Soft coral (Octocorallia, Alcyonacea) diversity and distribution along a latitudinal environmental gradient and the role of their chemical defense against predatory fish in the Red Sea

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PUBLICATIONS AND CONTRIBUTIONS OF AUTHORS

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Hoang B, Reinicke G, Al-Sofyani A, Sawall Y. *Patterns of Soft Coral (Octocorallia, Alcyonacea) diversity and distribution in coral reefs along strong latitudinal environmental gradients in the Saudi Arabian Red Sea.* **(Submitted manuscript to Marine Biodiversity)**.

Hoang collected soft coral data in the field. Al-Sofyani, Sawall designed, collected and analyzed environmental data in the field and the laboratory. Hoang and Reinicke identified soft coral in the laboratory. Hoang and Sawall analyzed data. Hoang wrote the paper. Reinicke, Sawall and Al-Sofyani commented on and made corrections to manuscript drafts

Paper 2

Hoang B, Reinicke G. *Patters of Xeniidae (Octocorallia, Alcyonacea) communities impacted by different environmental parameters in the Red Sea.* (**Submitted manuscript to Saudi Journal of Biological Sciences).**

Hoang collected soft coral data in the field. Hoang and Reinicke identified soft coral in the laboratory. Hoang analyzed data. Hoang wrote the paper. Reinicke commented on and made corrections to manuscript drafts.

Paper 3

Ben Hoang, Yvonne Sawall, Abdulmohsin Al-Sofyani, Martin Wahl. *Chemical versus mechanical defense against fish predation in two dominant soft coral species (Xeniidae) in the Red Sea.* (**Submitted manuscript to Aquatic Biology, 2nd revised version).**

Hoang and Wahl designed for chemical extraction and experimental setup in the field and the laboratory. Hoang conducted experiments in the field and the laboratory. Hoang and Wahl analyzed data. Hoang wrote the paper. Wahl, Sawall and Al-Sofyani commented on and made corrections to manuscript draft.

SUMMARY

The Red Sea located between 30°N and $12^{\circ}30'$N separates Africa and Asia. It has a length of 1,840 km, an average width of 280 km and a total area of approximate 4,600,000 km^2. The Red Sea harbors complex ecosystems such as coral reefs, sea grass beds and mangrove forests. Soft corals are an important component of the reef communities and contribute substantially to the biological diversity in coral reefs of tropical Indo - Pacific region, and indeed globally.

This study not only assessed the soft coral distribution along the Saudi Arabian Red Sea including diversity, abundance and coverage but also valuated their relation with environmental parameters along the large scale latitudinal gradient and at the local scale. Moreover, this study asks whether the conspicuous dominance of xeniid soft corals in the Red Sea reef systems may be due to their chemical defenses against predator reef fishes.

Rapid ecological assessments (REA) and line intercept transect (LIT) methods were used in the field along the Saudi Arabian coast to record the cover and abundance of soft coral species. For a comprehensive diversity assessment, around 1,000 soft coral samples were collected at 24 sites along the Saudi Arabian coast from shallow (1 m) to deep reefs (38 m) during three subsequent field trips. Further, the environmental parameters such as nutrients, temperature, sedimentation, turbidity and reef types were also recorded during these expeditions. The field surveys were carried out in February and September 2011, and February/March 2012 and the laboratory experiments were conducted from September 2013 to March 2014 at GEOMAR in Kiel, Germany.

Seventeen genera of alcyonacean soft corals belonging to five families were found along the Saudi Arabian Red Sea coast by REA: *Tubipora, Rhytisma, Klyxum, Cladiella, Sarcophyton, Lobophytum, Sinularia, Anthelia, Xenia, Ovabunda, Heteroxenia, Paralemnalia, Litophyton, Sterenonephtya, Nepthea, Dendronephthya* and *Siphonogorgia*. The highest numbers of genera (fifteen genera) were found in the northern reefs. The southern reefs featured the lowest number of soft corals with eight genera. The most abundant genera throughout the Red Sea included*, Sinularia, Xenia/Ovabunda, Sarcophyton* and *Tubipora*. These were found at all reef sites. In contrast, the genera *Cladiella, Stereonephtya, Heteroxenia* and *Siphonogorgia* were

found in few areas only. Overall, the genera *Xenia/Ovabunda* and *Sinularia* featured highest abundances contributing most to the coverage of soft corals throughout the Red Sea. The LIT determined the average soft coral areal cover was 11% (± 3.8 SE), relative cover was lowest at southern reefs (Farasan: 0.6% ± 0.9) and highest in the northern reefs (Al-Wajh: 27% ± 2.1).

Eightytwo soft coral species were identiied belonging to Alcyoniidae (six genera, 40 species), Xeniidae (five genera, 24 species), Nephtheidae (six genera, 15 species), Nidaliidae, Briareidae and Tubiporidae (one species each). This study reported new distribution of soft coral species records for the Red Sea. Bray-Curtis clustering of soft coral species composition and abundance grouped the sites into three main clusters: representing northern (Maqna and Al-Wajh), central (Yanbu, Jeddah, Rabigh, Mastura and Al-Lith) and southern (Doga and Farasan) reef areas respectively.

The factors affecting the pattern of soft coral communities along coastal reefs of Saudi Arabia are substrate, depth, slope morphology, temperature, nutrients, sedimentation and turbidity. These factors, in combination, explained 65% of the total variation in soft coral community structure. The northern section had highest soft coral coverage (27% ± 4.1 SE) and diversity (44 species) and was characterized by lowest temperatures, low nutrient concentrations, steep reef slopes and low sedimentation. The southern section had lowest soft coral coverage (0.6% ± 0.9) and diversity (26 species), and was characterized by high temperature, high nutrient concentration, mostly shallow reef slopes and high sedimentation. The central section was intermediate in cover, diversity and the key environmental factors.

Xeniids, notably *Xenia/Ovabunda* species*,* were important components of soft coral communities in the Saudi Arabian Red Sea. Xeniids occupied 80% of soft coral cover in some areas. The relative coverage of xeniids ranged from 7.5% (± 2.1 SE) to 14.4% (± 1.9) in the off-shore reefs, and from 0.6% (±1.1) to 8.5% (±3.3) in the near-shore reefs, in response to major differences in water quality parameters. Eighteen species were recorded at the off-shore sites and 13 species in near-shore locations at Al-Wajh, Yanbu, Mastura/Rabigh and Jeddah. Multivariate analyses showed that xeniid communities differed between the eight reef sites surveyed. The xeniid communities were significantly different between inshore and offshore at Yanbu, Mastura/Rabigh and Jeddah reefs. They not only differ in coverage but also in the predominating genera and species diversity varies under different habitat conditions.

Community composition partly varied according to anthropogenic impacts at some locations.

The crude extract of two xeniid species deterred reef fishes in the field at the Red Sea to 86% (*Ovabunda crenata)* and 92% (*Heteroxenia ghardaqensis.* In the laboratory, natural concentration of crude extract deterred the reef fish *Thalassoma lunare* (moon wrasse) to 83% and 85%, respectively. Crude extract still showed unpalatable for moon wrasse even when reduced to 12.5% of the natural concentration in both species. While *Heteroxenia ghardaqensis* lacking sclerites, the sclerites of *Ovabunda crenata* species did not deter moon wrasses in the laboratory even under the increasing double natural concentration suggesting that sclerites provide structural support rather than antifeeding defenses. We conclude from that, the role of chemical defense against predation contributes to the conspicuous abundance of these soft coral species in the Red Sea.

ZUSAMMENFASSUNG

Das Rote Meer liegt zwischen den Breitengraden 30°N und 12°30'N und trennt Afrika und Asian voneinander. Es ist 1.840 km lang, 280 km breit und bedeckt eine Fläche von ungefähr 4.600.000 km². Das Rote Meer beherbergt komplexe Ökosysteme wie Korallenriffe, Seegraswiesen und Mangrovenwälder. Weichkorallen sind ein wichtiger Bestandteil von Riffgemeinschaften und tragen erheblich zur biologischen Vielfalt der Korallenriffe im Indo-Pazifik bei, und sogar weltweit.

Diese Studie untersuchte nicht nur die Verteilung der Weichkorallen entlang der saudi-arabischen Rote Meer Küste inklusive Diversität, Häufigkeit und Bedeckungsgrad, sondern auch deren Bezug zu den Umweltbedingungen entlang des groß-skalaren Gradienten über die Breitengrade, als auch auf lokaler Ebene. Weiterhin geht es in dieser Studie um die Frage, ob die auffällige Dominanz von xeniiden Weichkorallen in den Riffen des Roten Meeres mit der chemischen Abwehr von Fraßfeinden zu tun haben könnte.

Die Methoden "Rapid ecological assessments" (REA, wörtlich: schnelle ökologischen Einsschätzungen) und "line intercept transects" (LIT, wörtlich: Linenabschnitte entlang von Transekten) wurden benutzt, um in den Riffen entlang der saudi-arabischen Küste Bedeckung und Vorkommen von Weichkorallen zu bestimmen. Für eine ausgedehnte Diversitätseinschätzung wurden circa 1.000 Proben von Weichkorallen an 24 Standorten entlang der saudi-arabischen Küste in 1 bis 38 m Tiefe gesammelt, während drei aufeinanderfolgenden Expeditionen. Weiterhin wurden während dieser Expeditionen auch die Umweltparameter Nährstoffkonzentrationen, Temperatur, Sedimentation, Trübung und Riff-Typ gemessen beziehungsweise dokumentiert. Die Untersuchungen im Feld wurden im Februar und September 2011 und im Februar/März 2014 durchgeführt, während die Laborexperimente von September 2013 bis März 2014 am GEOMAR Kiel, Deutschland, durchgeführt wurden.

17 Gattungen von alcyonacea Weichkorallen zugehörig zu 5 Familien wurden entlang der saudi-arabischen Rote Meer Küste mit der REA Methode gefunden: *Tubipora, Rhytisma, Klyxum, Cladiella, Sarcophyton, Lobophytum, Sinularia, Anthelia,*

Xenia, Ovabunda, Heteroxenia, Paralemnalia, Litophyton, Sterenonephtya, Nepthea, Dendronephthya und *Siphonogorgia*. Die höchste Anzahl an Gattungen (15) wurde im nördlichen Abschnitt gefunden. Die südlichen Riffe beherbergten die geringste Anzahl mit nur acht Weichkorallengattungen. Die Gattungen, die am häufigsten vorkamen im gesamten Roten Meer beinhalten *Sinularia, Xenia/Ovabunda, Sarcophyton* und *Tubipora*. Diese kamen an allen Riffen vor. Im Gegensatz dazu wurden die Gattungen *Cladiella, Stereonephtya, Heteroxenia* und *Siphonogorgia* nur in manchen Gebieten gefunden. Generell zeigten die Gattungen *Xenia/Ovabunda* und *Sinularia* das höchste Vorkommen und steuerten somit den höchsten Bedeckungsgrad an Weichkorallen im gesamten Roten Meer bei. Mit der LIT Methode wurde ein mittlerer Bedeckungsgrad von Weichkorallen von 11% (± 3.8 SE) festgestellt, während die niedrigste Bedeckung im südlichen Abschnitt (Farasan: 0.6% ± 0.9) und die höchste Bedeckung im nördlichen Abschnitt (Al-Wajh: 27% ± 2.1) gefunden wurde.

82 Weichkorallenarten wurden identifiziert welche zu den Familien Alcyoniidae (6 Gattungen, 40 Arten), Xeniidae (5 Gattungen, 24 Arten), Nephtheidae (6 Gattungen, 15 Arten), Nidaliidae, Briareidae und Tubiporidae (jeweils eine Art) gehören. Innerhalb der Studie wurden auch neue Arten im Roten Meer entdeckt. Bray-Curtis Clustering der Artenzusammensetzung und der Häufigkeit gruppierte die untersuchten Riffe in drei Haupt-Cluster, welche durch den nördlichen (Maqna und Al-Wajh), den zentralen (Yanbu, Jeddah, Rabigh, Mastura and Al-Lith) und den südlichen (Doga and Farasan) Abschnitt repräsentiert wurden.

Die Hauptfaktoren, die das Verteilungsmuster der Weichkorallengemeinschaften entlang der Küste von Saudi-Arabien bestimmen, sind Substrat, Tiefe, die Morphologie des Hanges, Temperatur, Nährstoffe, Sedimentation und Trübung. Diese Faktoren erklären in Kombination 65% der Gesamtvariation in der Struktur der Weichkorallengemeinschaft. Der nördliche Abschnitt hatte die höchste Weichkorallenbedeckung (27% ± 4.1 SE) und Diversität (44 Arten) und wies die niedrigste Temperatur, niedrigste Nähstoffkonzentration, steilsten Riffhänge und niedrigste Sedimentationsrate auf. Der südliche Abschnitt hatte die niedrigste Weichkorallenbedeckung (0.6% ± 0.9) und Diversität (26 Arten) und wies die höchste Temperatur, höchste Nährstoffkonzentration, zumeist recht flache Riffhänge und hohe Sedimentationsraten auf. Der zentrale Sektor wies mittlere Bedeckung und Diversität auf, und auch mittlere Werte bei den Umweltfaktoren.

Xeniidae, beziehungsweise *Xenia/Ovabunda* Arten, waren wichtiger Bestandteil der Weichkorallengemeinschaften im saudi-arabischen Roten Meer. In manchen Gebieten beanspruchten die Xeniide bis zu 80% der gesamten Weichkorallenbedeckung. Die relative Bedeckung der Xeniidae, reichte von 7.5% (± 2.1 SE) bis 14.4% (± 1.9) in küstenfernen Riffen, und von 0.6% (±1.1) bis 8.5% (±3.3) in küstennahen Riffen, je nach Wasserqualität. In küstenfernen Riffen wurden 18 Arten gefunden, 13 Arten wurden in küstennahen Riffen gefunden bei Al-Wajh, Yanbu, Mastura/Rabigh und Jeddah. Multivariate Analysen zeigten, dass die Xeniiden-Gemeinschaften unterschiedlich waren zwischen den 8 untersuchten Riffen. Die Xeniiden-Gemeinschaften waren signifikant unterschiedlich zwischen küstenfernen und küstennahen Riffen bei Yanbu, Mastura/Rabigh und Jeddah. Sie unterschieden sich nicht nur im Bedeckungsgrad, sondern auch in den dominierenden Gattungen und in der Artenvielfalt welche je nach Habitateigenschaften schwankte. Die Zusammensetzung der Gemeinschaften variierte je nach Stärke des menschlichen Einflusses.

Das Rohextrakt von zwei Xeniide Arten wehrte Rifffische im Roten Meer in 86% (*Ovabunda crenata)* und in 92% (*Heteroxenia ghardaqensis*) aller Fälle ab. Unter Laborbedingungen wehrte das Rohextrakt in natürlicher Konzentration den Rifffisch *Thalassoma lunare* (Mondsichel-Lippfisch) in jeweils 83% and 85% aller Fälle ab. Das Rohextrakt war immer noch ungenießbar für den Mondsichel-Lippfisch bei einer Konzentration von 12,5% der natürlichen Konzentration in beiden Weichkorallenarten. Während *Heteroxenia ghardaqensis* keine Sklerite besitzt, haben die Sklerite von *Ovabunda crenata* keinen Effekt in der Abwehr von dem Mondsichel-Lippfisch gezeigt, selbst bei doppelter Menge der natürlich vorkommenden Konzentration. Das bedeutet, dass Sclerite höchstwahrscheinlich nur zur strukturellen Stütze vorhanden sind und nicht zur Abwehr von Fraßfeinden dient. Wir schließen daraus, dass die chemische Abwehr gegen Fraßfeinde zum erheblichen Erfolg dieser Weichkorallenarten im Roten Meer beiträgt.

GENERAL INTRODUCTION

1. Coral reefs

Coral reefs are a complex ecosystem with high diversity, biological productivity and provide habitat for a vast number of species. Hence, they are considered to be the rainforest of the sea (Connell 1978). The tropical reefs are distributed between $30°$N and $30°$S where the surface temperature rarely falls below $20°$C (Fig.1). By using different methods, the estimate of global coral reef areas ranges from 255,000 to 3,930,000 km^2 and approximately occupies 0.1 - 0.5% of the ocean floor (Smith 1978; Copper 1994; Kleypas 1997; Spalding and Grenfell 1997).
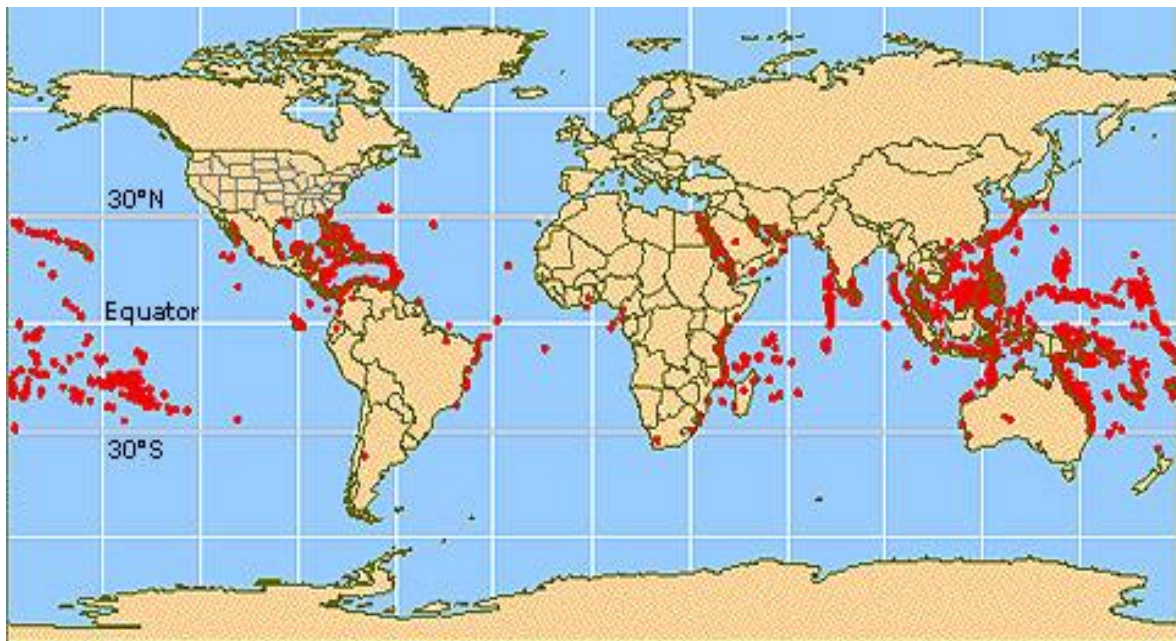
Figure 1: Global tropical coral reef distribution (Source: http://oceanservice.noaa.gov)

The most recent estimation calculated that the coral reefs total area amounts to 284,300 km^2 and the total reef area comprises less than 1.2% of the world's continental shelf areas (Spalding et al. 2001), (Tab.1). The distribution of tropical coral reefs can be divided into four main biogeographic regions: the Indo-West Pacific, East Pacific, West Atlantic and East Atlantic (Paulay 1997). Among these regions, the area of coral reef of the Indo-Pacific region is highest, occupying approximately 92% of total coral reef area (Spalding et al. 2001).The tropical reefs are distributed along the coastal lines of 80 countries of the world; where the lowest extension of coral reef

areas reaches in Israel (ca. 10 km^2), while Indonesia is the country with coral reef areas occupying about 51,000 km^2 (Spalding et al. 2001).

Table 1: Estimate of global reef areas in the world (Source: Spalding et al. 2001).

Regions	Area (km^2)	% of world total
Caribbean	21,600	7.0
Atlantic	1,600	0.6
Red Sea and Gulf of Aden	17,400	6.1
Arabian Gulf and Arabian Sea	4,200	1.5
Indian Ocean	32,000	11.3
Southeast Asia	91,700	32.3
Pacific	117,500	41.4
Total	**284,300**	**100**

Coral reefs are among the ecosystems with highest diversity of species with around 93,000 macroscopic species described to date (Reaka-Kudla 1997). Among corals and allied taxa, around 5,350 species have been described, including octocorals, scleractinians, hydrocorals and antipatharians (Williams and Cairns 2013). However, these tallies of species are incomplete because it is estimated that approximately 91% of the species of the oceans are still to be described (Mora et al. 2011) and only around 62% - 79% of Hexacorallia and Octocorallia species have been described to date (Ward et al. 2012).

Although coral reefs occupy less than 1.2% of earth's continental shelf, they provide numerous renewable and non-renewable resources and ecosystem services (including physical structure service, biotic service, biogeochemical service, information service and social/culture service, Moberg and Folke 1999).

Martínez et al. (2007) calculated that the ecosystem service products amounted to approximately 172 billion US dollars per year. For example, 1 km^2 of coral reef in a good condition could provide the protein source for over 300 people (Jennings and Polunin 1996). Cesar et al. (2003) estimated the global economic

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benefits from coral reefs at approximately 30 billion USD per year, which includes fisheries (5.7 billion), coastal protection (9.0 billion), tourist/recreation (9.6 billion) and biodiversity value (5.5 billion).

Soft corals (Octocorallia, Alcyonacea) represent major components of the sessile benthos contributing to the diversity of tropical reef communities (Dinesen 1983; Fabricius and Alderslade 2001), including the coral reefs of the Red Sea (Benayahu and Loya 1977, 1981; Benayahu 1985; Reinicke 1997) and the Atlantic Ocean (Cortes 1997; Chiappone et al. 2001).

More than 200 genera of Octocorallia (Bayer 1981) and around 90 genera belonging to 23 families of alcyonacean soft coral have been described from the Central-West Pacific, Indian Ocean and the Red Sea region (Fabricius and Alderslade 2001). Williams and Cairns (2013) calculated around 3,400 Octocorallia species which contributed 64% of the total species of the class Anthozoa. The Indo-Western Pacific is known to be the 'hotspot' of soft coral diversity, in the world's center for coral reefs (Fig. 1, Dinesen 1983; Fabricius and Alderslade 2001; Hoeksema and Putra 2000).

In general, diversity of soft corals increases towards the equator or decreases both with increasing latitude and longitude away from the diversity centre (Ofwegen 2000; Benayahu et al. 2003). For example, the species richness of Octocorallia was found to be greatest in the northern region, between 11° and 13° latitude in the Great Barrier Reef (Fabricius and Alderslade 2001; Fabricius and De'ath 2001).

2. Biology of soft coral

Soft corals belong to the order Alcyonacea, subclass Octocorallia, class Anthozoa and phylum Cnidaria (Bayer 1981). The most important feature of Octocorallia distinguishing them from the others is that each polyp bears eight tentacles and usually one or several rows of pinnules on both sides of the tentacle. Moreover, unlike stony corals with structural skeletons, the small sclerites embedded in the coenenchyme in most soft corals are another different characteristic between hard and soft corals.

Along with the hard scleractinian corals, soft corals play an important role as components of coral reef benthic assemblages, influencing primary productivity and providing a source of food and habitats for other organisms (Fabricius and Alderslade

2001). Moreover, the sclerites of fleshy soft coral like genus *Sinularia* consolidated on the substratum could contribute to the reef building (Jeng et al. 2011)

2.1. Colony growth forms

The variable colony shapes is one of the characteristics of soft corals. Each kind of colony shape of the soft corals consists of different parts such as stalk, lobe, disc and capitulum. Bayer et al. (1983) defined the various growth forms and used technical terms such as membranous, encrusting, digitate, massive, arborescent shapes (Fig. 2) for the description of Octocorallia. Although, in some soft corals the colony form could be variable within species (Benayahu et al. 1998); the colony shape is one of the important characteristics for taxonomical classifications (Bayer et al. 1983).
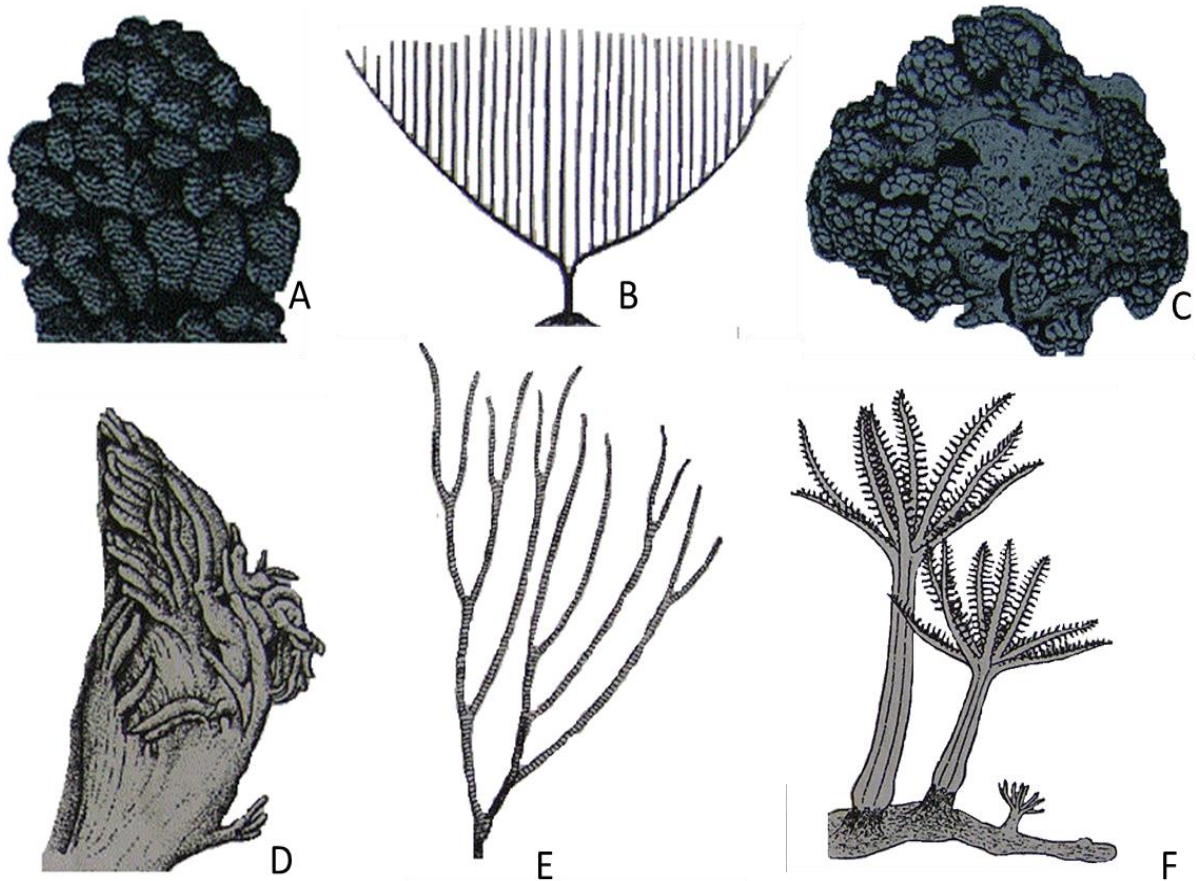

Figure 2: The various soft coral forms. Note: A: Lobate form (*Cladiella kremfi*), B: Arborescent (lyrate) form (*Ctenocella pectinata*), C: Encrusting form (*Cladiella tenuis*), D: Digital form (*Sinularia capilosa)*, E: Arborescent (dichotomus) form (*Ascolepis splendens*) and F: Stolonate growth form (*Clavularia harma = Briareum hamrum*). Adapted from Bayer et al. (1983).

2.2. Polyp structure

Two types of polyps are found in soft corals: autozooid and siphonozooid (Ashworth 1899; Pratt 1906). Autozooids contain eight tentacles including eight septa to connect with pharynx while siphonozooids have a simple structure with reduced size and still eight rudimentary tentacles (Hyman 1940) (Fig. 3).
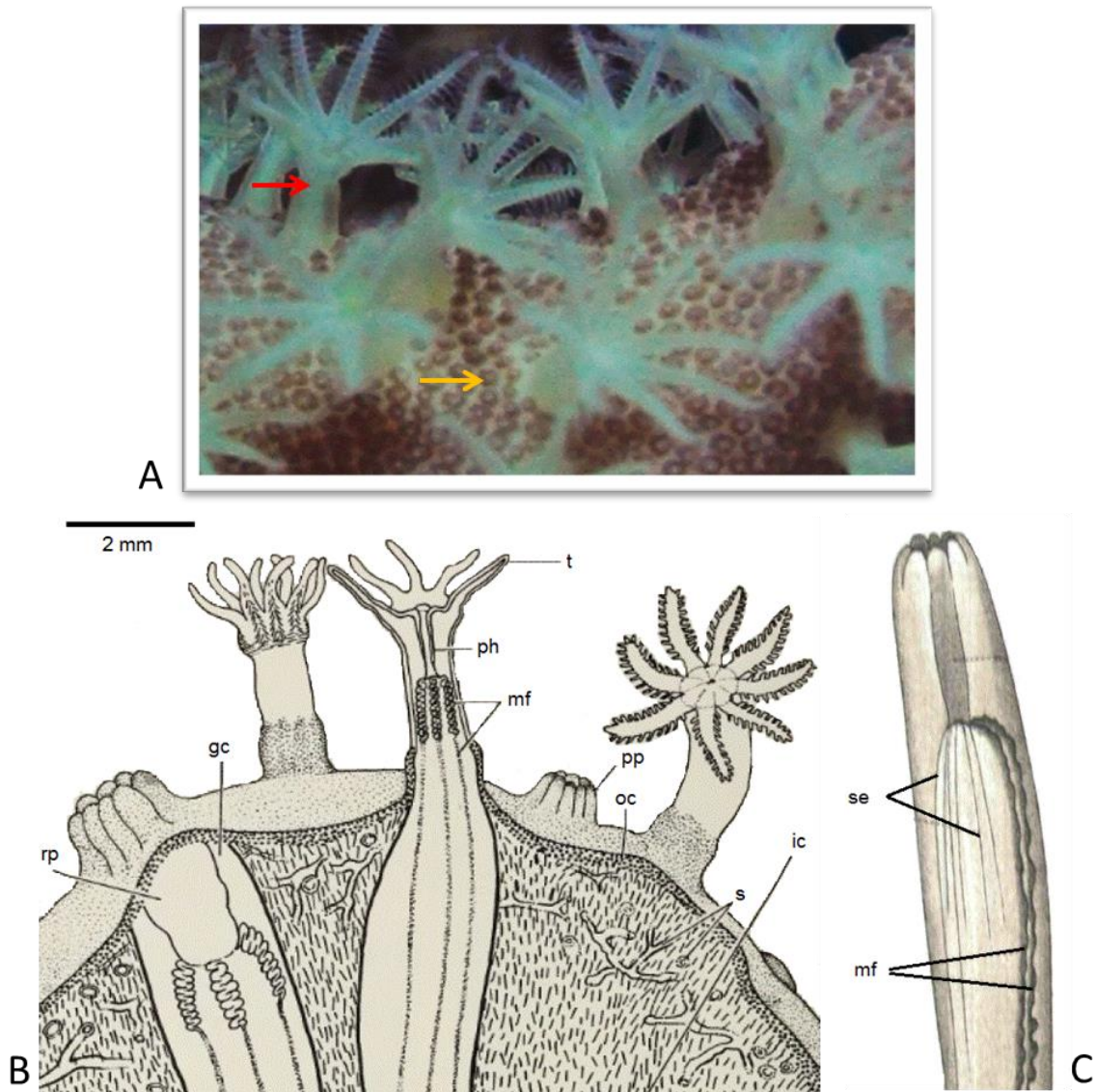
Figure 3. A The surface of soft corals with expanded autozooid polyps (red arrow) and numerous small rounded siphonozooids (yellow arrow) Adapted from Fabricius' photo in Fabricius and Alderslade (2001). B Autozooid structure. Adapted from Williams (1986). C: Siphonozooid structure. Adapted from Ashworth (1899). Notes: rp, retracted polyp; gc, gastric cavity; mf, mesenterial filament; ph, pharynx; pp, proximal region of polyp; oc, outer coenenchyme; ic, internal coenenchyme; s, solenial tubes; se, septa; t, tentacle.

The polyp of soft corals constitute three layers: the outer layer of tissue is called the epidermis which contains mucus producing cells, sensory cells and nematocysts. The inner layer is called the gastrodemis covering the gastric cavity, mesenterial filament, pharynx. The layer between epidermis and gastrodemis is called the coenenchyme and consists of fiber, amoeboid cells and calcareous sclerites (Fabricius and Alderslade 2001).

The function of the two types of polyp is different, the autozooid is responsible for capture of prey and sexual reproduction while siphonozooids maintain irrigation of the colony and take small suspended food particles (Fabricius and Alderslade 2001). The total length of autozooid and siphonozooid are not only variable among species (Pratt 1906) but can also vary within the same species (Ashworth 1899). The numbers of siphonozooids present on the surface of colonies and the distance between siphonozooid and autozooid are also important characteristics for identification of some soft coral species (Verseveldt 1982, 1983).

2.3. Symbiotic algae

Soft corals can be differentiated into two groups by the presence or absence of their symbiosis with dinoflagellate algae called zooxanthellae (genus *Symbiodinium*) embedded in their gastrodermal cells. The colour variation of most zooxanthellate soft corals is influenced by the density of the symbiotic algae present (Gohar 1940). Moreover, different colors even occur within the same species (Verseveldt 1969). The diameter of zooxanthellate cells have been found to be between 8 - 12μm in corals and their densities usually range between $1 - 2 \times 10^6$ cm^{-2} (Muller-Parker and D'Elia 1997).

Based on the genetic sequence, the genus *Symbiodinium* is divided into 9 groups (= clades) abbreviated as A-I (Barneah et al. 2004; Van Oppen et al. 2005; FitzPatrick et al. 2012). Trench (1987) suggested that the post-larval stages of soft coral could acquire the dinoflagellate in two ways: (1) The acquisitive direction in which larvae receive algae from parental mature source by brooding reproduction, called vertical transmission and (2) to receive algae from ambient environment, called horizontal transmission. In vertical transmission the host can completely obtain its symbiotic algae from parents and thus quickly adapt to the new life conditions, while in horizontal transmission, the juvenile stages may take up different clade types of algae

from the surrounding environment, which may result in reduced or enhanced adaptation of the holobiont towards environmental conditions.

Barneah et al. (2004) reported that the vertical transmission belongs to *Symbiodinium* clade A while horizontal transmission belongs to the predominant *Symbiodinium* clade C in the soft corals. However, it appears possible that all suitable clades may be either vertically or horizontally transmitted, depending on the biology of the coral host. Most xeniiid species exhibit brooding reproduction (Kahng et al. 2011), and hence it could be that most of them uptake symbiotic algae by vertical transmission (e.g. in *Ovabunda macrospiculata* (Benayahu and Schleyer 1998); and *Anthelia glauca* (Achituv et al. 1992)).

2.4. Sclerites

Calcium carbonate spicules are common attributes in Octocorallia, as well as in many Porifera, Echinodermata and Ascidiacea (Kingsley 1984). The sclerites are embedded in the coenenchyme of soft corals and they vary in shapes and concentration between species or different parts of colony of the same species (Sammarco et al. 1987; Van Alstyne et al. 1992). However, the density and length of sclerites can also vary along the depth gradient (West 1998; Clavico et al. 2007). Sizes and shapes of the spicules are uasually species-specific and are used as taxonomic tools (Bayer et al. 1983).

Most of the studies available suggested that the main function of sclerites is to support the structural polyp and colony (Lewis and Von Wallis 1991; Van Alstyne et al. 1992; O'Neal and Pawlik 2002) or act as defensive tools against predators like carnivorous fishes (Van Alstyne et al. 1992, 1994). However, some soft corals lack sclerites (Gohar 1940), and hence their function is still under debate (Kelman et al. 1999; O'Neal and Pawlik 2002)

2.5. Reproduction

Soft corals reproduce both sexually and asexually. Sexual reproduction includes both gonochorism and hermaphroditism. In gonochorism, males and females form separate colonies (up to 89% of soft corals). In hermaphroditism, mature colonies consist of both male and female (Kahng et al. 2011). Three types of sexual reproduction are known in Octocorallia and spawning time differs between season and species (Gohar 1940; Benayahu and Loya 1983, 1984b; Benayahu 1991): (1)

Broadcasting sperm and eggs - the sperm and eggs are expelled synchronously by the mature colonies into the water where the fertilization occurs (2) internal brooding - the fertilization occurs inside the female colonies and (3) External surface brooding - the eggs are fertilized and remain on the surface of female colonies where they develop into larvae (Fig. 4).
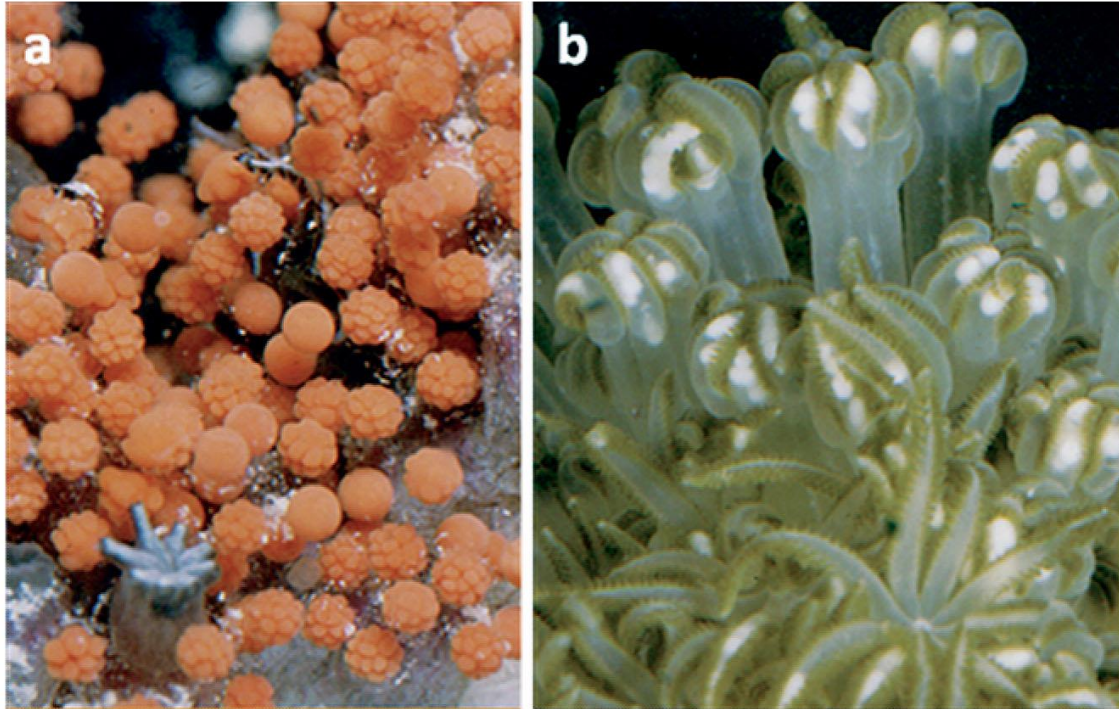
Figure 4: Sexual reproduction in soft corals. (a) External surface brooding (*Briareum hamrum*), (b) internal brooding (*Heteroxenia fuscescens*). (Source: Kahng et al. 2011).

The ratio of broadcasting spawning species (49%) is approximately equal to those internally brooding (40%) plus external brooding (11%) in the sexual reproduction of soft corals (Kahng et al. 2011). Interestingly, some species may also show different sexuality in different regions, for example *Heteroxenia elizabethae* is described to be gonochoric in the Great Barrier Reef but hermaphroditic in the Red Sea; *Sarcophyton glaucum* is gonochoric in the Red Sea but mixed in South Africa (Kahng et al. 2011). It could be that the environmental conditions may be responsible for the various sexuality of soft corals or that sibling species are present in these species.

Asexual propagation is a common type of reproduction in soft corals (Fabricius and Alderslade 2001) including colony fragmentation, fission or budding. These asexual strategies are performed on different parts of colonies within and between species. For example *Sinularia flexibilis* produces small buds on the edge or base of

colonies (Fabricius and Alderslade 2001), *Ovabunda macrospiculata* buds the second polyp around 3-4 months after settlement on the substratum (Benayahu and Loya 1984a). Asexual reproduction, as for example by fragmentation, is one of the reasons for successful growth and recovery of some soft corals on disturbed reefs (Highsmith 1982).

2.6. Nutrition

Most soft corals acquire nutrients by two pathways: feeding and photosynthesis. Azooxanthellate soft corals get the nutrients by feeding on small particles or capture prey from the ambient environment. In contrast, zooxanthellate soft corals uptake energy through photosynthesis by symbiotic dinoflagellate but also gain additional nutrition (nitrogen, phosphorous, trace elements etc.) by trapping food from the ambient environment (Fabricius and Alderslade 2001).

Feeding: Suspension feeding by selected asymbiotic soft corals targets small particulate organic matter (<20 size µm) including phytoplankton, ciliates, dinoflagellates, diatoms, bacterioplankton or microzooplankton (Fabricius et al. 1995a; Fabricius et al. 1995b; Ribes et al. 1998). Currents of medium speed (ranging 8 - 15 cm s^{-1}) provide good feeding conditions for soft corals. Stronger currents reduce feeding efficiency by bending the polyps and increasing speed of particles (Fabricius et al. 1995b).

Nematocysts used in prey capture are embedded in the outer layer of soft coral tissue (epidermis) (Fig. 5). These nematocysts are simpler in comparison to other animals like jellyfish, hydroids and sea anemones. Thus, the prey capture capacity of soft coral nematocysts is limited to weakly swimming organisms, including bivalve or gastropod larvae, while zooplankton with stronger swimming activity can often escape after being captured (Fabricius et al. 1995b). Hence the proportion of carbon and nitrogen contributed by prey capture is less than that from suspension feeding in nutrition of soft corals (Fabricius et al. 1995a; Ribes et al. 1998).

Photosynthesis: Although the zooxanthellate soft corals can acquire nutrients by prey capture, they acquire more energy from photosynthesis by their symbiotic algae. Conversely, the waste products obtained by prey capture or suspension feeding are transported to zooxanthellae by their host coral. Muscatine (1990) reported that symbiotic algae can provide up 90% energy by photosynthesis for

fulfilling the nutrient requirement of the host. However, the supply of photosynthetic products to the host coral differs among *Symbiodinium* clades (Stat et al. 2008).

Some studies have suggested that tropical soft coral species increase the density of zooxanthellae in their tissues in the winter season, in response to the low light conditions; and also that azooxanthellate soft corals are more abundantly distributed in areas of high turbidity (Muller-Parker and D'Elia 1997; Fabricius and McCorry 2006), where zooxanthellate species may receive insufficient illumination and/or be stressed by sedimentation.
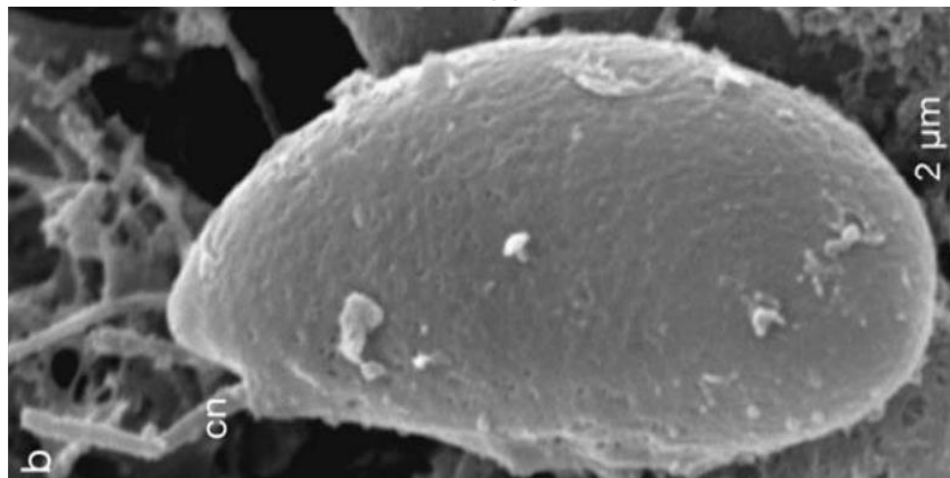
Figure 5: The nematocytes (arrows) in the gastrovascular cavity of *Heteroxenia fuscescens* (A) and view of a nematocyte (B) note: mf. Mesenteries (Source: Yoffe et al. 2012).

2.7. Anti-predator defense of soft corals

Predation is known to be one of the factors influencing or controlling populations of many marine invertebrates, including soft corals, presumably driving natural selection for the evolution of defense mechanisms. Soft corals deter their predators by physical defense, chemical defense or both (La Barre et al. 1986; Sammarco and Coll 1992; Van Alstyne et al. 1994; O'Neal and Pawlik 2002).

Chemical defense is defined as the production of metabolites by the prey to defend itself against predators through toxicity or unpalatability (Pawlik 2012). Toxicity means that the metabolites produced by soft corals can cause damage to, or death of, the predators. Unpalatability is achieved through the production of secondary metabolites that can deter predators by distastefulness without harming the predators. Anti-predatory defenses of soft corals exhibit temporal and spatial variation in response to environmental conditions (Slattery et al. 2001).

Additive and synergistic phenomena are apparent in chemical defense by soft corals (Pawlik 2012). For example, single compounds of soft corals could not deter predation when tested separately. However, anti-predator defense did occur when different compounds were combined (Epifanio et al. 2007). Single compounds have also proven less effective at predator deterrence than the sum of effects of all active compounds (Fenical and Pawlik 1991; Pawlik and Fenical 1992).

Unlike the stony corals that have the skeleton for support, most soft coral species have small sclerites in the coenenchyme, which may provide a means of physical defense. However, such physical defense by sclerites may be effective only in those parts of the colony where their concentration is particularly high (Puglisi et al. 2000). Moreover, the defensive role of sclerites depends on their shape, size, abundance and the arrangement of sclerites on the polyp or colony (Sammarco et al. 1987; Van Alstyne et al. 1992; Koh et al. 2000; Burns and Ilan 2003).

Some soft coral species showed a deterrence of predators both through physical and chemical defense (Van Alstyne and Paul 1992; Koh et al 2000; O'Neal and Pawlik 2002). The combination of both physical and chemical defense was found to be a more effective deterrent than their activity when separated (Burns and Ilan 2003). For example, the incorporation of sclerites and crude extracts was more unpalatable to predators because of reduced food quality (Duffy and Paul 1992). The

penetration of chemicals into the tissue was aided by sclerite damage to the mouth of the predator (Burns and Ilan 2003).

3. Environmental conditions and their influence on soft corals distribution

These parameters may act independently or together in structuring coral communities. For example, water motion, depth and slope angle are important abiotic factors that can affect local distribution patterns, cover and morphology of soft corals (Fabricius and De'ath 1997).

3.1. Temperature

Temperature is a limiting factor for distribution of zooxanthellate soft corals. Some species of the symbiotic algae in soft coral can become physiologically stressed by temperature extremes, typically when the temperature is lower than 18°C or above 31°C, particularly if such extremes are present for extended periods. Rising temperatures can cause bleaching in corals through loss of the symbiotic zooxanthallae, the *Symbiodinium* from their tissues.

Typically bleaching is a three step process: initiation of signal factors (e.g. rising temperature), appearance of symptoms (losing pigment in the symbiont algae and/or coral host) and induction of bleaching mechanism (the response of symbiont algae and the coral host to signal factors) (Douglas 2003). Susceptibility to temperature related bleaching differs between soft coral species (Strychar et al. 2005). Corals are more resistant in some regions where the temperature is more variable (Guest et al. 2012). Azooxanthellate soft corals are not affected by bleaching, facilitating their distribution in certain regions unfavorable or inimical to the zooxanthellate taxa, and to temperate zones and deep water (Fabricius and Alderslade 2001).

3.2. Light conditions

Like terrestrial plants, the zooxanthellate soft corals need light for photosynthesis of their symbiotic algae. As zooxanthellae provide photosynthetic products to their coral hosts, light conditions may become a limiting factor for the distribution of soft corals. Photosynthesis of symbiotic algae is important for calcification in corals (review by Tambutté and Ferrier-Pagès 2008). Soft coral diversity can shift from zooxanthellate to azooxanthellate species along a gradient of

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turbidity (Fabricius and De'ath 2001), which means that the ambient light condition, like temperature, is an important factor in the structure and distribution of soft coral communities.

3.3. Sedimentation

Soft corals are more sensitive to sediment deposition than hard corals (Riegl 1995). Deposited sediments can affect corals by preventing feeding and/or photosynthesis and reducing available substrates suitable for coral settlement (Huston 1995; Pastorok and Bilyard 1985; Birrell et al. 2005). Sediments deposited on the surface of soft corals can cause necrotic tissue in colonies after several days and bleaching in some parts of the colony or death after several weeks (Riegl 1995).

Moreover, like hard corals, the impact to soft corals of sediment deposition depends on a wide variety of factors, including the amount and types of sediment, and the impact varies between species (Fabricius 2005). Soft corals can use their mucus as a sheet to protect themselves against sedimentation (Riegl and Branch 1995), and sediments may also be dislodged from their surface by current motion or gravity (Riegl 1995). Substratum selection for settlement can influence colony development and survival rate (Benyahu and Loya 1984b).

3.4. Human impacts

Direct or indirect impacts of human activities have significant effects on the distribution, abundance and community structure of soft corals. These can include oil pollution, sewage pollution, nitrate, phosphate and sulphur enrichment and inputs of other pollutants in river runoff and from shipping, destructive and overfishing and recreational activities (Pastorok and Bilyard 1985; Ammar et al. 2007; Tilot et al. 2008; Klaus et al. 2008; Mohammed 2012).

3.5. Predation and competition

As introduced above in Section 2.7, some soft coral species, notably of the families Xeniidae and Alcyoniidae, contribute to the diet of coral reef fishes (Gohar 1940). Some taxa known to feed on soft corals are egg cowry (*Ovula ovum*) and carnivorous coral fishes. Predation can be a major force structuring reef communities. For example, in 27 years (1985-2012) the major decline in hard coral cover on the Great Barrier Reef declined to 42% was mainly due to predation by the crown-of-

thorns starfish *Acanthaster planci*, but also from impacts of tropical storms, bleaching and pollution in river runoff (De'ath et al. 2012). However, such major declines in soft coral cover from predation across an entire reef tract so far have not been documented.

Competition for space is common among the sessile organisms dwelling on coral reefs. Benayahu and Loya (1981) suggested that stony corals and algae are major groups competing for space with soft corals on the reef flat. However, soft corals can respond to such space competition by using a variety of strategies. For example, some soft corals can cause necrosis of tissue in stony corals when the colonies are in contact (Sammarco et al. 1985); or kill stony corals in their direct vicinity by releasing allelopathic chemicals into the surrounding sea water (Sammarco et al. 1983). Moreover, moving to occupy new space or moving away from each other via asexual reproduction are strategies used by soft corals to avoid competition (Benayahu and Loya 1981; La Barre et al. 1986).

3.6. Storms and disease

As noted above, tropical storms (variously known as cyclones, typhoons or hurricanes) can cause significant declines in coral cover, as for example on the Great Barrier Reef (De'ath et al. 2012) and in the Caribbean Sea. However, such storms also provide new substratum for settlement and recruitment.

Coral diseases are becoming increasingly important, with 18 coral diseases of zooxanthellate corals currently known from the Caribbean and Indo-Pacific regions (review in Sutherland et al. 2004). Coral diseases are more common in hard corals (0.3%) than soft corals (less 0.03%) in the central Pacific and 0.63% coral disease reported in the northern Red Sea (Williams et al. 2011; Mohamed et al. 2012). It could be that soft coral are more resistant towards the impacted disease than hard corals (Williams et al. 2011).

4. Soft corals in the Saudi Arabian Red Sea

The Red Sea is the north-western extension of the tropical Indo-Pacific and includes complex ecosystems, mainly coral reefs, sea grass beds and mangroves.

Environmental parameters such as temperature, salinity, chlorophyll a and nutrients vary along a gradient from north to south in the Red Sea (Morcos 1970; Sawall et al. 2014). For example, temperature on the sea surface ranges between 20-26°C in the northern Red Sea and 26-33°C in the southern Red Sea. The highest salinity value is 41.2 psu in the North and 37.4 psu in the South and chl a ranges between 0.01 µg l^{-1} in the North to 1.98 µg l^{-1} in the South (Fig. 6).
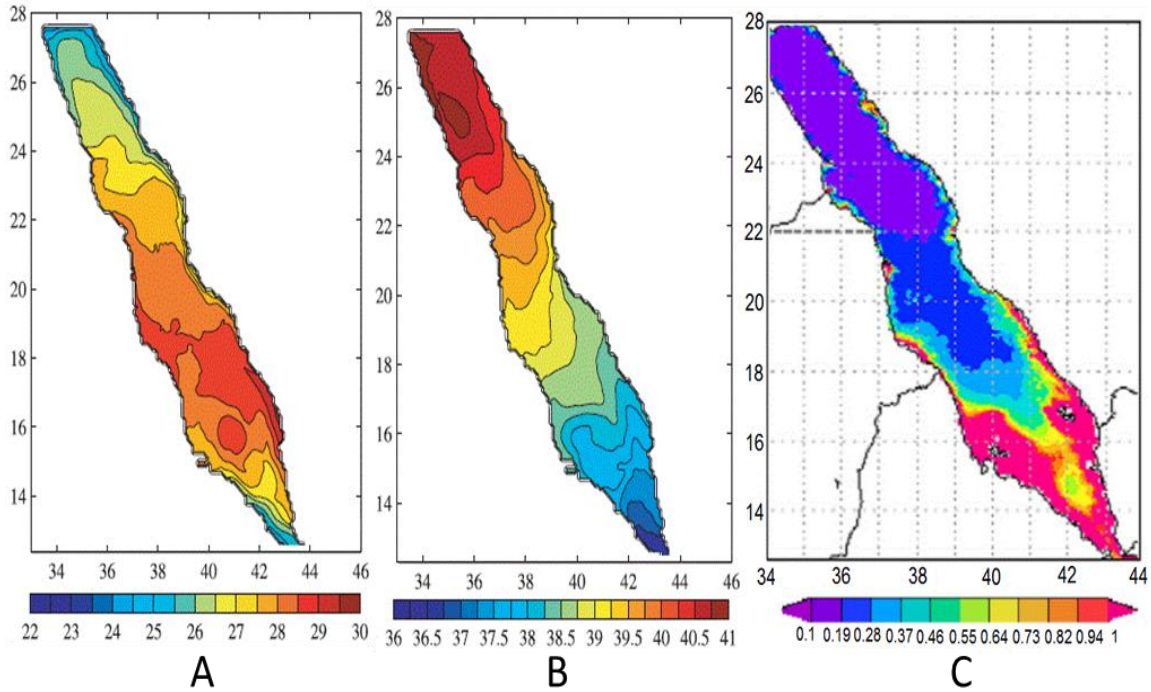
Figure 6: Mean of sea surface temperatures $^{\circ}$C (A), salinity psu (B) and chlorophyll a content (mg m^{-3}) in the Red Sea (A, B: Miami Isopycnic Coordinate Ocean Model average over the last 9 years of simulation. Source: Sofianos and Johns 2003; C: Field-of-View sensor average of chl a concentration for the Red Sea from Jan. 1998 to Dec. 2004. Source: Acker et al. 2008).

The total area of coral reefs in the Red Sea is estimated to be approximately 17,640 km^2 of which around 6,660 km^2 is present in the Saudi Arabian area, representing about 2.34% of world's total shallow water reef area (Spalding et al. 2001) (Fig. 7). The three general types of reefs in the Red Sea include patch, fringing and barrier reefs. While the Gulf of Aqaba in the northern Red Sea is characterized by fringing reefs along the coast, the central and northern Red Sea exhibit all reef types: barrier reefs on submerged limestone platforms, fringing reefs along the coast and around various islands and diverse patch reefs. Towards the South the slope of the coastal sea bed decreases slowly and fringing reefs around islands (Farasan banks and islands) and patch reefs are most common (Sheppard et al. 1992).

Figure 7: Coral reef distribution in the Red Sea (Adapted from: Wilkinson 2008)

The Red Sea has a long history of coral reef research. First observations about soft coral diversity were carried out by Forskål as early as 1775. The knowledge of soft coral diversity in the Red S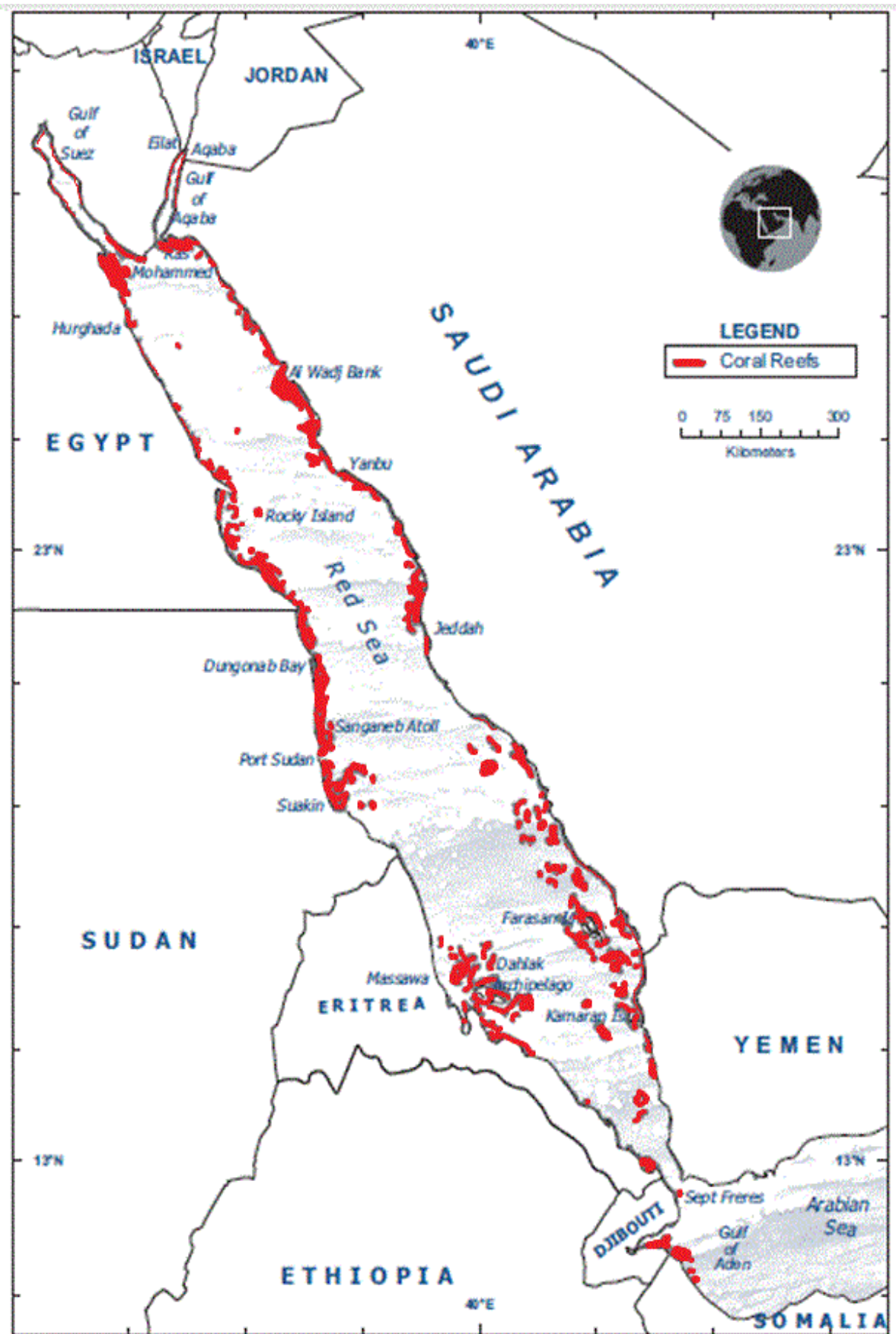ea increased following various expeditions. Benayahu (1985) reviewed the soft coral diversity in the northern Red Sea and reported 183 species from this region, including 18 new species and 29 new geographical records. Benayahu et al. (2002) in a study of soft corals in the southern Red Sea, listed 28 species, among them five genera and 16 species were recorded for the first time in the South. Ofwegen's (2000) revision of the genus *Sinularia* indicated that this genus in the Rea Sea exhibits the highest diversity among the different reef regions of the world. Reinicke (1997) reported 34 species of xeniid soft corals, some of which were first records in the Red Sea. Halász et al (2013) reexamined the xeniid samples and reported 11 species belonging to new genus *Ovabunda* Alderslade (2001) in the Red Sea.

During recent years, the rapid economic development and costal activities in Saudi Arabia have led to increasing pressure on coral reef systems, especially impacting shallow inshore reefs on local scales (PERSGA 2010). For example, the amount of wastewater discharged into the sea in Jeddah city was 800,000 m^3/day (Kotb et al. 2008) and the metal pollution in sediments was recorded to be in a high concentration at Yanbu, Rabigh and Jeddah, where there are many industrial and human activities along the coast line (Badr et al. 2009).

These are potentially significant point sources impacting coral reef communities in the adjacent near-shore areas. Scuba diving has also been found to impact coral communities as it increases both the amount of dead coral and coral rubble (Tratalos and Austin 2001). Recreational activities such as scuba diving and trampling on coral reefs are common in some areas of the Red Sea, though not in Saudi Arabia (Hawkins and Roberts 1993).

The desalination plants of Saudi Arabia, which supply potable water to towns and cities, pump out about 2.27 million m^3/day of salty water into the sea (Hoepner and Lattemann 2002; Dawoud and Al-Mulla 2012). Hence impact from anthropogenic activities may be an important factor affecting local coral reefs along some sections of Saudi Arabia coastline, as indeed elsewhere in the Red Sea.

5. Thesis outline

Soft corals in the Red Sea are a dominant component of diversity and abundance of coral reef benthos. Indeed, diversity of soft corals in the Red Sea is among the highest in the tropical coral region. Given that environmental conditions such as temperature, salinity and chlorophyll a all change along a gradient from north to south in the Red Sea, this gradient could be considered as a 'natural experiment' to investigate soft coral diversity and abundance for comparison with other regions.

Moreover, human activities are increasing along the Saudi Arabian coast. Several important questions are: whether or not there is a clear relation between soft coral abundance and diversity and the environmental gradient in the Red Sea, how human activities impact to soft coral communities in the near-shore and what factors influence relative abundance of soft corals on the coral reefs? Moreover, survey of the soft coral communities from the northern to the southern Saudi Arabian Red Sea will contribute to a better understanding of biodiversity and large scale distribution patterns in the Red Sea.

To address the above questions, this study of soft coral communities in the Red Sea undertook to resolve three main aspects:

- How do the soft coral communities alter in diversity and distribution patterns along the gradient of environmental conditions from the northern to the southern Red Sea?
- How do the soft coral communities respond under differing conditions of impact from different pollution sources?
- Why are some soft coral species dominant where generalist carnivorous fish are prevalent on the reefs; and how do physical or chemical defences of soft corals confer protection against predator fish?

The first question was addressed in chapter one: *Patterns of soft coral (Octocorallia, Alcyonacea) diversity and distribution along a strong latitudinal environmental gradient in the coastal reefs of the Saudi Arabian Red Sea*. This chapter focuses on the relative abundance of genera and diversity of alcyonacean soft coral species along the Saudi Arabian Red Sea coastline as well as their relation with ecological parameters influencing the distribution patterns.

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The second question of effects of pollution was addressed in chapter two: *Patterns of Xeniidae (Octocorallia, Alcyonacea) communities impacted by different environmental parameters in the Red Sea*. The aim of this chapter is the comparison of xeniid assemblages in the Al-Wajh, Yanbu, Matura/Rabigh and Jeddah areas on the Saudi-Arabian Red Sea coast between near-shore and off-shore reef sites under differing conditions of impact from human pollution sources. The study also includes the results of substratum coverage surveys and relative abundance of alcyonacean soft corals at genus level at reefs effected by different environmental conditions.

The third question of chemical defense of soft coral against predatory fishes was addressed in chapter three: *Chemical versus mechanical defense against fish predation in two dominant soft coral species (Xeniidae) in the Red Sea*. In this chapter, the chemical and sclerites defense of two abundant xeniid species in the Red Sea *Ovabunda crenata* and *Heteroxenia ghardaqensis* were tested against predatory fishes both in the field (Jeddah, Saudi Arabia) and in the laboratory (Geomar, Germany).

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Patterns of Soft Coral (Octocorallia, Alcyonacea) diversity and distribution in coral reefs along strong latitudinal environmental gradients in the Saudi Arabian Red Sea

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Abstract

Alcyonacean soft corals were surveyed and sampled in 14 regions over 1840 km from the northern to the southern Saudi Arabian Red Sea and related to prevailing gradients in nutrients and temperature, as well as to changes in bathymetry and substrate condition. In total, 82 soft coral species were identified belonging to the families Alcyoniidae (6 genera, 40 species), Xeniidae (5 genera, 24 species), Nephtheidae (6 genera, 15 species), Nidaliidae, Briareidae and Tubiporidae (one species each). Using cluster analysis, the soft coral species composition and abundance found at the surveyed sites grouped the sites into three main clusters, a northern (Maqna and Al-Wajh), central (Yanbu, Jeddah, Rabigh, Mastura and Al-Lith) and southern cluster (Doga and Farasan). The northern section, featuring lowest temperatures (up to 29°C), low nutrient concentrations, steep reef slopes and low sedimentation, harbored the highest soft coral abundance (Al-Wajh: 27% ± 4.1SE substrate coverage) and diversity (Maqna and Al-Wajh: 44 species). The southern section, characterized by high temperature (up to 33°C), high nutrient concentration, mostly rather shallow reef slopes and comparatively high sedimentation, harbored lowest soft coral abundance and diversity (Farasan: 0.6% ± 0.9 and 26 species, respectively). The characteristics of the central section mainly lay between the northern and southern section. Furthermore, near-shore reefs close to a source of pollution (Rabigh, Jeddah and Yanbu) generally featured a lower soft coral abundance

and diversity, if compared to their respective non-polluted off-shore site. In addition, new zoogeographical records of soft coral species were made in the central and southern section of the Red Sea, where *Xenia actuosa, Sarcophyton pauciplicatum, Sinularia dissecta, S. gyrosa* and *S. inelegans* were recorded for the first time.

Key words: Soft coral; biodiversity; distribution pattern; community structure; environmental gradient; latitudes; Red Sea.

Introduction

Soft corals (Octocorallia, Alcyonacea) were considered the wild flowers in coral reefs, because of their hidden charms (Allen and Steene 1994). They represent major components of the sessile reef benthos and diversity in tropical Indo-Pacific reef communities (Dinesen 1983; Fabricius and Alderslade 2001) including the coral reefs of the Red Sea (Benayahu and Loya 1977, 1981; Benayahu 1985; Reinicke 1997). Along with the hard scleractinian corals, soft corals play an important role as components of coral reef benthic assemblages, influencing primary productivity and providing a source of food and habitats for other organisms (Fabricius and Alderslade 2001).

The narrow trench of the Red Sea extends from the north-west to the south-east over 2,200 km between the latitudes 30°N and 12°N. It covers an area of 4.6 x 10^{5} km^{2} between the African and Asian continental plates. The coastline of the Saudi Arabian Red Sea extends roughly over 1,840 km. Four biogeographic zones were described for the Saudi Arabian Red Sea (UNEP/IUCN 1988): (1) the Gulf of Aqaba and (2) the northern half of the main Red Sea, both zones mainly characterized by well-developed steep fringing reefs as well submerged limestone platforms, (3) the southern half of the main Red Sea characterized by less steep fringing reefs and patch reefs, as well as large reef flats (4) the coastal zone characterized by less developed fringing reefs, in particular where sedimentation is high.

Studies on Red Sea soft corals started as early as 1775, when Forskål conducted first diversity studies. During the last century, the knowledge about soft coral diversity and physiology increased steadily, when researchers explored the Red Sea coral reefs during various expeditions (e.g. Thomson and McQueen 1907; Kükenthal 1913; Gohar 1940; Verseveldt 1965, 1969, 1970, 1974, 1982; Verseveldt and Cohen 1971; Verseveldt and Benayahu 1978, 1983; Reinicke 1997). Many

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species were originally described from the Red Sea and later also found in other tropical regions (Benayahu 1985). A high soft coral diversity in the Red Sea was confirmed by Benayahu, who counted 183 species in the reefs around the Sinai Peninsula (northern Red Sea, Benayahu 1985) and 28 species in the most southern reefs of the Red Sea (Eritrea and Yemen, Benayahu et al. 2002). The common genus *Sinularia* was found to be the most species rich genus in the Red Sea, if compared to other Indo-Pacific coral reef regions (Ofwegen 2000).

Soft corals in the Red Sea are not only highly diverse, but also show considerable abundance on the reefs with coverage values reaching up to 50% in some shallow reef areas (~4m depth) forming extensive carpets (Benayahu and Loya 1981; Reinicke 1997). The high success of soft corals in the Red Sea was previously related to the fact that soft corals do not only reproduce sexually, but also intensively by asexual propagation, thereby efficiently outcompeting potential space competitors (Benayahu and Loya 1977, 1981). Additionally, some soft coral species such as *Xenia (= Ovabunda) macrospiculata* feature a very short planktonic phase and quickly propagate by polyp budding after settlement, which contributes to their high success in Red Sea coral reefs (Benayahu and Loya 1984). Furthermore, some soft corals species in the Red Sea such as *Rhytisma fulvum fulvum, Ovabunda macrospiculata, Sarcophyton glaucum* are also known to feature a strong chemical defense against predation or microbial activity (Kelman et al. 1998, 1999, 2006).

Like stony corals, the distribution of soft corals strongly depends on water quality, including for example the availability of light, the strength of water movement and the occurrence of sedimentation (Fabricius and De'ath 1997), as well as on biotic controls such as predation and competition (Fabricius and Alderslade 2001). Changes in octocoral community patterns along water quality gradients were reported for example from the Great Barrier Reef (Fabricius et al. 2005) and South China Sea (Fabricius and McCorry 2006). There, overall soft coral diversity decreased, while the abundance of azooxanthellate octocorals taxa increased when water quality decreased (increase of nutrients, sedimentation and turbidity). Furthermore, living soft coral cover and diversity is usually higher on exposed reef slopes than on reef flats or back reefs, due to stronger water movement and higher water clarity at exposed reefs (Dinesen 1983; Evans et al. 2011; Chanmethakul et al. 2010).

In the Red Sea, the environmental and habitat conditions change over the latitudes. From north to south, average annual surface water temperature increases

by ~6°C, salinity decreases (42 to 38 psu), nutrient concentrations and turbidity increase particularly in the South, and the bathymetry changes from steep reefs to slightly sloping reefs. These changes were found to influence the community structures of hard corals (Sheppard et al. 1992) and do most likely also shape the soft coral community structures. So far, this, however, can only be inferred from comparative studies performed at the very northern (Gulf of Aqaba) and at the very southern end of the Red Sea (Eritrea and Yemen) (Benayahu 1985; Benayahu et al. 2002), while systematic and continuous surveys along the latitudinal environmental gradients are still lacking.

Furthermore, increasing human activities in coastal areas cause changes in water quality and habitat structure in consequence of, for example, petroleum oil pollution, eutrophication, sediment input, overfishing and recreational activities (Ammar et al. 2007; Tilot et al. 2008; Klaus et al. 2008; Mohammed 2012). These most likely affect near-shore soft coral communities, as well, particularly at shallow inshore reefs close to regions of rapid economic development and increasing coastal activities (PERSGA 2010).

The aim of the present study was to assess potential shifts in the structure of alcyonacean soft coral communities along the latitudinal environmental gradients in the Red Sea and to relate coral diversity and relative abundance to prevailing environmental conditions. Additionally, the potential effect of land-based anthropogenic alterations of environmental conditions was investigated.

Methods and materials

Studying area: Fourteen reef sites within 7 regions (distance between regions ~300 km) were investigated along the Saudi Arabian Red Sea coast between 16°34'N and 28°31'N (Fig. 1, Tab. 1). The northernmost site Maqna (MAQ) is located near-shore in the Gulf of Aqaba and the southernmost sites are located about 50 km off the mainland, close to the Farasan islands (FAR).

The study sites are listed as followed from north (superscript 1) to south (superscript 7) and donated with 'N' (superscript) for non-polluted reefs and 'P' (superscript) for reefs close to a potential source of pollution: Maqna (MAQ[1N]), Al-Wajh (WAJ[2N] and WAJ[2P]), Yanbu (YAN[3N] and YAN[3P]), Mastura (MAS[4N]), Rabigh (RAB[4P]), Jeddah (JED[5N] and JED[5P]), Al-Lith (LIT-N[6P] and LIT-S[6P]), Doga (DOG[6N]) and Farassan (FAR-S[7N] and FAR-S[7N]). The six reefs categorized as potentially polluted

are located less than 500 m away from a sources of pollution which varied in type and intensity (specified in Tab.1). It should be noted that this categorization is based on circumstantial evidence only, since no environmental monitoring is conducted in these regions.

Environmental parameters: The values of the environmental parameters temperature, chlorophyll a, total nitrogen and phosphorous, particulate carbon of the study sites/regions were derived from Sawall et al. (2014) for September in 2011 (late summer) and March in 2012 (late winter). The data was averaged over the two months, providing a rough estimation of the average annual environmental condition.

The study sites of Sawall et al. (2014) were the same as in this study. Additionally the silicate concentration was determined from the same batch of water samples as used for the aforementioned parameters. For this triplicate water samples (15 ml) were filtered by gravity through a 0.2 μm membrane filter and kept in scintillation vials at -20°C until analysis. Silicate was determined photometrically following the standard procedure described by Grasshoff et al. (1983).

Soft coral composition and reef structure: Each reef site was surveyed using two techniques: (1) the line intercept transect (LIT) was used to assess the composition of substratum coverage and (2) the rapid ecological assessment (REA) was used to estimate the abundance and diversity of Alcyonacea genera at each site.

For the LIT, a measuring tape of 100 m length was laid out at 3 m depth parallel to the reef contour and the underlying substrate was recorded every 0.5 m (English et al. 1997). The substrate was categorized into the living categories 'hard coral', 'soft coral', 'macro-algae' and 'others' (e.g. sponge, anemone, tunicates) and into the non-living categories 'rock' (dead coral boulders and rock), 'rubble' (small dead coral pieces max. 15 cm long), 'sand' and 'silt'. Percentage cover of each substrate was calculated.

The REA method (Devantier et al. 2000a,b; Fabricius and De'ath 2001; Fabricius and McCorry 2006) was chosen to assess soft coral composition and habitat structure. It is a highly efficient method considering the amount of data retrieved per unit of time spent under water (Dinesen 1983), and considering its power to detect rare and heterogeneously distributed taxa within a large range of reefs (Fabricius and De'ath 2001; Fabricius and McCorry 2006). Surveys were conducted at 2 - 4 m and 5 - 10 m depth always of the same diver (here B. Hoang), who was slowly swimming

over the reef for 30 minutes covering a section of 100-150 m length and recorded the following data:

- The relative abundances of each alcyonacean soft coral on a scale from 0 to 5, with 0 = absence, 1 = few colonies covering < 1 %, 2 = uncommon, covering 1 - 5%, 3 = common covering 6 - 10%, 4 = dominant, covering 11 - 20% and 5 = highly abundant, covering > 20% (Fabricius and McCorry 2006). Due to difficulties distinguishing between the two genera *Xenia* and *Ovabunda* (previously being one genus *Xenia* - Alderslade 2001), they were summarized as '*Xenia*' (*Xenia/Ovabunda*). Samples, however, were retrieved and identified later (see description below).

- The sediment deposit on the reef substratum was assessed by fanning with the hand and rated on a scale from 0 to 4, with 0 = no dispersion of sediment , 1 = low dispersion, referring to a thin layer of sediment, 2 = medium dispersion referring to a medium thick layer of sediment and 3 = high dispersion referring to a thick layer of rather fine sediment (Fabricius and McCorry 2006). Additionally, the turbidity (water clarity) was estimated based on the horizontal visibility (V) and was categorized on a 3-point scale: 1 (V = 0 – 5 m), 2 (V = 6 - 10 m) and 3 (V > 11 m) labeled as 'turbid', 'moderate' and 'clear', respectively.

Furthermore, the angle of reef slope was recorded and assigned to one of the three categories 'flat' (0 to ~15° angled slope = 1), 'sloping' (15°~ 45° angled slope = 2) and 'steep' (45°~ 90° slope = 3). All surveyed reefs were facing towards the open sea and exposed to full sunlight.

Diversity of alcyonacean soft corals: Reference material of soft corals was collected for identification during expeditions along the Saudi Arabian Red Sea coast in February 2011, September-October 2011 and March 2012, from a total of 24 reef sites (previously described sites + additional neighboring sites). This resulted in approximately 1000 specimens, which were collected between 1 and 38 m water depth. In some southern reefs (Al-Lith and Farassan), where the depth range was less than 38 m depth, collection took place down to the maximum depth of reef distribution. Prior to collections, colonies were photographed *in situ*. After collection, samples were fixed in 4% formalin, rinsed with fresh water after 24h and transferred to 70% ethanol for long term preservation and examination.

Tissue samples from different colony parts (polyp, surface layer of the colony top, interior of the colony top, surface layer of the colony base and interior of the base) were examined separately after dissolving the organic matter in 10% sodium hypochlorite to observe the sclerites under an optical microscope at magnifications of x 40, x 100 and x 400. All samples were divided and distributed between the following institutions as taxonomic vouchers and reference material: GEOMAR in Kiel (Germany), KAU in Jeddah (Saudi Arabia) and Deutsches Meeresmuseum in Stralsund (Germany).

Data analysis

All data analyses were performed by multivariate statistics using the software Plymouth Routines in Multivariate Ecological Research-PRIMER 6 (Clarke and Gorley 2006) and PERMANOVA (Anderson et al. 2008).

To assess the similarity between the alcyonacean soft coral community structures based on the REA, a resemblance matrix was calculated based on Bray-Curtis similarity, followed by a hierarchical cluster analysis (based on group averages). No data transformation was necessary for the resemblance matrix, since the data was categorical.

In order to assess potential relationships between alcyonacean communities and environmental parameters, the same soft coral resemblance matrix was used to perform a Principal Coordinate Analysis (PCO) to which the environmental data set was added based on Pearson correlations (symbols represent soft coral communities, vectors represent environmental parameters).

The environmental parameters included temperature, all nutrient-related data (Chlorophyll a (chl a), total nitrogen (TN), total phosphorous (TP), particular carbon (PC) and silicate (Si), as well as sediment deposits, visibility and slope. The environmental data was normalized in order to avoid artificial effect from different units. PCO was chosen over Principal Component Analysis (PCA, same principal of analysis), since it is a more general procedure able to use any kind of distance measure, not only Euclidean distance, as it is the case for PCA (Anderson et al. 2008).
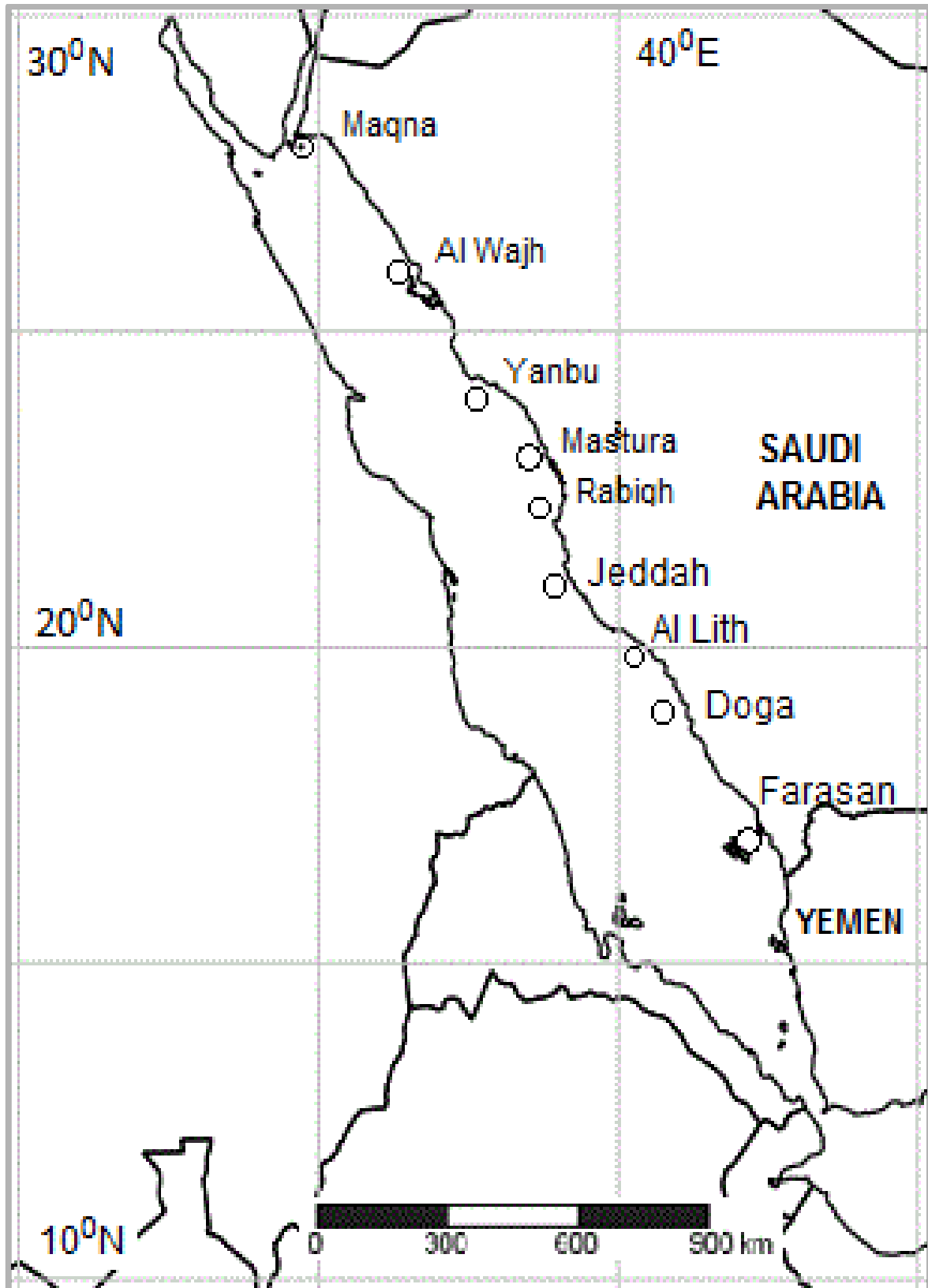
Figure 1: Studied reef locations (O) along the coastline of the Saudi Arabian Red Sea
(The map was designed following SimpleMappr; Shorthouse 2010).

Table 1: Description of the study sites from north to south. Superscript number represents the region with 1= most northern and 7 = most southern. Superscript [N] = non-polluted, superscript [P] = polluted/reefs close to a source of pollution.

Regions	Sites	Latitude	Longitude	Remarks
Maqna	MAQ[1N]	28°31′31.0″	34°48′15.9″	Inshore
Al Wajh	WAJ[2N]	26°04′06.2″	36°20′23.7″	Offshore
	WAJ[2P]	26°14′28.3″	36°26′51.6″	Inshore (close to a desalination plan)
Yanbu	YAN[3N]	23°56′50.7″	38°10′31.5″	Offshore
	YAN[3P]	23°57′08.0″	38°12′18.5″	Inshore (close to a petro-chemicals factory, construction)
Mastura	MAS[4N]	23°02′36.2″	38°46′38.3″	Offshore
Rabigh	RAB[4P]	22°37′33.1″	39°03″08.9″	Inshore (close to a cement factory, oil refinery and power plant)
Jeddah	JED[5N]	20°45′19.8″	38°57′71.0″	Offshore
	JED[5P]	20°35′57.4″	39°06′23.9″	Inshore (waste water discharge)
Al-Lith	LIT-N[6P]	20°04′22.3″	40°00′18.8″	Offshore (close to an aquacultural waste water discharge)
	LIT-S[6P]	20°18′51.4″	40°15″57.6″	Inshore (close to an aquacultural waste water discharge)
Doga	DOG[6N]	19°36′50.6″	40°38′07.6″	Offshore
Farasan	FAR-N[7N]	17°05′44.5″	41°54′21.3″	Near island
	FAR-S[7N]	16°34′16.2″	42°08′57.8″	Near island

Results

Environmental parameters: A detailed description of water quality parameters at the reef sites is provided and discussed by Sawall et al. (2014). The averaged environmental data is presented in table 2. From north to south, water temperatures ranged from 21°C to 28°C in winter and from 27°C to 32°C in summer. Most nutrient-related parameters showed a slight increase from north to south with sudden peaks at the most southern reefs around the Farasan islands (FAR).

Some reefs close to a source of pollution (YAN[3P], RAB[4P] and JED[5P] near-shore reefs) revealed substantial variation in water quality, if compared to their corresponding non-polluted reefs (YAN[3P], MAS[4N] and JED[5N] off-shore reefs). Here, chl a, TN and TP were about 1.5 to 2-folds higher and particular carbon up to 15-folds higher at the reefs close to a source of pollution (Table 2).

The sediment deposit on the reefs increased from north to south, as well as from off-shore to near-shore sites. In the North (MAQ and WAJ), no sediment was dispersed by fanning, in the central Red Sea sediment dispersion ranged between the categories 0 and 0.25 (MAS[4N]: 0, YAN[4N]: 0.25 and JED[5N]: 0) and between 0.5 and 1.75 at their corresponding near-shore reefs (RAB[4P]: 0.5, YAN[4P]: 1.5 and JED[5P]: 1.75), and in the South sediment dispersion ranged from 0.5 to 2.25 (FAR-N[7N], FAR-S[7N]: 0.5 and LIT-N[6P]: 2.25).

Benthic cover: In 3 m depth, mean hard coral cover throughout all surveyed sites was 41.5% ± 4.8SE and soft coral cover was 11% ± 3.8. Soft coral cover generally increased from south to north with lowest cover found at FAR-N[7P] (0.6% ± 0.9) and highest cover at WAJ[2P] (27% ± 4.2, Fig. 2). The living coral cover (hard and soft coral) was strongly reduced at the two sites YAN[3P] (31.3%) and RAB[4P] (10%), both being close to a source of pollution, if compared to their respective non-polluted reefs (YAN[3N]: 81.3%%, MAS[4P]: 68.8%). Macroalgae abundance was generally very low with highest cover in the South around the Farasan islands (FAR-N[7N]: 5.0% ± 1.3 and FAR-S[7N]: 3.8% ± 1.7). Coral rubble increased towards the South, while the highest cover was found at polluted Al-Lith (LIT-S[6P]: 28.8% ± 5.4, Fig. 2). The coverage of non-coral zoobenthos taxa was overall inconspicuous ranging from 0.6% ± 1.1 to 1.3% ± 1.5 cover (Fig. 2) and was mainly represented by sponges.
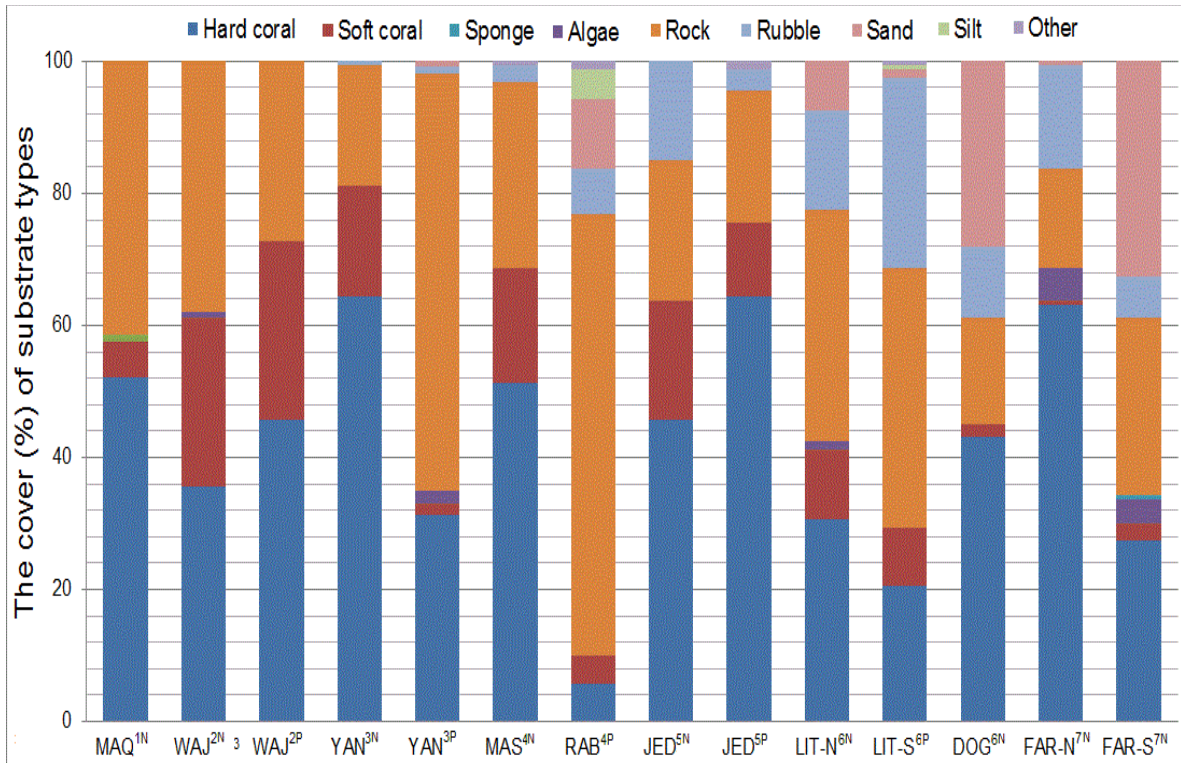
Figure 2: The mean cover of substrate types (%) at each survey site along the coastline of the Saudi Arabian Red Sea.

Table 2: The summarized environmental parameters (±SE). The data calculated the average of winter and summer value.

Parameters	Remark	Maximum	Minimum
Chl a ($\mu g\ l^{-1}$)	Polluted sites	0.47 ± 0.02 (LIT-S[6P])	0.29 ± 0.01 (WAJ[2P])
	Non-polluted sites	1.98 ± 0.52 (FAR-N[7N])	0.16 ± 0.04 (WAJ[2N])
TN ($\mu mol\ l^{-1}$)	Polluted sites	6.46 ± 1.30 (FAR-N[7N])	3.13 ± 0.12 (MAS[4N])
	Non-polluted sites	12.17 ± 4.48 (JED[5P])	6.12 ± 1.12 (RAB[4P])
TP ($\mu mol\ l^{-1}$)	Polluted sites	0.59 ± 0.24(FAR-N[7N])	0.17 ± 0.05 (MAS[4N])
	Non-polluted sites	0.55 ± 0.02 (JED[5P])	0.33 (0.04) (WAJ[2P])
PC ($\mu g\ l^{-1}$)	Polluted sites	1,150 ± 453 (RAB[4P])	79.70 ± 3.10 (WAJ[2P])
	Non-polluted sites	259.9 ± 91.18 (FAR-S[7N])	66.1 ± 26.7 (MAQ[1N])
PN ($\mu g\ l^{-1}$)	Polluted sites	34.10 (10.60) (RAB[4P])	79.70 ± 3.10 (WAJ[2P])
	Non-polluted sites	36.90 ± 5.13 (FAR-S[7N])	11.80 ± 0.40 (MAQ[1N])
Si ($\mu mol\ l^{-1}$)	Polluted sites	1.49 ± 0.20 (JED[5P])	0.73 ± 0.01 (RAB[4P])
	Non-polluted sites	1.21 ± 0.11 (MAQ[1N])	0.50 ± 0.04 (MAS[4N])
Temperature (^0C)	September	31.85 ± 0.35 (FAR-N[7N])	26.96 ± 0.54 (MAQ[1N])
	March	28.52 ± 0.31 (DOG[6N])	21.45 ± 0.21 (MAQ[1N])

The abundance of soft coral genera grouped the 14 sites into three main clusters from north to south (Tab. 3): The first group includes the northern reefs MAQ[1N], WAJ[2N] and WAJ[2P], the second group includes the central reefs YAN[3N], MAQ[4N], RAB[4P], JED[5N], JED[5P], LIT-N[6P] and LIT-S[6P] and the third group includes the southern reefs DOG[6N], FAR-N[7N], and FAR-S[7N], as well as the near-shore reef YAN[3P] from the central Red Sea.

The clusters could be clearly related to the environmental conditions, particularly slope, visibility, and sediment deposit and temperature (Fig.3). In the northern cluster most genera occurred, the reef slope was steep, visibility was high and silicate concentrations were slightly increased. In contrast, in the southern cluster, where abundance and diversity of soft coral was low, sediment deposit, chl a concentrations, TP and temperature were high. The central group showed intermediate levels of the aforementioned parameters, but featured highest levels of TN and PC (Fig 3.).

Diversity of alcyonacean soft corals: Identification of more than 1000 soft coral reference samples from 24 sites throughout the Red Sea revealed 82 species belonging to 20 genera and 6 families (see appendix). The family Alcyoniidae showed highest diversity with 6 genera and 40 species, followed by Xeniidae with 5 genera and 24 species, and Nephtheidae with 6 genera and 15 species. The other 3 families Nidalidae, Briareidae and Tubiporidae were only represented by one species each.

The species diversity was highest in the northern and central Saudi Arabian Red Sea ranging from 44 to 47 species, while it was rather low in the southern region with only 25 to 29 species. The most common species included *Tubipora musica* (Tubiporidae), *Rhytisma fulvum fulvum*, *Sinularia dissecta, S. leptoclados* (Alcyoniidae), *Paralemnalia thyrsoides* (Nephtheidae), *Ovabunda biseriata, Heteroxenia elizabethae* (Xeniidae), which were found at most investigated sites. Rare species included *Sarcophyton trocheliophorum*, *S. muqeblae, S. vrijmoethi* (Alcyoniidae), *Sympodium caeruleum, Xenia actuosa* (Xeniidae) and were found only once amongst all sampled specimen.
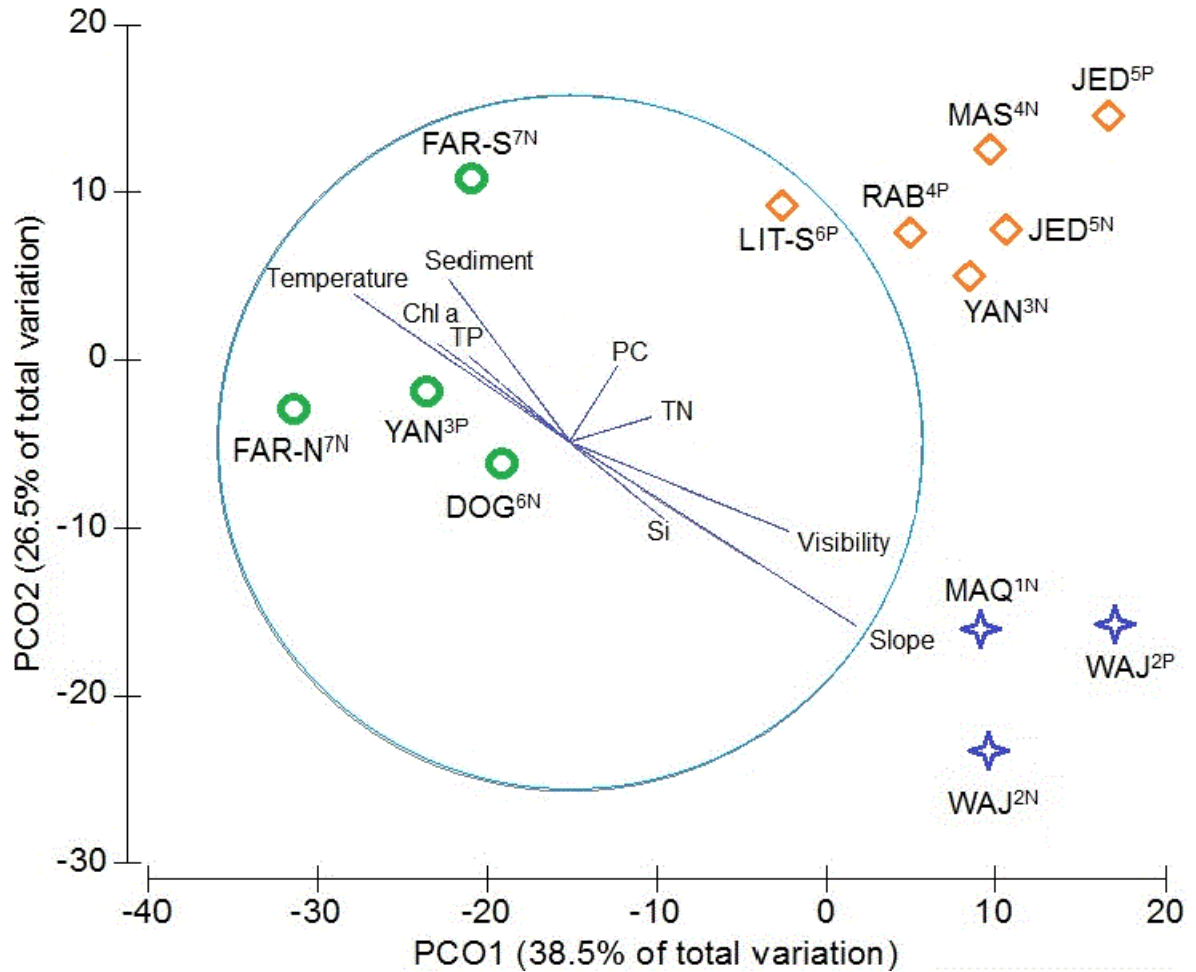
Figure 3: The principle coordinate analyses (PCO) of the alcyonacean community pattern (number of genera and abundance). Different symbols characterize the different clusters determined by cluster analysis. The environmental parameters are presented as vectors: direction and the length of the vector represent the correlation between the environmental parameter and alcyonacean community pattern and the strengths of correlation, respectively.

Table 3: Relative abundance of alcyonacean genera recorded during the rapid ecological assessment (REA). Sites are clustered into 3 groups (cluster analysis - northern, central and southern) according to their alcyonacean community composition (number of genera and abundance).

Degrees of relative abundance are indicated as: ∘ = few, ● = uncommon, ●● = common, ●●● = dominant and ●●●● = abundance.

	Group 1 (Northern)			Group 2 (Central)							Group 3 (Southern)			
	MAQ[1N]	WAJ[2N]	WAJ[2P]	YAN[3N]	MAS[4N]	RAB[4P]	JED[5N]	JED[5P]	LIT-N[6P]	LIT-S[6P]	YAN[3P]	DOG[6N]	FAR-N[7N]	FAR-S[7N]
Tubipora	●	●	●	●	●●	●	●	●	●	●	●	●	●	●
Rhytisma	∘	∘	∘	∘	●●∘	∘	●	●	●		●	∘	∘	∘
Klyxum	●●	●	●	∘	∘	∘	∘	∘						
Cladiella	●●	∘	●●	∘				∘						
Sarcophyton	●	●	●	●	●	●	●	●●	●●	●	●	●	∘	●
Lobophytum	∘	∘	∘	∘	∘	∘	●	●	●	●	●	●	●	●
Sinularia	●●	●●●●	●●●●	●	●	●●	●●	●●	●●	●	●	●	●	●
Xenia/Ovabunda	●●	●●	●●	●●●●	●●●●	●●	●●●●	●●●	●●●	●●●	●	●	●●	●●
Anthellia	●	●●	●	∘	∘	∘	∘	∘						
Heteroxenia	∘	∘	∘	∘	∘		∘		∘					
Paralemnalia	●		●			∘		∘					∘	∘
Litophyton	●	∘	∘	∘	∘		∘	∘						
Sterenonephthya	∘	∘		∘	∘			∘		∘				
Nepthea	●●	●●	●●		∘	∘				∘		∘		
Dendronephthya	∘	∘			∘	∘				∘			∘	∘
Siphonogorgia		∘												

Discussion

In this study, we confirmed a high soft coral diversity and abundance in the Red Sea. Some genera, such as Xenia/Ovabunda, Sinularia and Sarcophyton, are not only the most abundant concerning soft coral cover, but are also the most diverse. Moreover, we provided a comprehensive data set relating soft coral communities to the strong latitudinal environmental gradients and change in habitat structure. Results showed clear reductions in soft coral cover, abundance and diversity from north to south, which could be related to an increase in temperature and turbidity, as well as to a change in habitat structure. Furthermore, we found that octocoral communities are clearly affected by poor water quality at some near-shore reefs close to a source of pollution.

Abundance and diversity of alcyonacean soft corals: Among the 16 soft coral genera recorded during the REA surveys; the six genera *Xenia/Ovabunda* (Xeniidae) *Sinularia, Sarcophyton, Rhytisma* (Alcyoniidae) and *Tubipora* (Tubiporidae) were the most abundant. Thereof, the genera *Sinularia, Sarcophyton* and *Rhytisma* are generally known as 'dominant' genera in the Indo-Pacific, as evidenced in Madagascar (Evans et al. 2011), the Great Barrier Reef (Dinesen 1983; Fabricius and Alderslade 2001), the Indian and South China Sea (Chanmethakul et al. 2010), in southern Taiwan (Benayahu et al. 2004) and in Vietnam (Hoang 2010).

The strong dominance of the genera *Xenia/Ovabunda*, however, particularly in the central section (<15% substrate coverage, >80% to the total soft coral cover in YAN[3N] and JED[5N]; Ben Hoang, unpublished data), seems to be specific for the Red Sea. Also previous studies reported high coverage rates of *Xenia/Ovabunda*, reaching up to 50% in some shallow reef areas of the Red Sea (~4m depth), where they form extensive carpets of several square meters in size (Benayahu and Loya 1981; Reinicke 1997). In reefs close to a source of pollution, the genus *Rhytisma,* mainly represented by the polymorphic species *Rhytisma fulvum fulvum* (Haverkort-Yeh et al. 2013), was most abundant. Here, the particularly high abundance of dead corals and rubble seems to serve as an ideal substrate for this species, which is known to coat large surface areas with a thin tissue (2-4 mm thick) including overhanging substrate, (Benayahu 1985; Fabricius and Alderslade 2001).

Highest soft coral diversity, including the number of genera as well as the number of species samples, was found in the northern and central Red Sea. The most

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diverse genus was *Sinularia* with 21 species and confirms the striking diversity of *Sinularia* species reported previously from the Red Sea (38 species, Ofwegen 2000). *Sinularia* is a widely distributed genus growing in most reef habitats, from shallow water to more than 30 m deep and from turbid to clear water environments (Fabricius and Alderslade 2001). Three species of *Sinularia* (viz. *S. dissecta, S. gyrosa* and *S. inelegans*), as well as one species of the genus *Sarcophyton* (*S. pauciplicatum)* were found in the southern Red Sea for the first time, rising the species number of *Sinularia* and *Sarcophyton* in southern Red Sea to 10 and 3 species, respectively.

The genera *Klyxum, Cladiella, Sympodium* and *Anthelia,* however, were lacking in the southern Red Sea, as previously reported from the Dahlak Archipelago and Kamaran island (Eritrea and Yemen Benayhu et al. 2002), as well. The rare occurrence of *Siphonogorgia* in this study (only found at Al-Wajh) is in agreement with a former study around the Sinai Peninsula (Benayhu 1985).

The most common and highly diverse soft coral family Xeniidae comprises currently about 34 species (Reinicke 1997). Thereof, 11 species belong to the relatively new genus *Ovabunda* (Halász et al. 2013), which differ from their former genus *Xenia* by their large micro-corpuscular sclerites (Alderslade 2001). In this study, we identified 10 out of the 11 *Ovabunda* species with *O. crenata, O. macrospiculata, O. impulsatilla* and *O. biseriata* being present in most regions. Within the genus *Xenia*, some species were found for the first time in some regions, such as *X. membranacea* in the central section (Jeddah) and *X. lillieae* (Doga, Farasan) and *Heteroxenia elizabethae* (Farasan) in the southern section of the Red Sea.

The doubtful presence of *Xenia garciae* BOURNE, 1895, in the Red Sea (Reinicke 1997) could be dispelled by our findings, since we found specimens of this species at a near-shore reef in front of Jeddah (JED[5P]). The species *X. actuosa,* so far only known from the Bismarck Sea in Papua New Guinea (Verseveldt and Tursch 1979), was found in the Red Sea for the first time (Farasan). Its presence and taxonomic identity, however, needs further proof (i.e. more material and genetic identification).

Factors affecting soft coral distribution: The decrease in soft coral cover and diversity from north to south is most likely related to the increase of nutrient concentration and temperature. In particular, the increase in nutrients, as well as in sedimentation and turbidity were previously found to negatively affect the abundance

and diversity of octocorals (Van Woesik et al. 1999; Fabricius and De'ath 2001; Fabricius et al. 2005). In consequence, only few genera could be found in the south, with *Xenia/Ovabunda, Sinularia, Sarcophyton* and *Lobophytum* (Farasan, Doga) being the most abundant ones. In particular, *Sinularia* and *Sarcophyton* are known to cope with a large range of turbidity levels (Fabricius and Alderslade 2001). Also some species of the genus *Xenia* are known to grow in turbid habitats, as described from other regions in the Red Sea (Benayahu 1985). In contrast, the genera *Nephthea* and *Dendronepthya* are known to favor clear waters (Fabricius and Alderslade 2001) and were therefore rare in the South.

Another potential challenge for soft corals are high temperatures, as they occur in the South, particularly in summer, (>32°C for several weeks Sawall et al. 2014). Like hard corals, also soft corals can lose their symbiotic unicellular algae (zooxanthellae) in consequence of heat related damage, a process called bleaching (Douglas 2003). The susceptibility to thermal stress, however, varies between soft coral genera (Floros etal. 2004; Marshall and Baird 2000). Rather heat tolerant genera include *Sinularia, Sarcophyton* and *Lobophyton,* (Strychar et al. 2005), which would explain their dominance in the South.

Substrate condition is another important factor, which determines the success of soft corals. Therefore, changes in substrate conditions from north to south contributed to the explained variation of soft coral community structures in the Red Sea. In the northern reefs, the reef slopes are rather steep, consist of mostly solid substrate and reach down deeper than 40 m. These changes gradually towards the South, where rather gently sloping reefs are found covered by larger areas of soft substrate (i. e. sand). Consequently, species predominantly known from deeper reefs, such as of the genera *Cladiella* and *Siphonogorgia* (Loya 1972)*,* were only found in the North (see also Benyahu 1985). Furthermore, intermediate reef depth (10-30m) and steep slopes are generally known to harbor a higher soft coral species diversity compared to shallow and rather flat reef areas (Loya 1972; Riegl and Velimirov 1994; Sheppard 1980; Reinicke and Van Ofwegen 1999; Huston 1985; Liddell and Ohlhorst 1987).

In order to discriminate, however, between the effects of the different environmental parameters which change more or less simultaneously from north to south, experimental studies are required. Those should test for the effect of

temperature, nutrients, sedimentation and substrate availability individually and combined on soft corals from the northern and southern Red Sea.

The soft coral communities also changed with changing water quality between near-shore reefs close to a source of pollution and non-polluted off-shore reefs. Increased nutrient levels, turbidity and higher sedimentation at most near-shore reefs, could be related to a lower soft coral abundance and diversity.

This effect was strongest at YAN[3P], a reef close to the industrial city Yanbu with factories processing petro-chemicals and with extensive coastal construction work. Strong impacts on the soft coral community were also found at RAB[4P], a reef close to an oil refinery, cement factory and power plant of the city Rabigh. At these sites, the generally rather dominant genera *Tubipora, Rhytisma, Lobophytum, Sinularia, Sarcophyton* and *Xenia/Ovabunda,* revealed a very low relative abundance at these impacted sites. Furthermore, the overall soft coral cover was strongly reduced (YAN[3P]: 1.8 %, RAB[4P]: 4.4 %), although the hard coral coverage was still rather high at least at YAN[3P] (31.3%). This indicates that soft corals are generally more susceptible to water quality degradation than hard corals (Fabricius et al. 2005).

The concomitant low soft coral and low hard coral cover at RAB[4P], however, may not only related to pollution, but also to previous coral bleaching events (1998, 2010) in that region (Devantier et al. 2000a; Furby et al. 2013). Further south, the reef LIT-S[6P], close to the aquacultural waste water discharge of a large shrimp farm in Al-Lith, seemed to be affected by nutrient enriched and polluted effluents leading to a particularly low soft coral diversity (15 species).

Although, we could not find a significant relationship between soft coral cover and sediment deposits in this study (Spearman Rank, r_s = 0.14, P > 0.05), unlike reported from other regions before (Loya 1976), shifts in the abundance of different soft genera were found. While some genera could not be found in near shore reefs with high sediment deposits, other genera such as *Sinularia, Sarcophyton, Lobophytum* were still present. Those are considered more tolerant towards elevated levels of sedimentation due to their morphology, which include a high profile growth form, a flexible talk and disk or a pliable shape (Schleyer and Celliers 2003). Moreover, soft corals diversity was reduced in some regions where high sediment deposited were found, as previously reported from the Great Barrier Reef (Fabricius and De'ath 2001). Overall, considerable changes in soft coral community structures

close to major industrial sites were found along the Saudi Arabian Red Sea coast, likewise along the Egyptian Red Sea coasts as previously reported (Mohammed 2006; Mohammed et al. 2009).

In conclusion, this is the first study, which systematically investigated the soft coral community structures along the latitudinal environmental gradients of the Red Sea. It confirms an extraordinary high soft coral diversity in the Red Sea, including many species found in the wider Indo-Pacific and some new zoogeographical records, such as the species *Xenia actuosa, Sinularia dissecta* and*, Sarcophyton pauciplicatum*. Soft coral communities, however, strongly changed from north to south along the Saudi Arabian Red Sea coast, considering soft coral cover, diversity and abundance. This could be related to various environmental factors, which changed from north to south, generally creating a less soft coral friendly environmental in the southern Red Sea, where temperatures, nutrient input and turbidity are high and substrate conditions are less favorable for larvae settlement. Here, only the more tolerant genera, such as *Sinularia* and *Sarcophyton* were found, covering rather small areas. Near shore reefs close to industrial areas were generally characterized by high sedimentation, which lowered soft coral diversity and cover. The results of this study form an important base line on soft coral community structures in the Red Sea and provide information on potential changes in soft coral communities in consequence of environmental changes.

Acknowledgments

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Appendix

List of alcyonacean soft coral species identified from the Saudi Arabian Red Sea coast

Species	Areas								
	MAQ	WAJ	YAN	MAS	RAB	JED	LIT	DOG	FAR
Tubiporidae Ehrenberg, 1828									
Genus Tubipora Linnaeus, 1758									
Tubipora musica Linnaeus, 1758	+	+	+	+	+	+	+	+	+
Alcyoniidae Lamouroux, 1812									
Genus Rhytisma Alderslade, 2000									
Rhytisma fulvumfulvum (Forskäl, 1775)	+	+	+	+	+	+	+	+	+
GenuaKlyxum Alderslade, 2000									
Klyxum flaccidum (Tixier-Durivault, 1966)	+	+				+		+	
Klyxum utinomii (Verseveldt, 1971)	+	+				+			
Genus Cladiella Gray, 1869									
Cladiella brachyclados Ehrenberg, 1834	+	+	+						
Cladiella pachyclados (Klunzinger, 1877)	+	+	+			+			
Cladiella sphaerophora (Ehrenberg, 1834)	+					+			
Genus Lobophytum Von Marenzeller, 1886									
Lobophytum crassum Marenzeller, 1886			+				+		

Species	Areas								
	MAQ	WAJ	YAN	MAS	RAB	JED	LIT	DOG	FAR
Lobophytum depressum Tixier-Durivault, 1966		+	+						
Lobophytum pauciflorum (Ehrenberg, 1834)		+	+		+	+	+	+	+
Genus Sarcophyton Lesson, 1834									
Sarcophyton auritum Verseveldt & Benayahu, 1978	+						+		
Sarcophyton boletiforme Tixier-Durivault, 1958	+	+	+			+		+	
Sarcophyton crassocaule Moser, 1919		+							
Sarcophyton digitatum Moser, 1919				+				+	
Sarcophyton ehrenbergi Von Marenzeller, 1886					+	+		+	
Sarcophyton glaucum (Quoy & Gaimard, 1833)	+	+			+	+	+	+	+
Sarcophyton pauciplicatum Verseveldt & Benayahu, 1978	+		+			+	+	+	+
Sarcophyton serenei Tixier-Durivault, 1958								+	
Sarcophyton trocheliophorum Marenzeller, 1886			+						
Genus Sinularia May, 1898									
Sinularia compressa Tixier-Durivault, 1945						+			+
Sinularia cruciata Tixier-Durivault, 1970			+	+					
Sinularia dissecta Tixier-Durivault, 1945	+	+	+		+	+	+	+	+
Sinularia erecta Tixier-Durivault, 1945		+	+	+	+	+	+	+	+
Sinularia flexuosa Tixier-Durivault, 1945	+	+	+						
Sinularia gardineri (Pratt, 1903)		+	+	+		+			+

Species	Areas								
	MAQ	WAJ	YAN	MAS	RAB	JED	LIT	DOG	FAR
Sinularia gyrosa (Klunzinger, 1877)	+	+	+	+		+		+	+
Sinularia heterospiculata Verseveldt, 1970		+	+					+	
Sinularia hirta (Pratt, 1903)		+	+			+			
Sinularia inelegans Tixier-Durivault, 1970		+	+			+	+		+
Sinularia leptoclados (Ehrenberg, 1834)	+	+	+	+		+	+	+	+
Sinularia loyai Verseveldt & Benayahu, 1983	+	+							
Sinularia minima Verseveldt, 1971	+	+	+						
Sinularia muqeblae Verseveldt & Benayahu, 1983				+					
Sinularia notanda Tixier-Durivault, 1966	+	+	+						
Sinularia prattae Verseveldt, 1974	+							+	
Sinularia polydactyla (Ehrenberg, 1834)	+	+							+
Sinularia querciformis (Pratt, 1903)	+	+	+	+		+	+		
Sinularia rigida (Dana, 1846)		+	+			+			
Sinularia vrijmoethi Verseveldt, 1971							+		
Nephtheidae Gray, 1862									
Genus Nephthea Audouin, 1826									
Nephthea acuticonica Verseveldt, 1974	+	+	+		+			+	
Nephthea albida (Holm, 1894)			+			+			
Nephthea chabrolii Audouin, 1828	+		+		+				

Species	Areas								
	MAQ	WAJ	YAN	MAS	RAB	JED	LIT	DOG	FAR
Genus Dendronephthya Kükenthal, 1905									
Dendronephthya ehrenbergi Kükenthal, 1904							+		+
Dendronephthya formosa Gravier, 1908		+					+		+
Dendronephthya hemprichi (Klunzinger, 1877)	+	+		+				+	+
Dendronephthya klunzingeri (Studer, 1888)		+							+
Genus Paralemnalia Kükenthal, 1913									
Paralemnalia eburnea Kükenthal, 1913	+		+			+			
Paralemnalia thyrsoides (Ehrenberg, 1834)	+	+	+		+	+	+	+	+
Litophyton acutifolium Kukenthal, 1913	+	+					+	+	
Litophyton arboretum Forskäl, 1775	+	+	+		+			+	
Genus Stereonephthya Kükenthal, 1905									
Stereonephthya bellissima Thomson & Dean, 1931	+					+			
Stereonephthya cundabiluensis Verseveldt, 1965	+	+	+			+	+		+
Stereonephthya imbricans Thomson & Dean, 1931	+	+					+		
Genus Scleronephthya Studer, 1887									
Scleronephthya corymbosa Verseveldt and Cohen, 1971	+					+			
Nidallidae Gray, 1869									
Genus Siphonogorgia Kölliker, 1874									
Siphonogorgia fragilis Verseveldt, 1965		+				+			

Species	Areas								
	MAQ	WAJ	YAN	MAS	RAB	JED	LIT	DOG	FAR
Briareidae Gray, 1859									
Genus Briareum Blainville, 1830									
Briareum hamrum (Gohar, 1948)					+			+	
Xeniidae Wright &Studer, 1889									
Genus Sympodium Ehrenberg, 1834									
Sympodium caeruleum Ehrenberg, 1834		+							
Genus Anthelia Lamarck, 1816									
Anthelia glauca Lamarck, 1816	+	+	+	+		+		+	
Genus Ovabunda Alderslade, 2001									
Ovabunda ainex (Reinicke, 1995)	+	+			+	+			
Ovabunda biseriata (Verseveldt & Cohen, 1971)	+	+	+	+		+	+	+	+
Ovabunda crenata (Reinicke, 1995)	+		+	+		+	+	+	
Ovabunda gohari (Reinicke, 1995)						+			
Ovabunda hamsina (Reinicke, 1995)	+		+			+			
Ovabunda impulsatilla (Verseveldt & Cohen, 1971)	+	+	+	+		+	+		+
Ovabunda macrospiculata (Gohar, 1940)	+		+	+	+	+	+		
*Ovabunda verseveldti (*Benayahu, 1990)	+					+		+	
Genus Xenia Lamarck, 1816									
Xenia actuosa Verseveldt &Tursch, 1979									+

Species	Areas								
	MAQ	WAJ	YAN	MAS	RAB	JED	LIT	DOG	FAR
Xenia garciae Bourne, 1895						+			
Xenia hicksoni Ashworth, 1899			+	+	+	+			
Xenia lillieae Roxas, 1933	+	+						+	+
Xenia mayi Roxas, 1933			+						
Xenia membranacea Schenk, 1896						+			
Xenia miniata Reinicke, 1995						+			
Xenia ternatana Schenk, 1896			+						
Xenia umbellate Lamark, 1816			+			+			+
Genus Heteroxenia Kölliker, 1874									
Heteroxenia elizabethae Kölliker, 1874	+	+	+	+		+	+		+
Heteroxenia fuscescens (Ehrenberg, 1834)						+		+	
Heteroxenia ghardaqensis Gohar, 1940	+			+		+			
Total (82 species)	**44**	**44**	**46**	**20**	**15**	**47**	**25**	**29**	**26**

Patters of Xeniidae (Octocorallia, Alcyonacea) communities impacted by different environmental parameters in the Red Sea

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Abstract

Xeniid communities were studied at eight reef sites in near- and off-shore positions of the Saudi Arabian Red Sea, where the water quality parameters showed different conditions. 20 xeniid species belonging to five genera were recorded at all study sites, with 18 species recorded at the off-shore sites and 13 species in near-shore locations at Al-Wajh, Yanbu, Mastura/Rabigh and Jeddah. The relative coverage of xeniids ranged from 7.5% (±2.1SE) - 14.4% (±1.9) in the off-shore reefs and 0.6% (±1.1) - 8.5% (±3.3) in the near-shore reefs. The relative abundance of Alcyonacea genera was also different between both sets of reef areas. Multivariate analyses showed that xeniid communities differed among eight reef sites surveyed. The results demonstrate that the xeniid communities were significantly different between inshore and offshore at Yanbu, Mastura/Rabigh and Jeddah reefs, but showed no significant differences at Al-Wajh in and offshore. Our study showed that the xeniid community patterns relate to water parameters and environmental conditions in different reefs. They not only change in the coverage but also predominating genera and species diversity varies under different habitat conditions. The results strongly suggest that the abundance, diversity and distribution patterns of soft corals like Xeniidae have influenced, if not controlled by environmental nutrient levels.

Key words: Xeniidae; diversity; distribution; nutrient; Red Sea.

Introduction

The Red Sea is known as an outstanding area of coral reefs distribution situated at the north-western edge of the tropical Indo-Pacific region. First studies of the diversity and distribution of coral reefs in the Red Sea started in the 18th century by Forskål since his "*Arabia Felix*"-expedition in 1761. However, the knowledge of soft coral diversity in the Red Sea has substantially increased only following the time of traveling expeditions during the early and ongoing 20th century (e.g. Kükenthal 1904, 1913; Verseveldt 1965, 1969, 1970, 1974, 1982; Verseveldt and Cohen 1971; Verseveldt and Benayahu 1978, 1983; Reinicke 1997; Benayahu et al. 2002; Halász et al. 2013)

The relationships between octocoral communities and water quality parameters on inshore reefs were investigated in the Great Barrier Reef (Fabricius et al. 2005) and the South China Sea (Fabricius and McCorry 2006). The distribution patterns of soft corals showed strong relations with physical environmental parameters such as light, water motion or sedimentation (Fabricius and De'ath 1997).

Living soft coral cover was recorded highest on outer shelf reef slopes and low diversity levels were observed on shallow reef flats in the Great Barrier Reef (Dinesen 1983), the highest abundance and diversity of alcyonacea was found on exposed reefs under high water clarity in Northern Madagascar (Evans et al. 2011). Soft corals were also recorded dominant on reef slopes and lower reef zones in the Andaman Sea and the Gulf of Thailand (Chanmethakul et al. 2010).

In the Red Sea soft corals as parts of the benthic coral communities were not only impacted by severe natural disaster such as coral bleaching (Devantier et al. 2000a; Furby et al. 2013) but are also effected by human local to regional activities such as pollution by petroleum oil, uranium, phosphate and sulphur enrichment during their loading and shipping, overfishing and recreational activities (Abu-Hilal 1994; Ammar et al. 2007; Tilot et al. 2008; Mohammed 2012). A recent coral reef monitoring program in the South Sinai reefs indicated a moderate decline in coral coverage during recent decades (Tilot et al. 2008).

Environmental parameters such as surface temperature, salinity, turbidity, nutrient concentrations reveal a gradient from north to south in the Red Sea (Sheppard et al. 1992) also influencing, if not controlling coral reefs distribution. The latitudinal attenuation was related to distribution of soft coral diversity at both species

and genus level (Benayahu 1985; Benayahu et al. 2002). The presence of hard substrata for juvenile settlement is a major factor limiting the distribution of soft corals in the Red Sea reefs (Benayahu 1985). In some areas soft corals were controlled by sedimentation rates, direct exposure, wave action and hydrodynamic exposure (Dar et al. 2012).

The soft coral family Xeniidae (Wright and Studer, 1889) is distinguished from all other Octocorallia by their soft, fleshy texture growing as polyp bearing membranes or upright lobes, often with sterile stems carrying more or less distinct branches or capitula covered with polyps (Ashworth 1899). Regular pulsating tentacle movements are a unique feature of some xeniid species (Reinicke 1997b). The family is one of the most common and widely distributed octocoral families and comprises of 34 accepted species reported in the Red Sea (Reinicke 1997a). Here it reaches substrate coverage rates of up to 50% in some shallow reef areas (~4m depth) forming extensive carpets (Benayahu and Loya 1981; Reinicke 1997). Depending on available light intensities (turbidity), depth distribution may extend down 40 and 70 m depth in the northern (Gulf of Aqaba, Reinicke 1997b) and central Red Sea (Reinicke 1997a), respectively.

Studies on the biology of Xeniidae in the Red Sea by Benayahu and Loya (1977, 1981) investigated the space partitioning and competition among coral reef sessile organisms on the coral reefs. Observations of planulae shedding and post larval development of *Xenia macrospiculata* suggested that this species exhibits high reproductive potential maintaining conspicuous dominance in Red Sea coral reefs (Benayahu and Loya 1984). Yoffe et al. (2012) studied characteristic nematocysts of *Heteroxenia fuscescens* species in the Red Sea revealed that two types of nematocysts are a trichous isorhiza and a novel macrobasic-mastigophore. Kremien et al. (2013) demonstrated benefits of tentacle pulsation could be enhancement of their photosynthesis in some xeniid species colonies. In the field of chemical defense, results of Kelma et al. (2006) revealed an active compound of Red Sea xeniids such as the antimicrobial activity of *Ovabunda macrospiculata,* and an anti-predatory, repelling activity against coral reef fish in *Ovabunda crenata* and *Hereroxenia ghardaqensis* (Hoang, work in progress).

The aim of this study is the comparison of xeniid assemblages in the Al-Wajh, Yanbu, Mastura/Rabigh and Jeddah areas on the Saudi-Arabian Red Sea coast, including near-shore and off-shore reef sites under differing conditions of impact from

different pollution sources. The study also includes the results of substratum coverage surveys and relative abundance of alcyonacean soft corals at genus level at reefs effected by different environmental conditions.

Method and materials

Study area: Four coral reef areas at Al-Wajh (WAJ), Yanbu (YAN), Mastura/Rabigh (MAS/RAB) and Jeddah (JED) with four non-impacted (off-shore sites WAJ1, YAN1, MAS and JED1) and four reefs close to potential sources of pollution (near-shore sites WAJ2, YAN2, RAB and JED2) were selected for this study (Fig. 1). The details of reef topography recorded during diving on coral reefs at each sites, the different natural and anthropogenic disturbances at the different sites were quantitatively estimated by surveying team in the field. All information are presented at table 1 and figure 2.

- Al-Wajh area: two reef sites selected: off-shore fringing reef about 11 km far from mainland (WAJ1 at $26°11'06.2"$ N, $36°21'23.7"$E), and a near-shore fringing reef about 60 m from the shore (WAJ2 at $26°14'28.3"$N, $36°26'52.3"$E).
- Yanbu area, two reef sites selected: off-shore patch reef about 4 km far from mainland (YAN1 at $23°56'50.7"$N, $38°10'31.8"$E), and a near-shore fringing reef about 1 km from the shore (YAN2 at $23°57'18.0"$N, $38°12'18.5"$E).
- Mastura/Rabigh area, off-shore patch reef about 1 km far from mainland (MAS at $23°02'36.2"$N, $38°46'38.3"$E) and near-shore fringing reef about 150 m from the shore (RAB at $22°37'33.1"$N, $39°02'28.9"$E).
- Jeddah area, two reef sites selected: off-shore patch reef about 14 km far from the mainland (JED1 at $21°45'11.4"$N, $38°57'45.9"$E), and a near-shore fringing reef at about 100 m from the shore (JED2 at $21°35'38.5"$N, $39°06'17.3"$E).

The potential sources of pollution were within the proximity of about 500 m and varied in type and intensity: WAJ2 was located close to a desalination plant in front of the small city of Al-Wajh. YAN2 was located close to a petro-chemicals factory and construction site. RAB was close to the oil refinery, cement factory and power plant in Rabigh city. JED2 was located in proximity of a domestic waste water discharge of the major city Jeddah. All other reef sites were categorized as non-impacted/polluted (off-shore reefs) since there was no potential source of pollution within the range of at least 3 km.

Environmental parameters: The values of the environmental parameters chlorophyll a (chl a), total nitrogen (TN), total phosphorous (TP), particulate carbon (PC), particular nitrogen (PN), Nitrite (NO_2), Nitrate (NO_3) and Silicate (Si) of the study sites were derived from Sawall et al. (2014). Nutrient related parameters were measured in water samples derived at the experimental depth in September 2011 and March 2012 following the standard procedure Grasshoff et al. (1983). The sediment deposits on the reef substratum were recorded by rating on a 0 - 4 scale applied by fanning (Fabricius and McCorry 2006): 0 = none; 1: thin layer; 2: medium; 3: thick. Water clarity: The turbidity was estimated as horizontal visibility at each survey site. The visibility (V) was categorized on a 3-point scale: 1 (V = 0-5 m), 2 (V= 6-10 m) and 3 (V>11 m) labeled as "turbid", "moderate" and "clear", respectively.

Survey methods for coral reefs: Each reef site was surveyed using two techniques: (1) the line intercept transect method (LIT) was applied to assess the coverage of substrata and (2) the rapid ecological assessment (REA) was used to estimate the abundance and diversity of alcyonacean soft coral genera.

- *The line intercept transect (LIT) method*: Transects of 20 m length and were laid out leaving 5 m gaps towards the neighbouring transect line. Four replicate transects were laid at 3 m depth in parallel to the reef contour for all the selected reef sites. Thus, a total of 32 transects were surveyed at all eight sites studied (8 sites x 4 transects each). Substrate types were recorded every 0.5 m (English et al. 1997). The substrate was categorized into living categories as hard coral, soft coral, macro-algae and others (e.g. sponge, anemone, tunicates) and into the non-living categories as rock (dead coral boulders and rock), rubble (small dead coral pieces max. 15 cm long), sand and silt.

- *Rapid ecological assessment (REA) method:* This method had been used successfully for studying and monitoring coral reef communities since the 1970s. REA was chosen for its advantages in terms of efficiency of surveys carried out per unit of time spent in the field (Dinesen 1983) and its power of detecting rare and heterogeneously distributed taxa within a large range of reefs (Fabricius and De'ath, 2001; Fabricius and McCorry 2006). The genera *Xenia* and *Ovabunda* were not visually differentiated in the field, thus recorded as "*Xenia/Ovabunda*" in the survey. Species ID for these genera was done in the lab yielding the list of species in table 3. Eight reefs were surveyed by modifying the one-off REA methods (Devantier et al. 2000b; Fabricius and

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De'ath 2001; Fabricius and McCorry 2006). Each survey was carried out visually for 30 minutes within a range of approximately 100-150 m length. The surveys were conducted at two depths 2-4 m (labeled as "shallow") and 5-10 m (labeled as "deep") depending on the reef morphology. For each survey the data were recorded as follows: The relative abundances of Alcyonacea (RA) genera were graded according to the rating scale of 0-5 (Fabricius and McCorry 2006): 0 = absence; 1: one or few colonies covering < 1%; 2: uncommon, covering 1- 5%; 3: common covering 6 - 10%; 4: dominant, covering 11 - 20% and 5: abundant, covering > 20%.

Diversity of Xeniids: Approximately 200 samples were collected by boat and SCUBA diving from 1 m to 30 m depth or to the bottom end of the coral reefs deep extension at some sites. Prior to collections, most of the colonies were photographed in situ, the presence of pulsation, colours of the colonies and water depth were recorded. The samples were fixed in formalin (4%), rinsed with fresh water after 24 h and transferred into ethanol (70%) to further preservation and study. The taxonomic identification was based on the literature of (Roxas 1933; Gorha 1940; Verseveldt and Cohen 1971; Benayahu 1990; Reinicke 1997a; Alderslade 2001; Hala'sz et al. 2013). All samples were deposited at KAU in Jeddah (Saudi Arabia) and Deutsches Meeresmuseum (Stralsund) in Germany (Taxonomic voucher).

Data analysis: The percentages of substrate categories were calculated according to the following formula: Percentage cover of each category = Intercept length/Transect length x 100.

The coverage of xeniids data were analysed using ANOVA (with Bonferroni post-hoc comparisons) to determine the different significance between sites. Analyses were performed with the software Statistica 8.

To assess the similarity between the alcyonacean soft coral community structures based on the REA, the hierarchical cluster analysis was conducted using clusters with group average. Prior analysis a resemblance matrix was calculated based on Bray-Curtis similarity. Since the data is already categorical, no data transformation was necessary.

Multivariate analyses were performed using Plymouth Routines in Multivariate Ecological Research PRIMER 6 (Clarke and Gorley 2006). Non-parametric multidimensional scaling (MDS) was performed with variations of xeniid communities

between eight reefs (including abundance, species richness and cover). ANOSIM comparisons were run as one-way tests (Analyse of similarities), where ANOSIM showed significant differences between sites (P<0.05), the SIMPER (Similarites Percentage) were used to assess the different xeniid communities between reefs.

PERMANOVA (Anderson et al. 2008) used to to assess the relations between alcyonacean communities and environmental parameters, Principal Coordinate Analyses (PCO) were conducted with the soft coral data set and the environmental data were correlated post-analysis based on Pearson correlation. The xeniid data was the same as for the cluster analysis and the environmental parameters included temperature, all nutrient-related data (chl a, TN, TP, PC, NO_2, NO_3, Si) as well as sediment deposits. The environmental data was normalized in order to avoid artificial effect from different units. Principal coordinates analysis (PCO) was chosen as a more general procedure than Principal Component Analyses (PCA), PCO can be based on any resemblance matrix, allows using any distance measure and a projection of the points onto axes that minimise residual variation in the space of the resemblance matrix. The ordination plot representing the sites is based on the Bray-Curtis similarity.

Table 1: Observations of reef topography reefs and quantitative evaluation of different natural and anthropogenic disturbances impacts at the different sites listed. Degrees of impacts are indicated from – (no impact) to + (minor) ++ (moderate) and   +++ (high) impact. (Nut.: Nutrients, Plas.: Plastic waste, Cons.: Constructions, Ind.: Industry, and Por.: Ports).

Area	Topography	Nut.	Plas.	Cons.	Ind.	Por.
WAJ1	Type: fringing reef. Inshore island (200m) and offshore mainland (11km) Reef flat: 3m. Reef slope: steep (6-18m). Bottom: sand (25m)	-	-	-	-	-
WAJ2	Type: Fringing reef. Near shore (60m). Reef flat: 2-3m. Reef slope: Steep (6-18m). Fore reef: sand (20m)	+	+	+	+	-
YAN1	Type: Patch reef. Near shore (4 km) Reef flat: 2-3m. Reef slope: steep 7-10m. Fore reef: sand (15m)	+	-	-	-	-
YAN2	Type: Fringing reef. Near shore (1 km). Reef flat: 2-4m. Reef slope: low. Fore reef: sand (11m)	++	+	+	+++	++
JED1	Type: Patch reef. Offshore (14 km) Reef flat: 1-2m. Reef slope: steep (10m). Fore reef: sand (20m)	+	-	-	-	-
JED2	Type: Fringing reef. Near shore (100m). Reef flat: 1-3m. Reef slope: steep (7-10m). Fore reef: sand (20m)	++	++	+++	+	+
MAS	Type: Fringing reef. Near shore (1 km). Reef flat: 2-3m. Reef slope: steep (5-10m). Fore reef: sand (16m)	+	-	-	-	-
RAB	Type: Fringing reef. Near shore (150m). Reef flat: 3m. Reef slope: steep (3-6m). Fore reef: sand (8m).	+	++	+	+++	+
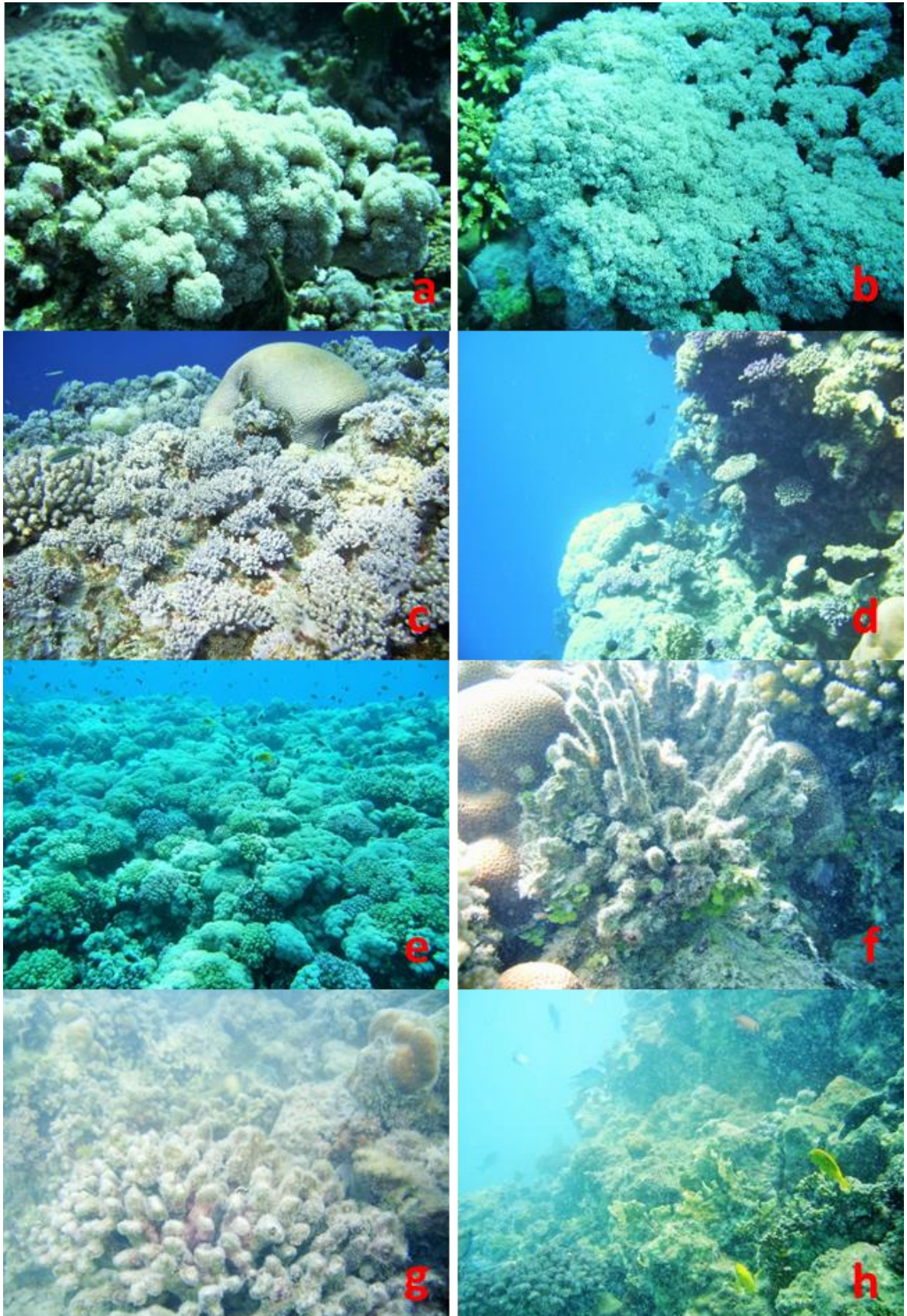
Figure 2: Photos of typical community structures and reefs at. a: cover on the xeniid reef flat at WAJ1; b: Xeniid reef flat at Mastura; c: Colonies of the *Sinularia spp* on reef flat at WAJ1; d: reef slope at WAJ2; e: Coverage on the reef flat at YAN1; Recently dead covered by sediment at YAN2 (f) and RAB (g); h: The particle load of sediment on the reef at JED2.

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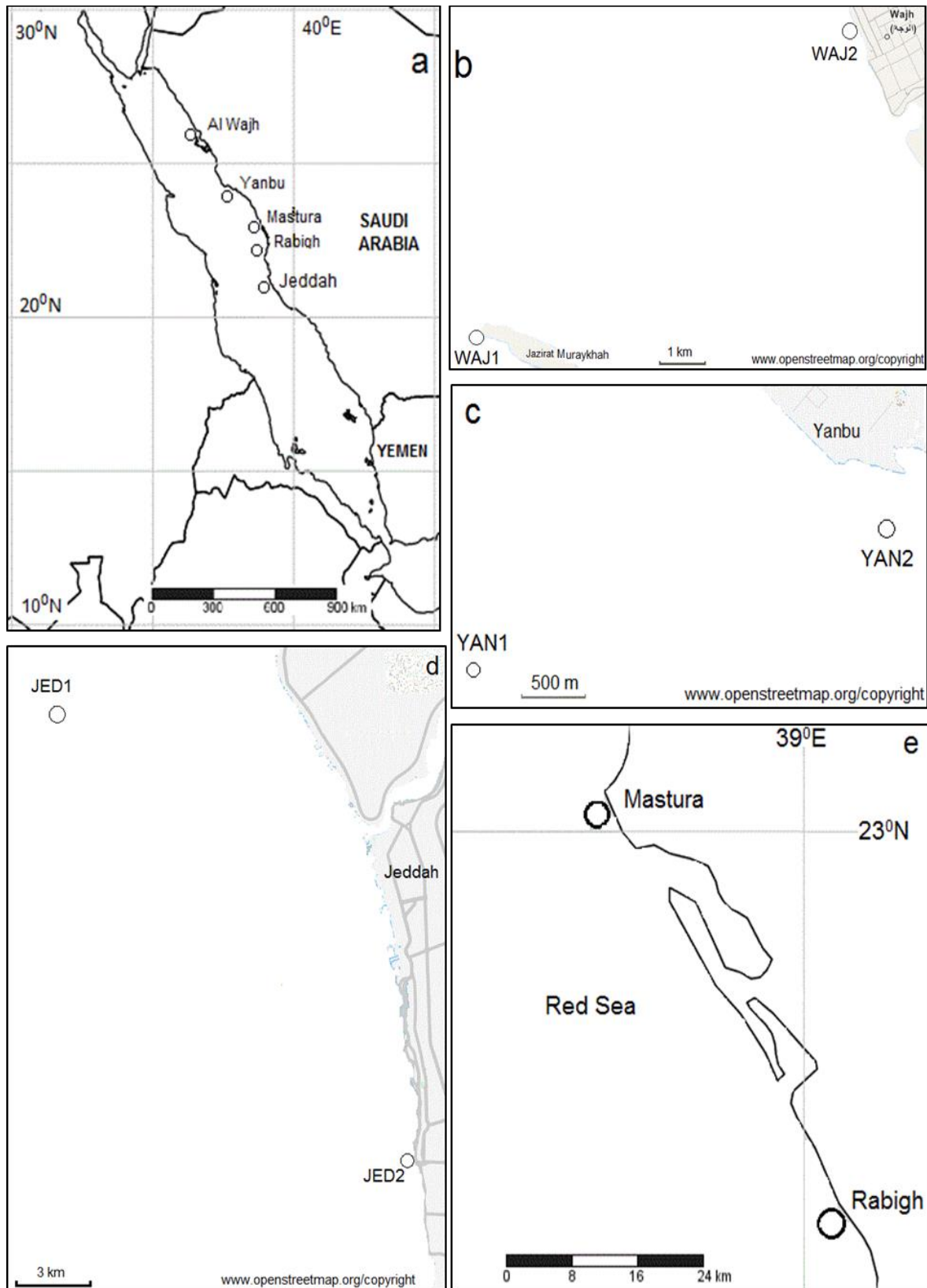
Figure 1: Map of study locations and sites (a), Al Wajh (b), Yanbu (c) Mastura/Rabigh (e) and Jeddah (d) areas. Map designed by following SimpleMappr; Shorthouse 2010 (a, e) and openstressmap (b,c and d).

Results

Environmental parameters: The results of water quality data showed that almost all environmental parameters differed between near-shore and off-shore reef sites, most environmental indices showed higher values in the near-shore (WAJ2, YAN2, RAB and JED2) than the off-shore sites (WAJ1, YAN1, MAS and JED1). A detailed description of water quality parameters at the reef sites was given and discussed in Sawall et al. (2014) and summarized in figure 3.

Near-shore reefs, close to a source of pollution, showed clearly different values as compared to the corresponding off-shore reefs. The chl a ranging from 0.29 to 0.43 µg L^{-1}, TN: 6.12 to 12.17 µmol L^{-1}, TP: 0.33 to 0.55 µmol L^{-1}, PC: 79.7 to 1150 µg L^{-1}, PN: 11.8 to 34.1 µg L^{-1}, NO$_2$: 0.04 to 0.09 µmol L^{-1}, NO$_3$: 0.12 to 1.18 µmol L^{-1} and Si 0.73 to 1.49 µmol L^{-1}. Meanwhile, in the off-shore reefs the water quality values were lower with the chl a ranging from 0.16 to 0.26 µg L^{-1}, TN: 3.13 to 4.79 µmol L^{-1}, TP: 0.17 to 0.33 µmol L^{-1}, PC: 84.3 to 131.4 µg L^{-1}, PN: 10.7 to 17.0 µg L^{-1}, NO$_2$: 0.02 to 0.04 µmol L^{-1}, NO$_3$: 0.04 to 0.23 µmol L^{-1} and Si: 0.5 to 1.02 µmol L^{-1}.

Amounts of sediment deposits on the reef substratum and turbidity values also differed between near- and off-shore reefs. The sediment deposits at YAN2, RAB and JED2 were "medium" layers and horizontal visibilities were turbid (V < 5 m). On all off-shore reefs no sediment deposit were recorded and the water clarity in terms of horizontal visibility ranged from 6 to over 15.
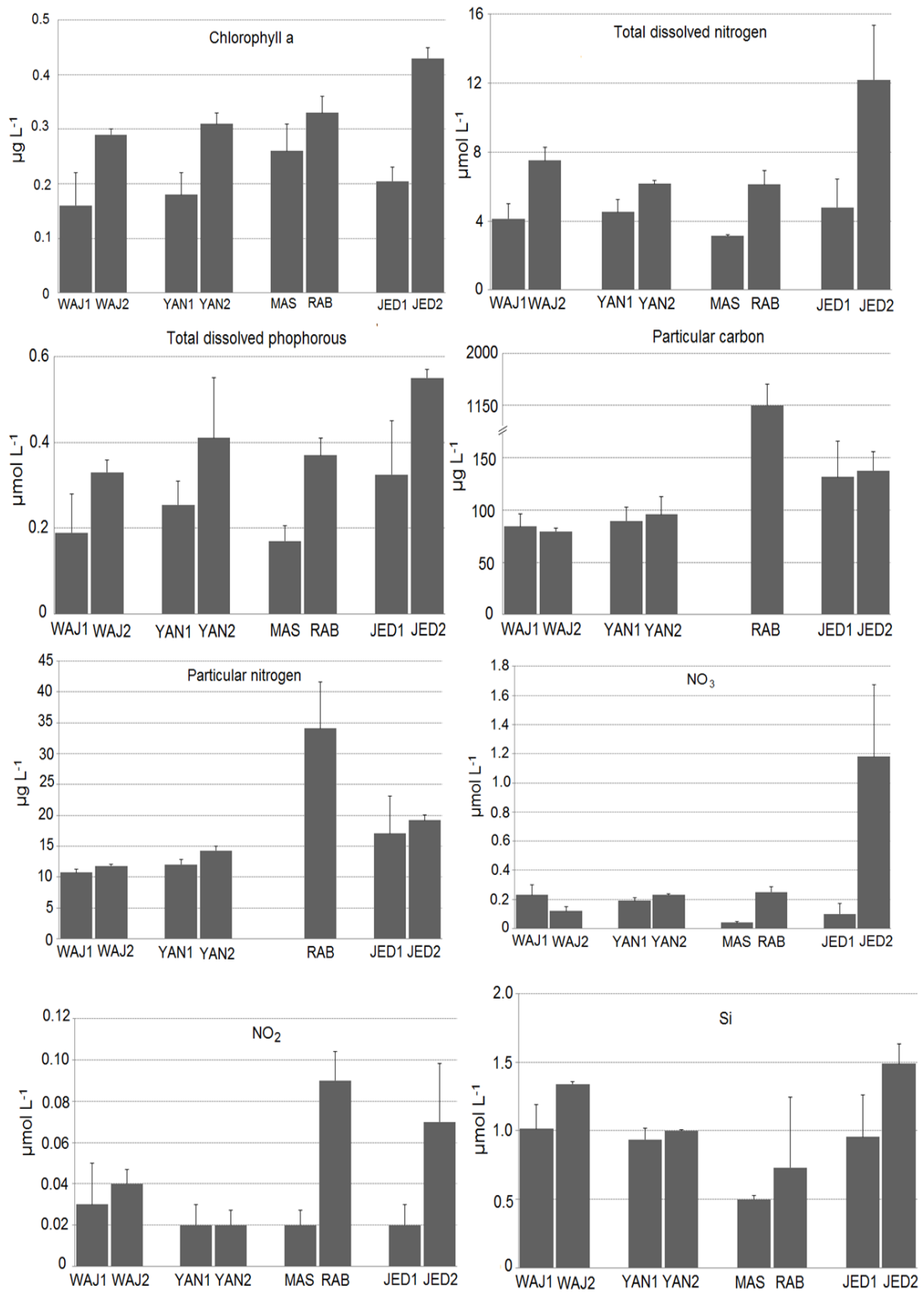
Figure 3: The environmental parameters in study sites.

(The data calculated the average of winter and summer value, bars ±SE).

Benthic coverage and abundance of Alcyonacea: Results from the LIT method showed that the coverage of living coral was quite high at all study sites (Tab. 2). The overall values of living coverage ranged from 10.0 % (RAB) to 81.3 % (YAN1). The soft coral coverage was high at WAJ2 and WAJ1 (27.0 % ± 4.1SE and 25.6 % ± 3.5, respectively) and lower at YAN2 and RAB (only 1.8 % ± 1.2 and 4.4 % ± 0.6, respectively).

Table 2: The mean of coverage (%) of substrate types at each study site.

(The value in the parentheses showed ±SE)

Substrate types	Study sites							
	WAJ1	**WAJ2**	**YAN1**	**YAN2**	**MAS**	**RAB**	**JED1**	**JED2**
Hard coral	35.5 (4.1)	45.8 (4.9)	64.4 (3.2)	31.3 (3.6)	51.3 (1.8)	5.6 (0.6)	45.6 (3.9)	64.4 (4.4)
Soft coral	25.6 (3.5)	27.0 (4.1)	16.9 (2.7)	1.8 (1.2)	17.5 (1.1)	4.4 (0.6)	18.1 (1.9)	11.3 (3.4)
Algae	1.0 (1.1)	0.0 (0)	0.0 (0)	2.0 (1.5)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Sponge	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
Rock	37.9 (4.5)	27.3 (3.6)	18.3 (2.3)	63.1 (3.2)	28.1 (3.2)	66.9 (3.0)	21.3 (3.8)	20.0 (3.6)
Rubble	0.0 (0)	0.0 (0)	0.5 (1.2)	1.3 (1.5)	2.5 (0.5)	6.9 (0.6)	15.0 (3.4)	3.1 (2.1)
Sand	0.0 (0)	0.0 (0)	0.0 (0)	1.3 (1.5)	0.0 (0)	10.6 (3.4)	0.0 (0)	0.0 (0)
Silt	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	4.4 (3.0)	0.0 (0)	0.0 (0)
Other	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.6 (0.3)	1.3 (0.4)	0.0 (0)	1.3 (0.4)

16 genera of Alcyonacea belonging to 5 families were recorded from the REA surveys, including *Tubipora, Rhytisma, Klyxum, Cladiella, Sarcophyton, Lobophytum, Sinularia, Anthelia, Xenia/Ovabunda** (** not recorded separately in the field), *Heteroxenia, Paralemnalia, Litophyton, Sterenonephtya, Nepthea, Dendronephthya,*

Siphonogorgia. The genera diversity recorded was highest at WAJ1 (16 genera) and lowest at YAN2 (6 genera). *Xenia/Ovabunda* and *Sinularia* were the two most common taxa dominating at the study sites (Tab. 3).

Table 3: Alconacean community composition show the relative abundance (RA) of each genus in the study sites. Degrees of RA are indicated that ∘: few ●: uncommon, ●●: common, ●●●: dominant and ●●●●: abundance.

	Al-Wajh		Yanbu		Mastura/Rabigh		Jeddah	
	WAJ1	WAJ2	YAN1	YAN2	MAS	RAB	JED1	JED2
Tubipora	●	●	●	●	●●	●	●	●
Rhytisma	∘	∘	∘	●		●●∘	∘	●
Klyxum	●	●	∘		∘	∘	∘	∘
Cladiella	∘	●●	∘					∘
Sarcophyton	●	●	●	●	●	●	●	●●
Lobophytum	∘	∘	∘	●	∘	∘	●	●
Sinularia	●●●●	●●●●	●	●	●	●●	●●	●●
Xenia/Ovabunda	●●	●●	●●●●	●	●●●●	●●	●●●●	●●●
Anthellia	●●	●	∘		∘	∘	∘	∘
Heteroxenia	∘	∘	∘		∘		∘	
Paralemnalia		●				∘		∘
Litophyton	∘	∘	∘		∘		∘	∘
Sterenonephthya	∘		∘		∘			∘
Nepthea	●●	●●			∘	∘		
Dendronephthya	∘				∘	∘		
Siphonogorgia	∘							

Xeniids community: Generally, the xeniid communities showed differences between near- and off-shore reefs in this study (Fig. 4; Tabs. 2 and 3). The ANOVA was used to compare the mean xeniid cover showing significant difference (d.f = 1 and 5, P<0.0001), the Bonferroni post-hoc comparisons showed the differences of xeniids cover between YAN1 and YAN2, MAS and RAB, JED1 and JED2 reefs were significant (P<0.05), but at Al-Wajh the reefs showed no significant difference xeniid communities between WAJ1 and WAJ2 (P>0.05).
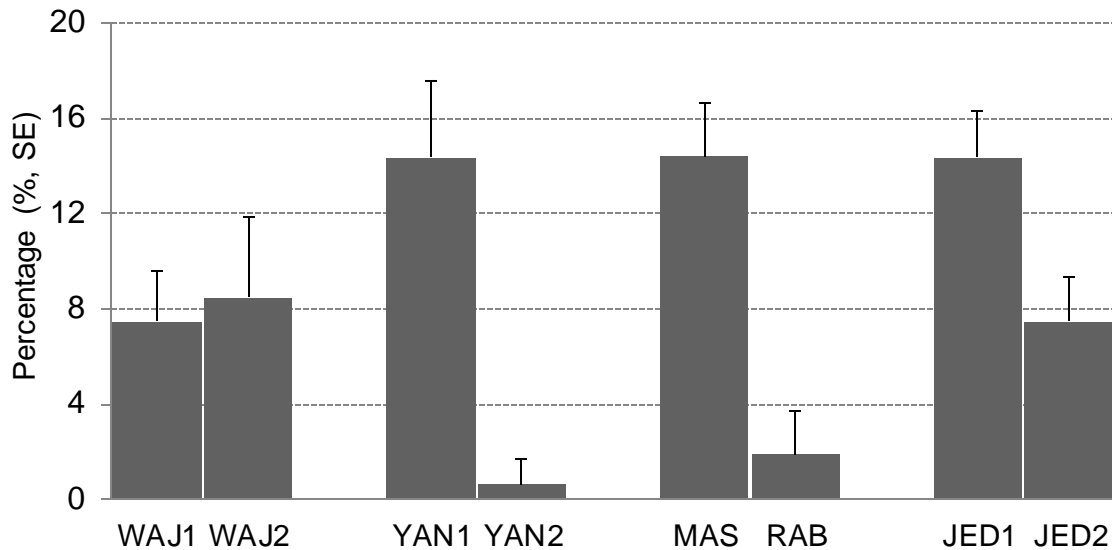
Figure 4: The cover of xeniids at the studying sites

Multivariate analyses (MDS and PCO) showed that the xeniids communities differed between the eight reefs surveyed (Figs. 5 & 6). ANOSIM results confirmed the conclusion (Global R = 0.64, P<0.01). The Pair-wise comparisons revealed that the xeniid communities were significantly different at YAN1 and YAN2 reefs (P<0.01), at MAS and RAB (P<0.05), at JED1 and JED2 reefs (P<0.05), but no difference was detected at WAJ1 and WAJ2 (P>0.05). SIMPER analyses indicated that the differences between the xeniid community at Yanbu and Mastura/Rabigh reefs related from the strong decrease of xeniid richness, cover and abundance at YAN2 and RAB, between Jeddah reefs difference were due to a reduced contribution of xeniid cover and abundance at JED2.
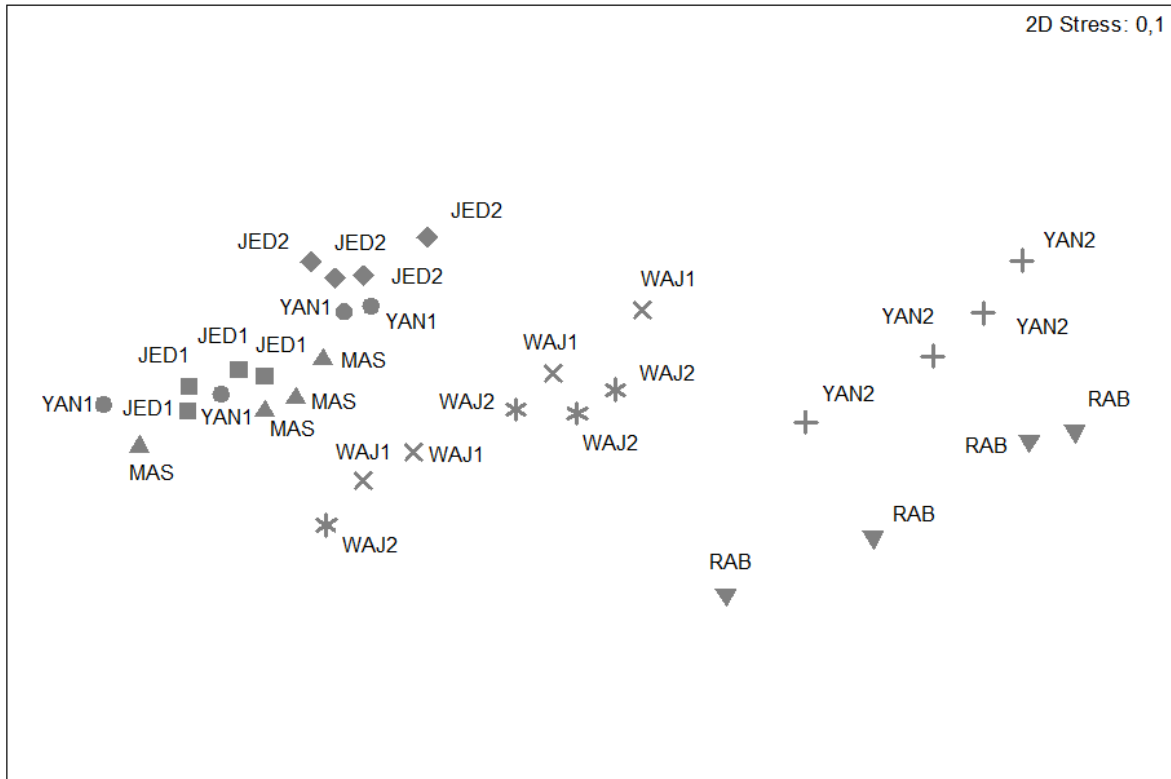
Figure 5: Multidimensional ordinations (MDS) of xeniid communities structure at eight reef sites surveyed.
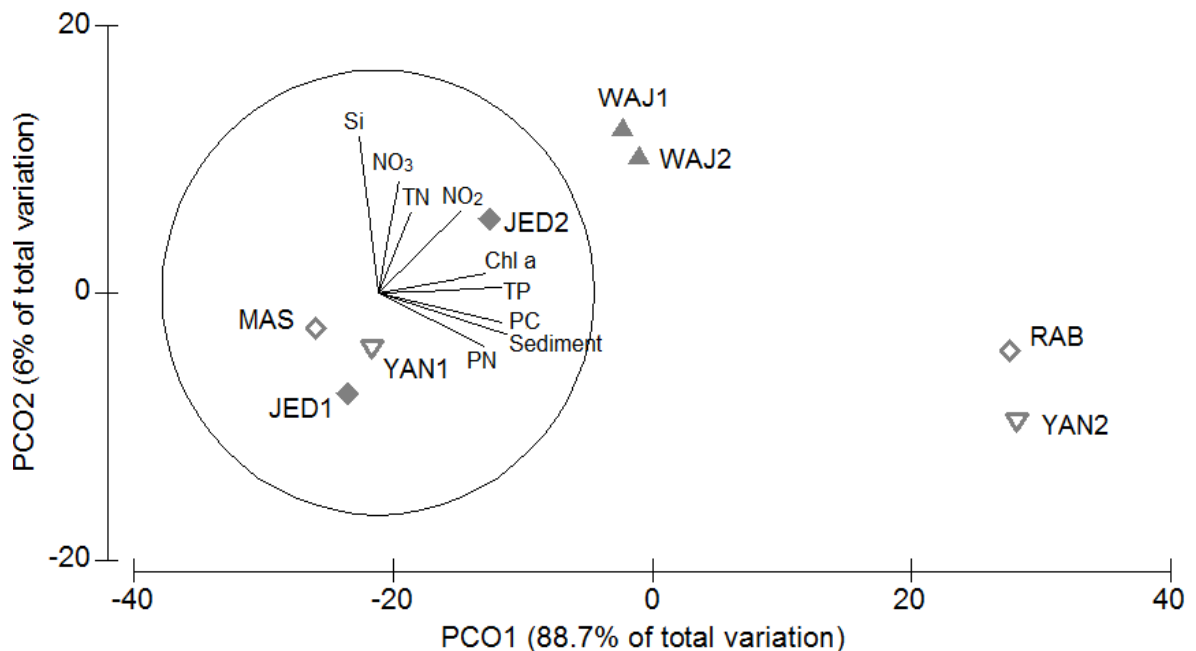
Figure 6: Results of principle coordinate analyses (PCO) of the alcyonacean community pattern (diversity, cover and relative abundance). The environmental parameters are presented as vectors: direction and the length of the vector represent the correlation between the environmental parameter and alcyonacean community pattern and the strengths of correlation, respectively.

This result recorded 20 species belonging to 5 genera. They are shown in table 4.

Table 4: Xeniidae (Wright & Studer, 1889) species recorded at the study sites. (1: WAJ1, 2: WAJ2, 3: YAN1, 4: YAN2, 5: MAS, 6: RAB, 7: JED1, 8: JED2)

Genera/Species	Study sites							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Genus *Sympodium* Ehrenberg, 1834								
Sympodium cœruleum Ehrenberg, 1834	+							
Genus *Anthelia* Lamarck, 1816								
Anthelia glauca Lamarck, *1816*	+	+	+		+		+	+
Genus *Ovabunda* Alderslade, 2001								
Ovabunda ainex (Reinicke, 1995)	+	+				+		+
Ovabunda benayahui (Reinicke, 1995)			+					+
Ovabunda biseriata (Verseveldt & Cohen, 1971)	+	+	+		+		+	+
Ovabunda crenata (Reinicke, 1995)				+	+		+	
Ovabunda faraunensis (Verseveldt & Cohen, 1971)		+	+		+			
Ovabunda gohari (Reinicke, 1995)							+	
Ovabunda hamsina (Reinicke, 1995)			+					
Ovabunda impulsatilla (Verseveldt & Cohen, 1971)	+	+		+	+			+
Ovabunda macrospiculata (Gohar, 1940)			+	+	+	+	+	+
Ovabunda miniata (Reinicke, 1995)								+
Ovabunda verseveldti (Benayahu, 1990)							+	
Genus Xenia Lamarck, 1816								
Xenia garciae Bourne, 1895								+
Xenia hicksoni Ashworth, 1899					+	+	+	
Xenia lillieae Roxas, 1933	+							
Xenia ternatana Schenk, 1896			+					
Xenia umbellate Lamarck, 1816			+				+	+
Genus *Heteroxenia* Kölliker, 1874								
Heteroxenia elizabethae Kölliker, 1874	+	+	+	+	+		+	+
Heteroxenia ghardaqensis Gohar, 1940							+	+
Total (20 species)	**7**	**6**	**9**	**4**	**8**	**3**	**10**	**11**

Of these, the genus *Ovabunda* was most diverse with 11 species, the genus *Xenia* was represented by 5 species, *Heteroxenia* by two species, *Sympodium* and *Anthelia* were recorded by one species each. Some species such as *Ovabunda impulsatilla, Heteroxenia elizabethae* and *Anthelia glauca* were present and abundant at most of the study sites. However, nine xeniid species were only recorded at one site and absent at all the other sites.

The diversity of species also differed between near- and off-shore reefs. In off-shore reefs (WAJ1, YAN1, MAS and JED1) the total of 18 xeniid species recorded represent 5 genera, while 13 xeniid species belonging to 4 genera were recorded on the near-shore reefs (WAJ2, YAN2, RAB and JED2). Comparison between areas yielded higher numbers of species at YAN1, WAJ1 and MAS than at YAN2, WAJ2 and RAB. JED2 reef the highest number of xeniid species (11) was recorded, while the lowest number (only 3 and 4 species) was observed at RAB and YAN2, respectively (Tab. 4).

Discussion

The xeniid communities were difference between near-shore and off-shore where the environmental conditions varied by activities from mainland and the shift in xeniid communities included covering, abundance and species richness related to water quality in this study.

Water quality data revealed that environmental parameter concentrations showed higher values at near-shore (close to the coastline including potential sources of impact pollution) as compared to off-shore sites due to elevated levels of (diffuse) land-based nutrient input. The water parameters showed a decline at reefs located close to a source of impact pollution, which was evident at YAN2 lying close to a petro-chemical factory and construction site, and JED2 close to an inlet of domestic waste water. For examples, at YAN2 the difference is supported by 2-fold values of the chlorophyll a and nitrite, JED2 showing from 2 to 10-fold higher concentrations of nitrite, nitrate, total nitrogen if compared to the corresponding reef sites off-shore.

The water parameter data at Al-Wajh area showed that WAJ2 seemed to be largely unaffected by the nearby desalination plant and potential effluents by the Al-Wajh town if compared to WAJ1, this result suggesting either low input levels of nutrients or rapid dilution (or both). Moreover, at YAN2, RAB and JED2 higher

amounts of sediment deposits on the reef substrata (labeled 2 with "medium" layers) indicate less water exchange than in the off-shore reefs. Our water quality data supported that the rapid economic development of the Saudi Arabian coast leads to locally elevated nutrient levels in near-shore waters at the Red Sea coast (PERSGA 2010), such as phosphate, hydrocarbons, sedimentation, temperature, salinity and dissolved oxygen (Ammar et al. 2007; Mohammed 2012; Dar et al. 2012).

In the Al-Wajh area, 16 genera of Alcyonacea were recorded by REA method in this study. However, the data showed that the relative abundances of Alcyonacea largely agree between WAJ1 (16 genera) and WAJ2 (13 genera). Some genera such as *Sinularia*, *Xenia/Ovabunda* and *Nepthea* are common on the reefs.

The cover of Xeniidae was higher at WAJ2 than WAJ1 but this difference between both reef sites was not significant. Our survey demonstrated that this area was characterized by high horizontal visibility (>10m), and no significant sediment deposition on the reef. Previous studies demonstrated that low visibility featured strong negative relation with the abundance and diversity of octocorals on inshore reefs of the Great Barrier Reef (Fabricius and De'ath 2001b; Fabricius et al. 2005). Some soft coral genera such as *Nepthea* are most abundant at clear-water locations and negatively affected by turbidity (Fabricius and Alderslade 2001). The presence of *Nepthea* species on both reefs at Al-Wajh provides evidence to support this finding.

The differences of water quality parameter data between both reefs appear less distinct. For example, values of chlorophyll a concentration, total nitrogen and phosphorus were higher at WAJ2 than at WAJ1, while nitrite, nitrate, silicate concentrations were higher at WAJ2 than WAJ1. This may indicate that the reef site WAJ2 does not exhibit distinct pollution source pattern from the mainland, or potential nutrient inputs may get rapidly diluted by physical factors such as waves and currents.

In the Yanbu area, YAN2 appeared strongly impacted by a landbased source of pollution as compared with the off-shore reef at YAN1. The coverage of xeniids was 14.4 % ± 3.2 SE at YAN1, significantly higher than at YAN2 with only 0.6 % ± 1.1, with 10 xeniid species recorded at YAN1 and only 4 at YAN2. Only two species *Ovabunda macrospiculata* and *Heteroxenia elizabethae* were observed at both reefs. The abundant presence of *O. macrospiculata* species was also reported from many Red Sea reef locations (e.g. Sanganeb-Atoll, Reinicke 1995). However, more detailed studies about the resilience of soft coral communities under impacted environmental conditions would be needed to evaluate the distribution patterns of this species.

Generally, the diversity of Alcyonacea with only 16 species recorded also was lowest at YAN2 as compared with the other sites (Hoang, work in progress). Six genera *Tubipora, Rhytisma, Lobophytum, Sinularia, Sarcophyton* and *Xenia/Ovabunda* were recorded at YAN2 by the REA method with very low relative abundances of each genus and most of these genera distributed over a wide range of habitat types from turbid to clean environments (Fabricius and Alderslade 2001). The generic abundance of soft corals showed a low value and the water quality presented high concentration at YAN2 suggesting that alcyonacean abundance demonstrates negative correlate with turbidity, suspended particulate matter and total organic sediment contents (Van Woesik et al. 1999).

Moreover, some taxa missing in this reef as compared with YAN1 further confirmed that water quality effects xeniid richness. The YAN2 was located close to a petro-chemicals factory, the cover of living coral at YAN2 showed the lowest while the algae exhibited the highest value (2 % ± 1.5SE) as compared with the other study reefs supported that impacts from the petro-chemical plant lead to decreasing living coral and increasing algae and sea urchin abundance in the Red Sea (Ammar et al., 2007). The significant differences in the hard coral communities were evident towards some reefs close to a source of impact pollution such as YAN2 featuring a general decrease of coral abundance (Sawall et al. 2014). The difference of soft and hard coral coverage (1.8 % ± 1.2SE and 31.3 % ± 3.6, respectively) under impacted environmental conditions at YAN2 also reflects that soft corals tend to react more sensitively and specifically to modified water conditions than do hard corals (Fabricius et al. 2005).

Rabigh area showed the status of xeniid communities similar to YAN2 with low xeniid cover and species richness. The xeniid cover at RAB was 1.9% ± 1.6SE and only 3 species were recorded, further overall observations suggested that the living coral in this area might be affected by the regional bleaching events in 1998 (Devantier et al. 2000a) and 2010 (Furby et al. 2013), as well as by continuing or sporadic effects by pollution sources from the mainland. Thus, anthropogenic activities appear to play a role influencing the coral community's distribution in the near shore areas of the Saudi Arabian coast line.

The genus *Rhytisma* characteristically grow as attached membranes over non-living or overhanging substrates (Benayahu 1985; Fabricius and Alderslade 2001). Colonies of the genus *Rhytisma* which was newly established by Alderslade (2000) for

species separated from the taxon *Parerythropodium*. In this study the Red Sea polymorphic species *Rhytisma fulvum fulvum* (Haverkort-Yeh et al., 2013) was recorded dominant at RAB where were characterized by high shares of rock (66.9% ± 3.0SE) and rubble (6.9% ± 0.6) cover on the reef providing extended substrata for the colony spreading colony shapes of this species are thin-encrusting about 2 - 4 mm thick and often overgrowing dead substrate (Fabricius and Alderslade 2001).

In the Jeddah area, JED2 lay close to a domestic waste water inlet (200 m), the environmental parameters showed significant differences towards the off-shore site at JED1. The sediment deposits on the reef at JED2 scored "medium" (2) and the horizontal visibility was "turbid" (<5 m). Rising sewage effluents are potentially increasing impact coral reef communities (Pastorok and Bilyard 1985). The xeniids were reported to settle in turbid habitats of the Gulf of Suez (Benayahu 1985). As opportunistic colonizers their planktonic larvae distribute and successfully colonize suitable substrates under sufficient light exposition to meet developmental needs (Benayahu and Loya 1984; Reinicke 1997b).

Two xeniid species, *Ovabunda impulsatilla* and *O. biseriata* were dominat at JED2 while being absent at JED1, *O. impulsatilla* was also recorded dominant at YAN2. *O. biseriata* occurred with high frequency at Farassan island (Southern Red Sea) where environmental conditions featured high nutrient concentrations, sedimentation and low visibility (Hoang, work in progress). The frequent, abundant occurrence of these two species at impacted (polluted) sites (YAN2 and JED2) indicates their robustness and stress-tolerance towards turbidity. The *Heteroxenia fuscescens* was a common species and widely distribute in the Red Sea (Gohar 1940; Benayahu 1985; Reinicke 1997), although this species not encountered at study sites but it was recorded at the other reefs in the Jeddah, Farassan (Hoang, work in progress).

In Conclusion, this study shows that variations in xeniid communities distribution patterns reflect differences in water and environmental habitat parameters of reef sites at four surveyed locations. The xeniid communities not only vary in coverage but also in dominance of the genera and species diversity shifts the status under different impact conditions. The variability of alcyonacean communities reflects alterations of environmental conditions. Survey sites at Yanbu (YAN2), Rabigh (RAB) and Jeddah (JED2) being subjects to significant impacts from landbased pollution sources feature decreasing values of coverage and diversity of Alcyonacea.

Meanwhile the Al-Wajh area (WAJ1, WAJ2) showed no detectable differences between living benthic and alcyonacean communities patterns, reflecting the predominant environmental parameters quality exhibiting no detectable (significant) deviation from overall conditions, that influence the Alcyonacea an patterns in this area.

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Chemical versus mechanical defense against fish predation in two dominant soft coral species (Xeniidae) in the Red Sea

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Abstract

Soft corals of the family Xeniidae are particularly abundant in Red Sea coral reefs. Their success may be partly due to a strong defense mechanism against fish predation. In field and laboratory experiments we assessed the antifeeding activity of their secondary metabolites. In feeding deterrence assays the soft coral crude extract of secondary metabolites was mixed at natural or reduced concentrations into food pellets made of freeze-dried squid and phytagel. The feeding bioassays showed that at natural concentration the metabolites of both investigated species deterred reef fishes in the field (Red Sea) to 86% (*Ovabunda crenata)* and 92% (*Heteroxenia ghardaqensis).* In the laboratory, natural concentration of crude extract deterred the reef fish *Thalassoma lunare* (moon wrasse) to 83% and 85%, respectively. Moon wrasse feeding was even reduced at extract concentrations as low as 12.5% of the natural concentration in living soft coral tissues. When individual fish were fed repeatedly the same moderately deterrent feed (25% of natural concentration), their acceptance of the pellet decreased by 3 to 8% with each successive trial suggesting learned avoidance. To assess the potential of a physical anti-feeding defence, sclerites of *O. crenata* were extracted and mixed into food pellets at natural or double natural concentration combined with crude extract. The sclerites did not show any effect on the feeding behavior indicating that sclerites provide structural support rather than antifeeding defenses. *Heteroxenia ghardaqensis* species lacks sclerites. The remarkable chemical deterrence detected is likely to contribute to the conspicuous abundance of these soft coral species in the Red Sea.

Key words: chemical defence; feeding deterrence; sclerites; soft coral; *Ovabunda*; *Heteroxenia*; Red Sea.

Introduction

Soft corals (Octocorallia, Alcyonacea) are a major component of the sessile coral reef benthos and feature a high diversity in tropical Indo-Pacific coral reefs (Dinesen 1983; Fabricius and Alderslade 2001), including the Red Sea (Benayahu and Loya 1977, 1981; Benayahu 1985; Reinicke 1997). Some soft corals species of the families Xeniidae and Alcyoniidae contribute to the diet of coral reef fishes (Gohar 1940). Secondary metabolites of some soft corals have been shown to possess ecological functions including anti-predatory protection (La Barre et al. 1986), allelopathy (Sammarco et al. 1983, 1985) and antifouling activity (Limna Mol et al. 2010, Changyun et al. 2008).

These chemical defenses may be as effective as the biomineralized skeleton protecting hermatypic corals from predation by most reef fishes (Sammarco and Coll 1992). Some Alcyoniidae species (e.g. *Sinularia polydactyla, Rhytisma fulvum fulvum*) were shown for example, to possess secondary metabolites, which protect the soft corals against predation by carnivorous fish (Wylie and Paul 1989; Van Alstyne et al.1994; Kelman et al. 1999). A survey by Coll et al. (1982) showed a high prevalence of toxic species among the soft coral order Alcyonacea (>50% of the species) in the central Great Barrier Reef, suggesting that secondary metabolites which are active against predators are common in the Alcyonacea. In an extensive study by La Barre et al. (1986) it was found that the majority of soft coral taxa in the Great Barrier Reef are defended against fish predation, but that toxicity and repellence are not necessarily related.

Chemical defense against predation may already be present in eggs, embryos or larvae of some soft corals (Coll et al. 1989; Kelman et al. 1999; Slattery et al. 1999; Lindquist 2002) hinting at the importance of chemical antifeeding defense in soft corals throughout life history. In addition to their well-studied antifeeding role, secondary metabolites of soft corals may also serve to combat fouling on their surface (Bhosale et al. 2002; Limna Mol et al. 2010) and to protect corals against viral infections (Ahmed et al. 2013). The conspicuous richness of chemical defenses in soft corals (Rocha et al. 2011) may contribute to their remarkable invasion potential (Lages et al. 2006; Fleury et al. 2008).

Chemical defense could be supplemented by mechanical defense such as mucus secretion (La Barre et al. 1986; Sammarco et al. 1987; Harvell and Fenical 1989) or elevated spicule concentration in the tissue (Van Alstyne et al. 1992). Calcium carbonate spicules are common attributes in Octocorallia, as well as in Porifera, Echinodermata and Ascidiacea (Kingsley 1984). Size and shape of the spicules are often species-specific and used as taxonomic tools (e.g. Bayer et al. 1983). They are thought to mainly function as structural support of the polyps and colonies (Lewis and Von Wallis 1991; Van Alstyne et al. 1992; O'Neal and Pawlik 2002), but can also function as defensive structures. The latter was demonstrated for some soft coral species, where fishes rejected sclerite containing artificial food (Van Alstyne et al. 1992, 1994), but not for others (Kelman et al. 1999; O'Neal and Pawlik 2002).

The antifeeding defense by sclerites may be effective only in those parts of the colony, where their concentration is particularly high (Puglisi et al. 2000). Where sclerites do play a defensive role, their shape, size and abundance determine their protective efficiency, traits which may differ throughout a coral colony (Sammarco et al. 1987; Van Alstyne et al. 1992; Koh et al. 2000). Similarly, Ilan and Burns (2003) found that in sponges only spicules larger than ~250 µm deterred predation.

The family Xeniidae comprises 34 species and is one of the most common and widely distributed octocoral families in the Red Sea (Reinicke 1997). Here, it can cover up to 50% of the substrate in some shallow reef areas (~4m depth) forming extensive carpets (Benyahu and Loya 1981; Reinicke 1997).

The family differs from all other Octocorallia by the soft, fleshy consistency of the colony and by its non-retractile polyps (Ashworth 1899). Some xeniid species lack stinging nematocysts (Janes 2008), which might reduce their capacity for protection against predators (Vermeij 1978; Bakus 1981; McIlwain and Jones 1997). Their competitiveness, nevertheless, is high presumably due to the motility as adults, their rapid asexual reproduction (Benayahu and Loya 1981), and the widespread allelopathy against space competitors and hard coral recruitment (Sammarco et al. 1983; Atrigenio and Alino 1996). Secondary metabolites with antimicrobial (Kelman et al. 1998, 2006) and anti-fouling activity (König et al. 1989) also seem to abound. Indeed, xeniids, like many other soft coral taxa, are remarkably rich in bioactive secondary metabolites (König et al. 1989; El-Gamal et al. 2005). Some chemical

compounds were isolated from xeniid species considered to be useful candidates in the field of medicine such as blumiolide A and B (*Xenia blumi)*, a range of xeniolide (*X.blumi, X.novaebrittanniae, X.umbellata*) and different umbellacins (*X. umbellate*) (e.g. anti-tumor activity, El-Gamal et al. 2005, 2006; Bishara et al. 2006). Their potential chemical defense against fish predation, which could contribute to their high abundance in the Red Sea, has to the best of our knowledge not been investigated so far.

In this study we investigated the chemical defense against fish predation in two particularly abundant xeniid species in the Red Sea, *Ovabunda crenata* and *Heteroxenia ghardaqensis*. We further studied whether or not chemical defense is enhanced by the presence of sclerites. To this purpose artificial food was made and charged with crude extract (i) at natural concentration and fed to the reef fish community in situ and, (ii) at natural and reduced concentrations, with and without the addition of sclerites, and fed to the moon wrasse fish *Thalassoma lunare* in aquaria.

Materials and Methods

Sample collection and identification: The soft coral samples were collected near the city of Jeddah, Saudi Arabia, in the central Red Sea. Here, the cover by living coral (hard and soft coral) was 36 to 61% to which the family Xeniidae contributed with 7.5 - 14% (unpublished data of line intercept transects in 3-4 m depth). The two xeniid soft coral species were collected by SCUBA diving in 3–6 m depth. The species *Ovabunda crenata* was collected at off-shore reefs (10 km from shore) while *Heteroxenia ghardaqensis* was collected near-shore (50 m from shore), where the respective species dominated the soft coral populations in the reefs. Five replicate samples of each species were collected with about 0.5 kg wet weight per sample. The samples were brought to the laboratory, the volume was determined immediately by water displacement (live colonies), and their identity was verified under the microscope following the identification criteria of Reinicke (1997).

Chemical extraction: The extraction was carried out in two steps in order to guarantee maximum metabolite extraction of a wide polarity spectrum. For the first extraction, fresh samples (whole colonies) were immersed in ethyl acetate for 24h at room temperature (Lages et al. 2006). The gained crude extract was filtered through a

paper filter and the solvent was removed with a rotary evaporator. The extracted coral tissue was stored in a freezer at -20°C until further processing. A second extraction followed, for which the frozen coral sample was freeze-dried, chopped into small pieces of about 0.5 cm^3 and weighed (dry weight). The tissue was then immersed in a solvent consistent of a 1:1 (v/v) mixture of dichloromethane and methanol (DCM:MeOH) for 24h at room temperature (Wylie and Paul 1989). This second crude extract was also filtered through filter paper and the solvent was evaporated until dryness. Finally, the crude extracts of the first and second extraction were combined and kept at -20°C until further processing. The calculation of the natural concentration of crude extract was based on the volume of samples. The values were 32 mg ml^{-1} for *O. crenata* and 35 mg ml^{-1} for *H. ghardaqensis* and were used as reference for the preparation of the food pellets.

Sclerite preparation: In order to obtain pure sclerites of the soft corals, each colony of *O. crenata* species was cut into small pieces and immersed in 12% sodium hypochlorite to dissolve the tissue and leave the sclerites. *H. ghardaqensis* does not contain sclerites. After 12 hours the supernatant was carefully decanted and new sodium hypochlorite was added. This process was repeated until the tissue was completely dissolved. The sclerites remained on the bottom of the tube. They were collected and rinsed 3 times with distilled water, dried in an oven (80°C, until completely dry) and weighed. The natural concentration of sclerites was calculated by dividing the dry weigh of sclerites by the dry weigh of the colony.

Field assay: The frozen crude extract was re-dissolved in ethanol. Food pellets were produced after Pawlik and Fenical (1992) with some modifications: the basis of the food pellets was made by mixing and boiling of 1.30 g phytagel (Sigma- Aldrich Company, USA), 1.38 g of freeze-dried powdered squid and 30 ml distilled water. After the mixture cooled down to ~40°C the crude extract dissolved in ethanol (1.1 ml of *O. crenata* or 1.08 ml of *H. ghardaqensis*) was added at natural concentration as found in the soft coral tissue. The viscous mixture was poured into a plastic mould containing a piece of mosquito net with a mesh size of 1 mm^2. After the matrix cooled down, the solidified gel was removed from the mould and cut into pieces of three different sizes: 1, 2 and 3 cm^2. From each extract (n=5) 3 pellets were made, resulting in 15 pellets (replicate and sub-replicate) for each species.

The feeding assay was conducted at the same off-shore reef and the same depth, where the xeniid samples had been collected. The procedure was similar to the method described by Van Alstyne et al. (1992, 1994), where pellets were individually weighed and fixed to a fishing line. Each size class (1, 2, or 3 cm²) was represented as a pair with one pellet containing crude extract and the other pellet (of identical size) containing ethanol only. The distance between the pellets of a pair was 5 cm and the distance between pairs was 25 cm. A buoy at one end and a weight at the other end held the rope in a vertical position in the reef. The lowest pair was 1 m above the ground. The feeding activity of the reef fish was observed by SCUBA divers from about 3 m distance. The ropes were re-collected after one of the control or treatment pellets on each rope were eaten completely by reef fishes. The pellets were re-weighed to determine the percentage consumed.

Aquarium experiment: The food pellets for the aquarium experiment were made after Pawlik et al. (1995). Here the crude extract dissolved in ethanol was mixed with 0.3 g alginic acid and 0.5 g powdered squid. Distilled water was added to obtain a final volume of 10 ml. The mixture was stirred until it was homogeneous, and then loaded into a 10 ml syringe. The tip of the syringe was immersed into a 0.25 M $CaCl_2$ solution and the content of the syringe was slowly expelled into the $CaCl_2$ solution to form noodle-like food pellets. After several minutes, the solidified "noodles" were rinsed with sea water and cut into 2-5 mm long pieces.

The effectiveness of the antifeeding activity was assessed at different concentrations of crude extract in the food pellets. This was done to assess the efficiency of secondary metabolites, which may vary in concentrations within the soft coral tissue seasonally, among populations, among organs and/or among life stages (Slattery et al. 1999, 2001). Thus, we produced pellets with 100%, 50%, 25% and 12.5% of the natural extract concentration. In order to assess the potential anti-feeding effect of the sclerites, sclerites were added to the food pellets (without extract) in their natural concentration (0.13 g sclerites g^{-1} soft coral dry weigh). Additionally, sclerites were added to food pellets containing reduced concentrations of crude extract (25% of the natural concentration) in different concentrations (50%, 100% and 200% sclerites of natural sclerite concentration) to determine the potential interactive effect of sclerites and secondary metabolites. We used 25% extract concentration not to mask any potential sclerite effect by a dominant chemical effect.

The feeding experiment in aquaria was carried out in Kiel, Germany, using the climate rooms of the GEOMAR institute. The moon wrasse, *Thalassoma lunare,* (bought from the company Aqua Inspiration, Bonn, Germany) was chosen, because it is an abundant species in the central Red Sea and known to be a generalist feeder on a wide assortment of benthic invertebrates including soft corals (Randall 1983; Rotjan and Lewis 2008). Furthermore, this species has been used frequently for aquarium bioassays (Pawlik et al. 1987; Harvell et al. 1988; Kelman et al. 1999; Epifanio et al. 2007), due to its wide prey spectrum, its fast adaptation to aquarium conditions and slow satiation (Pawlik et al. 1987). Each fish (n=9) was placed in a separate aquarium filled with 40-l artificial sea water with a salinity of 35psu, a temperature of 25°C and a 12h light : 12h dark rhythm.

The feeding choice test was done by feeding the fish alternatingly with control and treatment pellets loaded with extract and/or sclerites. In case the fish ignored the treatment pellet, another control pellet was offered in order to discriminate between the repellence of the treatment pellet and satiation. A pellet was considered rejected, when it was ignored or spit out by the fish and the fish consumed a control pellet thereafter. The feeding tests were repeated with 10 control and 10 treatment pellets at a time with each of the 9 fish. The number of pellets consumed or rejected was recorded. Different treatments were tested at different days, with 3-5 days of rest between each test. During resting time, fish were fed with artificial food (fish food).

Analyses: The feeding deterrence in the field assays was assessed by comparing the consumption rates on the pairwise deployed pellets using Repeated Measures ANOVA according to Molis et al. (2006) which takes account of the spatial dependence of the two pellets with and without extract forming a pair. Only the data of the large pellets were used, because in this case the control pellets were not entirely consumed. Prior to the analysis, all data were Box-Cox-transformed to ensure normality (see Molis et al. 2006).

The learning capacity of the fish in the aquaria experiment, which were repeatedly (10x) fed an identical extract pellet (intermittently with a control pellet), was assessed as the % decrease of acceptance between successive offerings during a given test day (i.e. increasingly experienced fish) relative to the acceptance at the first offering of an extract-loaded pellet (i.e. naive fish). These slopes were calculated for the pellets containing 25% of the natural extract concentration, because with full concentration the acceptance in most cases reached zero too early to calculate

reliable slopes and at concentrations below 25% repellence and learning were almost absent. Because the fish showed some learning capacity, only the acceptance or rejection of the first treatment pellet (i.e. the reaction of a naive fish) was used for the statistical assessment of the extract defense strength.

The discrimination between control and extract pellet was tested by Fisher's exact test for the two soft coral species separately. Replication was done on the extract side (n = 5 colonies extracted) and on the consumer side (n = 9 fish individuals tested). This procedure assesses the difference in proportion of eaten relative to rejected pellets between pellets with versus without extracts for the 5 replicate extracts per soft coral species offered to 9 fish. Analyses were performed with the software Statistica 8.

Results

In the field experiment, food pellets containing extracts of both soft coral species at natural concentration were avoided by the reef fish community relative to the pellets without coral extract (F=44.6, p<0.001; Fig. 1, Tab. 1). In contrast to the control pellets (97% ±2.5 SE and 92% ±2.9), only 14.4% (±3.9) and 8.7% (±3.2) of the pellets containing *O. crenata* extract and *H. ghardaqensis* extract, respectively, were eaten by the fishes.

Repellency did not differ significantly between the two xeniid species (F=0.07, p=0.8, Tab.1). The main fish species observed feeding on the pellets were *Thalassoma lunare, T. rueppellii, Pomacentrus sulfureus, Sufflamen albicaudatum, Oxycheilinus digramma* and *Cephalopholis argus.* In addition, some allegedly herbivorous fishes such as parrot fishes and surgeon fishes fed on the pellets occasionally.
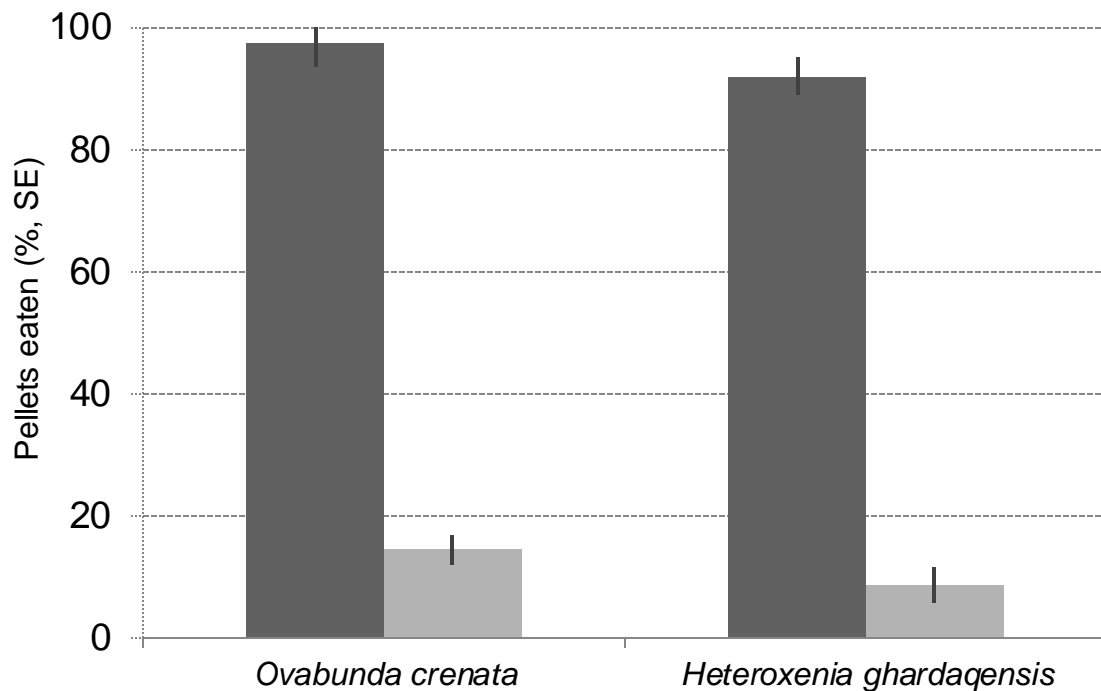
Figure 1: Field assay. Mean percentage of pellets consumed by reef fishes in field. Dark grey columns: pellets without crude extract, light grey columns: pellets containing crude extracts at natural concentration.

Table 1: Results of repeated measures analysis of variance (repANOVA) on the consumption rates of natural reef communities on pellets loaded with either *Ovabunda crenata* or *Heteroxenia ghardaqensis* extracts (factor "Extract") at natural concentrations relative to pellets not containing any coral extract. The comparison of feeding on the pair-wise deployed control and extract pellets is represented by the "R1" term. Shown are: df = degrees of freedom, SS = sum of squares, MS = mean squares, F = test statistic, and p = significance.

	SS	df	MS	F	p
Intercept	13.43845	1	13.43845	18.70672	0.002529
Extract	0.0507	1	0.0507	0.07057	0.797225
Error	5.747	8	0.71838		
R1	30.62576	1	30.62576	44.63039	0.000156
R1*Extract	0.0301	1	0.0301	0.04387	0.839335
Error	5.48967	8	0.68621		

In the aquarium experiment the fish quickly adapted to the new condition and readily accepted the control food pellets (without extract). For most concentration levels of both crude extracts most fish individuals learned to recognize and avoid the

repellent pellets during the series of 10 subsequent encounters with a given pellet type. For the 25% natural concentrations, we assessed the slope of decreasing acceptance by increasingly experienced fish. The average slopes of the learning curves of the 9 fish, i.e. increasing rejection with increasing experience, were -3.3 (±1.6 SE) and -8.6 (±2.7) for *Heteroxenia* and *Ovabunda* extracts, respectively. This means, that each time the fish faced a further extract-loaded pellet they, on average, accepted it 3.3% to 8.6% less often than at the preceding encounter. Between the first and the tenth encounter the acceptance thus decreased by 33% and 86% for *Heteroxenia* and *Ovabunda* extracts, respectively. The difference in learning speed of fish with regard to the 2 potential prey species was, however, not significant (t-test, df = 11, t= 1.6, p = 0.13).

At the first encounter between pellet and the naive fish, the control pellets were always eaten, while the treatment pellets containing the natural concentration of crude extracts were rejected by the moon wrasse to different degrees. On average, only 21% (±6.4 SE) of the pellets containing crude extract of *O. crenata* and 26% (±8) of the pellets containing crude extract of *H. ghardaqensis* were consumed by the naive moon wrasse (Fig. 2), which in both cases was significantly less than the feeding on control pellets (repANOVA and Fisher's Exact test p< 0.0001, Tabs.1 and 2).

The repellent activity decreased with decreasing crude extract concentration for both soft coral species (Fig. 2). This trend appeared slightly stronger in *H. ghardaqensis* compared to *O. crenata*, but both species showed a significant repellence even at the lowest tested concentration of crude extract (12.5%) (Tab. 2). Comparing the treatment pellets of the two species only (Fig. 2), *Ovabunda* extracts appear less repellent than *Heteroxenia* extracts (Tab. 3). However, only at 25% natural concentration was this difference significant.

Sclerites of *O. crenata* did not affect the feeding behavior of moon wrasses at any sclerite concentration (50%, 100% or 200% of natural sclerites) when added to food pellets without coral extract or in combination with 25% of crude extract concentration (Fig. 3, Tab. 4).
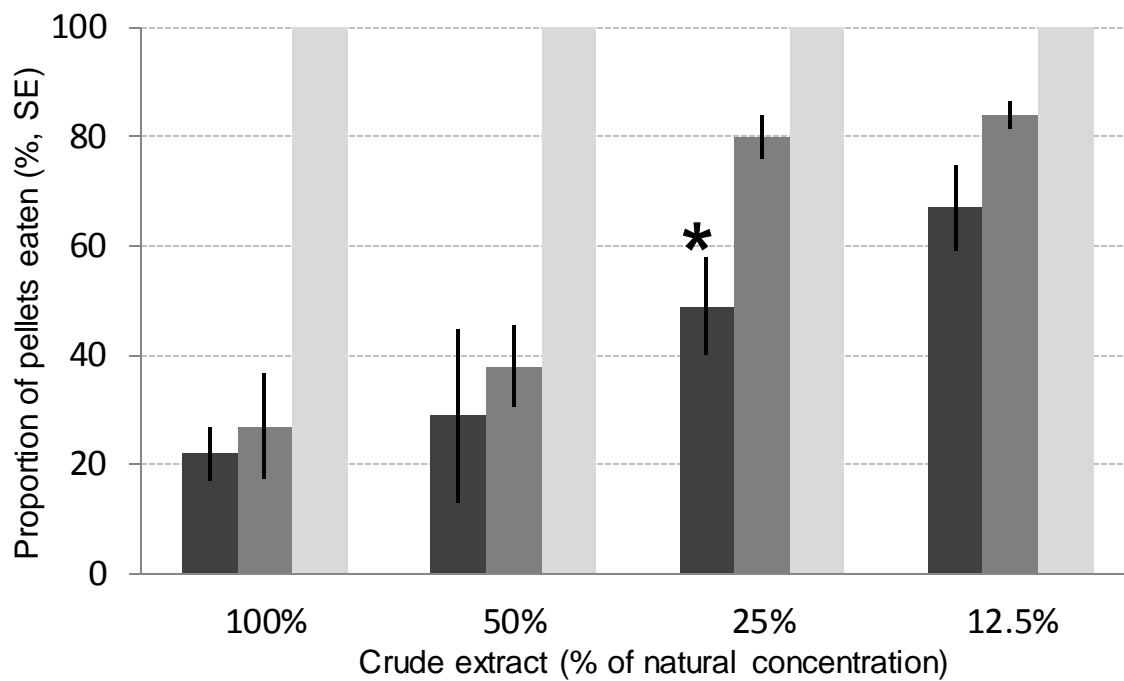
Figure 2: Proportion of pellets containing different natural concentration of crude extract of *Ovabunda crenata* (dark grey) and of *Heteroxenia ghardaqensis* (medium grey) consumed by moon wrasse fish. Pellets without coral extract (light grey, 100% eaten in all tests). (* significant difference with p<0.05 between pellets containing *Ovabunda crenata* and *Heteroxenia ghardaqensis* extracts).

Table 2: Feeding discrimination of fish between pellets with versus without coral extracts in the aquaria assays analysed by Fisher's Exact test. "Extract %" = concentration of coral extract in % of natural concentration. "Fisher's p" = 2-sided p-value.

Species	Extract (%)	Chi²	Fisher's p
Ovabunda crenata	100	54	<0.0001
	50	47	<0.0001
	25	29	<0.0001
	12.5	13	<0.001
Heteroxenia ghardaqensis	100	49	<0.0001
	50	38	<0.0001
	25	7.9	0.0025
	12.5	5.6	0.0121

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Table 3: Repellence (assessed as proportion of pellets consumed) of *Ovabunda* versus *Heteroxenia* extracts compared by Fisher's Exact test at different extract concentrations. "Extract %" = concentration of coral extract in % of natural concentration. "Fisher's p" = 2-sided p-value.

Extract (%)	Chi²	Fisher's p
100	0.06	0.81
50	0.69	0.37
25	8.2	0.004
12.5	2.9	0.08
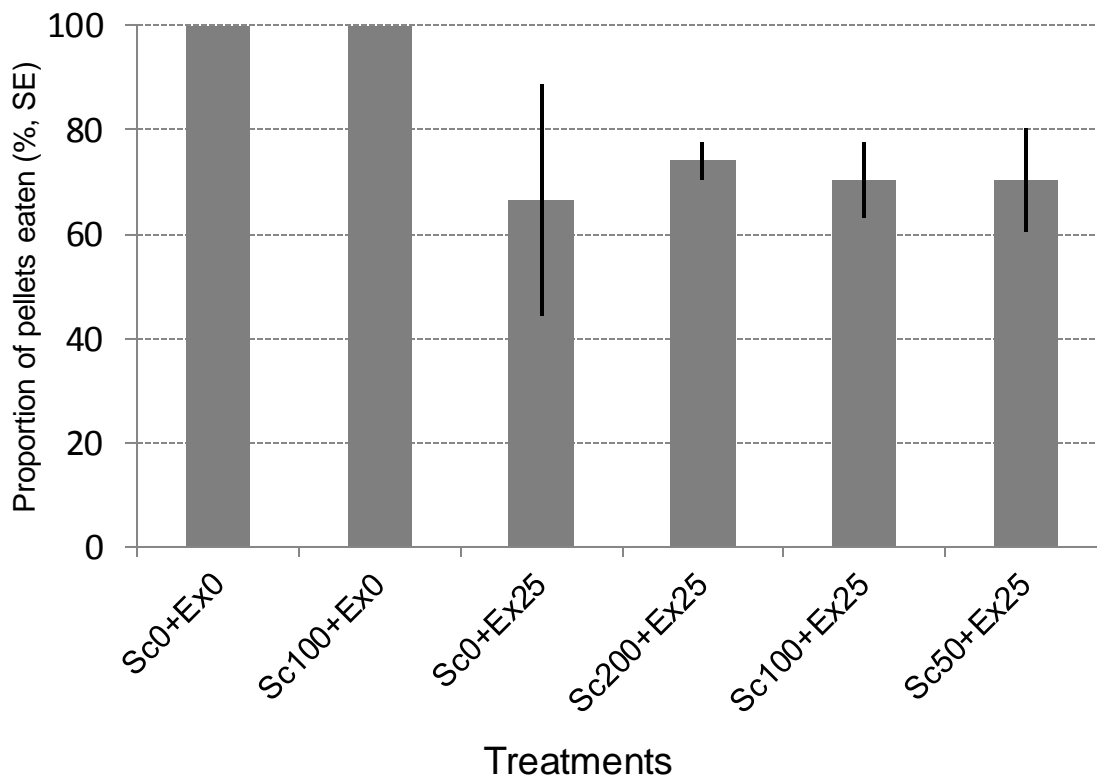
Figure 3: Proportion of pellets containing different crude extract and sclerite treatments of *Ovabunda crenata* consumed by moon wrasse fish. Sc = sclerite, Ex = *Ovabunda crenata* extract, numbers behind these abbreviations indicate the concentration of extract and sclerites of the natural concentration in percent.

Table 4: Repellence (assessed as proportion of pellets consumed) of various combinations of *Ovabunda* extracts and sclerites loaded pellets compared by Fisher's Exact test. "Extract %" = concentration of coral extract in % of natural concentration. "Fisher's p" = 2-sided p-value.

Extract (%)	Spicule (%)	Chi²	Fisher's p
25	0	8.5	0.002
0	100	0	1
25	200	5.9	0.01
25	100	7.2	0.004
25	50	7.2	0.004

Discussion

Our results show that the crude extracts from two highly abundant soft coral species in the Red Sea, *O. crenata* and *H. ghardaqensis,* strongly deter reef fishes from feeding on their polyps. This protective effect is not only detected at natural concentrations but even at 4-fold reduced concentrations, highlighting the efficiency of the involved secondary metabolites. Consequently, these soft coral species are likely to be well defended against fish consumption even if the defense metabolite concentration fluctuated to some extend among individuals, populations, life history stages or seasons. This antifeeding defense most likely contributes to the success and remarkable abundance of these soft coral species in the reefs along the Saudi Arabian Red Sea coast.

Sclerites, in contrast, did not show any deterring effect against fish predation. A negative relation between sclerite armament and chemical defense, suggestive of a defensive role of the sclerites has previously been reported by Sammarco et al. (1987) for some soft coral taxa (*Sinularia, Lemnalia, Heteroxenia*).

The similarity of the results found in both experiments, the field and laboratory assays, suggests that the secondary metabolites of xeniid soft corals are "broad-band" repellents against predation of various fishes rather than against specific species only (e.g. *T. lunare*). Xeniids are known as a rich source of terpenoids with antifouling activity (König et al. 1989; Bishara et al. 2006) or substances with potential antitumor activity (El-Gamal et al. 2005). Although, the chemical composition of the crude extracts in our study species is not yet known, the fact that they inhibited feeding by a wide variety of fish species even at concentrations substantially below natural

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concentrations indicates an impressive activity. Similar chemical anti-feeding defenses have been described for other soft coral species such as *Sinularia polydactyla, S.maxima* (Wylie and Paul 1989) and *Rhytisma fulvum fulvum* (Kelman et al. 1999). Such effective predator deterrence may be due to the combined effect of several different compounds (Van Alstyne et al. 1994), and it might therefore be rewarding in a follow-up study to assess the composition of effective metabolites, and whether they act additively or synergistically.

Although, the crude extract of both soft coral species was similarly repellent at natural concentrations, repellence decreased slightly faster with decreasing extract concentration for *H. ghardaqensis* than for *O. crenata* extracts. Concomitantly, fish seemed to learn avoiding pellets faster when they were loaded with *Ovabunda* extracts than with *Heteroxenia* extracts. Whether this was attributable to the stronger chemical activity or a more characteristic or stronger olfactory cue in *Ovabunda* extracts is not clear at the moment. It should be noted that our extraction procedure did not capture the most polar metabolites of the soft corals. Possibly, highly water-soluble cues were missed as a consequence. If not, the slightly more active repellence and the more pronounced recognition value might confer a better antifeeding protection to *Ovabunda* as compared to *Heteroxenia*.

In the field, we also observed fish behavior suggestive of learned avoidance when certain chemicals of the treatment pellets were sensed. Thus, some fishes approached the treatment pellets but then did not take a bite. In contrast to the fish in the laboratory, the natural reef population of fishes was presumably not naive. Given the abundance of the two soft coral species in these reefs, the fishes must encounter them regularly and learn how to recognize them by chemical cues. The prevalence of these highly deterrent chemical cues in soft corals is not necessarily related to toxicity, as described by La Barre et al. (1986). A capacity of fishes to use olfactory or visual cues to avoid unpalatable organisms has been suggested (Pawlik et al. 1995; Miller and Pawlik 2013).

It is conceivable that the chemical repellence is complemented by other, e.g. morphological or behavioural protective adaptations in this coral species. In both regards, the two species differ to a certain degree. The colonies of *O. crenata* species reach a total height of 3 cm, while *H. ghardaqensis* colonies can reach 12 cm in height. *Ovabunda* polyps do not show any pulsating activity, whereas the polyps of

Heteroxenia feature continuous pulsation (Gohar 1940; Reinicke 1997). Whether these traits increase or decrease the species' susceptibility to fish consumption is unknown so far.

Many xeniid species are known to release mucus upon mechanical stress (Gohar 1940; Ducklow and Mitchell 1979). If this mucus bears olfactory signals it might enhance the avoidance behaviour of reef fishes. As a further distinctive property with potential relevance to predation, *Ovabunda* in contrast to *Heteroxenia* possesses sclerites. These, however, even at double natural concentration did not affect fish feeding in the lab experiments. In contrast, the presence of calcareous sclerites in other prey species was reported to enhance the efficiency of chemical anti-feeding defences by neutralizing the digestive enzymes in the stomachs of various consumers, including fishes (Hay and Kappel 1994). Also high concentrations of sclerites (31-82% of total tissue dry weight) of some Octocorallia (*Sinularia maxima, S.polydactyla, Annella mollis*) were found to deter fish feeding (Van Alstyne et al. 1992; Puglisi et al. 2000). On the other hand, the soft coral *Rhytisma fulvum fulvum,* which harbours sclerite concentrations of almost 80% of tissue dry weight, did not deter feeding (Kelman et al. 1999). Reasons for the lack of anti-feeding activity of the *O. crenata* sclerites may be (i) that the natural (13% of coral dry weigh) and even the doubled sclerite concentration is too low to affect the predator's enzymatic functionality and/or (ii) that the sclerite size and shape may be harmless to predator fishes (Van Alstyne et al. 1992). The latter reason is underpinned by results from Ilan and Burn (2003), who found that sponge spicules deterred fish only when larger than ~250 μm. The size of *O. crenata* sclerites in this study were below 50 μm in length and the sclerite morphologies were simple flat discs of roundish to oval shape (Reinicke 1997; Halász et al. 2013). Those might therefore only play a role as structural support (Van Alstyne et al. 1992; Lewis and Von Wallis 1991). In *H. ghardaqensis,* which lack sclerites, structural support is provided by the mesoglea which is particularly strong and well-developed compared to the mesogloea of other xeniid species (Reinicke pers. comm.).

In conclusion, the chemical defence of the two xeniid species clearly prevents fish-feeding, while the sclerites, where present, seem to serve as structural support only or have other functions unrelated to defense. The high anti-feeding efficiency of the metabolites most certainly contributes to the robustness, perseverance and considerable abundance of xeniid species in the Red Sea. The chemical repellency of the soft corals may be enhanced by the capacity of the fish to learn recognizing defended prey.

Acknowledgements

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GENERAL DISCUSSION

1. Pattern of soft coral community structure

In general, the results revealed that soft corals decrease in diversity, abundance and coverage from north to south along the Saudi Arabian coastline, and also display different communities among sites and areas (Figs. 1 & 2).
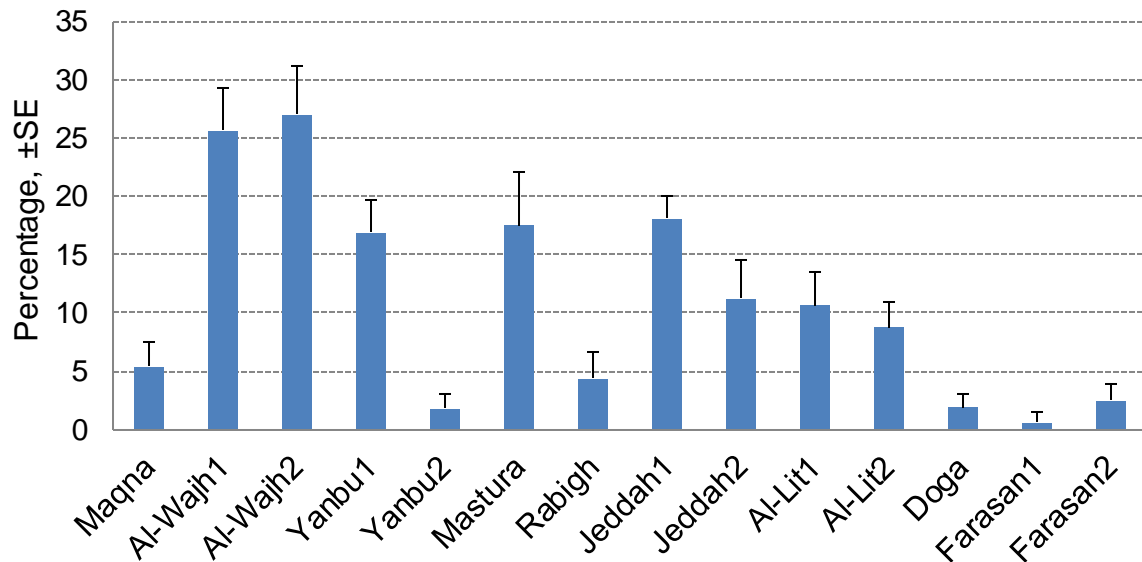

Figure 1: Soft coral cover along the Saudi Arabian Red Sea
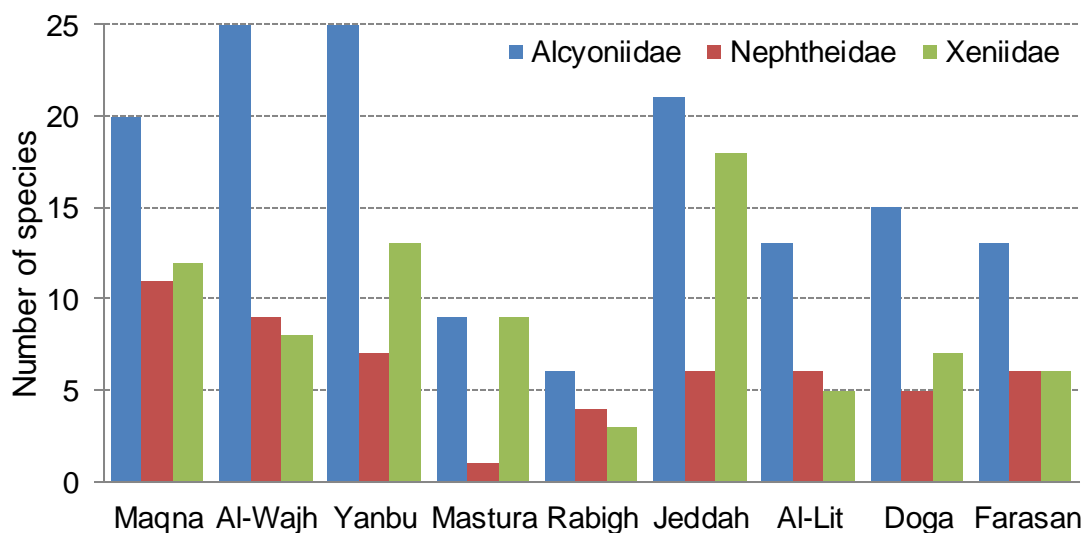(±SE: standard error obtained from replicate transects).

Figure 2: Species richness of three main families of soft corals distribution at 9 areas from north to south along the Saudi Arabian Red Sea.

Although soft coral communities showed different coverage, diversity and abundance between studied sites, a significant positive relationship was not found between high soft coral coverage and high species richness. For example, Maqna in the North had a high diversity of species (ca. 44 species) but the coverage was only 5.4%. At Jeddah, the coverage was 15% and species richness was ca. 47 species. Moreover, the relation between coverage and genera richness showed no significant difference. Fabricius and De'ath (2001) did find a relationship between soft coral genera richness and low soft coral coverage (less than 8% cover of substrate), and the authors also explained that the substitution of less tolerant by more tolerant species can cause increasing coverage but decreasing diversity. Based on the present results, this reason seems to be not valid for the Red Sea.

The most diverse soft coral communities occurred in the northern section (Maqna and Al-Wajh) with 57 species and 19 genera, representing 70% of the total soft coral species recorded in this study. These results were consistent with prior studies that revealed the importance of the northern Red Sea for soft coral diversity (Benayahu 1985; Benayahu et al. 2002), possibly related to the suitability of biotic and abiotic conditions in the North. These not only provide a reef refugium for hard corals (Fine et al. 2013) but also for soft coral communities.

Some species such as *Tubipora musica* (Tubiporidae), *Rhytisma fulvum fulvum*, *Sinularia dissecta, S. leptoclados, Sarcophyton pauciplicatum, Lobophytum pauciflorum* (Alcyoniidae), *Paralemnalia thyrsoides* (Nephtheidae), *Dendronephthya hemprichi* (Nephtheidae), *Ovabunda biseriata, Heteroxenia elizabethae* (Xeniidae) were dominant and occurred at almost all study areas, suggesting that they exhibit a wide distribution in the Red Sea and are more resilient towards the different environmental conditions along the gradient.

In contrast, species such as *Cladiella pachyclados, C. brachyclados, C. sphaerophora* and *Siphonogorgia fragilis* were only found in the northern and central sections but not in the southern section. It could be that the physical environmental conditions in the South are factors limiting their distribution. However, more studies or experiments are required to confirm the relationship between their distribution and environmental conditions.

The present study also adds new geographic records of some soft coral species such as *Sinularia loyai, S. muqeblae, S. auritum, Sarcophyton pauciplicatum*

(Alcyoniidae), *Xenia membranacea, X. actuosa X. lillieae*, and *Heteroxenia elizabethae* (Xeniidae). These results suggest that previous studies have not been sufficiently detailed over the geographic scale to detect all species present in the study region.

Based on the abundance of soft coral genera in this study, three main clusters of soft coral distribution were apparent, separating among northern, central and southern sections (see chapter 1). The northern section (Maqna and Al-Wajh) was found to have the highest number of genera (16); a result that lends support to this section being the most diverse for soft coral in the Red Sea.

In general, the dominant genera in the northern section are distributed quite equally among sites, and ranged between 5-10% coverage overall. The genus *Sinularia* was the main contributor to soft coral cover. The central section is less diverse than the northern section and the genera are distributed unequally, with 1-20% coverage. Xeniid corals are the main contributors to soft coral cover in this section. The southern section is characteristically less diverse and has less coverage when compared to the other sections. Interestingly, in contrast to coverage, the abundance of genera correlated significantly with species richness, because genera such as *Sinularia, Ovabunda, Xenia* were both abundant and the most diverse of genera on the studied reefs.

Previous studies revealed that soft coral diversity increases towards the equator or decreases both with increases in latitude and longitude (Ofwegen 2000; Benayahu et al. 2003). However, in this study the soft coral diversity decreased in the direction of the equator (from north to south in the Red Sea). This can be explained by the local conditions in the study region, as physical factors of the environment (discussed below) affect soft coral diversity distribution in the Red Sea.

Clearly, diversity and coverage are not only different between sites (near-shore and off-shore) due to variation among the environmental parameters (see chapter 2), but the soft coral coverage was also different among the off-shore sites (un-impacted sites, Fig.1) in this study. This may be explained by the patchy distribution of soft coral communities in the Red Sea and elsewhere (Tursch and Tursch 1982; Benyahu and Loya 1977; Dinesen 1983). This may be one of the reasons for the differences in soft coral cover between the un-impacted sites investigated in this study. Benayahu (1985) reported that the patchiness of soft coral distributions also changed with species

diversity. However, the changing diversity composition was not found in this study, which detected a significant relation between genera abundance and species richness but not between cover and diversity.

2. Factors impacting soft coral communities in the Saudi Arabian Red Sea

Soft coral communities, like other sessile communities, are strongly influenced by both the abiotic and biotic 'environment', the main limiting factors regulating their distribution. This study investigated the relative contribution and importance of the main physical parameters, including nutrients, slope types, depth, sediment and temperature, in structuring soft coral community distribution in the Red Sea. Any relation between dominant soft corals and water quality was also investigated.

2.1. Depth, substrate and slope conditions

As presented above, the abundance and diversity of soft corals are highest at northern reefs. There the substratum is mainly hard or solid, reefs continue down to deeper greater depths and slopes are steeper when compared to the rather flat, rubble/sand substratum and gently sloping reefs in the South.

Soft coral communities vary in diversity, composition and cover with depth (Tursch and Tursch 1982; Dinesen 1983). Previous studies have reported that soft coral species are most diverse between 5-35 m (Reinicke and Van Ofwegen 1999; Huston 1985; Riegl and Velimirov 1994; Liddell and Ohlhorst 1987). In this study, soft coral species were found to be most diverse between 5 - 25 m depth.

The depth gradient effect observed among the study sites, notably reduced soft coral diversity in shallow water, may be related to the lack of structural skeleton structure. In shallow water, where stronger wave action prevails, soft corals typically occur as small or flexible colonies (Fabricius and Alderslade 2001). Moreover, soft coral communities distributed in deeper zones may be subjected to reduced competition for space with other benthic organisms. Soft corals are known to be less successful competitors for space in comparison to stony corals and algae in reef flats of the Red Sea (Benayahu and Loya 1981). Furthermore, in this study, where the hard substratum (as reef rock or massive dead coral) was exposed without algae cover, more soft coral cover was present than in places covered by rubble, sand or silt (see

chapter 1). This suggested that the substrate condition is one of the main factors for soft coral settlement and growth in the Red Sea (Benayahu 1985).

The angle of the reef slope is another key factor affecting soft coral distribution in the Saudi Arabian Red. In the North and Central sections, reefs have characteristic steep slopes (angle of slope from $45° \sim 90°$) while in the South section the reefs are much less steep. Difference in slope morphologies between areas explained 32.6% of variation in soft coral communities in this study (Fig. 3). This is consistent with the results of Fabricius and De'ath (1997), who showed that 45% of variation in soft coral cover was explained by slope and location at Davies Reef (Great Barrier Reef).

Different soft coral communities occurred on reefs of different slope angle along the Saudi Arabian coast, consistent with the fact that soft coral genera have preferred angles of substratum. Chanmethakul et al. (2010) also found that soft coral distributions were affected by angle of substratum in the sea around India and Gulf of Thailand. Similarly Fabricius and De'ath (1997) reported that distribution of the genus *Nephthea* was related to slope angle. In this study, the genus *Nephthea* and some other genera including *Klyxum, Litophyton* and *Cladiella* were commonly found in the northern section yet were absent or rare in the other sections. The distribution of these genera in the Saudi Arabian Red Sea appear correlated with slope angle, although further investigations are required to confirm the strength of this relationship between distribution and slope.

2.2. Nutrients, sedimentation, turbidity and temperature

Nutrient concentrations not only strongly increased from the North to the South during both the winter and summer expeditions but also differed between impacted and un-impacted sites along the Saudi Arabian coast (Sawall et al. 2014). Conversely with nutrient concentrations, soft coral communities decreased in coverage, abundance and diversity along the Saudi Arabian coast from north to south, and structure of the communities also changed among sites.

The combined effect of nutrients, sedimentation and turbidity explained 52.8% of soft coral variation along the gradient, while turbidity explained 19.3%, sedimentation 13% and nutrients 49%, respectively (Fig. 3). This result showed that sedimentation and turbidity are not strongly correlated or overlapping, because the combination of turbidity and sedimentation explained 29.3% of variation in soft coral distribution. This result is similar to the result of Fabricius and De'ath (2001) that

underwater visibility (a proxy for turbidity) and sediment explained 24.5% of the variation of soft coral richness and both factors seem not to overlap each other in the Great Barrier Reef.

Sedimentation is another important parameter, as soft corals are less diverse in some sites such as Rabigh and Yanbu with high sediment deposition on the reef substrata. Conversely, Al-Wajh and Maqna have high soft coral diversity and no deposited sediment. Sedimentation also caused local loss of soft coral taxa in the Great Barrier Reef (Fabricius and De'ath 2001). The result of this study provided additional supporting information about the status of soft coral communities in the Saudi Arabian coast affected by anthropogenic activities such as petroleum production, industrial pollution and sewage.
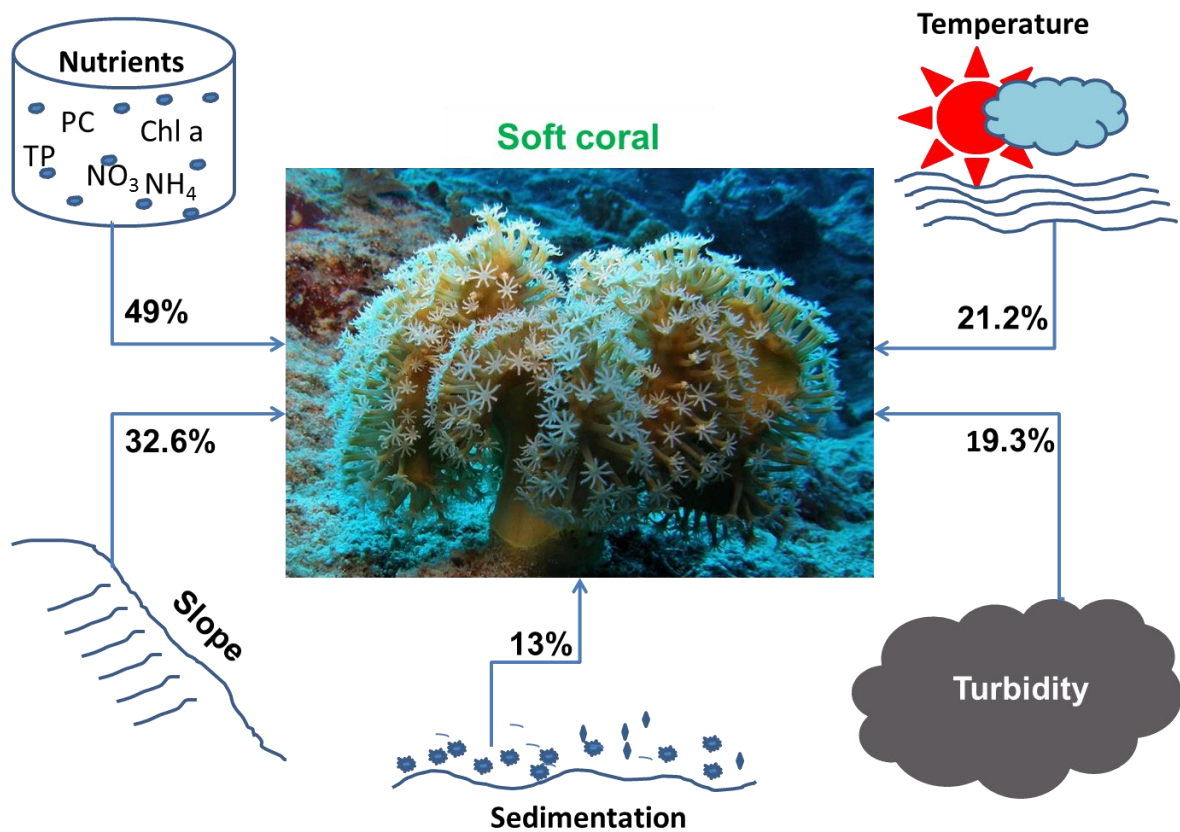
Figure 3: Proportion of variation in soft coral distribution pattern explained by parameter factors (The overall variation is 65% while total factors sum up to more than 100%, it means that some factors are correlated each other, producing overlap in variability).

Moreover, the relation between soft coral communities with nutrients and sedimentation was also reported from Madagascar (Evan et al. 2011), the Chagos Archipelago (Reinicke and van Ofwegen 1999) and the Egyptian Red Sea shores (Mohammed 2012). Clearly, the Red Sea features an extended gradient of environmental conditions, and these, along with cover and dominance of soft coral, are required to assess the shift of soft coral communities in the Red Sea. In this study, there was a strong signal of the key environmental parameters in explaining the variation of soft coral communities, as measured by diversity composition, coverage and dominance of genera along the Saudi Arabian coast. These results strongly emphasized that the environmental gradient conditions affected the soft coral distribution along the Red Sea coast.

Increasing temperature is one of the triggers of bleaching (Douglas 2003) leading to loss of symbiotic algae in the tissue of soft corals. Approximately 21% of variation of soft coral communities in the Saudi Arabian Red Sea was explained by different temperature along the gradient (Fig. 3). The genera *Sinularia, Sarcophyton* and *Lobophytum* were dominant on the southern reefs (where the temperature can reach 32°C in summer). Interestingly, Strychar et al. (2005) reported that *Sarcophyton ehrenbergi* can tolerate temperature of 34°C for more than 39 h and *Sinularia sp* can survive after long time exposure of 32°C temperature. The results of this study suggest that the genera *Sinularia, Sarcophyton* and *Lobophytum* may be more resistant in terms of thermal tolerance in the southern Red Sea, although more focused experimental studies are needed to explain the significance of temperature in controlling soft coral distribution in the Red Sea.

The xeniid communities, as described by coverage, abundance and diversity pattern, differ between near-shore (impacted sites) and off-shore reefs (un-impacted sites). Difference in the relation of xeniid communities to environmental conditions in this study is similar to previous results. These showed that the abundance and diversity of octocorals exhibit strong negative correlations with suspended particulate matter, silicate and total organic sediment contents (van Woesik et al. 1999; Fabricius and De'ath 2001; Fabricius 2005). Sawall et al. (2014) reported that significant differences among the genera abundance of hard coral communities were evident in some reefs located close to a source of nutrient pollution. Nutrients impacted both hard and soft coral communities along the Saudi Arabian Red Sea coast.

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3. Chemical defense against fish predation in xeniid species.

Xeniid communities are dominant in the Red Sea, covering up to 14% of substratum or occupying 80% of soft coral coverage in some areas in this study. Like other soft corals, the capacity of anti-predator defense is a potential contributor to the abundance of these soft coral species in the Red Sea. Such defenses include both physical and chemical deterrents to predation, with chemical deterrents ranging from outright toxicity to unpalatability.

Crude extracts of *Ovabunda crenata* and *Heteroxenia ghardaqensis* strongly deterred reef fishes even when the natural concentrations were reduced 4-fold. This suggests that the chemical defenses of secondary metabolites still strongly affect predatory fishes, even allowing for significant natural fluctuations in concentration of chemical compounds in response to changing environmental conditions or other stimuli. Moreover, the strong anti-feeding response, even at low concentrations of crude extract, may compensate for the apparent lack of physical defense from sclerites of *Heteroxenia ghardaqensis* species.

Although not tested in the present study, the natural concentration of defensive chemicals also may vary between parts of colonies, such as polyp and stalk, in the same soft coral species (Van Alstyne et al. 1994; Harwell and Fenical 1989). Natural chemical concentration may be higher in the polyp than other colony parts, because polyps are more exposed to predation in closely adjacent stands of xeniid colonies, which may consist of numerous conspecific individuals occurring side by side on the reef (Gohar 1940). This growth mode can afford some protection to the stalk from carnivorous fishes, which may thus have lower levels of chemical (and other) defenses. Conversely, the polyp parts that are extended into the water column may need a high defense chemical concentration for their protection.

The two xeniid species tested here differed in morphology, including total height of colony, size of tentacles, pulsation of tentacles and the absence/presence of sclerites. The pulsation of polyps plays a role in enhancing photosynthetic respiration of xeniid species (Kremien et al. 2013). However, whether the pulsation of polyps could decrease or increase the attraction of fishes to attack the corals and consume the polyp tissue is presently unknown. The presence of high chemical defense against predatory fishes in both species used in this study suggests that there is no relation

between morphology and chemical defense. However, more studies are needed to confirm this observation.

Previous studies have revealed that some xeniids exhibit marked toxicity (Bakus 1981), or ranged from moderately toxic to non-toxic (Coll et al. 1982; Sammarco et al. 1987). Although the toxicity of chemical defense was not specifically tested for the two xeniid species *Ovabunda crenata* and *Heteroxenia ghardaqensis* in this study, it is likely that secondary metabolites in both species lack toxicity. The reason for this proposal is that the behaviour of generalist fishes in the field and moon wrasse in the laboratory did not change after consuming amounts of pellets with added chemical extract (the fish behavior after feeding observed following Coll et al. 1982). Possible reasons for apparent lack of toxicity in both species may be the high metabolic costs of producing toxins.

CONCLUSIONS

Briefly, this thesis provides the first assessment of the status of soft coral communities, including diversity, abundance and cover, from north to south of the Saudi Arabian coastline. This region has a strong latitudinal gradient in several key environmental parameters. The diversity, abundance and cover of soft coral communities strongly varied along this latitudinal environmental gradient, and also changed between near shore (impacted reefs) and off shore (un-impacted reefs).

The major parameters influencing community structure and distribution were also reviewed and examined in the field. The study found that each of the main parameters, including substrate, depth, slope, temperature, nutrients, sedimentation and turbidity, are important determinants of soft coral distribution in the Red Sea, at both local and regional scales. The key parameters explained 65% of the variation in soft coral communities from north to south.

Chemical defense against predatory fishes is one of the reasons why two species of xeniid soft coral exhibit robustness, perseverance and abundance in the Red Sea. Conversely, the role of sclerites in xeniid species, where present, seems to serve as structural support only, or perform other functions unrelated to defense.

LOOKING AHEAD

Soft coral communities in the Red Sea are among the most diverse in the tropical regions of the world, a finding confirmed in this study. In addition to the community structuring parameters examined, other abiotic and biotic factors may also be important. These include light and oceanographic current condition, wave action, competition between soft coral and other organisms on coral reef, other forms of predation, and potentially other community structuring forces.

Chemical defense against predation by xeniid soft corals in the Saudi Arabian Red Sea was demonstrated for the first time. However, this study was limited to the crude chemical extract of xeniids, and further research should be conducted to

determine which single chemical compound or combined compounds play an important role in affecting predator fishes. Moreover, such research should examine variation in secondary metabolism between seasons and along gradients. This will increase the knowledge of chemical defense of predators of xeniid soft corals, contributing to their dominance in the Red Sea.

Samples of some species belonging to families Alcyoniidae and Nephtheidae were not able to be identified in this study. These may be new species (or at least newly recorded for the zoogeographical region). These samples need systematic verification, potentially including genetic analyses, by taxonomic specialists to confirm their identities as either undescribed or new records in the Red Sea.

Global warming leads to rising sea temperatures, while acidification of the oceans and increasing anthropogenic activities will cause more impacts and pressure on coral reef ecosystems in the near future. More studies at local, regional and global level are needed to understand the impacts on coral reefs and provide the solution to protect the coral reefs.

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Eidesstattliche Erklärung

Hiermit bestätige ich, dass die vorliegende Arbeit mit dem Titel "***Soft coral (Octocorallia: Alcyonacea) diversity and distribution along latitudinal environmental gradient and the role of their chemical defense against predatory fish in the Red Sea***" von mir selbständig angefertigt wurde.

Ich habe keine als die angegebenen Hilfsmittel und Quellen verwendet und die Arbeit unter Einhaltung der Regeln guter wissenschaftlicher Praxis der Deutschen Forschungsgemeinschaft erstellt.

Die Arbeit wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren.

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