red Sea

Individual fungiid corals were characterized as healthy, bleached or lesioned along a 1300 km transect in the eastern Red Sea, and the proportions of corals displaying these health categories varied greatly between sites (Fig. 3). Bleaching of free-living corals could be related to multiple factors including irritation by sediment and inversion on the seafloor, as well as abnormal temperatures (Schuhmacher 1977). For this reason, although the study quantified bleaching, bleaching was not investigated further. Lesioned corals were further investigated, and lesions were found to affect 27% of fungiids throughout the reefs surveyed. On the broadest spatial scale, lesioned fungiids were more prominent on southern compared to northern Red Sea reefs (Fig. 4), and this trend is statistically significant (Mood median test, Chi-squared = 214 15.96, DF = 3, p = 0.001). On smaller scales, particularly in the central Red Sea, lesioned fungiids peaked to incidences of 97%, and were more prevalent north of the city of Jeddah, a major Saudi Arabian city on the coast (Fig. 4).

3.2 General properties of nutrients, microbial abundances and SST in the eastern Red Sea

Seawater inorganic nutrient concentrations were measured at 45 of the 52 sites surveyed for coral health (Supplementary Table 1). Concentrations of phosphate ranged

232 from 0.021 – 0.132 μM, (mean 0.062 μM), and were generally lower at the northernmost
233 sites (Supplementary Fig. 1A). Concentrations of nitrate + nitrite ranged between 0.004 -
234 0.528 μM (mean 0.181 μM) and were generally < 0.2 μM at the northernmost sites
235 (Supplementary Fig. 1B). Ammonium concentrations were mostly below detection,
236 ranging from 0.004 – 2.972 μM, with a mean concentration of 0.169 μM (Supplementary
237 Fig. 1C). Elevated concentrations of ammonium, 0.26 – 1.3 μM, were detected at three
238 sites just north and down current of the city of Jeddah. Silicate at all sites ranged from
239 0.305 – 1.152 μM with a mean concentration of 0.793 μM (Supplementary Fig. 1D).
240 Abundances of the major microbial groups were also measured at 38 of the 52
241 survey sites as an indirect indicator of water quality (Supplementary Table 1,
242 Supplementary Fig. 2). In the water above the reefs surveyed, heterotrophic bacteria
243 ranged from $3.6 \times 10^5 – 1.4 \times 10^6$ cells ml^{-1} (mean 5.8×10^5 cells ml^{-1}), with the highest
244 concentrations at the southernmost site of Sumayr (Supplementary Fig. 2A).
245 Concentrations of *Synechococcus* varied from $2.6 \times 10^3 – 2.2 \times 10^5$ cells ml^{-1} (mean $5.0 \times$
246 10^4 cells ml^{-1}), with a trend of fewer cells at the northern latitude reefs (Supplementary
247 Fig. 2B). *Prochlorococcus* cells ranged from undetectable to 1.1×10^5 cells ml^{-1} (mean
248 4.6×10^4 cells ml^{-1}) throughout the surveyed reefs (Supplementary Fig. 2C). Reefs
249 where *Prochlorococcus* were undetectable were located in the central Red Sea, offshore
250 and directly north of the city of Jeddah (spanning 21.6 - 22.4°N latitude). The remaining
251 sites contained at least 21,000 *Prochlorococcus* cells ml^{-1}. Picoeukaryote abundance
252 ranged from $90 – 7.5 \times 10^3$ cells ml^{-1} (mean 3.1×10^3) at all sites, with similar
253 concentrations throughout the basin (Supplementary Fig. 2D).

Prokaryotic metabolism, indirectly assessed using the ratio of heterotrophic to autotrophic (*Prochlorococcus* + *Synechococcus*) bacterial cells, exhibited a large range at the surveyed sites, 1.2 – 27.8 (mean 8.0). Ratios were generally lower (increased autotrophy) in the southern Red Sea (Supplementary Fig. 2E). Ratios at one site in the southern Red Sea (AQ3 at 19.1°N) was especially low, < 1.5, and one site in the northern Red Sea (Pisces I, 27.3°N) was exceptionally high, with a cellular ratio of 27.8.

SST was not directly measured at each site, but satellite data revealed that mean-annual SST averaged over three years for each study site ranged from 26°C to 29.5°C (Supplementary Figure 3). The highest temperatures were concentrated in the southern region.

3.3 *Relation of lesioned corals to Red Sea environmental conditions*

A principal component analysis (PCA) examined the relationship between the different environmental parameters measured at each site, as well as latitude and SST. This analysis indicated that sites with high numbers of lesioned corals (>60%) were associated with the PC2 axis, and were related to increasing concentrations of ammonium, as well as decreasing abundances of silicate, *Prochlorococcus* spp. and heterotrophic bacteria (Fig. 5). Sites with minimal percentages of lesioned corals associated more with the PC1 axis, and were related to higher latitude, lower SST, and decreased abundances of *Synechococcus* spp. Thus, SST, microrganisms, inorganic nutrients and geographic latitude were related to incidences of fungiid lesions across the eastern Red Sea.

The environmental parameters that were particularly identified as variables exhibiting a relationship with the presence or absence of lesioned corals were explored

277 individually in more detail. To examine SST as a potential factor influencing fungiid
278 lesions, three-year mean SST was examined against percentage of lesioned corals at each
279 site. A significant relationship exists, with higher incidences of lesions generally
280 occurring in the warmer water ($r^2 = 0.25555$, $p = 0.0021$ $n = 52$; Fig. 6).
281 Regression and correlation analysis of relationships between lesioned corals and
282 microbial cellular abundance revealed that significant interactions exist for
283 *Prochlorococcus* spp. ($r^2 = 0.20527$, $p = 0.0049$, $n = 38$; Fig. 7A), *Synechococcus* spp.
284 ($r^2 = 0.21463$, $p = 0.004$, $n = 38$; Fig. 7B) and picoeukaryote abundances ($r^2 = 0.17239$, p
285 $= 0.0106$, $n = 38$; Fig. 7C), compared to occurrence of coral lesions. The regression
286 analysis also indicated that *Prochlorococcus* spp. decreased as lesion occurrences
287 increased, whereas *Synechococcus* spp. and picoeukaryote abundances increased with
288 increasing percentage of lesions. There were no relationships between abundances of
289 heterotrophic bacteria and lesioned corals (Fig. 7D), and the ratio of heterotrophic to
290 autotrophic prokaryotes was also not significantly related to lesioned corals (Fig. 7E).
291 Similar to the findings for the PCA analysis, regression analysis of lesioned corals
292 compared to concentrations of ammonium ($r = 0.21835$, $p = 0.004$, $n = 38$; Fig. 8A) and
293 silicate ($r = 0.13991$, $p = 0.025$, $n = 38$; Fig. 8B) were found to be significant. Higher
294 ammonium concentrations were associated with greater percentages of lesions, and the
295 opposite relationship was found for silicate (low silicate when lesions were more
296 prevalent). However, it should be noted that although the relationship between
297 ammonium and lesioned corals was significant, at many sites concentrations were below
298 detection and this trend was only apparent at the local scale near the Red Sea's largest
299 city of Jeddah. No significant relationship was found between the percentages of coral

lesions at each site and concentrations of phosphate (Fig. 8C) or nitrate and nitrite (Fig. 8D).

3.4 Urban and aquaculture influences on coral lesions

The nutrient and microbial data in the eastern Red Sea suggest that there may be specific point-source impacts from the surrounding terrestrial environment. Lesioned corals were prominent south of Al-Lith, a city supporting a low population (<130,000 people; Central Department of Statistic) but a large shrimp aquaculture facility. The potential impact of aquaculture pollutants on lesioned corals was assessed using regression analysis with distance from the aquaculture outfall, and did not demonstrate a significant relationship (Fig. 9A).

A relationship between distances from the major urban center of Jeddah (population 3.4 M; Central Department of Statistics) was found using regression analysis. Specifically, abundances of lesioned corals were significantly related to distance from Jeddah (Fig. 9B). Populations of the other eastern Red Sea cities were considerably lower than Jeddah (25,568 – 233,236 people; Central Department of Statistics) and were not further investigated.

3.5 Urban water quality related to lesioned corals near Jeddah: a summary

The relationships between lesioned corals and water quality and proximity to Jeddah were further examined on a scale relative to point source pollutants. Oceanographic currents along the eastern Red Sea shore generally move from the south to the north, and both concentrations of ammonium and lesion occurrence reached

maximum values at the first site north of Jeddah (~40km), and then decreased with distance northward (Fig. 10). In the same sites immediately north of Jeddah, the oligotrophic bacteria *Prochlorococcus* spp. were absent. The lack of *Prochlorococcus* spp. cells near Jeddah coincides with the comparatively high concentrations of coastal-derived ammonium, which are orders of magnitude lower at all other reef sites examined. Collectively, these data provide evidence for decreased water quality (elevated ammonium, undetectable oligotrophic bacteria (*Prochlorococcus* spp.) and increased occurrences of coral lesions near the city of Jeddah; each signal diminishes with distance north from Jeddah.

4. Discussion

4.1 Prevalence of lesioned fungiids

The prevalence of lesioned *Fungiidae* corals along the eastern coast of the Red Sea was high (average 27%, peak prevalence of 97%) compared to previous quantifications of coral lesions in the Caribbean and Great Barrier Reef (Green and Bruckner 2000, Porter et al. 2001, Sato et al. 2009, Willis et al. 2004). These previous studies report 5-65% incidence of colonies affected by black band disease (BBD), white diseases, and YBD. In this Red Sea study, higher prevalence of lesioned corals was correlated to factors including seawater temperature and water quality, reflected by inorganic nutrients and microbial abundances. These data suggest that both regional climate (temperatures) and local pressures from urban areas affect the health of Red Sea corals.

4.2 Sea surface temperature (SST) related to lesioned corals

There was a clear pattern of higher prevalence of lesions on the mushroom corals in the southern Red Sea. The southern Red Sea typically experiences 1.5 – 2.5°C higher mean annual SST than the northern Red Sea. In particular, higher incidences of lesions were found in southern and central Red Sea reefs, and bleaching was a common phenomenon affecting fungiids in the northern reefs.

The relationship between elevated SST and increased lesions and/or coral disease is well documented (Alker et al. 2001, Cervino et al. 2004a,b, Cervino et al. 2008, Kushmaro et al. 1998, Selig et al. 2006, Toren et al. 1998). Studies by Ben-Haim and colleagues (2003a,b) have suggested that this relationship occurs because bacterial pathogens involved in the disease state are more virulent with high temperatures. Elevated temperatures could also impair coral immunity, rendering them more susceptible to infection (Porter et al. 2001). The continued warming expected for the future may have detrimental impacts on corals, including fungiids in the Red Sea. The sources of the pathogens as well as temperature-related impacts on coral disease are critical areas for future research.

Additional longer-term, large-scale studies are needed to monitor corals over time and differentiate between patterns of bleaching and lesions. It should be noted that at depths greater than 6m, fungiid corals will sometimes exhibit mottled patterns of bleaching in response to thermal stress (Hoeksema 1991). However, the pattern of bleaching described by Hoeksema (1991) differs from the lesion pattern observed in the Red Sea. Tolerance to bleaching can vary across depth and by species (Hoeksema 1991, Hoeksema and Matthews 2011).

Shorter-term surveys of coral health can often overlook unseen variables (Edmunds and Bruno 1996, Porter et al. 2001). For example, continued monitoring of the lesioned states would aid in determining if the condition is chronic. Seasonality and water temperature effects on the coral lesions could also be examined to confirm the sensitivity of lesions to SST. By continuing comparative regional studies of coral reef communities, particularly in the unique yet relatively poorly studied Red Sea, we may gain valuable insights into future coral health impacts from rising sea surface temperature as well as from local anthropogenic influences (Berumen et al. 2013).

4.3. Urban water quality related to lesioned corals near Jeddah

Several measurements of water quality proximal to the city of Jeddah were related to the presence of lesioned corals. Specifically, high incidences of lesioned corals were reported at sites corresponding to elevated concentrations of ammonium, often a signature for sewage or manure runoff in coastal areas (Duedell et al. 1975, Risk et al. 2009). In the same sites immediately north (down current) of Jeddah, *Prochlorococcus* spp. were absent. While *Prochlorococcus* spp. are able to utilize ammonium (and not nitrate) as a nitrogen source (Garcia-Fernandez et al. 2004), populations generally decrease or are absent in more eutrophic and brackish regions (Partensky et al. 1999). Studies of an urban coastal environment in Kaneohe Bay, Hawaii, report undetectable concentrations of *Prochlorococcous* spp., but detectable *Synechocccus* spp., inside the Bay (Apprill and Rappé 2011, Cox et al. 2006). The lack of *Prochlorococcus* spp. cells near Jeddah may be related to the comparatively higher concentrations of coastal-derived ammonium, which are orders of magnitude lower at other reef sites, and/or other coastal

392 pollutants, such as toxins and pharmaceutical products, that were not measured. The
393 signatures for low water quality are detected north and not south of Jeddah and are most
394 likely explained by the general direction of surface current movement when these
395 measurements were taken (Quadfasel 2001), as well as the fact that urban populations are
396 focused in northern Jeddah (Vincent 2003).

397 Jeddah's population is nearing three and a half million people, and has
398 experienced high growth over the last decade (Central Department of Statistics). A
399 number of environmental issues contribute to coastal runoff, including direct sewage
400 discharge and the high level of cesspool-influenced groundwater leaking into coastal
401 lagoons (Vincent 2003). The results presented here agree with previous studies
402 demonstrating declines in coral health near human population centers (e.g., Bruno et al.
403 2003, Green and Bruckner 2000, Harvell et al. 1999, Pastorok and Bilyard 1985, Porter et
404 al. 2001). In previous studies of the Gulf of Aqaba, Red Sea and Kaneohe Bay, Hawaii,
405 survivorship of corals was directly correlated with distance from sewage outfall (Smith et
406 al. 1981, Walker and Ormond 1982).

407 Coral disease has been linked with high nutrient levels, including but not limited
408 to ammonium. Bruno et al. (2003) found that adding a minimum of 1.0 μM nitrate, 0.9
409 μM phosphorus, and 1.0 μM ammonium could significantly increase incidence of some
410 marine diseases. The moderate change in ammonium observed by Bruno et al. (2003)
411 was approximately one third of the maximum concentrations observed on reefs in the
412 eastern Red Sea. Therefore, the elevated ammonium and subsequent alteration in the
413 microbial community may be reflecting or contributing to the increasing stress on
414 fungiids occurring near Jeddah.

Free-living scleractinians are unique in that their life history may include a phase in which they live on sandy substrate. Fungiids that are free-living often occur near the reef base and will survive limited flipping or burial in sediment (Chadwick 1988, Chadwick-Furman and Loya 1992, Goffredo and Chadwick-Furman 2000). Further study is needed on the sediment chemistry, as well as suspended sediment levels of the Red Sea, as this may be a factor affecting the health of these corals. However, fungiids have been found to be resilient to bleaching and sedimentation (Bongaerts et al. 2012, Furby et al. 2013, Schuhmacher 1977). The *Fungia*, *Herpolitha* and *Ctenactis* corals studied here are seemingly unique in their vulnerability to the sources of stress investigated in this study, and they may represent new indicator genera for coral stress within the Red Sea.

4.4. Aquaculture outfall not related to lesioned corals

One of the largest shrimp aquaculture facilities in the world is near the coast in Al Lith. This facility's effluent canal is less than a kilometer from several sites surveyed in this study. Despite the high sampling of reefs near Al Lith, nutrient levels at sites near the facility were not anomalously high, nor was the frequency of lesioned corals. Over 2 km away from fish pen aquaculture in the Phillipines, total inorganic nitrogen concentrations are over 14 μM (Garren et al. 2008). This is approximately an order of magnitude higher than concentrations measured <1km from the Al Lith facility outfall. Overall these results and the low incidences of lesioned corals surrounding Al Lith suggest that the aquaculture facility outfall may not be a major source of stress to fungiid corals in this region. A comprehensive survey of the abundance, distribution and health of diverse coral species as well as water quality parameters would be necessary to address the

438 impact of the Al Lith aquaculture outfall on corals.

439

440 *4.5. Nutrients and microbial abundances in the eastern Red Sea*

441 The inorganic nutrient and microbial measurements presented here are the most
442 comprehensive dataset available on water quality for the eastern Red Sea, a relatively
443 understudied region (Berumen et al. 2013). Reef water microbial and biogeochemical
444 loops have important implications for the health of corals (Dinsdale et al. 2008, Garren et
445 al. 2008, Pastorok and Bilyard 1985). However, there are a number of caveats associated
446 with this dataset, most notably the fact that water samples were collected during different
447 years, seasons and tidal fluctuations, due to availability of ship time. However, these data
448 provide some important and novel observations about Red Sea microbial
449 biogeochemistry.

450 Throughout the Red Sea, concentrations of inorganic nutrients were quite low;
451 average total dissolved inorganic nitrogen (DIN) was generally less than 0.55 µM. Levels
452 of ammonium rarely exceeded detectable ranges at nearly all but the Jeddah-proximal
453 sites. These concentrations are lower than detected for other coral reef environments,
454 where DIN ranges from 1 – 4 µM or more (Apprill and Rappé 2011, Dinsdale et al. 2008,
455 Szmant 2002). Thus, the observed ammonium enrichment near Jeddah may be
456 specifically problematic for Red Sea corals compared to corals regularly exposed to
457 higher concentrations.

458 Microbial metabolism exhibited a latitudinal relationship in the eastern Red Sea,
459 and the increased autotrophy in the southern Red Sea is likely related to elevated
460 seawater temperatures in this region. Both *Prochlorococcus* and *Synechocccus* spp.

461 generally exhibit higher growth rates in warmer waters (Moore et al. 1995), although the
462 ecotypes of these species have not been well studied in the Red Sea. Abundances of
463 heterotrophic bacteria at the study sites were similar to previous measurements in the Red
464 Sea (Weisse 1989). However, concentrations of heterotrophic bacteria, *Synechococcus*
465 spp. and picoeukaryotes were 0.5–1 order of magnitude lower than coastal Hawaiian
466 reefs (Apprill and Rappé 2011). Interestingly, although nutrient levels are higher in the
467 Line Island Reefs in the central Pacific (Dinsdale et al. 2008), microbial cell abundances
468 (heterotrophic and autotrophic bacteria) were comparatively higher in the Red Sea. These
469 limited results suggest that the microbial biogeochemistry of the Red Sea may be
470 different than other open-ocean reef environments, possibly due to the limited circulation
471 and water exchange and the oligotrophic nature of the Red Sea region.
472
473 **5. Conclusions**
474 This study represents a novel assessment of eastern Red Sea mushroom corals along 1300
475 km of Saudi Arabian coastline, where coral health, nutrient enrichment, and seawater
476 microbial communities were previously uncharacterized on a comparable scale. The
477 correlation of coral lesions with SST was the most significant relationship observed
478 throughout the eastern Red Sea. Elevated sea surface temperatures may serve to increase
479 the virulence of pathogens or diminish corals' immune defenses. The relationship
480 between ammonium and the prevalence of fungiid corals with lesions was significant at
481 the local scale near the Red Sea's largest city, Jeddah. Ammonium is an indicator of
482 sewage pollution, and together with the lack of *Prochlorococcus* spp., reflects poor water
483 quality in the region immediately down current from Jeddah. The relationship between

484 coral health and proximity to aquaculture effluent was also examined, but no correlations
485 were found. More focused studies would be necessary to draw conclusions regarding the
486 potential impact of pathogens from aquaculture outfall and coral health. Overall, this
487 large-scale geographic study provides an opportunity to examine the relationship between
488 environmental factors and coral health. As climate change continues to impact marine
489 ecosystems, studies of Red Sea corals will be critical for understanding how coral reefs
490 function under high temperature and increasing anthropogenic impact.
491

FIGURE LEGENDS

Figure. 1. Map of the reef sites spanning ~1300 km that were surveyed for coral health in the Red Sea. The large urban area of Jeddah, and the large aquaculture facility at Al Lith, are indicated. Image is courtesy of Google Earth (2010) under the academic print distribution guidelines, and include data from SIO, NOAA, U.S. Navy, NGA and GEBCO and images from U.S. Geological Survey, Cnes/Spot Image and 2001 DigitalGlobe

Figure. 2. Photographs of fungiid corals of various health status, including healthy (A, B), bleached (C, D) and lesioned (E, F). Close up photographs of typical lesions on fungiid corals (G, H).

Figure. 3. Percentages of fungiid corals categorized as healthy, bleached or lesioned at survey sites throughout the eastern Red Sea (2-4 transects per site).

Figure. 4. Distribution of lesioned corals at the survey sites (2-4 transects per site with standard error bars). The locations of Jeddah (large urban area) and Al Lith (large aquaculture facility) relative to the sampling sites are indicated.

Figure. 5. Principal component analysis (PCA) of the measured environmental variables at each sampling site, in relation to the percentage of lesioned corals. The vector overlays represent multiple correlations between ordination axes and environmental variables. Only the sites with complete environmental data sets are represented (n = 32).

Figure. 6. Comparison of percent abundance of lesioned corals (square root transformed) compared to three-year mean SST (n = 52).

Figure. 7. Regressions of microbial cellular abundances against percentage of lesioned corals, at sites surveyed for coral health, including *Prochlorococcus* spp. (A), *Synechococcus* spp. (B), picoeukaryotes (C), heterotrophic bacteria (D), as well as the ratio of heterotrophic to autotrophic bacteria regressed against lesioned corals (E) (n = 38).

Figure. 8. Regressions of the major inorganic nutrients ammonium (A), silicate (B), phosphate (C) and nitrate + nitrite (D) against percentage of lesioned corals (n = 38).

Figure. 9. Regression analysis comparing the percentage of lesioned corals to distance from the aquaculture facility in Al Lith (A) and the city of Jeddah (B).

Figure. 10. Summary diagram displaying the relationship between the percentage of lesioned fungiids at sites north and south of Jeddah, and concentrations of ammonia and *Prochlorococcus* spp. cells in the water at each site. The direction of coastal currents is also represented, generally traveling from S to N.

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544

545 **LITERATURE CITED**

546 Acker, J.G., Leptoukh, G., 2007. Online Analysis Enhances Use of NASA Earth
547 Science Data. Eos, Transactions of the American Geophysical Union 88, 17.
548 Acosta, A., 2001. Disease in zoanthids: dynamics in space and time. Hydrobiologia
549 460, 113–130.
550 Alker, A.P., Smith, G.W., Kim, K., 2001. Characterization of *Aspergillus sydowii*
551 (Thom et Church), a fungal pathogen of Caribbean sea fan corals. Hydrobiologia
552 460, 105–111.
553 Antonius, A., 1984. Human impact on corals in fringing reefs near Jeddah, Red Sea.
554 Proceedings of the Symposium for Coral Reef Environments Red Sea Jeddah,
555 363-389.
556 Apprill, A., Rappé, M.S., 2011. Response of the microbial community to coral spawning
557 in lagoon and reef flat environments of Hawaii, USA. Aquatic Microbial Ecology
558 62, 251-266.
559 Apprill, A., Hughen, K., Mincer, T. 2013. Major similarities in the bacterial communities
560 associated with lesioned and healthy Fungiidae corals, Environmental
561 Microbiology. 15: 2063-2072.

562 Armstrong F.A.J., Stearns C.R., Strickland J.D.H., 1967. The measurement of upwelling
563 and subsequent biological processes by means of the Technicon AutoAnalyzer
564 and associated equipment. Deep-Sea Research 14**,** 381-389.
565 Ben-Haim, Y., Thompson, F.L., Thompson, C.C., Cnockaert, M.C., Hoste, B., Swings, J.,
566 Rosenberg, E., 2003a. *Vibrio coralliilyticus* sp. nov., a temperature- dependent
567 pathogen of the coral *Pocillopora damicornis*. International Journal of Systematic
568 and Evolutionary Microbiology 53, 309–315.
569 Ben-Haim, Y., Zicherman-Keren, M., Rosenberg, E., 2003b. Temperature-regulated
570 bleaching and lysis of the coral *Pocillopora damicornis* by the novel pathogen
571 *Vibrio coralliilyticus*. Applied and Environmental Microbiology 69, 4236–4242.
572 Bernhardt, H., Wilhelms, A., 1967. The continuous determination of low-level iron,
573 soluble phosphate and total phosphate with the Autoanalyzer. Technicon
574 Symposia. Mediad Inc.: New York. pp 385-389.
575 Berumen, M.L., Hoey, A.S., Bass, W.H., Bouwmeester, J., Catania, D., Cochran, J.E.M.,
576 Khalil, M.T., Miyake, S., Mughal, M.R., et al., 2013. The status of coral reef
577 ecology research in the Red Sea. Coral Reefs DOI 10.1007/s00338-013-1055-8.
578 Bongaerts, P., Hoeksema, B.W., Hay, K.B., Hoegh-Guldbery, O. 2012. Mushroom corals
579 overcome live burial through pulsed inflation. Coral Reefs 31, 399.
580 Brown, O.B., Minnett, P.J., 1999. MODIS Infrared Sea Surface Temperature Algorithm
581 Theoretical Basis Document, Ver 2.0,
582 http://modis.gsfc.nasa.gov/data/atbd/atbd_mod25.pdf.
583 Brugère, C., Ridler, N., 2004. Global aquaculture outlook in the next decades: an analysis

584 of national aquaculture production forecasts to 2030. FAO Fisheries Circular. No.
585 1001, Rome, FAO.
586 Bruno, J.F., Petes, L.E., Harvell, C.D., Hettinger, A., 2003. Nutrient enrichment can
587 increase the severity of coral diseases. Ecology Letters 6, 1056-1061.
588 Bruno J.F., Selig E.R., Casey K.S., Page C.A., Willis B.L. et al., 2007. Thermal stress
589 and coral cover as drivers of coral disease outbreaks. PLoS Biol 5, e124.
590 Doi:10.1371/journal.pbio.0050124.
591 Central Department of Statistics, Kingdom of Saudi Arabia,
592 http://www.citypopulation.de/SaudiArabia.html, accessed 03/30/2014.
593 Cervino, J.M., Hayes, R., Polson, S., Polson, S.C., Goreau, T.J., Martinez, R.J. and
594 Smith, G.W., 2004a. Relationship of *Vibrio* species infection and elevated
595 temperatures to yellow blotch/band disease in Caribbean corals. Applied and
596 Environmental Microbiology 70, 6855–6864.
597 Cervino, J.M., Hayes, R., Goreau, T.J., Smith, G.W., 2004b. Zooxanthellae regulation in
598 yellow blotch/ band and other coral disease contrasted with temperature-related
599 bleaching: in situ destruction vs expulsion. Symbiosis 37, 63-85.
600 Cervino, J.M., Thompson, F.L., Gomez-Gil, B., Lorence, E.A., Goreau, T.J., Hayes, R.L.,
601 Winiarski-Cervino, K.B., Smith, G.W., Hughen, K., Bartels, E., 2008. The *Vibrio*
602 core group induces yellow band disease in Caribbean and Indo-Pacific reef-
603 building corals. Jour App Microbiol 105,1658-1671.
604 Cervino, J.M., Hauff, B., Haslun, J.A., Winiarski-Cervino, K., Cavazos, M., Lawther, P.,
605 Wier, A.M., Hughen, K., Strychar, K.B., 2012. Ulcerated yellow spot syndrome:
606 implications of aquaculture-related pathogens associated with soft coral

607 *Sarcophyton ehrenbergi* tissue lesions. Diseases of Aquatic Organisms 102, 137-
608 148.
609 Chadwick, N., 1988. Competition and locomotion in free-living fungiid coral. Journal of
610 Experimental Marine Biology and Ecology 123, 189-200.
611 Chadwick-Furman, N., Loya, Y., 1992. Migration, habitat use, and competition among
612 mobile corals (Scleractinia: Fungiidae) in the Gulf of Eilat, Red Sea. Marine
613 Biology 114, 617-623.
614 Cox, E.F., Ribes, M., Kinzie, R.A. III, 2006. Temporal and spatial scaling of planktonic
615 responses to nutrient inputs into a subtropical embayment. Marine Ecology
616 Progress Series 324, 19-35.
617 Dinsdale, E.A., Pantos, O., Smriga, S., Edwards, R.A., Angly, F., Wegley, L., Hatay, M.,
618 Hall. D., Brown, E., Haynes, M., Krause, L., Sala, E., Sandin, S.A., Thurber,
619 R.V., Willis, B.L., Azam, F., Knowlton, N., Rohwer, F., 2008. Microbial ecology
620 of four coral atolls in the Northern Line Islands. PLoS ONE 3, e1584.
621 doi:10.1371/journal.pone.001584.
622 Duedall, I.W., Bowman, M.J., O'Connors, H.B., 1975. Sewage sludge and ammonium
623 concentrations in the New York Bight apex. Estuarine and Coastal Marine
624 Science 3, 457-463.
625 Edmunds, P.J., Bruno, J.F., 1996. The importance of sampling scale in ecology:
626 kilometer-wide variation in coral communities. Marine Ecology Progress Series
627 143, 165-171.
628 Edmunds, P.J., 2002. Long-term dynamics of coral reefs in St. John, US Virgin Islands.
629 Coral Reefs 21, 357-367.

630 Erftemeijer, P.L.A., Riegl, B., Hoeksema, B.W., Todd, P.A., 2012. Environmental
631 impacts of dredging and other sediment disturbances on corals: A review. Marine
632 Pollution Bulletin 64, 1737-1765.
633 Fabricius, K.E., 2005. Effects of terrestrial runoff on the ecology of corals and coral
634 reefs: review and synthesis. Marine Pollution Bulletin 50, 125-146.
635 Furby, K.A., Bouwmeester, J., Berumen, M.L., 2013. Susceptibility of central Red Sea
636 corals during a major bleaching event. Coral Reefs 32, 505-513.
637 Garcia-Fernandez, J.M., de Marsac, N.T., Diez, J., 2004. Streamlined regulation and
638 gene loss as adaptive mechanisms in *Prochlorococcus* for optimized nitrogen
639 utilization in oligotrophic environments. Microbiology and Molecular Reviews
640 68, 630-638.
641 Garren, M., Smriga, S., Azam, F., 2008. Gradients of coastal fish farm effluents and their
642 effect on coral reef microbes. Environmental Microbiology 10, 2299-2312.
643 Gilmour, J.P., 2004. Asexual budding in fungiid corals. Coral Reefs 23, 595.
644 Goffredo, S., Chadwick-Furman, N., 2000. Abundance and distribution of mushroom
645 corals (Scleractinia: Fungiidae) on a coral reef at Eilat, Northern Red Sea.
646 Bulletin of Marine Science 66, 241-254.
647 Goreau, T.J., Cervino, J., Goreau, M., Hayes, R., Hayes, M.,
648 Richardson, L., Smith, G., DeMeyer, K., Nagelkerken, I., Garzon-Ferrera, J., Gil,
649 D., Garrison, G., Williams, E.H., Bunkley-Williams, L., Quirolo, C., Patternson,
650 K., Porter, J.W., Porter, K., 1998. Rapid spread of diseases in Caribbean coral
651 reefs. Revista de Biologia Tropical 46, 157-171.
652 Green, E.P., Bruckner, A.W., 2000. The significance of coral disease epizootiology

653 for coral real conservation. Biological Conservation 96, 347-361.
654 Harvell, C.D., Kim, K., Burkholder, J.M., Colwell, R.R., Epstein, P.R., et al., 1999.
655 Emerging marine diseases – Climate links and anthropogenic factors. Science
656 285, 1505.
657 Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., et al., 2002. Climate
658 warming and disease risks for terrestrial and marine biota. Science 296, 2158–
659 2162.
660 Harvell, C.D., Jordan-Dahlgren, E., Merkel, S., Rosenberg, E., Raymundo, L.,
661 Smith, G., Weil, E., Willis, B., 2007. Coral disease, environmental drivers, and
662 the balance between coral and microbial associates. Oceanography 20, 172-195.
663 Hayes, M.L., Bonaventura, J., Mitchell, T.P., Prospero, J.M., Shinn, E.A., Van Dolah, F.,
664 Barber, R.T., 2001. How are climate and marine biological outbreaks functionally
665 linked? Hydrobiologia 460, 213-220.
666 Hoegh-Guldberg, O., 1999. Climate change, coral bleaching and the future of the world's
667 coral reefs. Marine and Freshwater Research 50, 839-866.
668 Hoekesema, B.W., 1989. Taxonomy, phylogeny and biogeography of mushroom corals
669 (Scleractinia: Fungiidae). Zoologische Verhandelingen 254, 3-295.
670 Hoeksema, B.W., 1991. Control of bleaching in mushroom coral populations
671 (Scleractinia: Fungiidae) in the Java Sea: stress tolerance and interference by life
672 history strategy. Marine Ecology Progress Series 74, 225-237.
673 Hoeksema, B.W., Matthews, J.L., 2011. Contrasting bleaching patterns in mushroom
674 coral assemblages at Koh Tao, Gulf of Thailand. Coral Reefs 30, 95.
675 Hoeksema, BW. 2012a. Distribution patterns of mushroom corals (Scleractinia:

676 Fungiidae) across the Spermonde Shelf, South Sulawesi. Raffles Bulletin of
677 Zoology 60: 183-212.
678 Hoeksema, BW. 2012b. Evolutionary trends in onshore-offshore distribution patterns of
679 mushroom coral species (Scleractinia: Fungiidae). Contributions to Zoology 81:
680 199-221.
681 Holmes, R.M., Aminot, A., Kerouel, R., Hooker, B.A., Peterson, B.J., 1999. A simple
682 and precise method for measuring ammonium in marine and freshwater
683 ecosystems. Canadian Journal of Fisheries and Aquatic Science, 1801-1808.
684 Kushmaro, A., Rosenberg, E., Fine, M., Ben Haim, Y., Loya, Y., 1998. Effects of
685 temperature on bleaching of the coral *Oculina patagonica* by *Vibrio* AK-1.
686 Marine Ecology Progress Series 171, 131-137.
687 McClanahan, T., Polunin, N., Done, T., 2002. Ecological states and the resilience of coral
688 reefs. Conservation Ecology 6, 18.
689 Moore, L.R., Goericke, R., Chisholm, S.W., 1995. Comparative physiology of
690 *Synechococcus* and *Prochlorococcus*: influence of light and temperature on
691 growth, pigments, fluorescence and absorptive properties. Marine Ecology
692 Progress Series 116, 259-275.
693 Partensky, F., Blanchot, J., Vaulot, D., 1999. Differential distribution and ecology of
694 *Prochlorococcus* and *Synechococcus* in oceanic waters : a review. Bulletin de
695 l'Institut océanographique NS19, 457-475.
696 Pastorok, R., Bilyard, G., 1985. Effects of sewage pollution on coral-reef
697 communities. Marine Ecology Progress Series 21, 175–189.
698 Peters, E.C., 1984. A survey of cellular reactions to environmental stress and disease in

699 Caribbean scleractinian corals. Helgoländer Meeresunters 37, 113-137.
700 Porter, J.W., Dustan, P., Jaap, W.C., Patterson, K.L., Kosmynin, V., Meier, O.W.,
701 Patterson, M.E., Parsons, M., 2001. Patterns of spread of coral disease in the
702 Florida Keys. Hydrobiologia 460, 1.
703 Quadfasel, D., John, H.S., Karl, K.T., Steve, A.T., 2001. Red Sea Circulation, in:
704 Encyclopedia of Ocean Sciences, Academic Press, Oxford, pp. 666-676.
705 Risk, M.J., Lapointe, B.E., Sherwood, O.A., Bedford, B.J., 2009. The use of [delta]15N
706 in assessing sewage stress on coral reefs. Marine Pollution Bulletin 58, 793-802.
707 Rosenberg, E., Ben-Haim, Y., 2002. Minireview: Microbial diseases of corals and
708 global warming. Environmental Microbiology 4, 318–326.
709 Ruangpan, L., Kitao, T., 1991. *Vibrio* bacteria isolated from black tiger
710 shrimp, *Penaeus monodon* Fabricius. Journal of Fish Disease 14, 383-388.
711 Sato, Y., Bourne, D.G., Willis, B.L., 2009. Dynamics of seasonal outbreaks of black band
712 disease in an assemblage of *Montipora* species at Pelorus Island (Great Barrier
713 Reef, Australia). Proceedings of the Royal Society B 276, 2795-2803.
714 Schumacher, H., 1977. Ability of fungiid corals to overcome sedimentation. In:
715 Proceedings of the 3rd International Coral Reef Symposium. Rosentiel School of
716 Marine and Atmospheric Science, University of Miami.
717 Selig, E.R., Harvell, C.D., Bruno, J.F., Willis, B.L., Page, C.A., Casey, K.S., Sweatman,.
718 H., 2006. Analyzing the relationship between ocean temperature anomalies and
719 coral disease outbreaks at broad spatial scales, in: Phinney, J.T., Strong, A.,
720 Skrving, W., West, J., Kleypas, J., Hough- Guldberg, O. (Eds.) Coral reefs and

climate change: science and management, Coastal and Estuarine Series, vol. 61. American Geophysical Union Press, Washington, D.C., pp. 111-128.

Sheppard, C.R.C., 1979. Interspecific aggression between reef corals with reference to their distribution. Marine Ecology Progress Series 1, 237-247.

Smith, S.V., Kimmerer, W.J., Laws, E.A., Brock, R.E., Walsh, T.W., 1981. Kaneohe Bay sewage diversion experiment: perspectives on ecosystem responses to nutritional perturbation. Pacific Science 35, 279-395.

Szmant, A., 2002. Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? Estuaries 25, 743-766.

Toren, A., Landau, L., Kushmaro, A., Loya, Y., Rosenberg, E., 1998. Effects of temperature on adhesion of *Vibrio* strain AK-1 to *Oculina patagonica* and on coral bleaching. Applied and Environmental Microbiology 64, 1379-1384.

U.S. Environmental Protection Agency, 1983. Nitrogen, Ammonia. Method 350.1 (Colorimetric, Automated, Phenate). Methods for Chemical Analysis of Water and Wastes: Cincinnati, pp. 350-1.1 - 350-1.4.

Vincent, P., 2003. Jeddah's Environmental Problems. Geographical Review 93, 394-412.

Veron, J.E.N., 2000. Corals of the World. Stafford-Smith, M. (Ed.) Australian Institute of Marine Science, Townsville.

Walker, D.I., Ormond, R.F.G., 1982. Coral death from sewage and phosphate pollution at Aqaba, Red Sea. Marine Pollution Bulletin 13, 21-25.

Walton, C.C., Pichel, W.G., Sapper, J.F., 1998. The development and operational

742 application of nonlinear algorithms for the measurement of sea surface
743 temperatures with the NOAA polar-orbiting environmental satellites. Journal of
744 Geophysical Research 103, 27999-28012.
745 Weisse, T., 1989. The microbial loop in the Red Sea: dynamics of pelagic bacteria and
746 heterotrophic nanoflagellates. Marine Ecology Progress Series 55, 241-250.
747 Wilkinson, C.R., Souter, D., (Eds.) 2008. Status of Caribbean coral reefs after
748 bleaching and hurricanes in 2005. Global Coral Reef Monitoring Network, pp.1-
749 148.
750 Willis, B.L., Page, C.A., Dinsdale, E.A., 2004. Coral disease on the Great Barrier Reef,
751 in: Rosenberg, E., Loya, Y., (Eds.) Coral health and disease. Springer, New York,
752 pp. 69-104.
753 Work, T.M., Aeby, G.S., 2006. Systematically describing gross lesions in corals.
754 Diseases of Aquatic Organisms 70, 155-160.

Figure

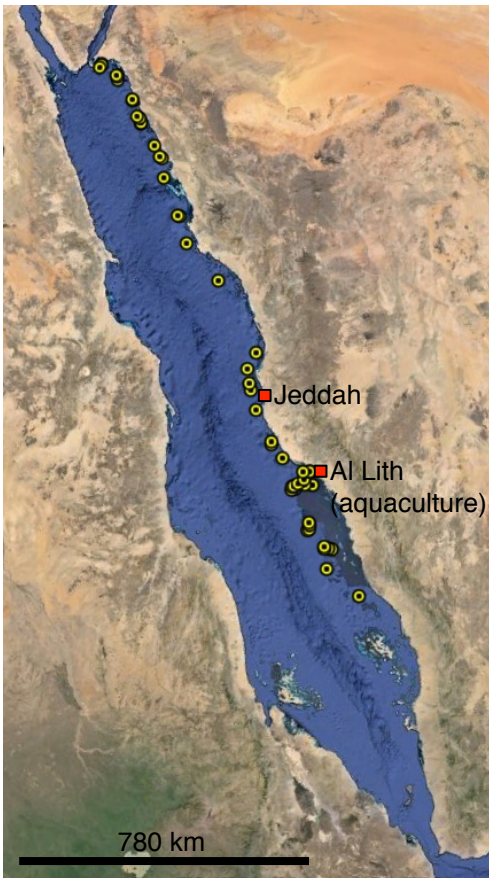

Figure 1.

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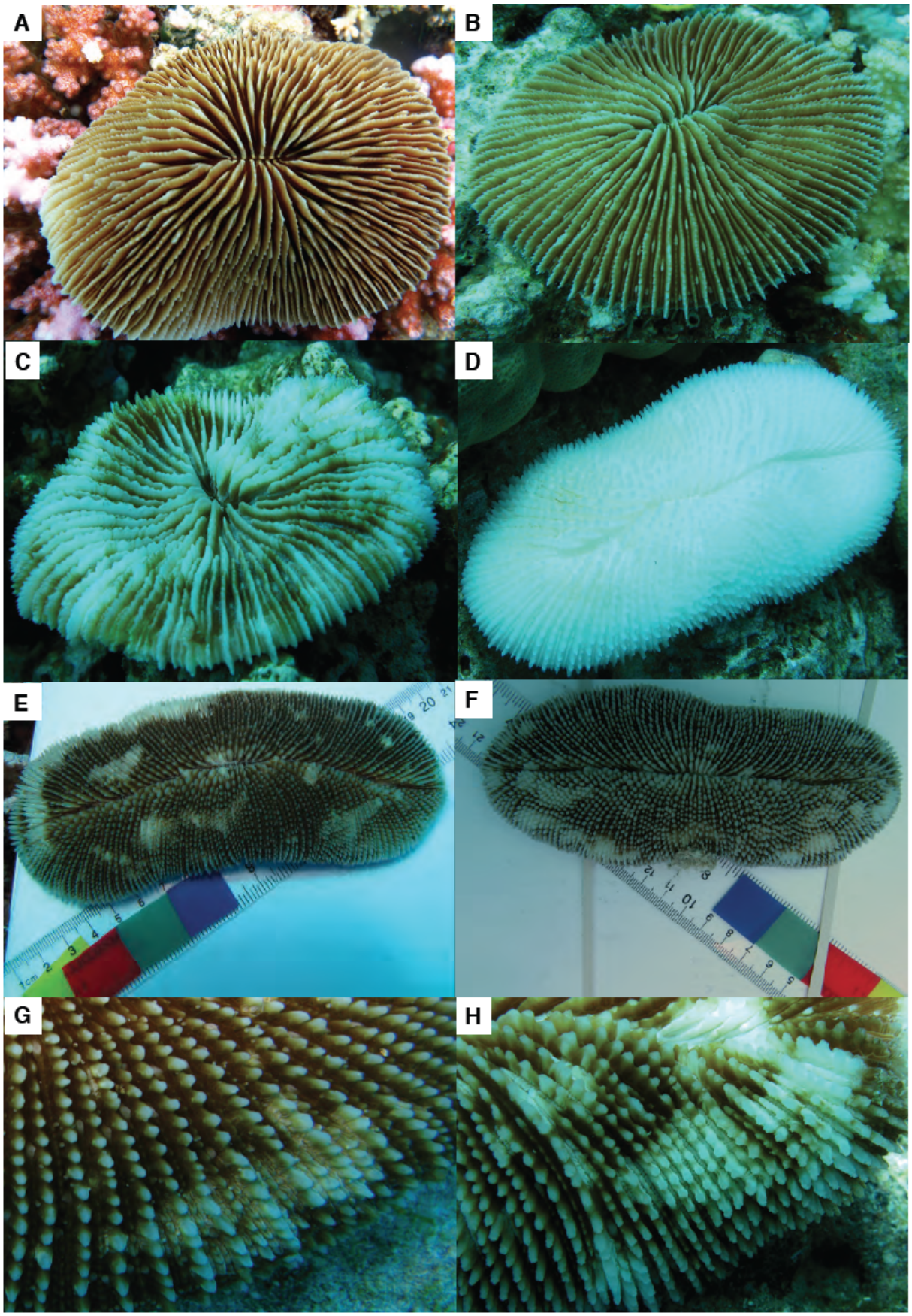

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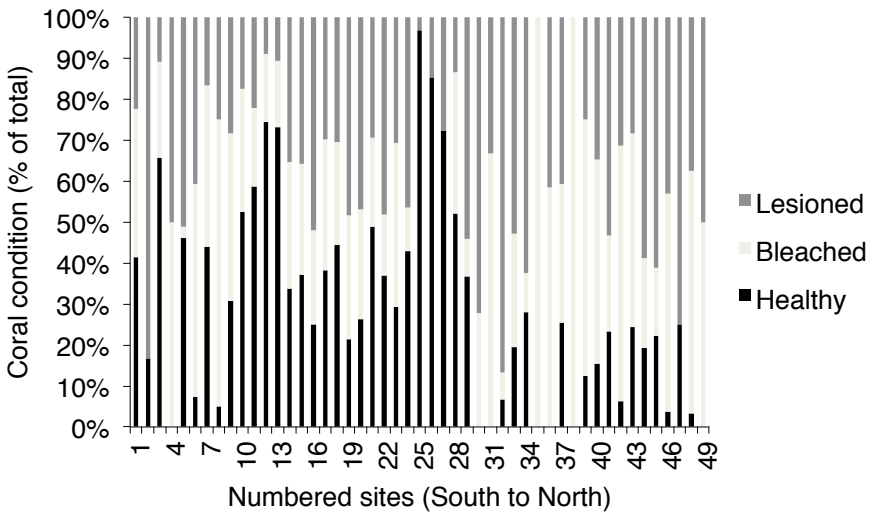

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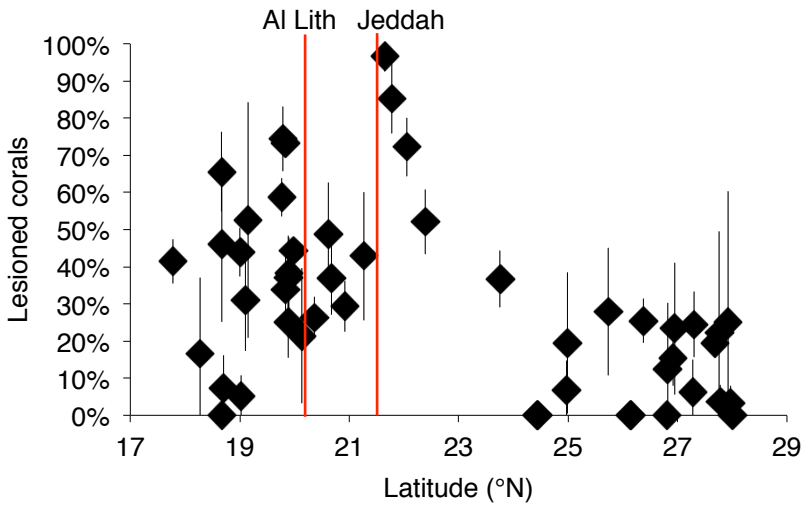

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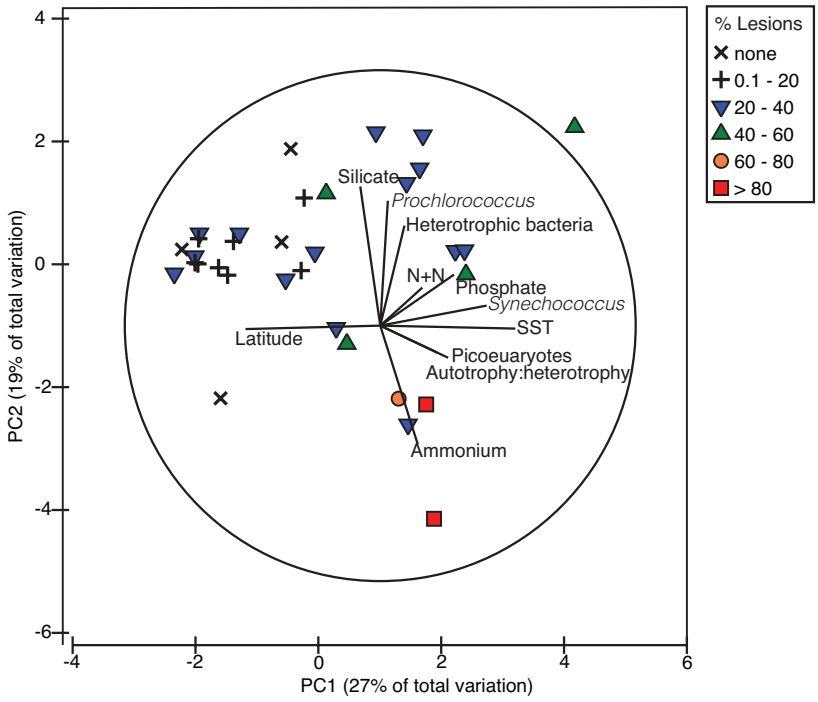

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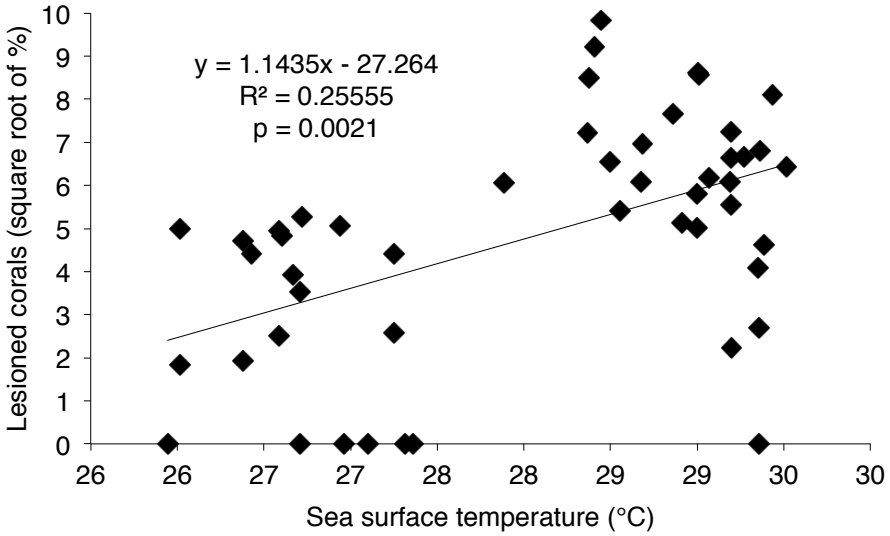

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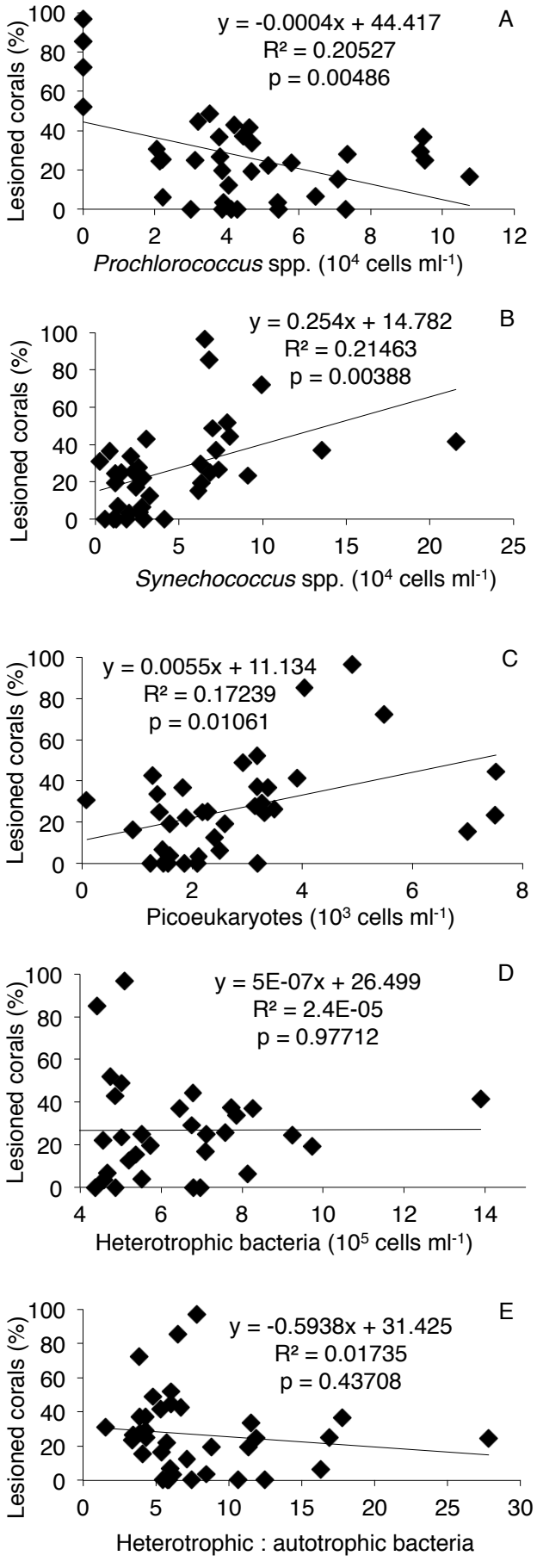

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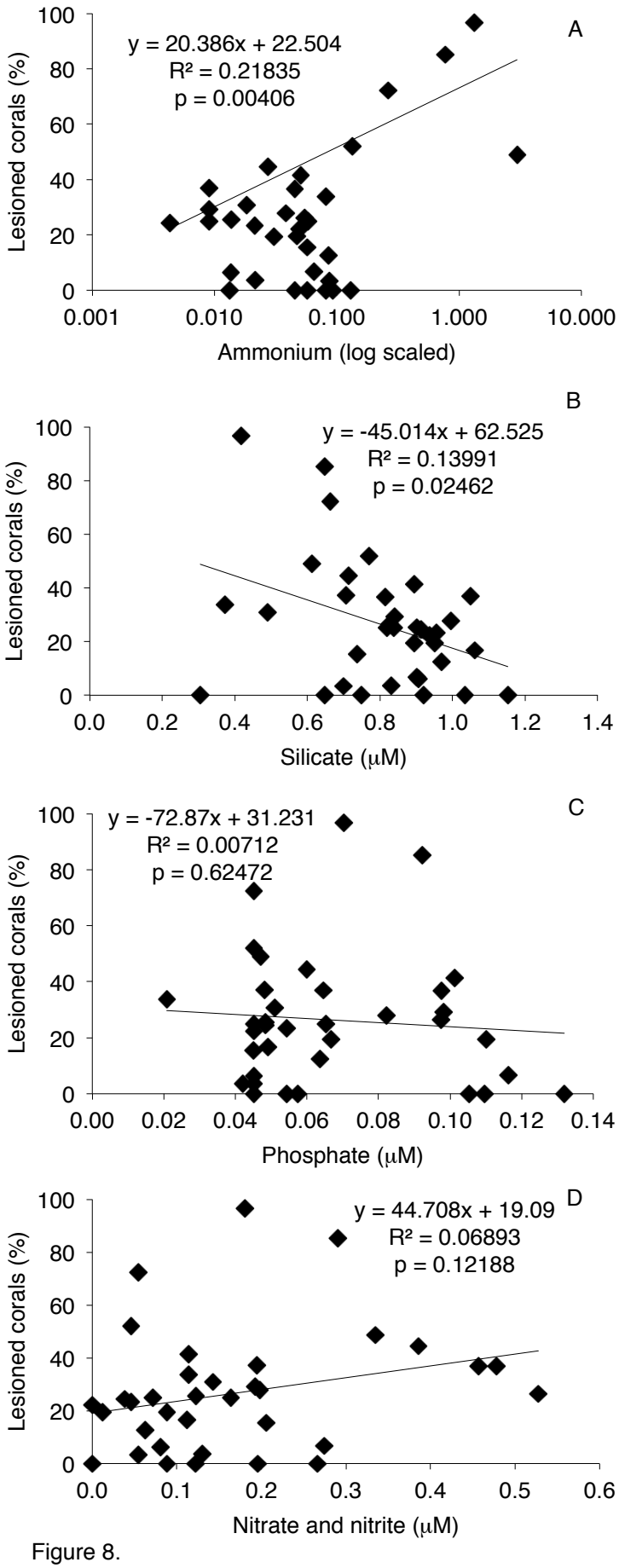

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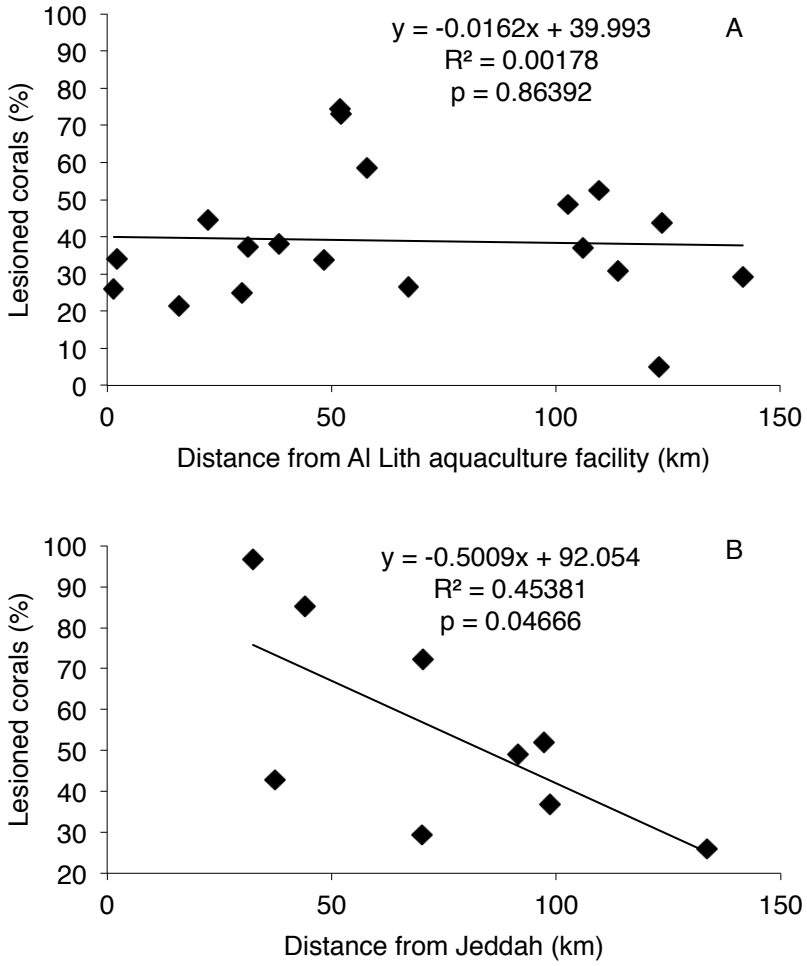

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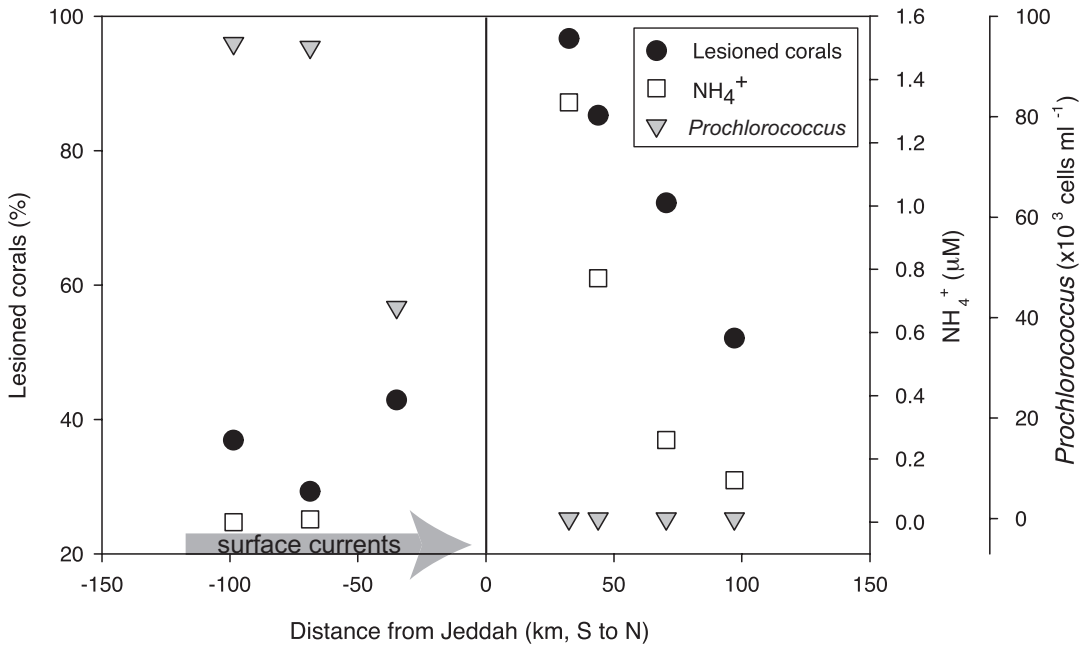


Figure 10.

Supplementary Material

Incidence of lesions on Fungiidae corals in the eastern Red Sea is related to water temperature and coastal pollution

Furby, K.A., Apprill, A., Cervino, J.M., Ossolinski, J.E., Hughen, K.A.

Supplementary Table 1. Comprehensive list of survey and sample sites.

Date Surveyed/Sampled	Site Name	Latitude	Longitude	Health survey	Microbial abundances	Inorganic nutrients
Oct 2009	Sumayr	17.7874	41.44173333	x	x	x
June 2009	Petit Murabit	18.00238333	40.28493333	x		
Oct 2009	Maghabiyah	18.27391667	40.7371	x	x	x
June 2009	Ablo 2	18.665	40.81281667	x		
June 2009	Ablo 3	18.66771667	40.65928333	x		
June 2009	Ablo 1	18.6751	40.73921667	x		
June 2009	Ablo 4	18.70673333	40.65361667	x		
June 2009	Murabit	19.02431667	40.31791667	x		
June 2009	AQ3	19.10641667	40.31775	x		
Oct 2009	AQ3	19.10877778	40.489	x	x	x
June 2009	AQ4	19.15483333	40.30113333	x		
June 2009	Long Reef	19.76643333	39.89223333	x		
June 2009	Al'Jabir	19.78848333	39.95683333	x		
June 2009	Dohra Reef	19.82893333	39.89853333	x		
June 2009	Mar Mar	19.84335	39.93358333	x		
Oct 2009	Mar Mar	19.84335	39.93358333	x	x	x
Oct 2009	Saut	19.88761667	40.15665	x	x	x
June 2009	Saut	19.88761667	40.15665	x		
Oct 2009	Canyon	19.89045	39.96083333	x	x	x
June 2009	Canyon	19.89051667	39.96068333	x		
June 2009	Shi'b Sulaym	19.89798333	40.00651667	x		
Oct 2009	Abulatt	19.9875	40.13238889	x	x	x

Oct 2009	Ron's Reef	20.13480556	40.10122222	x		
June 2009	Coast Guard 1	20.14931667	40.2441	x		
June 2009	Coast Guard 2	20.14955	40.23541667	x		
Oct 2009	Uhm Huj	20.3697	39.65158333	x	x	x
	Tawil			x	x	x
Oct 2009	Raghwan	20.62206667	39.39788333			
Oct 2009	Sagir	20.67591667	39.39385	x	x	x
Oct 2009	Shib Al'Kadir	20.92408333	39.16393333	x	x	x
Oct 2009	MisMari2	21.2693	39.01765	x	x	
Nov 2008	South Reef	21.64805	38.87393333	x		
Sept 2010	South Reef	21.64805	38.87393333		x	x
Nov 2008	Coral Gardens2	21.77915	38.83023333	x		
Sept 2010	Coral Gardens	21.77915	38.83023333		x	x
Nov 2008	Abu Modafi	22.05768333	38.76263333	x		
Sept 2010	Abu Modafi	22.05768333	38.76263333		x	x
Nov 2008	Amorita	22.39006667	38.91875	x		
Sept 2010	Amorita	22.39006667	38.91875		x	x
Sept 2010	Maria	22.79635	38.665017		x	x
Nov 2008	Abu Galawa	23.75345	37.97341667	x		
May 2010	Abu Galawa	23.75419444	37.97352778	x	x	x
Sept 2010	Argonaut	24.43858333	37.14830556			x
May 2010	Argonaut	24.43858333	37.14830556	x	x	x
May 2010	Marker 7	24.44522222	37.20686111	x	x	x
May 2010	Marker 3	24.49102778	37.12108333	x	x	x
May 2010	Boomerang	24.97897222	36.99188889	x	x	x
May 2010	Saddle	24.98852778	36.94813889	x	x	x
Sept 2010	Saddle	24.98852778	36.94813889			x
May 2010	Popponesset	25.73258333	36.54944444	x	x	x
Sept 2010	Popponesset	25.73258333	36.54944444			x
May 2010	Key West	26.12997222	36.45861111		x	x
	Deception			x	x	x
May 2010	Point	26.16047222	36.40291667			
May 2010	Skharu Luhs	26.37730556	36.25480556	x	x	x
	Skharu Luhs					x
Sept 2010	North					
May 2010	Pele	26.80922222	35.89091667		x	x
May 2010	Pele2	26.82713889	35.89125	x	x	x
Sept 2010	Pele2	26.82713889	35.89125			x
May 2010	Moonscape	26.92275	35.84605556	x		
May 2010	Western Cape	26.95569444	35.78186111	x	x	x
May 2010	Pisces II	27.27986111	35.63505556	x	x	x
Sept 2010	Pisces II	27.27986111	35.63505556			x
May 2010	Pisces I	27.30405556	35.62297222	x	x	x
May 2010	Jaz'ir Sila	27.68722222	35.22941667	x	x	x
Sept 2010	Jaz'ir Sila	27.68722222	35.22941667			x
May 2010	Julayjilah	27.75833333	35.21002778	x	x	x

May 2010	Walih	27.78563889	35.18355556	x	x	x
May 2010	Mini-Sanafir	27.92391667	34.77469444	x	x	x
May 2010	Semi-colon	27.97869444	34.8085	x	x	x
Sept 2010	Semi-colon	27.97869444	34.8085			x
May 2010	Shishah	28.00441667	34.80602778	x	x	x

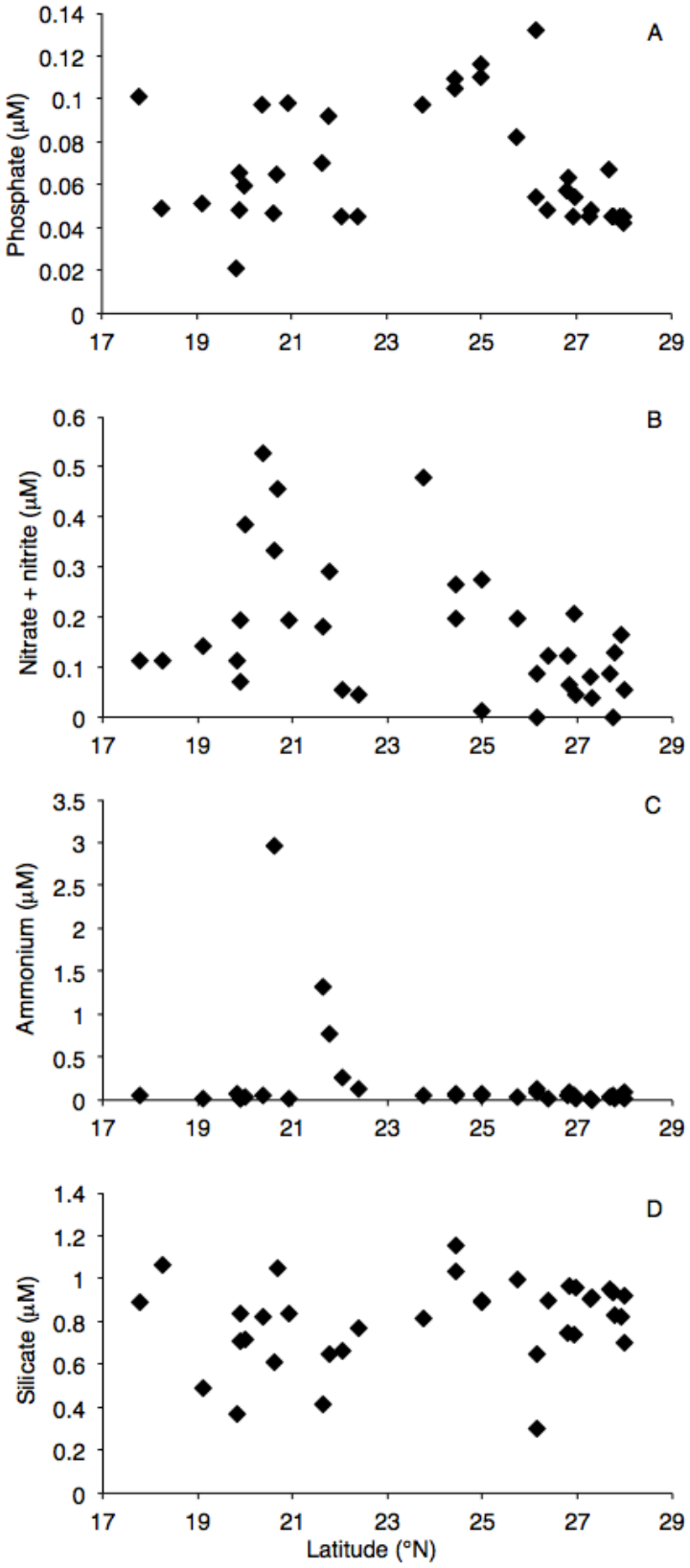
Supplementary Figure Legends

Supplementary Figure. 1. Concentrations of the inorganic nutrients phosphate (A), nitrate and nitrite (B), ammonium (C) and silicate (D) at the sites surveyed for coral health.

Supplementary Figure. 2. Abundances of heterotrophic bacteria (A), *Synechococcus* spp. (B), *Prochlorococcus* spp. (C), picoeukaryotes (D) as well as the ratio of autotrophic to heterotrophic microbial metabolism (E) at the reefs surveyed for coral health.

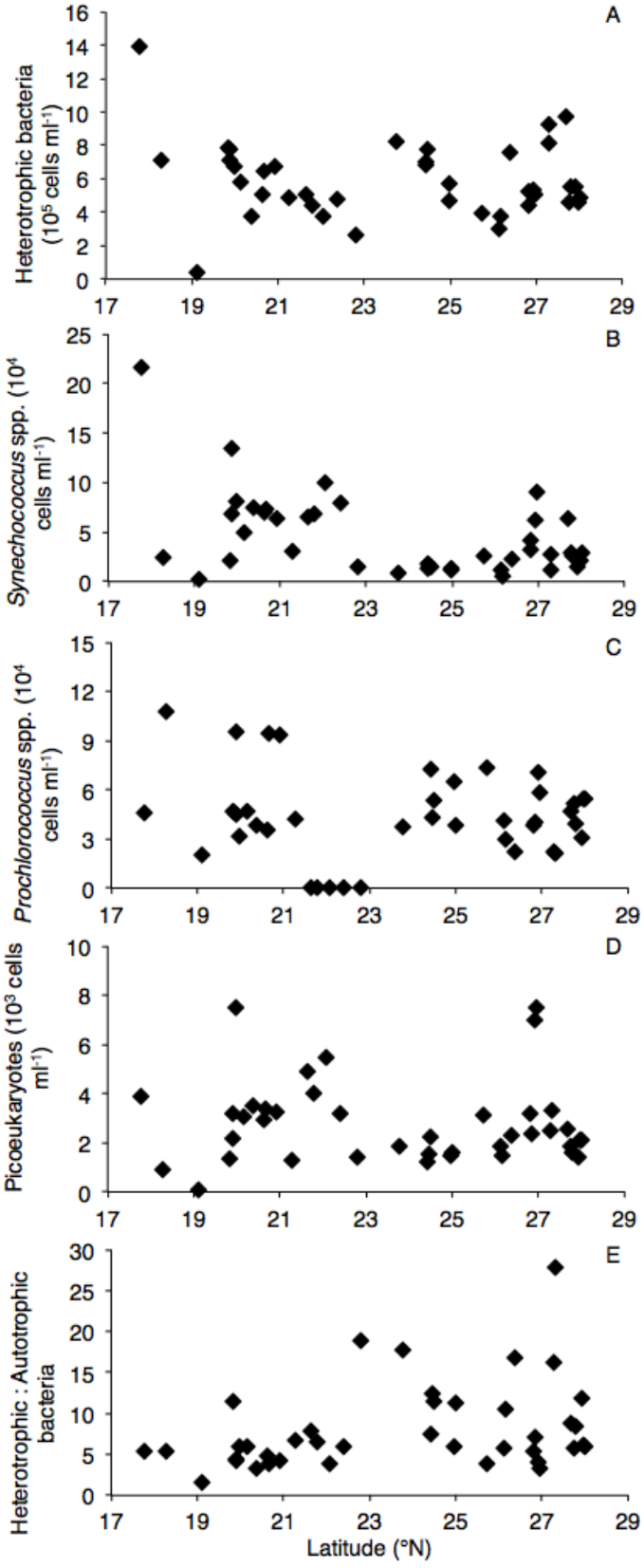
Supplementary Figure. 3. Three-year mean sea surface temperature (SST) for sites surveyed for coral health. SST are means for three years from October 2007 to October 2010.

Figure



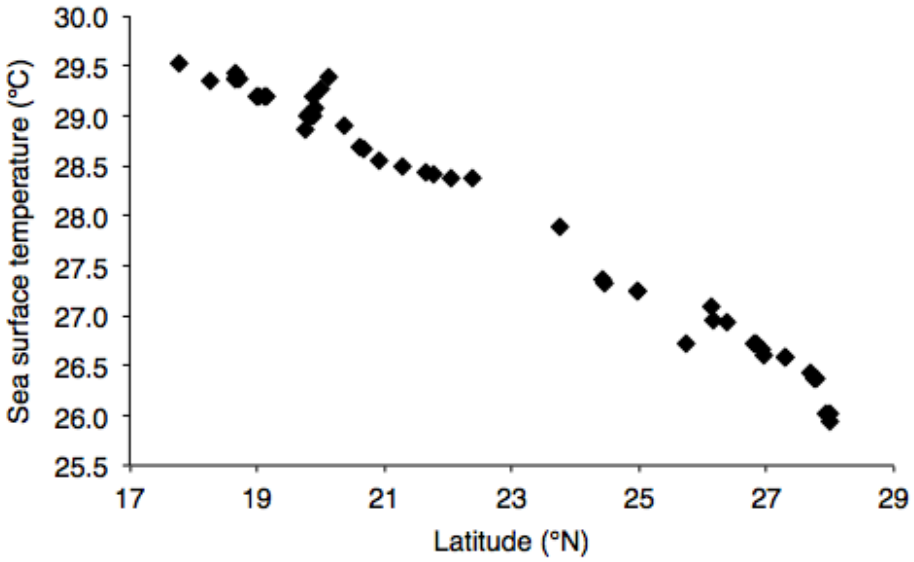
Supplementary Figure 1.

Figure



Supplementary Figure 2

Figure



Supplementary Figure 3.