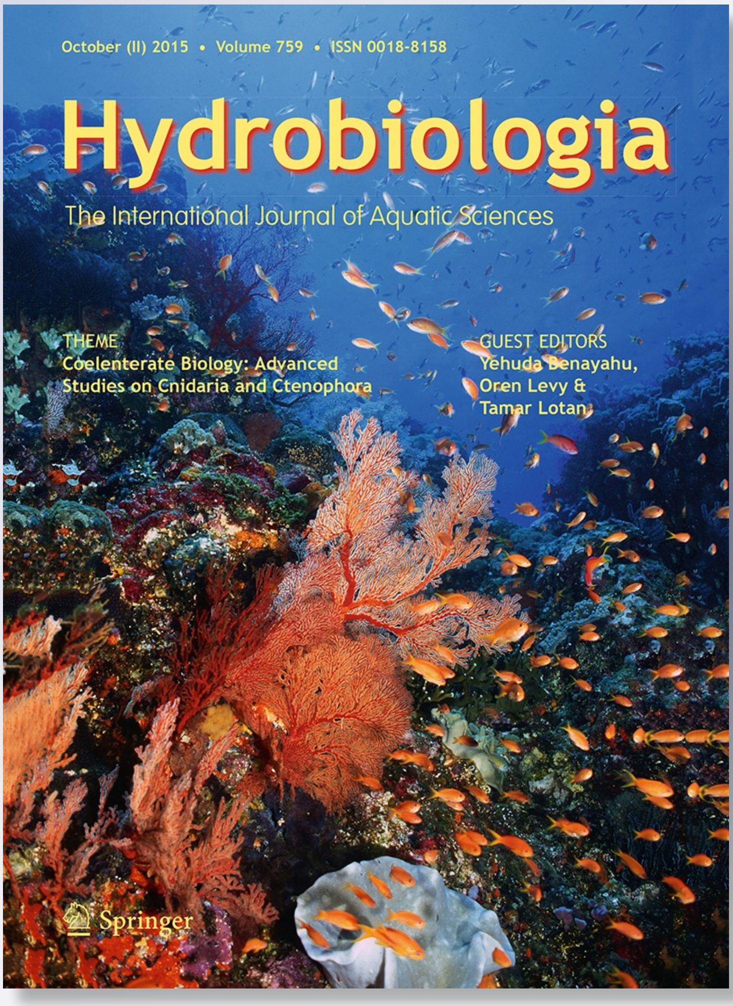
Occurrence and survivorship of azooxanthellate octocorals reflect recruitment preferences and depth distribution

Michal Grossowicz & Yehuda Benayahu

Hydrobiologia
The International Journal of Aquatic Sciences

ISSN 0018-8158
Volume 759
Number 1

Hydrobiologia (2015) 759:85-93
DOI 10.1007/s10750-015-2270-9



Springer

Your article is protected by copyright and all rights are held exclusively by Springer International Publishing Switzerland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com”.

Springer

Author's personal copy

Hydrobiologia (2015) 759:85–93
DOI 10.1007/s10750-015-2270-9

COELENTERATE BIOLOGY

Occurrence and survivorship of azooxanthellate octocorals reflect recruitment preferences and depth distribution

Michal Grossowicz · Yehuda Benayahu

Received: 28 March 2014 / Revised: 31 January 2015 / Accepted: 29 March 2015 / Published online: 12 April 2015
© Springer International Publishing Switzerland 2015

Abstract Like many other environmental factors, light limits the distribution of hermatypic corals along depth. Octocorals, accordingly, respond to light intensity, featuring a depth-related distribution. Among others, competition for space, resources, and settlement processes may determine their distribution. The azooxanthellate octocoral *Dendronephthya sinaiensis* inhabits flow-exposed vertical habitats such as reef slopes. The current study engages with its distributional patterns on both the southern and northern faces of the vertical pillars of the oil jetties at Eilat (northern Red Sea). It examines the possible role of light intensity and competition in determining its spatial distribution during recruitment processes. The distribution of *D. sinaiensis* along depth (14–32 m) was studied and light intensity was measured at both the light-exposed and shaded faces. The colonies were found mostly on the shaded faces, suggesting that *D. sinaiensis* might be adapted to low-light intensity, where zooxanthellate corals may be more restricted. Translocation of *D. sinaiensis* fragments from deep-to-shallow waters to either lit or shaded faces revealed their survival on the shaded faces, where they do not naturally occur, whereas they did not survive on the lit ones. This finding suggests a preference for deep water, which may reduce competition with zooxanthellate species. The occurrence of *D. sinaiensis* thus appears to be determined by both a selective preference to inhabit deep water and, at least partially, by light intensity.

Keywords Octocorals · Depth distribution · Translocation · Light intensity · Red Sea

Introduction

Octocorallia (Cnidaria: Anthozoa) comprise more than 3000 species, distributed worldwide, dwelling in a variety of habitats (Fabricius & Alderslade, 2001). The octocoral order Alcyonacea is the largest such order and encompasses both zooxanthellate and azooxanthellate species, commonly living side by side, including in illuminated shallow coral-reef habitats (Chanmethakul et al., 2010; Gori et al., 2012). Alcyonaceans constitute the second most important benthic component on many coral reefs (Fabricius & Alderslade, 2001), including in the Gulf

---

Guest editors: Yehuda Benayahu, Oren Levy & Tamar Lotan / Coelenterate Biology: Advanced Studies on Cnidaria and Ctenophora

M. Grossowicz · Y. Benayahu (✉)
Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv, 6997801 Tel Aviv, Israel
e-mail: yehudab@tauex.tau.ac.il

M. Grossowicz
Department of Marine Biology, L. H. Charney School of Marine Sciences, University of Haifa, 3498838 Haifa, Israel

Author's personal copy

of Aqaba (northern Red Sea) (Benayahu & Loya, 1977, 1981).

Octocorals of the genus *Dendronephthya* (family Nephtheidae) are azooxanthellate (Fabricius & Alderslade, 2001) and considered to be passive phytoplankton filter feeders (Fabricius et al., 1995a, b). They feature both sexual reproduction by gamete release and asexual propagation by means of numerous autonomous small detached fragments (Dahan & Benayahu, 1997a, b). On the northern Red Sea reefs the genus commonly inhabits flow-exposed habitats such as reef slopes (Benayahu, 1985) and flourishes there, especially on artificial structures (Perkol-Finkel & Benayahu, 2004, 2005; Ammar, 2009). Studies conducted on the underwater steel constructions of the oil jetties at Eilat (northern Gulf of Aqaba), revealed that *Dendronephthya* species are highly abundant there compared to the adjacent natural reefs (Dahan & Benayahu, 1997b). The vertical steel pillars of the jetties are characterized by a high-flow regime (Perkol-Finkel & Benayahu, 2004). In this artificial habitat *D. hemprichi* and *D. sinaiensis* display a distinct spatial distribution: the former inhabits the entire length of the pillars (1–32 m) while the latter occupies only the deeper section (14–30 m) (Grossowicz, 2008, Grossowicz & Benayahu, 2012).

The "fundamental niche" concept was first applied by Hutchinson (1958), who referred it to the set of resources or environmental factors that a species can utilize in the absence of competition or other biotic interactions (Krebs, 2001). The observed resource-usage of a given species in the presence of competition is considered as the species' "realized niche" (Hutchinson, 1958). Based on this concept, niche is determined not only by abiotic factors but also by biotic ones. A given species does not always occupy the optimal part of its fundamental niche but may be restricted to its periphery, for example by competition or predation (Krebs, 2001).

In the marine environment larval settlement takes place when their free-living state terminates and they select a substrate for attachment (Roth et al., 2013). Not only larvae but also asexual propagules, such as the small fragments detaching from *Dendronephthya* colonies, are subjected to recruitment processes (e.g., Dahan & Benayahu, 1997b). Most of these asexual propagules settle adjacent to the mother colonies, where the probability of occurrence of a suitable habitat is quite high (Dahan & Benayahu, 1997b). They are subjected to post-settlement processes such as predation, competition for space, or mortality due to diverse abiotic factors (see Ritson-Williams et al., 2009). The latter include for example light regime (Kahng et al., 2010), temperature (Bassim & Sammarco, 2003), hydrodynamics (Mullineaux, 1988), type of substrate and its complexity (Vermeij, 2005), sedimentation rate (Babcock & Davies, 1991), and salinity (Vermeij, 2006), all of which contribute to determining their niche (sensu Hutchinson, 1958).

Traditionally, light is considered a key factor in coral-reef survival, as it attenuates with depth and affects their distribution (e.g., Ettinger-Epstein et al., 2008; Kahng et al., 2010). Light also determines the depth distribution, size, and morphology of several anthozoan groups, such as hermatypic corals (e.g., Vermeij & Bak, 2002; Roth et al., 2013), black corals (Sanchez, 1999), and octocorals (Rocha et al., 2013). Kawaguti (1941) was the first to suggest that phototaxis of coral planulae may affect their vertical distribution, as was later confirmed (e.g., Gleason et al., 2005; Matterson, 2012). Studies have revealed a light-related distribution of several zooxanthellate octocorals (Xeniidae: Reinicke, 1997; *Cladiella* sp.: Chanmethakul et al., 2010; *Sinularia flexibilis*: Rocha et al., 2013). Similarly, a light-dependent distribution is exhibited by some azooxanthellate octocorals (*Chironephthya* sp.: Chanmethakul et al., 2010; *Eunicella singularis*: Gori et al., 2012; *Corallium rubrum*: Santangelo et al., 2012). In addition to light intensity, other factors may also determine larval recruitment on coral reefs. For example, Mundy & Babcock (2000) found that new recruits of stony corals translocated to deeper water survived there, although mature colonies are not usually found there. Those findings thus reject the hypothesis that patterns of adult distribution are determined by indiscriminant larval settlement, followed by differential depth-related, early post-settlement mortality. It was suggested that the choice of a particular recruitment site by larvae may reduce competition for space with co-occurring species (Edmunds et al., 2004). Such pre-settlement processes exhibited by the larvae may prevent recruitment where other environmental factors, such as light, might allow it (Ritson-Williams et al., 2009). Hence, it would seem that translocated recruits (e.g., Mundy & Babcock, 2000), in order to avoid competition, are able to survive in certain environments where their larvae would not naturally settle.

Author's personal copy

The current study addresses the question of whether recruitment processes determine the depth distribution of azooxanthellate octocorals. We tested the multiple hypotheses that (1) *D. sinaiensis* is a deep-water dweller; (2) preferentially appears on a certain face (north or south); (3) attenuated light intensity with depth determines in part the fundamental niche (Hutchinson, 1958) of *D. sinaiensis*; and (4) the pre-recruitment processes, such as selection of recruitment site, rather than only environmental factors, may reduce competition with its congener *D. hemprichi* and/or scleractinian corals that occupy the same habitat. The results also highlight the possible role played by competition for space in determining the spatial distribution of reef-inhabiting azooxanthellate octocorals.

Materials and methods

Study site and distribution of *D. sinaiensis*

The study was conducted at the oil jetties of the Eilat-Ashqelon Pipeline Company (EAPC), located 4 km south of the city of Eilat (Fig. 1). The jetties were constructed in the late 1960s and present an unplanned artificial reef, featuring diverse benthic communities (Dahan & Benayahu, 1997b; Perkol-Finkel & Benayahu, 2004) and fish assemblages (Rilov & Benayahu, 1998). Vertical steel pillars (0.65–1 m in diameter) support the jetties along their entire length, from the shallow water down to 32 m. For the purpose of the current study six vertical pillars at the deepest part (32 m) of the southern jetty were chosen. The abundance and distribution of *D. sinaiensis* on the pillars were determined along 0.6 m wide vertical belt transects, deployed from the base of the pillars to the water surface, with two belt transects to each pillar (one on its northern face and another on its southern one), along which the colonies were counted and their depth of appearance was recorded to the nearest 10 cm. For data analysis, each pillar was divided into eight depth sections, 4 m long, from the water surface to the bottom (0–4 m, 4–8 m, 8–12 m, etc.).

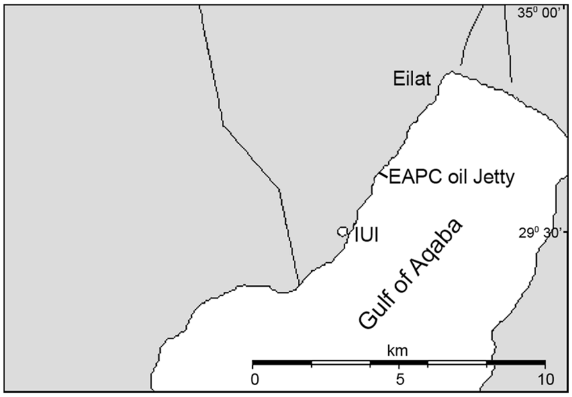


Fig. 1 Study site at Eilat, northern tip of the Gulf of Aqaba (Red Sea) (EAPC: Eilat-Ashqelon Pipeline Company, IUI: The Interuniversity Institute for Marine Sciences)

Translocation experiment

In order to uncover whether only environmental factors determine the distribution of *D. sianiensis* along the pillars, a translocation experiment was conducted. For this purpose, in January 2007 branches of *D. sinaiensis* were removed by scissors from ten randomly selected colonies growing on the pillars at 22 m depth ($n = 4{-}5$ branches from each colony). The branches were immediately transferred to the Interuniversity Institute for Marine Sciences in Eilat (IUI) and placed for acclimation in 200 L tanks supplied with flow-through seawater. A day later, ~1 cm fragments (5–8 polyps each) were carefully clipped from the branches and placed on individually tagged experimental PVC plates, measuring 5 × 10 × 0.3 cm (10–15 fragments per plate, $n = 48$ plates), all maintained in the running seawater system. A month later, following attachment of the fragments to the plates (see Barki, 1992; Dahan & Benayahu, 1997b), the plates were placed in zip-lock bags filled with seawater, brought to the jetty study site and attached by plastic clips to 5 mm diameter ropes on one of the pillars at 5, 12, and 22 m depth, on both its northern and southern faces. Eight plates were attached at each depth of the two faces, totaling 48 plates (8 plates × 3 depths × 2 faces). The fragments of *D. sinaiensis* were monitored and counted on each plate in March, April, and May 2007, constituting a time span falling within that of the studies by Dahan & Benayahu (1997b) and Perkol-Finkel & Benayahu (2009). For each plate, the relative survivorship of the fragments was calculated as the ratio between the number of fragments on a given date and the respective initial number of fragments, when introduced into the water (February 2007). The monthly average survival rate of the fragments per plate was then determined for each of the three depths of the two faces.

Author's personal copy

Light intensity measurements

Light intensity was measured along the pillars at the three depths (5, 12, and 22 m), corresponding to the position of the plates, on both the northern and southern faces, by a WALZ Diving-PAM. For calibration purposes, light measurement was taken at the sea surface (E_0). At each face and depth, measurements were taken during three consecutive days in July 2007 (Eilat mid-summer). The measurements were taken at 0.5 m distance from the pillar to avoid shade effect of any benthic organisms growing on its surface. The vertical light attenuation coefficient (K_d) was calculated according to the formula: $E_z = E_0 \cdot e^{-K_d z}$, where z is the depth (m) and E_z and E_0 are the measured light intensities at z and 0 m, respectively (Jerlov, 1976). K_d was calculated only for the southern face of the pillar, since the northern one was constantly shaded by the adjacent jetty's pillars.

Statistical analysis

Statistical analyses were performed by STATISTICA 10. Averages were compared by paired t test and variances were tested by Cochran C and ANOVA (one-way, two-way, and two-way repeated-measures), followed by Bonferroni post hoc test. Analysis of regression slope homogeneity was performed with ANCOVA. Normality of the dependent variables was examined by Kolmogorov–Smirnov test (KS) and, when required, a suitable transformation was conducted to obtain normality (see Results). All values are presented at a confidence interval of 95%.

Results

Abundance and distribution of *D. sinaiensis*

The belt transects conducted along the jetty pillars revealed that the uppermost (shallowest) colonies of *D. sinaiensis* were at the 16–20 m section (18.5 ± 4.1 m, $n = 6$ pillars). The highest number of colonies was recorded at the 20–24 m section, featuring 70.8 ± 53.7 colonies per 4×0.6 m^2 ($n = 6$ pillars, Fig. 2a). Colony count at each depth section was normally distributed (KS, $P > 0.2$ for each section), featuring a homogenous variance (Cochran C, $P = 0.06$). There were significant differences between the number of colonies among the eight depth sections of the pillars (one-way ANOVA, data $\sqrt[4]{X}$ transformed, $P = 0.006$). The deep sections of 20–24 and 24–28 m exhibited a significantly higher number of *D. sinaiensis* colonies than the others (post hoc Bonferroni, $P < 0.04$). Hence, no colonies were recorded at the 0–4, 4–8, and 8–12 m sections; low density at 12–16, 16–20, and 28–32 m; and the highest at 20–24 and 24–28 m (Fig. 2a). Out of the total 1083 *D. sinaiensis* colonies counted on the pillars, a higher percentage (63.4%) occurred on its southern face compared to the northern one (36.6%). The depth distribution of the colonies, when distinguishing between the northern and southern faces (Fig. 2b), resembled the general distribution on both faces (see Fig. 2a). The density of the colonies per depth section on both faces was significantly higher on the southern face compared to the northern one (paired t-test, $P = 0.04$). Likewise, 70.5% ($n = 758$) of the total number of colonies were found on a shaded surface of the pillar, facing its inner side, while the remaining colonies (29.45%, $n = 325$) were on the outer surface.

Translocation experiment

The survival rate of *D. sinaiensis* fragments placed on the southern face of the pillars (May 2007) was 0.01 at 5 m, 0.15 at 12 m, and 0.62 at 22 m (Fig. 3b), corresponding to the depth distribution findings (see above). On the northern face the survival rate was high at all depths (Fig. 3a: 0.75, 0.63, and 0.77 at 5, 12, and 22 m, respectively), compared to that recorded at 5 and 12 m on the southern face. The survival rate during the entire period exhibited a normal distribution (KS, $P > 0.2$ for each depth, face and time), with homogenous variance (Cochran C, $P > 0.2$ for each depth, face, and time). There were significant differences between the survival rate of all three counts (February to May 2007) between the pillar faces and depths (two-way repeated-measures ANOVA, data $\sin^{-1}\sqrt{X}$ transformed, $P = 0$, 0.0002, respectively, see Fig. 3). In May, the survival rate count at 22 m on the southern face was significantly higher than at 5 and 12 m (post hoc Bonferroni, data $\sin^{-1}\sqrt{X}$ transformed, $P < 0.003$, Fig. 3b) and similar to the northern face at all depths (post hoc Bonferroni, data $\sin^{-1}\sqrt{X}$ transformed, $P > 0.9$). Table 1 presents the

Author's personal copy

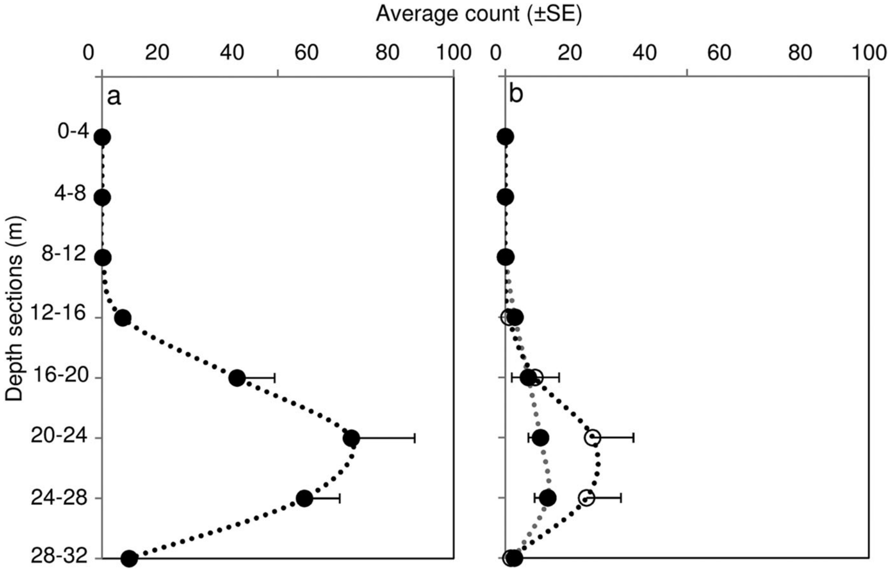


Fig. 2 Average colony count of *D. sinaiensis* per pillar along depth (±SE, $n = 6$ pillars). **a** Overall distribution along pillars, **b** *black* distribution along northern face, *white* along southern face

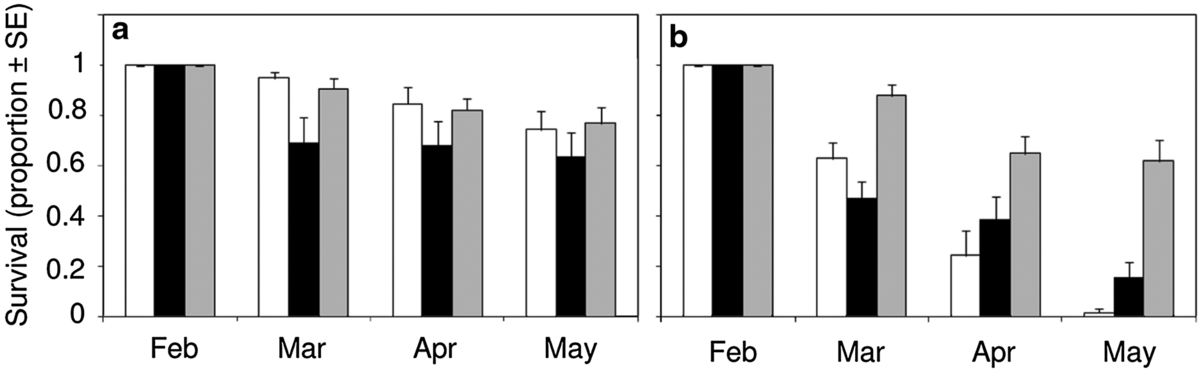


Fig. 3 Survival rates (±SE) of *Dendronephthya sinaiensis* by face. **a** Northern face, **b** southern face. *White*—5 m, *black*—12 m, *gray*—22 m

regression slopes of the survival rates during the three counts at each face and depth, revealing a moderate decrease at all depths of the northern face (Fig. 3a) and at 22 m of the southern one. At 5 and 22 m of the southern face the survival rate decreased acutely with time (Fig. 3b). The survival slopes significantly differed between faces (homogeneity of slopes ANCOVA, data $\sin^{-1}\sqrt{X}$ transformed, $P = 0.001$). At both 5 and 12 m, the survival rate on the southern face was significantly more moderate compared to the acute one on the northern face (post hoc Bonferroni, $P < 0.02$). The survival rate between 22 m on the southern face and northern one at all depths was similar ($P = 1$ between 22 m on southern face and each depth on the northern face). On the northern face the survival rate was similar at all depths ($P > 0.5$). The southern face exhibited a similar survival rate at 5 and 12 m ($P = 1$). Between 22 m and both 5 and 12 m on the southern face the survival rate was significantly different ($P < 0.001$), indicating that the survival rate

Table 1 Correlation coefficients of survival rate along time at each depth and face (R^2 in brackets) of the translocation experiment

	5 m	12 m	22 m
Northern face	−0.08 (0.98)	−0.11 (0.72)	−0.07 (0.98)
Southern face	−0.33 (0.98)	−0.26 (0.89)	−0.13 (0.93)

Author's personal copy

at 22 m was moderate compared to the sharp decline at 5 and 12 m.

Light intensity

The average water surface light intensity was $E_0 = 1892.5 \pm 527.9$ μE. A typical light attenuation curve was recorded at the southern face, featuring the highest intensity at 5 m, medium at 12 m, and lowest at 22 m. On the northern face the light intensity was similar at all three depths, yet still low, resembling the 22 m light intensity at the southern face, caused by the shade effect of the jetty itself. Table 2 presents the measured (E_z (μE), $z = 5$, 12, and 22 m) and calibrated light intensity (E_z/E_0), featuring normally distributed values (KS, $P > 0.2$) with homogenous variance (Cochran C, $P = 0.9$). The light intensity was significantly higher at the southern face of the pillar compared to the northern one (Table 2, two-way ANOVA, data $\sin^{-1} \sqrt{X}$ transformed, $P = 0.014$). The light intensity at 5 m on the southern face was significantly higher compared to all measurements taken on the northern face and that at 22 m on the southern face (post hoc Bonferroni, $P < 0.03$). The vertical attenuation coefficient for the southern face was $K_d = 0.08 \pm 0.04$ m^{-1}.

Discussion

The current study tested multiple hypotheses, all of which were proven valid (Table 3), with most *D. sinaiensis* colonies being recorded at 20–28 m on the southern pillar face. In addition, for the colonies that were found on a shaded surface of the pillars, facing their inner side and on the northern face, their survival rate was the highest at all depths, compared to that at 5 and 12 m on the southern face.

In the marine systems, environmental factors determine the recruitment of benthic organisms (Todd, 1998; Roth et al., 2013). These factors include among others temperature (Bassim & Sammarco, 2003), substrate availability (Grigg, 1977), substrate composition, and morphology (Vermeij, 2005), and sedimentation rate (Babcock & Davies, 1991). Other factors could be related to depth, such as currents (Mullineaux, 1988) and light (this study, Kahng et al., 2010). Previous studies have shown that different corals require specific light intensities for settlement (Vermeij & Bak, 2002). The current study revealed that colonies of the octocoral *D. sinaiensis* inhabit mostly the deep and shaded parts of the EAPC jetty pillars. The occurrence of benthic species, including zooxanthellate corals, along a depth gradient may reflect a response to environmental factors, including light (Baird et al., 2003). Therefore, it is suggested that depth distribution of the azooxanthellate *D. sinaiensis* is at least in part determined by light intensity. Nevertheless, distribution may also be affected by other depth-related factors, such as current regime, in which intensity displays moderate values in deeper compared to shallow water (Grossowicz, 2008).

The relationship between pillar face and its occurrence might thus be related to the light regime. Chanmethakul et al. (2010) demonstrated that octocorals exhibit species-specific habitat preferences; for example, members of the family Nephtheidae are often restricted to reef slopes and deep habitats. Sheppard (1980) found in Chagos (Indian Ocean) that slopes facing the open sea featured a typical species composition, with a more complex community on the slope facing the lagoon, comprising several taxa of stony and soft corals. The light intensity along the EAPC jetty is determined by the shade caused by the pillars constructing it and by light attenuation with

Table 2 Measured E_z (μE) and calibrated light intensity E_z/E_0 ($z = 5$, 12, 22 m) at the northern and southern faces (±SD, $n = 12$ measurements at each location)

	5 m	12 m	22 m
Northern face			
Calibrated	0.07 ± 0.05	0.06 ± 0.04	0.06 ± 0.04
Measured (μE)	139.5 ± 24.75	120 ± 2.82	114 ± 12.72
Southern face			
Calibrated	0.28 ± 0.16	0.14 ± 0.06	0.09 ± 0.05
Measured (μE)	529.5 ± 19.09	254.5 ± 24.75	168.5 ± 30.4

Author's personal copy

Table 3 Summary of tested hypotheses, conducted test results, and conclusions

Hypothesis	Test	Results and conclusions
D. sinaiensis displays a vertical distribution and appears mostly in deep water	Vertical belt transects	No colonies were recorded at 0–12 m, low density at 12–20, the highest at 20–28 m and none at 28–32 m
D. sinaiensis preferentially appears at a certain face (north or south)	Vertical belt transects at northern and southern faces	Higher percentage occurred on the southern face compared to the northern one
Depth distribution in part determined by light intensity	Light intensity measurement was conducted along vertical transects	Subject corals were found on the shaded surface of pillar, facing its inner side. On the northern face light intensity was low and uniform along entire depth, resembling the 22 m intensity at the southern face, caused by shade effect of the jetty itself
If environmental factors determine octocoral distribution, it will not survive at mid and shallow depths	Translocation experiment	On the northern face survival rate was highest at all depths, compared to that at 5 and 12 m on the southern face

depth. For example, the northern shaded side of the jetty features the low-light adapted azooxanthellate soft corals, whereas on the more illuminated southern side there are mostly zooxanthellate species (Barki, 1992; Grossowicz, 2008; Grossowicz & Benayahu, 2012), which may be competitors to azooxanthellate dwellers.

With respect to their fundamental niche (Hutchinson, 1958), larvae of benthic organisms may respond to cues for settlement supplied by the substrate itself or in the water overlying it (Ritson-Williams et al., 2009). For example, seawater salinity lower than normal increased both pre- and post-settlement mortality of coral planulae (Vermeij, 2006), while subsequent mortality due to predation or competition affected the recruits and their survivorship, thus reflecting the "realized niche". Mundy & Babcock (2000), who demonstrated that translocated zooxanthellate stony coral recruits survived at depths in which they did not naturally occur, concluded that the species' distribution was not depth-related. The azooxanthellate *D. sinaiensis* was found on the deeper and shaded parts of the jetty (>18.5 ± 4.1 m, Fig. 2a). Following translocation, the survival of *D. sinaiensis* asexual fragments on the south face of the jetty supports the hypothesis that attenuated light along depth determines its occurrence and that it does not survive in the shallow, well-illuminated, sections of the pillars. The survival of the translocated fragments on the north face at all depths was high within the duration of experiment (i.e., 90 days), thus falling within the findings of previous studies conducted in Eilat (Dahan & Benayahu, 1997b; Perkol-Finkel & Benayahu, 2009). *D. sinaiensis* was not recorded growing naturally at the mid and shallow depths, suggesting that light intensity is nevertheless not the only factor limiting its distribution in the deep section of the pillars. Similarly, as indicated by Mundy & Babcock (2000), it is suggested here that recruitment and subsequent survivorship of *D. sinaiensis* fragments determine their depth distribution. Only a few colonies of *D. sinaiensis* were found growing at depths shallower than 18 m (Fig. 2a), thus supporting the hypothesis of their preference for deep water. It is therefore concluded that *D. sinaiensis* is adapted to niches characterized by low-light intensity, insufficient for zooxanthellate species, and thus most probably avoids competition for space with the latter.

The current findings indicate that the *D. sinaiensis* niche on the EAPC jetty pillars is determined by pre-settlement preferences for both shaded and low-illuminated habitats. Depth, however, is not the sole contributing environmental factor. It is suggested that examining the role played by UV irradiance and possible competitive interactions with *D. hemprichi* and other benthic organisms, may highlight the relevance of the current results also to natural reef systems.

Acknowledgments We thank the Interuniversity Institute for Marine Sciences in Eilat (IUI) for the use of their facilities and assistance. We thank the Eilat-Ashqelon Pipeline Company (EAPC) for cooperation and the Israel Nature and National Parks Protection Authority for issuing the collection permit. We acknowledge A. Shlagman for curatorial help, N. Paz for

Author's personal copy

editorial assistance, and V. Wexler for digital editing. The study was in part supported by the Israel Cohen Chair in Environmental Zoology (Y. B.) and a grant from The Porter School of Environmental Studies (PSES) at Tel Aviv University. The article constitutes part of a MSc thesis in Ecology and Environmental Quality at Tel-Aviv University submitted by M. Grossowicz.

References

Ammar, M. S. A., 2009. Coral reef restoration and artificial reef management, future and economic. Open Environmental Engineering Journal 2: 37–49.

Babcock, R. & P. Davies, 1991. Effects of sedimentation on settlement of *Acropora millepora*. Coral Reefs 9: 205–208.

Baird, A. H., R. C. Babcock & C. P. Mundy, 2003. Habitat selection by larvae influences the depth distribution of six common coral species. Marine Ecology Progress Series 252: 289–293.

Barki, Y., 1992. Population ecology and genetic characteristics of the soft coral *Dendronephthya* in the northern Gulf of Eilat, Red Sea. M. Sc. Thesis, Tel-Aviv University, Israel (Hebrew, 79 p; English summary).

Bassim, K. & P. Sammarco, 2003. Effects of temperature and ammonium on larval development and survivorship in a scleractinian coral (*Diploria strigosa*). Marine Biology 142(2): 241–252.

Benayahu, Y., 1985. Faunistic composition and patterns in the distribution of soft corals (Octocorallia, Alcyonacea) along the coral reefs of Sinai peninsula. Proceedings 5th International Coral Reefs Congress, Tahiti 6: 255–260.

Benayahu, Y. & Y. Loya, 1977. Space partitioning by stony corals soft corals and benthic algae on coral reefs of northern Gulf of Eilat (Red-Sea). Helgoländer Wissenschaftliche Meeresuntersuchungen 30: 362–382.

Benayahu, Y. & Y. Loya, 1981. Competition for space among coral-reef sessile organisms at Eilat, Red-Sea. Bulletin of Marine Sciences 31: 514–522.

Chanmethakul, T., H. Chansang & S. Watanasit, 2010. Soft coral (Cnidaria: Alcyonacea) distribution patterns in Thai waters. Zoological Studies 49(1): 72–84.

Dahan, M. & Y. Benayahu, 1997a. Reproduction of *Dendronephthya hemprichi* (Cnidaria: Octocorallia): year-round spawning in an azooxanthellate soft coral. Marine Biology 129: 573–579.

Dahan, M. & Y. Benayahu, 1997b. Clonal propagation by the azooxanthellate octocoral *Dendronephthya hemprichi*. Coral Reef 16: 5–12.

Edmunds, P. J., J. F. Bruno & D. B. Carlon, 2004. Effects of depth and microhabitat on growth and survivorship of juvenile corals in the Florida Keys. Marine Ecology Progress Series 278: 115–124.

Ettinger-Epstein, P., S. Whalan, C. N. Battershill & R. de Nys, 2008. A hierarchy of settlement cues influences larval behavior in a coral reef sponge. Marine Ecology Progress Series 365: 103–113.

Fabricius, K., & P. Alderslade, 2001. Soft corals and sea fans: a comprehensive guide to the tropical shallow water genera of the central-west Pacific, the Indian Ocean and the Red Sea. Australian Institute of Marine Science and the Museum and Art Gallery of the Northern Territory.

Fabricius, K. E., Y. Benayahu & A. Genin, 1995a. Herbivory in asymbiotic soft corals. Science 268: 90–92.

Fabricius, K. E., A. Genin & Y. Benayahu, 1995b. Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnology and Oceanography 40: 1290–1301.

Gleason, D. F., P. J. Edmunds & R. D. Gates, 2005. Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral *Porites astreoides*. Marine Biology. doi:10.1007/s00227-005-0098-y.

Gori, A., L. Bramanti, P. Lopez-Gonzalez, J. N. Thoma, J. M. Gili, J. Grinyo, V. Uceira & S. Rossi, 2012. Characterization of the zooxanthellate and azooxanthellate morphotypes of the Mediterranean gorgonian *Eunicella singularis*. Marine Biology 159: 1485–1496.

Grigg, R. W., 1977. Population dynamics of two gorgonian corals. Ecology 58: 278–290.

Grossowicz, M., 2008. Niche partitioning among three azooxanthellate soft coral species in Eilat (northern Red Sea). M. Sc. Thesis, Tel-Aviv University, Israel (Hebrew, 75 p; English summary).

Grossowicz, M. & Y. Benayahu, 2012. Differential morphological features of two *Dendronephthya* soft coral species suggest differences in feeding niches. Marine Biodiversity 42: 65–72.

Hutchinson, G. E., 1958. Concluding remarks cold spring harbor symposium. Quantitative Biology 22: 415–427.

Jerlov, N. G., 1976. Marine Optics. Elsevier, Amsterdam: 231pp.

Kahng, S. E., J. R. Garcia-Sais, H. L. Spalding, E. Brokovich, D. Wagner, E. Weil, L. Hinderstein & R. J. Toonen, 2010. Community ecology of mesophotic coral reef ecosystems. Coral Reefs 29: 255–275.

Kawaguti, S., 1941. On the physiology of reef corals. V. The tropisms of coral planulae, considered as a factor of distribution on the reef. Palao Tropical Biology Station Studies 2: 319–328.

Krebs, C. J., 2001. Ecology: the experimental analysis of distribution and abundance. Benjamin Cummings, an imprint of Addison Wesley Longman Inc, San Francisco.

Matterson, K., 2012. Microscale variation in light intensity and its effects on growth of juveniles of the temperate coral, *Oculina Arbuscula*. Electronic Theses and Dissertations. Georgia Southern University, Paper 14.

Mullineaux, L. S., 1988. The role of settlement in structuring a hard-substratum community in the deep sea. Journal of Experimental Marine Biology and Ecology 120: 247–261.

Mundy, C. & R. C. Babcock, 2000. Are vertical distribution patterns of scleractinian corals maintained by pre- or post-settlement processes? A case of three contrasting species. Marine Ecology Progress Series 198: 109–119.

Perkol-Finkel, S. & Y. Benayahu, 2004. Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs. Coral Reefs 23: 195–205.

Perkol-Finkel, S. & Y. Benayahu, 2005. Recruitment of benthic organisms onto a planed artificial reef: shift in community structure one decade post-deployment. Marine Environmental Research 59: 79–99.

Perkol-Finkel, S. & Y. Benayahu, 2009. The role of differential survival patterns in shaping coral communities on

Author's personal copy

neighboring artificial and natural reefs. Journal of Experimental Marine Biology and Ecology 369: 1–7.

Reinicke, G.B., 1997. Different modes of adaptation to light conditions in Red Sea Xeniidae reflected by their depth distribution patterns (Octocorallia, Alcyonacea) Proceeding of the 6th International Conference on Coelenterate Biology 1995: 393–402.

Rilov, G. & Y. Benayahu, 1998. Vertical artificial structures as an alternative habitat for coral reef fishes in disturbed environments. Marine Environmental Research 45(4/5): 431–451.

Ritson-Williams, R., S. N. Arnold, N. D. Fogarty, R. S. Steneck, M. J. Vermeij & V. J. Paul, 2009. New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithsonian Contributions to the Marine Sciences 38: 437–457.

Rocha, R. J. M., J. Serôdio, M. Costa Leal, P. Cartaxana & R. Calado, 2013. Effect of light intensity on post-fragmentation photobiological performance of the soft coral *Sinularia flexibilis*. Aquaculture 388–391: 24–29.

Roth, M. S., T. Y. Fan & D. D. Deheyn, 2013. Life history changes in coral fluorescence and the effects of light intensity on larval physiology and settlement in *Seriatopora hystrix*. PLoS One 8(3): e59476. doi 10.1371/journal.pone.0059476

Sanchez, J. A., 1999. Black coral-octocoral distribution patterns on Imelda Bank, a deep-water reef, Colombia, Caribbean Sea. Bullatine of Marine Sciences 65(1): 215–225.

Santangelo, G., L. Bramanti, S. Rossi, G. Tsounis, I. Vielmini, C. Lott & J. M. Gili, 2012. Patterns of variation in recruitment and post-recruitment processes of the Mediterranean precious gorgonian coral *Corallium rubrum*. Journal of Experimental Marine Biology and Ecology 411: 7–13.

Sheppard, C. R. C., 1980. Coral cover, zonation and diversity on reef slopes of Chagos Atolls, and population structures of major species. Marine Ecology Progress Series 2: 193–205.

Todd, C. D., 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? Hydrobiologia 375(376): 1–21.

Vermeij, M. J. A., 2005. Substrate composition and adult distribution determine recruitment patterns in a Caribbean brooding coral. Marine Ecology Progress Series 295: 123–133.

Vermeij, M. J. A., 2006. Early life- history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy. Coral Reefs 25: 59–71.

Vermeij, M. J. A. & R. P. M. Bak, 2002. How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. Marine Ecology Progress Series 233: 105–116.