INTERNATIONAL JOURNAL OF ENVIRONMENTAL SCIENCE AND ENGINEERING (IJESE)
Vol. 5: 69- 80 (2014)
http://www.elac.pvamu.edu/pages/5779.asp,
Prairie View A&M University, Texas, USA

Distribution of *Symbiodinium* in corals of the Red Sea, Egypt

Muhammad Y. Dosoky[1], Fedekar F. Madkour[1,*], Mahmoud H. Hanafy[2] and Mohamed I. Ahmed[2]
1-Department of Marine Science, Faculty of Science, Port Said University, Port Said- 42526, Egypt
2- Department of Marine Science, Faculty of Science, Suez Canal University, Ismailia-41522, Egypt

ARTICLE INFO
Article History
Received: Sept. 15, 2014
Accepted: Oct. 25, 2014
Available online: Feb. 2015

Keywords:
Symbiodinium,
Red Sea
Total chlorophyll
Bathymetric distribution
Host variations.

ABSTRACT
Coral-*Symbiodinium* symbiosis is considered keystone component for coral reef ecosystem. To study changes in *Symbiodinium* parameters; *i.e*. density and chlorophyll content, along one of the most unique reefs at Egyptian coast of the Red Sea, five common species of scleractinian corals were collected from inshore and offshore reefs during 2012-2013. Results showed heterogeneous geographic patternin *Symbiodinium* parameters. Coral colonies of surface water were characterized by higher *Symbiodinium* densities than deeper ones. The current study also showed that pocilloporid corals host lower densities of *Symbiodinium* than acroporids. In oligotrophic waters, high densities of *Symbiodinium* in colonies grow at surface water reflects dependency of hosts on photosynthates produced by symbiont. Differences between coral hosts in densities of harbored *Symbiodinium* may relate to symbiont genetic identity. So, further studies are required to identify genetic affiliation of *Symbiodinium* clades associated with Red Sea corals. In addition, understanding of dynamics of coral's endosymbionts is restricted to resolving physiological differences of *Symbiodinium* within different host microbiomes.

1. INTRODUCTION
Although corals have wide biogeographic range of distribution from tropical to temperate regions, only corals between 30°N and 30°S are known to build reefs (Barnes and Hughes, 1999). Coral reefs that represent the largest bioconstructions had been primarily formed as a result of coral-*Symbiodinium*symbiosis (Allemand *et al.*, 2011). The process of coral calcification is controlled mainly by these endosymbionts (Kawaguti and Sakumoto, 1948). On the other hand, corals derive nutritional benefits while hosting *Symbiodinium* (Muscatine, 1990). In healthy corals and under normal environmental conditions, each endodermal cell of coral's polyp usually hosts one or more *Symbiodinium* cell(s) to reach densities of 0.5-5 × 10^6 cells/cm^2(Muscatine and Pool, 1979; Hoegh-Guldberg and Smith, 1989). However, densities of *Symbiodinium* are temporally fluctuated due to variation in environmental factors; e.g. seawater temperature, light intensity, solar radiation, and nutrients (Fitt *et al.*, 2001).

*Corresponding author: fedekarmadkour@ymail.com
ISSN 2156-7530

Increasing seawater temperature by a magnitude of 2°C above thermal tolerance limits of corals can induce partial or complete loss of *Symbiodinium* content (Glynn and D'Croz, 1990; Fitt and Warner, 1995).

The loss of *Symbiodinium* and/or their photosynthetic pigments synchronized with the presence of environmental stress is known as coral bleaching (Fitt *et al.*, 2001). In addition of being indicator of coral healthiness, *Symbiodinium* density is an indicator of coral biomass. So, increasing *Symbiodinium* density is an indicator of increasing coral tissue biomass (Fitt *et al.*, 2000).Other secondary factors, e.g. salinity, starvation, osmotic shock and Photosynthetic Active Radiation (PAR), may also affect the density of *Symbiodinium*(Titlyanov *et al.*, 2000; 2001).

Along depth gradient, scleractinian corals are distributed within photic zone (Veron, 2000). Light intensity is considered an important factor upon which *Symbiodinium* density depends. Increasing or decreasing light intensity, however, depends on water depth, turbidity, or host orientation. Accordingly, light intensity along reef tends to affect *Symbiodinium* density and their photosynthetic pigment concentration (Nir *et al.*, 2011). Adjusting photosynthetic pigments and/or abundance of coral endosymbionts along depth gradient is considered a strategy of coral-algal photoacclimation (Hennige *et al.*, 2008).Photoacclimation of corals involves changes in quality and quantity in photosynthetic pigments (Titlyanov, 1981). However, among photosynthetic pigments, chl*a* is considered a good indicator for all photosynthetic pigments changes (Frade *et al.*, 2008).

In most cases, different species of corals host genetically different *Symbiodinium* types (Coffroth and Santos, 2005). These types differ in their physiological responses to environmental changes. Consequently, corals harbor the most physiologically compatible and stressful tolerant types (Stat *et al.*, 2008; Stat and Gates, 2010). The physiological and the genetic differences between *Symbiodinium* types are not the only differences between coral's endosymbionts. Symbiont cell size also affects density of *Symbiodinium* within a particular host (Winters *et al.*, 2009). However, different coral species of different cell size may affect density of endosymbionts (Frade *et al.*, 2008). Most studies that focused on *Symbiodinium* photoadaptation were mainly based on experimental investigations. The main objective of the present study is to illustrate *in situ* changes in coral's endosymbiotic system along Egyptian coast of the Red Sea by investigating changes indensity and chlorophyll contentof *Symbiodinium*in different common coral species with depth.

2. MATERIAL AND METHODS

2.1. Study sites and coral samples collection

Samples of corals were collected from six sites along the Red Sea as represented in Figure 1, during 2012-2013. In the southern Gulf of Aqaba, coral samples were collected from two inshore reefs; Solomon Reef at Dahab (28° 29' 10" N and 34° 30' 52" E) and Marsa Ghozlani at RasMuhammad (27° 49' 20" N and 34° 15' 58" E). In the proper Red Sea, samples were collected from Marsa Samadai which is considered an inshore reef at Marsa Alam (25° 00' 50" N and 34° 55' 37" E). The other three sites were selected to represent offshore reefs. These sites were Fanous Reef at Hurghada (27° 15' 57" N and 33° 53' 3.0" E), Zabargad Island (23° 35' 51" N and 36° 12' 31" E), and Rocky Island (23° 33' 47" N and 36° 14' 33" E).

Among coral species, *Acropora-digitifera*, *Acroporahumilis*, *Acroporap-haraonis*, *Stylophorapistillata*, and *Pocilloporaverrucosa* were selected to be sampled based on their wide geographic distribution along the Red Sea. These species were identified following Veron (2000). However, *A. digitifera* from surface water of Rocky Island and *A. humilis* from

deep water of Zabargad Island were not collected.

To study bathymetric pattern of *Symbiodinium* abundance and chlorophyll content, coral fragments at Solomon Reef, Marsa Ghozlani, and Zabargad Island were collected by SCUBA from three depth ranges; surface (0-5m), mid (5-10m) and deep water (10-15m) during summer.

Collected coral samples were used to estimate *Symbiodinium* abundance and chlorophyll content except that collected from Marsa Samadai where *Symbiodinium* abundance were estimated only.

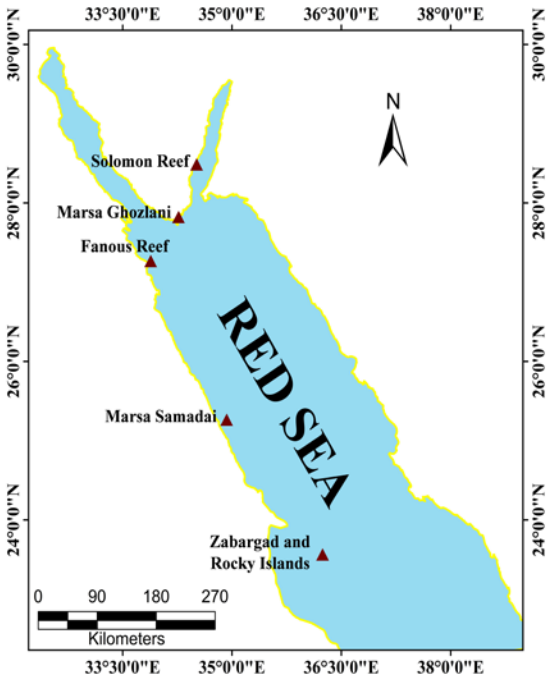

Fig. 1: Study sites at the Red Sea.

2.2 Isolation of *Symbiodinium* cells

The apical parts of the collected coral fragments were broken to avoid within branch variability (Anthony *et al.*, 2007). For each coral fragment, soft tissue was completely isolated in plastic bag by air-brushing. The resultant slurry was homogenized then centrifuged at 10,000 rpm for 15 min. The resultant *Symbiodinium* pellet was suspended into 20 ml of distilled water and well homogenized. About 2 ml of this suspension were further centrifuged at 10,000 rpm for 15 min. The supernatant was discarded, while *Symbiodinium* pellet was preserved at -20°C under dark conditions for chlorophyll analysis. For cell counting, the remaining 18 ml of *Symbiodinium* suspension were preserved in 4% formalin.

2.3 *Symbiodinium* density estimation

After tissue isolation, the surface area of hard skeleton of each coral fragment was estimated according to aluminum foil method (Marsh, 1970). Three subsamples of *Symbiodinium* suspension were loaded on haemocytometer slide. Cells of *Symbiodinium* were counted under 40x compound microscope. Average number of *Symbiodinium* cells was normalized to coral fragment surface area and expressed as number of cells per cm^2.

2.4 Determination of chlorophyll concentration

Total chlorophyll of *Symbiodinium* pellets were extracted in 5 ml acetone (90%). To ensure complete extraction, pellets in acetone were homogenized and incubated overnight at 4°C under dark conditions. Absorbances of samples as well as acetone blank were determined using spectrophotometer (Spectronic 601) at 630,

664, and 750nm. Concentrations of chlorophyll *a* and *c*, however, were determined following Arar (1997) using the following equations:

Chl*a* (µg/ml) = (11.85 E_{664}) - (0.08 E_{630})

Chl*c* (µg/ml) = (24.52 E_{630}) - (1.67 E_{664})

Where; E_{630}= ($A_{630sample}$-$A_{630blank}$) - ($A_{750sample}$-$A_{750blank}$)

E_{664} = ($A_{664sample}$-$A_{664blank}$) - ($A_{750sample}$-$A_{750blank}$)

Chlorophyll *a* and *c* content per cell (pg/cell) were estimated by dividing Chl*a* and *c* (µg/ml) by number of cells per 1 ml, respectively.

2.5 Statistical analysis

Data of density and chlorophyll content of *Symbiodinium* were represented as (Mean ± SE) and analyzed using SPSS (V.19). Appropriate statistical tests (ANOVA and Pearson correlation) were performed upon original or transformed data. For data of abnormal distribution, even after transformation, Kruskal-Wallis Test was used to analyze variance.

3. RESULTS

3.1. Spatial distribution

Spatial distribution of *Symbiodinium* density was derived from coral samples collected at surface water of all sites in summer. The average density of *Symbiodinium* (*n*= 91) along all sites was (0.57±0.04) × 10^6 cell/cm^2. The maximum density of *Symbiodinium* was recorded at Fanous Reef [(0.92±0.08) × 10^6 cell/cm^2; *n*=24]. The density of *Symbiodinium* displayed significant difference between sites ($p<0.05$) with higher densities in northern sites (Solomon Reef, Marsa Ghozlani and Fanous Reef) than southern sites, except Rocky Island (*n*=13). This difference was mainly due to Fanous Reef that varied significantly ($p<0.05$) from all other sites except Rocky Island. However, differences between other sites were not significant except that between Rocky Island and both of Zabargad Island (*n*=12) and Marsa Samadai. Although the large distance between inshore sites, no significant differences in *Symbiodinium* densities were observed between them. On contrast, the difference in *Symbiodinium* density was significant between offshore sites (Zabargad and Rocky Islands) which located within narrow geographical range.

Considering host identity, different species of corals showed significant difference ($p<0.05$) in *Symbiodinium* densities. This difference was exclusively originated from difference between *P. verrucosa* and both of *A. digitifera* and *A. humilis*. *A. digitifera* and *A. humilis* at Fanous Reef and *S. pistillata* at Rocky Island were found to host the highest densities of *Symbiodinium* which exceeded one million cells per cm^2. On the other hand, *P. verrucosa* showed the lowest density of *Symbiodinium* at all sites, except Zabargad and Rocky Islands where *A. pharaonis* hosted the lowest densities (Fig. 2). It is noteworthy that Marsa Samadai was the only site which had the five coral species hosted lower densities of *Symbiodinium* cells [(0.28±0.04) ×10^6 cell/cm^2].

Total chlorophyll estimatedper *Symbiodinium* cell (*n*=78) was higher in southern reefs (Zabargad and Rocky reefs) than that of northern ones, with the lowest chlorophyll content (0.36 ± 0.02 pg/cell) in samples collected from FanousReef (Fig. 3). Chlorophyll *a* or *c* per cell illustrated the same pattern which displayed by total chlorophyll with significant difference ($p<0.05$) between sites, especially at Fanous Reef.

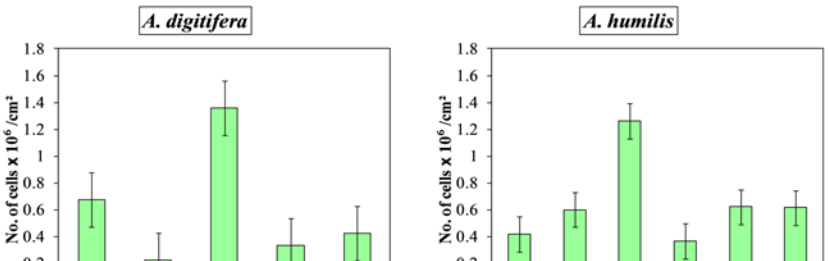

Fig. 2: Density of *Symbiodinium* (No. of cells × 10^6 /cm^2) in five studied species of corals at each site. (Note: *A. digitifera* was not collected from Rocky Island).

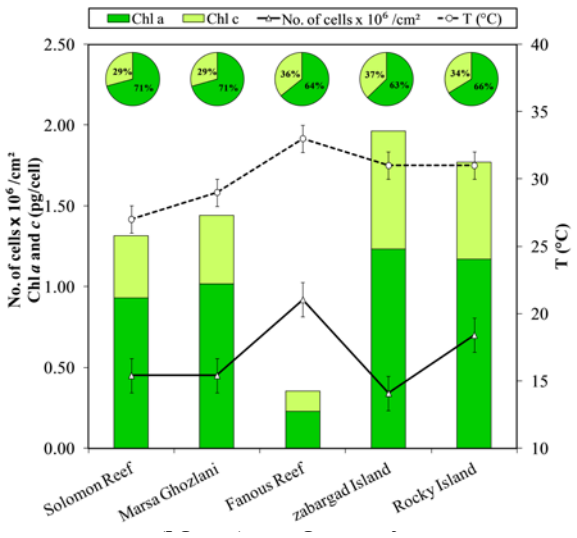

Fig. 3: Spatial distribution sity (No. of cells × 10^6 /cm^2). Top pie charts represent chl*a*/*c* ratio per *Symbiodinium* cell at each site.

3.2. Bathymetric distribution

Overall mean density of *Symbiodinium* at three depth ranges in five studied coral species collected from three sites (Solomon Reef, Marsa Ghozlani, and Zabargad Island) during summer was [(0.33±0.02)×10^6 cell/cm^2; *n*=115]. Generally, species of corals collected from surface water harbored higher densities of *Symbiodinium* than that recorded at mid or deep water. However, the variation of *Symbiodinium* density between surface and mid water or between mid and deep water was not significant. Only corals from surface were found to host significant higher densities ($p<0.05$) of *Symbiodinium* [(0.42±0.04)×10^6cell/cm^2; *n*=40] than that of deep water [(0.26±0.02) ×10^6cell/cm^2; *n*=42]. It was also noted that there is no significant difference in *Symbiodinium* densities (Two Way ANOVA; $p>0.05$) between Solomon Reef, Marsa Ghozlani, and Zabargad Island at three depth ranges (Fig. 4).

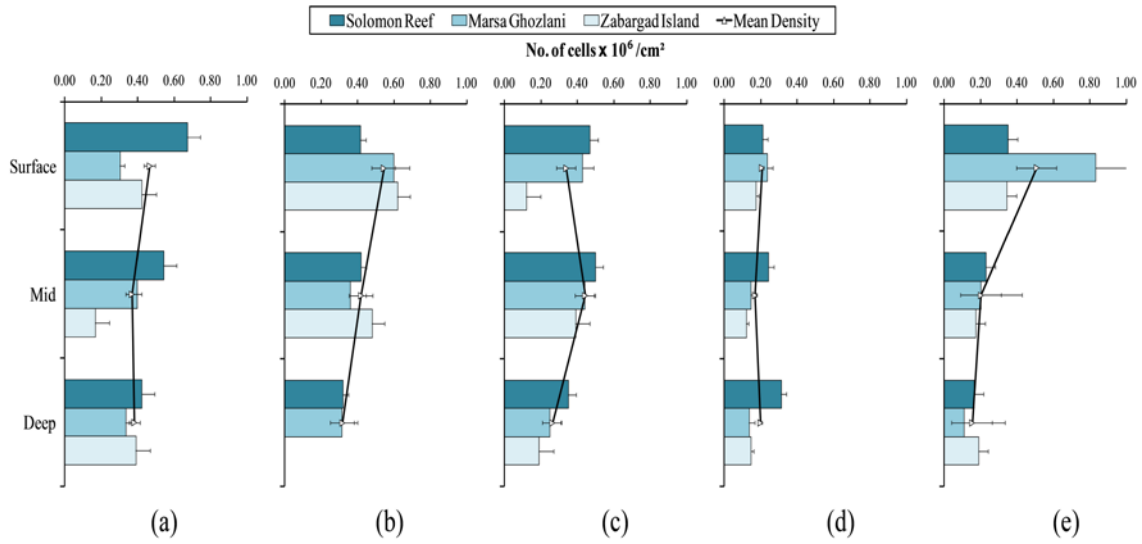

Fig. 4: Density of *Symbiodinium* (No. of cells × 10^6 /cm^2) with corresponding general trend in (a) *A. digitifera*, (b) *A. humilis*, (c) *A. pharaonis*, (d) *P. verrucosa*, and (e) *S. pistillata* along three depth ranges (surface, mid, and deep water) at Solomon Reef, Marsa Ghozlani, and Zabargad Island. *A. humilis* from deep water at Zabargad Island was not collected.

Total chlorophyll content and chl*a*/*c* ratio per *Symbiodinium* cell (*n*=105) obeyed the same pattern that displayed by density, giving non-significant gradual decrease ($p>0.05$) from surface to deep water (Fig. 5). Althoughchl*a* per cell displayed insignificant decrease with depth, chl*c* decreased significantly ($p<0.05$). Densities of *Symbiodinium* at three depth ranges showed insignificant correlation with total chlorophyll;chl*a*, chl*c*, and chl*a*/*c* ratio ($p>0.05$; r_p= -0.18, -0.17, -0.17, and 0.03; respectively).

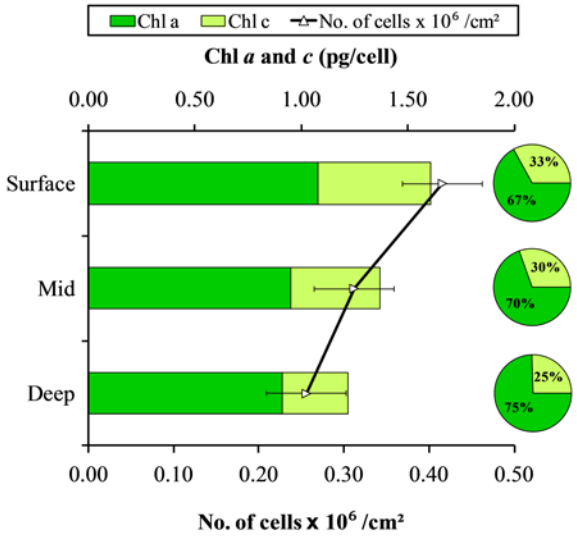

Fig. 5: Bathymetric pattern of chlorophyll per *Symbiodinium* cell (pg/cell) along with pattern of *Symbiodinium* density (No. of cells × 10^6 /cm^2).Right hand pie charts represent chl*a*/*c* ratio at each depth.

3.3 Host variation

Regardless variability in *Symbiodinium* density originated as a function of different sites or depths; there was significant variation ($p< 0.05$) between studied coral species (n=216). This variation was mostly obvious between acroporid and pocilloporid corals. Generally, acroporids (*A. digitifera*, *A. humilis*, and *A. pharaonis*) were found to host higher symbionts density than that of pocilloporid corals (*P. verrucosa*and *S. pistillata*) (Fig. 6). *P. verrucosa* was found to host the lowest number of *Symbiodinium* [(0.32±0.04) × 10^6 cells/cm^2; n=47].

There was no significant difference in chlorophyll content between host species ($p>0.48$; n=187). However, *A. humilis* was the only species that hosted *Symbiodinium* cells containing the highest levels of photosynthetic pigments. It was also noted that, *Symbiodinium* of three acroporid species had the same chl*a*/*c* ratio. *P. verrucosa* and *S. pistillata* were found to host lower density of *Symbiodinium* with high chl*a* and*c* contents per cell.

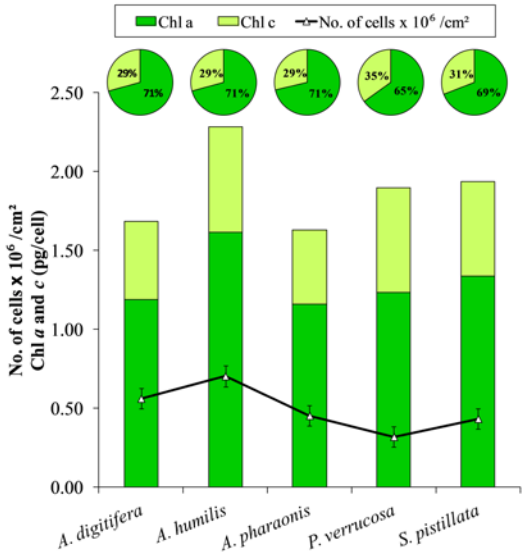

Fig. 6: Chlorophyll *a* and *c* content per *Symbiodinium* cell (pg/cell) along with *Symbiodinium* density (No. of cells × 10^6 /cm^2) in different host species. Top pie charts represents chl*a*/ *c* in each coral species.

4. DISCUSSION

Symbiosis represents essential component in coral reef ecosystem. However, coral-*Symbiodinium* relationshipis considered the most important relationship for coral reefs. Recently, monitoring changes in endosymbiotic systems of corals is of great concern (Mieog *et al.*, 2009; Winters *et al.*, 2009; Costa *et al.*, 2013). This importance originated primarily from consequences of such changes on corals healthiness.

The present study showed irregular geographic variation in *Symbiodinium* density and chlorophyll content along Egyptian coast of the Red Sea. Irregularity in spatial distribution of *Symbiodinium* abundance was explained by Baker *et al.* (2008) as a result of fluctuations in environmental conditions, differences in reef complexity, and background adaptive history of coral hosts. In our case, spatial variability was greatly linked to the distance of the reef from the coast where offshore reefs (Fanous Reef and Rocky Island) characterized by corals that harbor higher densities of *Symbiodinium* than inshore reefs (Solomon Reef, Marsa Ghozlani, and Marsa Samadai). The same distribution pattern of *Symbiodinium* density along Red Sea was previously noticed by Amer (2004) who attributed this distribution to the difference in water transparency between inshore and offshore reefs. According toRiegl (2003), the low effect of 2002 mass bleaching event on offshore reefs at Arabian Gulf might be due to efficient and continuous water circulation that dissipate influence of heat stress. Accordingly, water currents at offshore reefs act as a favorable condition that increase reef resilience even at high temperature by delocalize heat stress and eliminating toxic oxygen radicals produced by *Symbiodinium*, and consequently motivate coral's endosymbionts proliferation (Nakamura and van Woesik, 2001; Nakamura *et al.*, 2003; Baker *et al.*, 2008).

Regarding the variability in *Symbiodinium* density with depth, results showed no significant differences between surface (0-5m) and mid water (5-10m) or between mid and deep water (10-15m), which could be due to the narrow depth range with which differences in environmental conditions are not apparent; e.g. variation in light intensity. Otherwise, significant decrease in *Symbiodinium* density was noticed between surface (0-5m) and deep water (10-15m). Our results are in agreement with many field studies (e.g. Fitt *et al.*, 2000;Shu *et al.*, 2008). However, decreasing of *Symbiodinium* abundance from surface to deep water is not a common bathymetric pattern, such that many previous studies recorded higher densities of *Symbiodinium* in coral colonies at deep water than shallower relatives (Drew, 1972;Dustan, 1979;Battey and Porter, 1988;Kaiser *et al.*, 1993;Nir *et al.*, 2011). Recently, Al-Hammady (2013) reported that density of *Symbiodinium* in *Acroporahemprichii* decreased along depth gradient from reef flat to 25m south of Al-Qusier in the Red Sea. Such similar bathymetric pattern to the current study suggests that decrease in *Symbiodinium* density along with depth may be a common distribution pattern in corals inhabiting Red Sea.

Some experimental studies conducted that the bathymetric pattern of *Symbiodinium* abundance may be controlled by some physiological aspects such as growth, respiration, and metabolic rates of the host (Dustan, 1979;Lough and Barnes, 1992). They mentioned that corals at surface water grow faster than deeper ones. At such highly dynamic surface water, high growth rate of the host is paralleled with high respiration rate (Dustan, 1982; McCloskey and Muscatine, 1984). Additionally, compared with deep water, coral colonies at surface water are exposed to higher sea surface temperature which increases the metabolic rate of the host (Howe and Marshall, 2001). As a consequence, corals at the surface may require harboring higher densities of *Symbiodinium* to maintain high growth rate

or at least to compensate loss of energy in respiration and metabolic activities.

Cell size of symbiont in the same host at different depths is one of factors cause variation of *Symbiodinium* along with depth. Winters *et al.* (2009) indicated that *Symbiodinium* cells isolated from *S. pistillata*, collected from northern Red Sea, at surface water were smaller than those at deeper one. Reduction in cell size of symbiont may increase the capacity of host cell to harbor high number of endosymbionts (Jones and Yellowlees, 1997). This may explain the high densities of *Symbiodinium* at surface water recorded by the present study.

It is known that corals have the ability to photoacclimatize to different levels of Photosynthetic Active Radiation (PAR) by changing in density, photosynthetic pigments of endosymbionts and colony morphology (Baker *et al.*, 2008;Kuguru *et al.*, 2010). Along northern Red Sea, coral reef ecosystems are highly oligotrophic, which enables coral colonies at 80-120 m to receive sufficient light for phototrophic feeding (Acker *et al.*, 2008;Mass *et al.*, 2010). Accordingly, *Symbiodinium* cells at 15m depth can harvest sufficient light for photosynthesis. This may interpret the insignificant change in photosynthetic content per *Symbiodinium* cell along depth gradient in the current study. In coincidence to our results, Bhagooli (2003)suggested that insignificant differences of photosynthetic parameters of *Symbiodinium* in *Montiporacapitata* colonies collected from low and high light environments indicate sufficient light availability for photosynthetic performance at both environments. In addition, no correlation between density and chlorophyll content per *Symbiodinium* cell at different depths were recorded in the current study. This means that self shading due to density of cells does not affect chlorophyll content per cell along depth (Muscatine *et al.*, 1989).

The present results indicated that pocilloporid corals hosted significantly lower densities of *Symbiodinium* than acroporid species at spatial and temporal scales. In accordance with our results, the study ofAmer (2004) in the southern Gulf of Aqaba revealed that *S. pistillata* and *P. verrucosa* harbored lower densities of *Symbiodinium* than *A. humilis*. In contrast, Selim (2007) recorded that *S. pistillata* hosted higher *Symbiodinium* density than *Acropora tenuis*, while *Pocilloporadamicornis* hosted the lowest densities at Hurghada. Such difference between coral species may be explained on the basis of differences in genotypic identity, flexibility and specificity of *Symbiodinium* as well as phenotypic plasticity of host. Different coral species are known to host different *Symbiodinium* genotypes (Coffroth and Santos, 2005). This wide genetic diversity of *Symbiodinium* is usually associated with wide acclimation responses to environmental stressors (Baker *et al.*, 2004). On the other hand, the insignificant difference in photosynthetic pigments per *Symbiodinium* cell in different coral species is resulted from that all species of corals at specific location, depth, and season are mostly exposed to similar environmental factors.

Conclusively, the current study indicates that endosymbiont dynamics in scleractinian corals may be specific to local or regional scales. Abundance of *Symbiodinium* attained similar bathymetric patterns at both Gulf of Aqaba and Red Sea proper. Changes in *Symbiodinium* abundance may be more flexible than changes in photosynthetic parameters. Linking such dynamics with environmental parameters, however, may increase our understanding of adaptive responses of Red Sea corals to factors affecting their healthiness. Also, further studies are required to resolve genetic diversity of *Symbiodinium* along the Egyptian coasts of Red Sea.

5. ACKNOWLEDGEMENT

This study was funded and sponsored by Hurghada Environmental Protection and Conservation Association (HEPCA) as a part

of M.Sc. scholarship in Coral Reef Restoration.

6. REFERNCES

Acker, J.; Leptoukh, G.; Shen, S.; Zhu, T. and Kempler, S (2008). Remotely-sensed chlorophyll *a* observations of the northern Red Sea indicate seasonal variability and influence of coastal reefs. J. Mar. Syst., 69 (3): 191-204.

Al-Hammady, M. A. M (2013). The effect of zooxanthellae availability on the rates of skeletal growth in the Red Sea coral *Acropora hemprichii*. Egypt. J. Aquat. Res., 39 (3): 177-183.

Allemand, D.; Tambutté, É.; Zoccola, D. and Tambutté, S(2011). Coral calcification, cells to reefs. *In:* Dubinsky, Z. and Stambler, N. (eds.) Coral Reefs: An Ecosystem in Transition. Springer, 119-150.

Amer, M. A (2004). The role of zooplankton and water quality on some biological and ecological aspects of corals along the Egyptian Red Sea coast. Ph. D. Thesis, Suez Canal Univ. 293 pp.

Anthony, K.; Connolly, S. R. and Hoegh-Guldberg, O (2007). Bleaching, energetics, and coral mortality risk: Effects of temperature, light, and sediment regime. Limnol. Oceanogr., 52 (2): 716-726.

Arar, E. J (1997). In vitro determination of Chlorophylls *a*, *b*, *c*1+*c*2, and phaeopigments in marine and freshwater algae by visible spectrophotometry. Method 446.0. National Exposure Research Laboratory, Office of Research and Development, U.S. Environmental Protection agency, Cincinnati, Ohio., 25 pp.

Baker, A. C.; Glynn, P. W. and Riegl, B (2008). Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. Estuarine Coastal Shelf Sci., 80 (4): 435-471.

Baker, A. C.; Starger, C. J.; McClanahan, T. R. and Glynn, P. W (2004). Corals' adaptive response to climate change. Nature, 430:741-741.

Barnes, R. and Hughes, R(1999). An introduction to marine ecology. Blackwell Science Inc, 117-141.

Battey, J. and Porter, J. W (1988). Photoadaptation as a whole organism response in *Montastrea annularis*. Proc. 4th Int. Coral Reef Symp, 3:79-88.

Bhagooli, R (2003). Preliminary investigation on the effect of light on coral surface morphology and endosymbiont type in Montipora capitata. Hawaii Institute of Marine Biology. University of Hawaii, Technical Report, 43: 14-24.

Coffroth, M. A. and Santos, S. R (2005). Genetic diversity of symbiotic dinoflagellates in the genus *Symbiodinium*. Protist, 156:19-34.

Costa, C. F.; Sassi, R. and Gorlach-Lira, K (2013). Seasonal changes in zooxanthellae harbored by zoanthids (Cnidaria, Zoanthidea) from coastal reefs in northeastern Brazil. PANAMJAS, 8 (4): 253-264.

Drew, E. A (1972). The biology and physiology of alga-invertebrates symbioses. II. The density of symbiotic algal cells in a number of hermatypic hard corals and alcyonarians from various depths. J. Exp. Mar. Biol. Ecol., 9 (1): 71-75.

Dustan, P (1979). Distribution of zooxanthellae and photosynthetic chloroplast pigments of the reef-building coral *Montastrea annularis* Ellis and Solander in relation to depth on a West Indian coral reef. Bull. Mar. Sci., 29 (1): 79-95.

Dustan, P (1982). Depth-dependent photoadaption by zooxanthellae of the reef coral *Montastrea annularis*. Mar. Biol., 68 (3): 253-264.

Fitt, W. K.; Brown, B. E.; Warner, M. E. and Dunne, R. P (2001). Coral bleaching: interpretation of thermal

tolerance limits and thermal thresholds in tropical corals. Coral Reefs, 20 (1): 51-65.

Fitt, W. K.; McFarland, F. K.; Warner, M. E. and Chilcoat, G. C (2000). Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. Limnol. Oceanogr., 45 (3): 677–685.

Fitt, W. K. and Warner, M. E (1995). Bleaching patterns of four species of Caribbean reef corals. Biol. Bull., 189 (3): 298-307.

Frade, P. R.; Bongaerts, P.; Winkelhagen, A. J. S.; Tonk, L. and Bak, R. P. M (2008). In situ photobiology of corals over large depth ranges: A multivariate analysis on the roles of environment, host, and algal symbiont. Limnol. Oceanogr., 53 (6): 2711.

Glynn, P. W. and D'Croz, L (1990). Experimental evidence for high temperature stress as the cause of El Nino-coincident coral mortality. Coral reefs, 8 (4): 181-191.

Hennige, S. J.; Smith, D. J.; Perkins, R.; Consalvey, M.; Paterson, D. M. and Suggett, D. J (2008). Photoacclimation, growth and distribution of massive coral species in clear and turbid waters. Mar. Ecol. Prog. Ser., 369:77-88.

Hoegh-Guldberg, O. and Smith, G. J (1989). The effect of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. J. Exp. Mar. Biol. Ecol., 129:279–303.

Howe, S. A. and Marshall, A. T (2001). Thermal compensation of metabolism in the temperate coral, *Plesiastrea versipora* (Lamarck, 1816). J. Exp. Mar. Biol. Ecol., 259 (2): 231-248.

Jones, R. J. and Yellowlees, D (1997). Regulation and control of intracellular algae (=zooxanthellae) in hard corals. Philos. Trans. R. Soc. Lond. B, 352: 457-468.

Kaiser, P.; Schlichter, D. and Fricke, H. W (1993). Influence of light on algal symbionts of the deep water coral *Leptoseris fragilis*. Mar. Biol., 117 (1): 45-52.

Kawaguti, S. and Sakumoto, D (1948). The effect of light on the calcium deposition of corals. Bull. Oceanogr. Inst. Taiwan, 4:65-70.

Kuguru, B.; Achituv, Y.; Gruber, D. F. and Tchernov, D (2010). Photoacclimation mechanisms of corallimorpharians on coral reefs: Photosynthetic parameters of zooxanthellae and host cellular responses to variation in irradiance. J. Exp. Mar. Biol. Ecol., 394 (1): 53-62.

Lough, J. M. and Barnes, D. J (1992). Comparisons of skeletal density variations in *Porites* from the central Great Barrier Reef. J. Exp. Mar. Biol. Ecol., 155 (1): 1-25.

Marsh, J. A (1970). Primary productivity of reef-building calcareous red algae. Ecology, 51:255-263.

Mass, T.; Kline, D. I.; Roopin, M.; Veal, C. J.; Cohen, S.; Iluz, D. and Levy, O (2010). The spectral quality of light is a key driver of photosynthesis and photoadaptation in *Stylophora pistillata* colonies from different depths in the Red Sea. J. Exp. Biol., 213 (23): 4084-4091.

McCloskey, L. R. and Muscatine, L (1984). Production and respiration in the Red Sea coral Stylophora pistillata as a function of depth. Proc. R. Soc. Lond. B., 222 (1227): 215-230.

Mieog, J. C.; van Oppen, M. J. H.; Berkelmans, R.; Stam, W. T. and Olsen, J. L (2009). Quantification of algal endosymbionts (*Symbiodinium*) in coral tissue using real-time PCR. Mol. Ecol. Resour., 9:74-82.

Muscatine, L(1990). The role of symbiotic algae in carbon and energy flux in reef corals. *In:* Dubinsky, Z. (ed.) Ecosystems of the world. coral reefs. Elsevier, Amsterdam, 75-87.

Muscatine, L.; Falkowski, P. G.; Dubinsky, Z.; Cook, P. A. and McCloskey, L. R

(1989). The effect of external nutrient resources on the population dynamics of zooxanthellae in a reef coral. Proc. R. Soc. Lond. B., 236 (1284): 311-324.

Muscatine, L. and Pool, R. R (1979). Regulation of numbers of intracellular algae. Proc. R. Soc. Lond. B., 204 (1155): 131-139.

Nakamura, T. and van Woesik, R (2001). Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar. Ecol. Prog. Ser., 212:301-304.

Nakamura, T.; Yamasaki, H. and van Woesik, R (2003). Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata*. Mar. Ecol. Prog. Ser., 256:287-291.

Nir, O.; Gruber, D. F.; Einbinder, S.; Kark, S. and Tchernov, D (2011). Changes in scleractinian coral *Seriatopora hystrix* morphology and its endocellular *Symbiodinium* characteristics along a bathymetric gradient from shallow to mesophotic reef. Coral reefs, 30 (4): 1089-1100.

Riegl, B (2003). Global climate change and coral reefs: different effects in two high latitude areas (Arabian Gulf, South Africa). Coral Reefs, 22:433-446.

Selim, A. E. M (2007). Sedimentation threats to Red Sea corals: An ecological study of reefs in the Hurghada region, Egypt. Ph.D Thesis, Hull Univ. 207 pp.

Shu, L.; KeFu, Y.; Qi, S.; TianRan, C.; MeiXia, Z. and JianXin, Z (2008). Interspecies and spatial diversity in the symbiotic zooxanthellae density in corals from northern South China Sea and its relationship to coral reef bleaching. Chin. Sci. Bull., 53 (2): 295-303.

Stat, M. and Gates, R. D (2011). Clade D *Symbiodinium* in scleractinian corals: a "nugget" of hope, a selfish opportunist, an ominous sign, or all of the above? J. Mar. Biol., 2011: 10.1155/2011/730715.

Stat, M.; Morris, E. and Gates, R. D (2008). Functional diversity in coral–dinoflagellate symbiosis. Proc. Natl. Acad. Sci. U.S.A., 105 (27): 9256-9261.

Titlyanov, E. A(1981). Adaptation of reef-building corals to low light intensity. *In:* Gomez, E. D.; Birkeland, C. E.; Buddemeier, R. W.; Johannes, R. E.; Marsh, J. A.; Jr. and Tsuda, R. T. (eds.) Proc. 4th Int. Coral Reef Symp. Univ. Phillipines, 39-43.

Titlyanov, E. A.; Bil, K.; Fomina, I.; Titlyanova, T. V.; Leletkin, V. A.; Eden, N.; Malkin, A. and Dubinsky, Z (2000). Effects of dissolved ammonium addition and host feeding with *Artemia salina* on photoacclimation of the hermatypic coral *Stylophora pistillata*. Mar. Biol., 137 (3): 463-472.

Titlyanov, E. A.; Titlyanova, T. V.; Yamazato, K. and van Woesik, R (2001). Photoacclimation of the hermatypic coral *Stylophora pistillata* while subjected to either starvation or food provisioning. J. Exp. Mar. Biol. Ecol., 257 (2): 163-181.

Veron, J. E. N(2000). Corals of the World. Australian Institute of Marine Science & CRR Qld Pty Ltd, Australia, 490 pp.

Winters, G.; Beer, S.; Zvi, B. B.; Brickner, I. and Loya, Y (2009). Spatial and temporal photoacclimation of *Stylophora pistillata*: zooxanthella size, pigmentation, location and clade. Mar. Ecol. Prog. Ser., 384:107-119.