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Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment

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Abstract

Most artificial reef (AR) studies have examined the early colonization stages of benthic communities, while only a few have monitored the development of AR communities beyond the initial successional phases and evaluated the time scale needed for such development. In addition, despite the proliferation of AR studies, comparative studies between artificial and natural reefs (NRs) are scarce. We present here the monitoring results of initial (1–2 year) and progressed (10 year) stages of the developing benthic communities of a purpose-planned AR submerged at Eilat, Israel (Red Sea), and compare them to its adjacent NR. Visual surveys of macro-invertebrates were conducted on the initial stages and coral communities were characterized at the progressed stage, using belt transects. The results demonstrate a distinct shift in species composition of the AR communities along the monitoring periods: from a soft coral dominated community, comprised mainly of *Dendronephthya hemprichi*, in initial developmental stages of up to two years post-deployment, to a community dominated by the sponge *Crella cyatophora* at year 10. Distinct differences in coral species count, living cover and diversity were found between the AR and its neighboring NR. We estimate the time frame required to develop a progressed diverse AR community to be well over a decade, even in tropical ecosystems. The factors shaping the species composition of purpose-designed ARs in a coral reef environment, including structural design, spatial orientation, depth and age, are discussed.

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1. Introduction

The historical use of artificial reefs (ARs) in fisheries has been expanded to include control of beach erosion, mitigation of detrimental impacts on habitats, conservation of biodiversity and to test ecological theories (Baine, 2001; Seaman & Jensen, 2000). In recent years, great strides have been made in the understanding of artificial habitat ecology, although many questions regarding their performance and environmental impacts remain unanswered (Carr & Hixon, 1997). One of the reasons for the poor understanding of the ecology of ARs is the lack of knowledge of their effect on their surrounding natural environment (Sheng, 2000; Svane & Petersen, 2001). Hence, it is of prime importance to engage in comparative studies between artificial and natural reefs (NRs) (Perkol-Finkel & Benayahu, 2004; Rilov & Benayahu, 2000; Svane & Petersen, 2001).

Unplanned ARs, such as sunken ships, oil and gas platforms and breakwaters, offer substratum for settlement of benthic invertebrates and fish. This type of AR is common worldwide and can be considered as a natural experiment in community development on ARs, accessible for monitoring (e.g., Perkol-Finkel & Benayahu, 2004; Rilov & Benayahu, 2000; Wendt, Knott, & Van Dolah, 1989). Another type of AR is that of a designed structure, pre-planned for this function, and with the advantages of being a means for creating carefully planned habitats, integrating biology and engineering (Bohnsack, Johnson, & Ambrose, 1991). Nowadays, most ARs are purpose-planned structures, built according to accepted principles of safety, durability and effectiveness (Baine, 2001; CARPG, 1998; Seaman & Jensen, 2000).

When designing ARs several factors should be taken into consideration, including type of materials (reviewed in Baine, 2001), size and orientation (e.g., Oren & Benayahu, 1997; Rilov & Benayahu, 2000), and complexity and durability (Connell & Jones, 1991). The environmental factors to be considered when positioning an AR should include geographical location, surrounding substratum, proximity to natural habitats, depth and water conditions in the area of deployment (Sheng, 2000). Furthermore, different designs of ARs may offer an array of particular environmental conditions, such as light and current regimes or sedimentation load, that may influence recruitment onto the ARs (Abelson & Denny, 1997). Only purpose-planned ARs can offer a specific design that, according to their primary goals, will produce maximum yield, making them a potential tool to examine species' response to different conditions and to test ecological theories (Bohnsack, Ecklund, & Szmant, 1997; Connell & Slatyer, 1977). The application of planned ARs for conservation and restoration of marine habitats, including coral reefs, has greatly increased over the years (Clark & Edwards, 1999; Pickering, Whitmarsh, & Jensen, 1998). However, an assessment of their performances indicates that many do not meet their goals (reviewed in Baine, 2001).

Several studies have examined early stages of colonization of ARs (Bailey-Brock, 1989; Cummings, 1994; Palmer-Zwahlen & Aseltine, 1994). These stages follow the inhibition model of succession as suggested by Connell and Slatyer (1977), in which initial settlers dominate the substratum, thus delaying the appearance of secondary ones. Only after a shift in community structure has occurred will additional species follow and succession progress to the point where earlier settlers change the surrounding in a way that makes it suitable for later ones (Connell & Slatyer, 1977). Although several AR studies have described such phases in community changes via short-term monitoring (Cummings, 1994; Fitzhardinge & Bailey-Brock, 1989; Palmer-Zwahlen & Aseltine, 1994), only a few studies have evaluated the time scale needed for their development beyond the initial successional phases (Carr & Hixon, 1997). Most of the long-term studies found differences between artificial and natural reef communities, including higher presence of large individuals of corals and sponges at the NRs, as well as higher coral diversity in NRs than in ARs (Wendt et al., 1989; Wilhelmsson, Ohman, Stahl, & Shlesinger, 1998).

The current study presents monitoring results of initial (1–2 year) and progressed (10 year) stages of the developing benthic communities of a planned AR, submerged in 1992 at the northern tip of the Gulf of Eilat, Israel (Red Sea). This was the first planned AR submerged in the area and was designed specifically for research purposes, as a pilot experiment for a possible deployment of future ARs designed for recreational use in the area. We studied the benthic communities on the AR and compared them to that of its adjacent NR. The results demonstrate a distinct shift in the species composition of the AR communities along the monitoring periods and distinct differences in coral species count, living cover and diversity from the neighboring NR. We assess the time frame required to develop a progressed diverse coral community on an AR. The factors shaping the species composition of purpose-designed ARs in a coral reef environment, including structural design, spatial orientation, depth and age, are discussed.

2. Materials and methods

2.1. Study site

The studied AR was submerged on April 1992 at 32 m depth on a sandy bottom at the northern end of the Gulf of Eilat, Israel (Fig. 1(a)). The AR was deployed in spring in order to provide the substratum with three months of acclimation prior to the main reproduction season (summer) of most corals in the area (e.g., Benayahu, 1997; Loya, 1986). The AR consists of two truncated square metal pyramids (Fig. 1(b)), a large outer one (Fig. 1(c) and (d)) and a smaller inner one (Fig. 1(e) and (f)), termed hereon Pyramid-AR. Its design followed the conclusions of a previous study on benthic and fish communities developed on two oil jetties in Eilat (150 and 250 m long, respectively) constructed in the late 1960s (Goren, 1992; Rilov & Benayahu, 1998). Vertical steel pillars (0.65–1 m in diameter) located on a moderate sandy slope supported these jetties and most of the pillars were partially surrounded by barbed

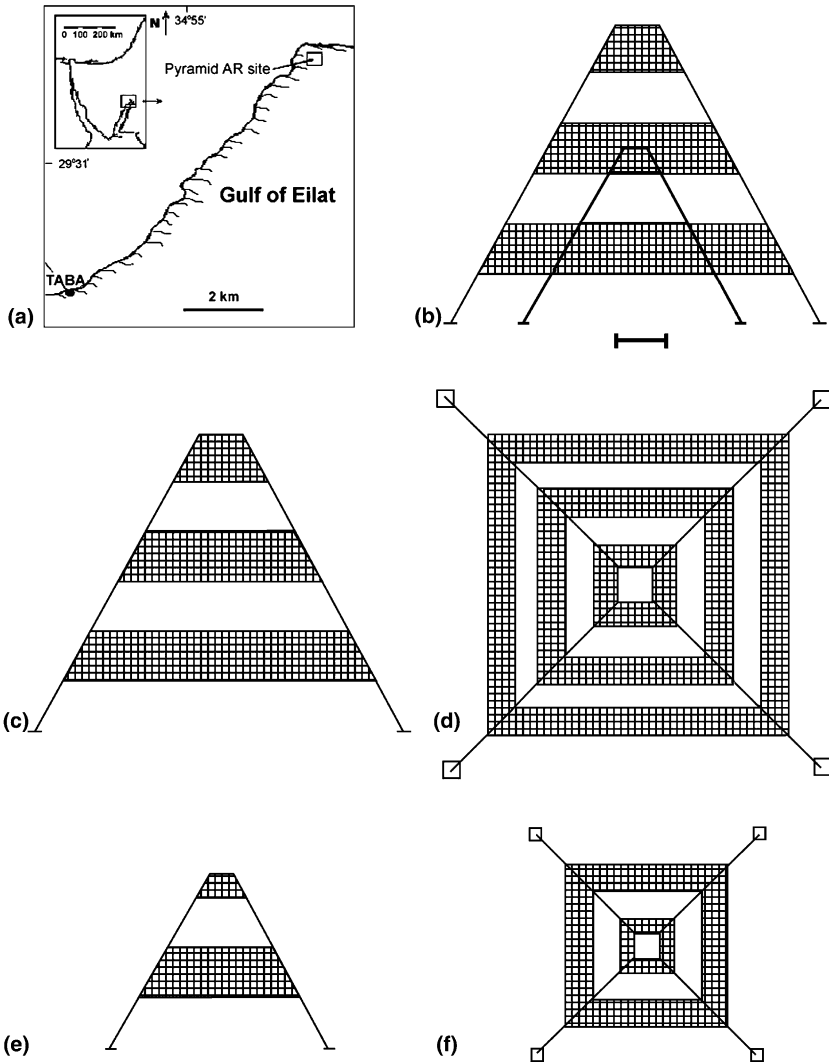


Fig. 1. Pyramid artificial reef (Pyramid AR). (a) The study site. Schematic illustrations; (b) two truncated square pyramids; (c) side view of outer pyramid; (d) view from above of outer pyramid; (e) side view of inner pyramid; (f) view from above of inner pyramid. Scale bar in (b), 200 cm, applies to (b)–(f).

wire, adding much to their structural complexity. The pillars and the barbed wire had rapidly become covered by diverse benthic organisms, including stony and soft corals (Goren, 1992; personal observations).

In the current study the faces of the two pyramids were inclined at an angle of 62° (Fig. 1(b)). Each face consisted of three parallel 2-m wide belts (outer pyramid: Fig. 1(c)) and one 2 m + one 1 m wide belt (inner pyramid: Fig. 1(e)), made of 8-mm thick

reinforced welded metal mesh (10 × 10 cm), supported by a horizontal metal frame. The belts alternated at 2-m intervals, from the bottom of each pyramid and up to its truncated top (Fig. 1(b)–(f)). The inclined supporting frames of each face were made of steel pipes (diameter: 15 cm) onto which the mesh belts were welded. The outer pyramid had a height of 12 m (20 m below sea surface) and a 15-m base-side (Fig. 1(c) and (d)); its belts (all four faces) were set at depths of 30–27 m (deep), 25–23 m (middle) and 21–19 m (shallow), with a total surface area of ca 96, 64 and 24 m², respectively. The inner pyramid had a height of 7 m and a 9 m base-side (Fig. 1(e) and (f)). Its belts were set at 30–27 m (deep) and 20–19 m (shallow), with a total surface area of 48 and 10 m², respectively. The total surface area of the Pyramid-AR mesh was thus ca. 242 m². The structural design of the AR was aimed at maximizing its stability, while the mesh supplied ample surface area for settlement of benthic organisms. The bottom depth was dictated by diving limitations to 30 m and its upper height to avoid hazard to marine traffic.

The adjacent NR surveyed for comparison was at a depth of 19–27 m, continuous in its deep portion, and comprising scattered patches of hard substratum at its shallower end. The deepest part of the NR was situated 15 m from the base of the Pyramid-AR, gradually ascending to 15 m depth and a distance of up to 50 m from the Pyramid-AR.

Data collection throughout the whole survey required ca. 150 SCUBA dives.

2.2. Early stages of colonization by benthic invertebrates

We monitored recruitment of benthic organisms onto the AR during the first two years following its deployment by conducting visual examination of the macro-invertebrates that had appeared as early as one month after deployment. Samples of fouling organisms were collected, preserved and sent to specialists for identification when needed. Once stony and soft corals began to appear, quantitative coral surveys were performed at two time points: one year (March–May 1993) and two years (March–July 1994) post-deployment. Since data collection required long bottom time, diving safety dictated spread of the dives over each time point. During each survey, the whole surface area of the Pyramid-AR was carefully examined. At the one-year survey, all settled fouling organisms were noted. Stony and soft coral recruits were identified to species level, measured to the nearest cm (see also below) and individually marked with numbered PVC tags for population census. The recruits on the Pyramid-AR were recorded in relation to their location on the inner or outer pyramid; deep, middle or shallow mesh belt; and north, south, east or west facing.

2.3. Monitoring of *Dendroneophthya* soft corals

Since colonies of the soft coral, genus *Dendroneophthya*, were the predominant recruits at the early stages of the study (see Section 3.2), they were counted and measured at the two initial survey points (see above) as well as at a third time-point (December 2002), ca. 10 years after deployment of the Pyramid-AR. *Dendroneophthya*

colonies were tagged and recorded as described above. The length of each colony was measured when fully inflated along its vertical axis, from the point of attachment to the tip of its longest branch. Data analysis was performed using the STATISTICA program (see Section 2.5.1).

2.4. Community studies on the Pyramid-AR and NR

The community structure of stony and soft corals was studied from a series of 10-m belt transects, following the methodology developed by Loya (1972). The surveyed area along a transect consisted of a 5-cm belt at each side of the line, thus forming a belt transect of 10×0.1 m. This modification of Loya's method increased the probability of recording data from the mesh-made surface. All stony and soft corals intercepted by the transect were recorded and their maximal projected length was measured (for further details see Perkol-Finkel & Benayahu, 2004). The hermatypic hydrozoan *Millepora dichotoma* was also included in this study, as well as the sponge *Crella cyathophora*, which was found to be an important component of the living cover at the Pyramid-AR during preliminary observations. Transects on the Pyramid-AR were made on the outer faces of the mesh belt surfaces. All transects originated from the northern edge of the western face of the pyramid (Fig. 1(b)–(f)), with a random starting point of the transects along the frame of the mesh belt. Transects ran parallel to the bottom at the three depth belts. Transects on the inner pyramid comprised the two deeper depth belts. As dictated by the dimensions of the pyramid-faces, transects in the 19 m (outer pyramid) and 24 m (both outer and inner pyramids) depth belts ran along more than one face of the pyramid. Four transects were made for each depth belt on each of the two pyramids. On the NR, transects were placed at respective depths, ($n = 3$ for each depth). The transect surveys of the outer Pyramid and of the NR were conducted during August–November 1999. A visual census of stony and soft coral species was done in August 2000 in order to obtain a total species list for the Pyramid-AR. The inner Pyramid was surveyed during April–May 2002. The prolonged periods of data collecting were mainly due to diving limitations.

The relative abundance (RA) of each species (see Rilov & Benayahu, 1998) was calculated according to its contribution to living cover: $RA = P_i/P_{\text{total}} \times 100$, where P_i is the pooled living cover of the i th species from all transects at a given site and P_{total} the pooled total living cover of all species in all transects at a given site. RA was calculated separately for stony and soft corals. The resulting values were then transformed into abundance categories (%): not recorded ($RA = 0$), rare ($0 < RA < 0.1$), uncommon ($RA = 0.1–1$), common ($RA = 1–10$), abundant ($RA = 10–20$) and dominant ($RA > 20$). RA was also calculated for stony and soft corals pooled together, termed here as total living cover. Species cover diversity (H'_c) was calculated using the Shannon–Weaver function (Shannon & Weaver, 1964), applied to stony and soft corals separately by using values of species contribution to living cover (Loya, 1972). All averaged values of the community features are presented with 95% confidence intervals (CI).

2.5. Statistical analyses

2.5.1. Univariate analyses

Comparison of *Dendronephthya* colony length among survey time points was performed by ANOVA (using the STATISTICA program) on $\log(x)$ transformed data. Factorial ANOVA was performed to detect differences in colony length of *Dendronephthya* among the time points (1, 2 and 10 years), depth belts (deep, middle and shallow) and facings (north, south, east or west). Analyses were performed on pooled recruitment data derived from both the inner and the outer pyramids.

Comparisons of living coral cover, species count and H'_c between the Pyramid-AR and NR were performed by ANOVA (using the STATISTICA program), run separately for stony and soft corals. In order to meet ANOVA assumptions, the stony and soft living cover and species count analyses were done on transformed data ($\log(x)$ and \sqrt{x} , respectively). We considered the inner pyramid 19-m depth belt as a missing value. Initial analyses tested for differences between the inner and the outer pyramids and the NR, followed by Scheffe tests, after which all statistical analyses were performed on pooled inner and outer pyramids versus the NR (see Section 3.3.2).

2.5.2. Multivariate analysis

Two multivariate techniques were used to detect community patterns and performed using the PRIMER (V 5.2.9) software program (Clarke & Warwick, 2001). Data sets included percentage cover for the stony and soft coral species (rows) in each of the belt transects (columns). A two-dimensional non-metric multidimensional scaling (MDS), based on the rank order of the Bray–Curtis similarities (Bray & Curtis, 1957), was used to define and visualize community patterns. A $\log(x + 1)$ transformation was applied to the raw data. K -dominance curves (Lambhead, Platt, & Shaw, 1983) were performed on both Pyramid-AR and NR. All analyses were performed on a full data set including both stony and soft corals.

3. Results

3.1. Early stages of colonization by benthic invertebrates

During the first 2–10 months post-deployment various fouling invertebrates appeared on the mesh of the Pyramid-AR, of which 11 species were very prominent. *P. aegyptiaca* and *Pteria macroptera* (Bivalvia, Mollusca) were conspicuous mainly on the mesh of the outer pyramid, with densities up to 6–8 individuals per 10×10 cm. Patches of the colonial Ascidiacea (Tunicata) *Didemnum granulatum*, *Didemnum* sp. and the solitary species *Pyura momus* were also abundant. Among the Bryozoa *Acaethodesia savartii*, *Bugula neritina*, *Celloporina costazzii* and *Schizoporella errata* covered large portions of the Pyramid-AR intermingled with the Hydrozoa species *Pennaria disticha* and *Tubularia crocea*. All the aforemen-

tioned species together covered almost the entire steel surface. During this first year additional organisms appeared, including the sponges *Negombata magnifica* and *Siphonochalina* sp.; however their densities were much less conspicuous.

The first soft coral recruits to the Pyramid-AR were of *Dendronephthya hemprichi*, already observed on the mesh surface 8 months after deployment (September 1993) and they rapidly became the most dominant coral recruit there (see below). At the first time point we recorded the soft corals *Xenia* sp., *Nephthea* sp., *Acabaria biserialis* and the stony coral *Stylophora pistillata*, each species represented by a single colony. At the second time point *Dendronephthya* colonies outnumbered all other coral recruits, predominantly represented by *D. hemprichi* and rarely intermingled with *D. sinaiensis*. At this time point a few colonies of other soft coral species were also recorded, including *Scleronephthya corymbosa*, *Stereonephthya cundabuluensis*, *Heteroxenia fuscescens*, *Xenia* sp. and *A. biserialis*.

3.2. Monitoring of *Dendronephthya* soft corals

At the first time point *Dendronephthya* recruits were found only on the outer pyramid, with only a few having recruited also to the inner pyramid by the second survey and hardly any additional ones by the third (10 year) survey; therefore all analyses were conducted on data pooled for the inner and outer pyramids. Temporal changes in the population of *Dendronephthya* on the Pyramid-AR are well indicated in the total colony count recorded for each time point (Table 1). Their number increased from 81 in year 1 to 359 in year 2 and then decreased to only 25 in year 10. The average colony length of *Dendronephthya* colonies was 10.39 ± 6.43 , 19.44 ± 19.96 and 12.67 ± 13.43 cm, indicating significant differences among the respective time points (Table 1, one way ANOVA: $F_{(df=2)} = 8.10$, $P < 0.001$). Minimal colony length at all time points was 2 cm, while the maximal length changed over time from 32 to 120 and then 64 cm. Notably, during the second year post-deployment of the Pyramid-AR several *Dendronephthya* colonies reached what proved to be a maximum length of 120 cm. Size distribution of *Dendronephthya* over time revealed that most colonies (66–91%, depending on the time point) ranged between 1 and 20 cm in length (Fig. 2). No significant differences were found in their length on the different facings and mesh belts of the Pyramid-AR (data not shown, two way ANOVA-facings: $F_{(df=2,3)} = 0.32$, $P > 0.05$; Belts: $F_{(df=2,2)} = 0.62$, $P > 0.05$).

Table 1
Dendronephthya colonies at the Pyramid-AR

Time point	Total # of colonies	Avg \pm SD (cm)	Size range (cm)
1 year	81	10.39 \pm 6.43	2–32
2 years	359	19.44 \pm 19.96	2–120
10 years	25	12.67 \pm 13.43	2–64

Total number of colonies, average length (\pm SD) and size range at three time points.

Length Distribution of *Dendronephthya*

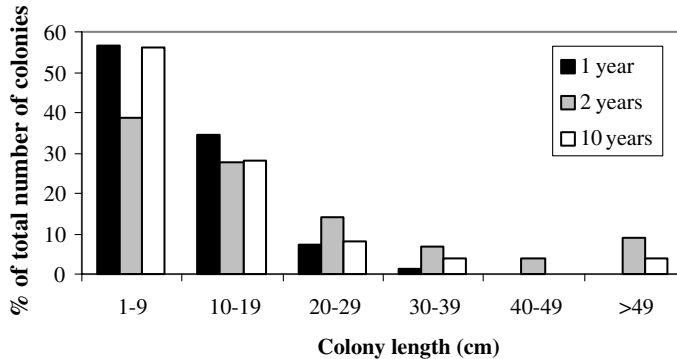


Fig. 2. Size distribution of *Dendronephthya* colonies on the Pyramid-AR 1 year ($n = 81$ colonies), 2 years ($n = 359$) and 10 years ($n = 25$) after deployment. Data for each size group are given as the ratio between the number of colonies in each group and the total number of colonies.

3.3. Community studies on Pyramid-AR and NR

3.3.1. Species composition

A total of 69 stony coral species (including the hydrozoan *M. dichotoma* and the antipatharian *Antipathes* sp.) and 20 soft coral species were found in the transects conducted on the Pyramid-AR and NR (Tables 2 and 3). Additional species were added from the visual surveys as indicated in these tables, adding 15 stony coral and two soft coral species to the Pyramid-AR list. The total number of stony coral species in the NR was more than double that in the Pyramid-AR (65 and 30, respectively, Table 2). *Psammocora nierstraszi* and *Seriatopora caliendrum* were the most common species in the NR, each contributing 9–10% of the total stony coral cover, along with *Pavona varians* and *Favites pentagona*, each of which accounted for 6–7% of the total stony coral cover. *P. nierstraszi* was also abundant in the Pyramid-AR, contributing 16% of the stony coral cover, followed by *Pocillopora danae*, which accounted for 13%. Of the common stony coral species in the Pyramid-AR, *Porites lutea* contributed the highest cover (7%) followed by *Cladopsammia gracillis* and *Cyphastrea chalcidicum*, each accounting for 6–7%. The additional stony coral species yielded from the visual census were from five families, including *Acropora scandens*, which did not appear in any of the belt transects. The majority of the species added to the Pyramid-AR by the census were from the Faviidae (Table 2), most of which appeared on the narrow horizontal panels that comprised the inner frame of the mesh belts.

The total number of soft coral species was similar in both Pyramid-AR and NR (Table 3). *Xenia biseriata* dominated, contributing a third of the soft coral cover, while two other xeniids were also abundant there: *Xenia hicksoni* and *Heteroxenia fuscescens* (17% and 14%, respectively). Xeniids were also dominant in the Pyramid-AR, particularly *X. hicksoni*, contributing nearly 40% of the soft coral cover while

Table 2

Relative abundance (RA: see Section 2.4) of stony corals occurring in the transects at the Pyramid-AR and NR, according to their contribution to living cover

Family	Species	AR	NR
Acroporidae	<i>Acropora eurystoma</i>	—	**
	<i>Acropora hemprichi</i>	**	***
	<i>Acropora scandens</i>	◆	—
	<i>Acropora variabilis</i>	**	***
	<i>Astreopora myriophthalma</i>	—	***
	<i>Montipora danae</i>	**	**
	<i>Montipora erythraea</i>	◆	**
	<i>Montipora granulata</i>	***	***
	<i>Montipora lobulata</i>	—	**
	<i>Montipora meandrina</i>	—	**
	<i>Montipora</i> sp.	***	**
	<i>Montipora tuberculosa</i>	—	**
Pocilloporidae	<i>Pocillopora danae</i>	****	*
	<i>Seriatopora angulata</i>	***	**
	<i>Seriatopora caliendrum</i>	***	***
	<i>Seriatopora</i> sp.	***	—
	<i>Stylophora pistillata</i>	***	**
	<i>Stylophora prostrata</i>	—	**
Oculinidae	<i>Galaxea fascicularis</i>	—	**
Siderastreidae	<i>Coscinaraea monile</i>	***	**
	<i>Psammocora nierstraszi</i>	****	***
	<i>Siderastrea lilacea</i>	—	*
Agariciidae	<i>Gardineroseris planulata</i>	—	*
	<i>Leptoseris fragilis</i>	***	**
	<i>Leptoseris tubulifera</i>	***	**
	<i>Pavona clavus</i>	—	**
	<i>Pavona decussata</i>	◆	***
	<i>Pavona gardineri</i>	◆	***
	<i>Pavona varians</i>	***	***
Fungiidae	<i>Fungia</i> sp.	**	***
	<i>Padobacia crustacea</i>	—	***
Pectiniidae	<i>Echinophyllia aspera</i>	***	***
	<i>Mycedium tubifex</i>	**	***
Dendrophylliidae	<i>Balanophyllia gemmifera</i>	—	**
	<i>Cladopsamia gracillis</i>	***	—
	<i>Turbinaria</i> sp.	—	**
Caryophylliidae	<i>Gyrosmitia interrupta</i>	—	***
	<i>Plerogyra sinuosa</i>	◆	**
Mussidae	<i>Acanthastrea echinata</i>	◆	***
	<i>Blastomussa</i> sp.	—	**
	<i>Cynarina</i> sp.	***	**
	<i>Lobophyllia corymbosa</i>	—	***
	<i>Lobophyllia hemprichii</i>	◆	**

Table 2 (continued)

Family	Species	AR	NR
Faviidae	<i>Cyphastrea chalcidicum</i>	***	***
	<i>Cyphastrea microphthalma</i>	***	***
	<i>Echinopora gemmacea</i>	◆	**
	<i>Favia doreyensis</i>	–	**
	<i>Favia fавus</i>	***	**
	<i>Favia speciosa</i>	◆	***
	<i>Favia</i> sp.	**	**
	<i>Favites abdita</i>	**	***
	<i>Favites halicora</i>	***	***
	<i>Favites pentagona</i>	***	***
	<i>Goniastrea pectinata</i>	◆	**
	<i>Leptastrea bottae</i>	◆	**
	<i>Leptastrea transversa</i>	◆	***
	<i>Leptoria phrygia</i>	–	**
	<i>Platygyra lamellina</i>	**	***
	<i>Platygyra subdentata</i>	–	**
	<i>Plesiastrea mammillosa</i>	◆	***
Poritidae	<i>Alveopora daedalea</i>	–	**
	<i>Goniopora</i> sp. 1	–	***
	<i>Goniopora</i> sp. 2	–	**
	<i>Goniopora</i> sp. 3	–	**
	<i>Porites lutea</i>	***	***
	<i>Porites mayeri</i>	–	**
	<i>Porites</i> sp.	–	**
Milleporidae	<i>Millepora dichotoma</i>	**	**
Antipatharia	<i>Antipathes</i> sp.	**	–

Species are listed according to families; with the following categories of relative abundance (%): –, not recorded; *, rare ($0 < RA < 0.1$); **, uncommon ($RA = 0.1-1$); ***, common ($RA = 1-10$); ****, abundant ($RA = 10-20$); *****, dominant ($RA > 20$). Species recorded in visual census are marked ◆.

X. umbellata accounted for 24%. *Xenia* and *Ovabunda* species appeared in high densities on the Pyramid-AR with numerous aggregated colonies. *Dendronephthya hemprichi* was common in the Pyramid-AR (11%), but did not appear at all in the NR (see above).

The 10 top-ranked species in the AR and NR, similarly based on their relative contribution to living cover, with stony and soft corals pooled together, are presented in Fig. 3. All the other corals that were found at the two reefs contributed the remaining cover. The sponge *Crella cyatophora* was included in the top 10 species due to its immense contribution to the total living cover in the AR (see also below). Both the Pyramid-AR and the NR had an almost even number of stony and soft coral species among the 10 top-ranked species and five of them were common to both reefs. Two of the soft corals common to the Pyramid-AR and NR were *Xenia hicksoni*, ranked second in both, and *Heteroxenia fuscescens*, fifth in the NR and tenth in the AR. On the other hand, some of the top 10 species found in one reef did not appear among the top 10 of the other, nor were they recorded in that reef at all.

Table 3

Relative abundance (RA: see Section 2.4) of soft corals occurring in the transects at the Pyramid-AR and NR according to their contribution to living cover

Family	Species	AR	NR
Tubiporidae	<i>Tubipora musica</i>	***	***
Alcyoniidae	<i>Cladiella pachyclados</i>	—	**
	<i>Rhytisma fulvum fulvum</i>	****	***
	<i>Sarcophyton glaucum</i>	—	***
	<i>Sinularia</i> sp.	—	***
Nephtheidae	<i>Dendronephthya hemprichi</i>	****	—
	<i>Dendronephthya sinaiensis</i>	**	—
	<i>Litophyton</i> sp.	**	***
	<i>Paralemnalia thyrsoides</i>	**	***
	<i>Scleronephthya corymbosa</i>	**	—
	<i>Stereonephthya cundabiluensis</i>	◆	***
Xeniidae	<i>Anthellia glauca</i>	—	**
	<i>Heteroxenia fuscescens</i>	***	****
	<i>Ovabunda macrospiculata</i>	—	***
	<i>Ovabunda obscuronata</i>	***	—
	<i>Xenia biseriata</i>	—	*****
	<i>Xenia hicksoni</i>	*****	***
	<i>Xenia impulsatilla</i>	—	***
	<i>Xenia umbellata</i>	*****	—
	<i>Xenia</i> sp.	**	—

Footnote as in Table 2.

Such was the case for the top ranked species in the NR, *X. biseriata*, as well as for the second and fourth ranked species in the Pyramid-AR, *X. umbellata* and *D. hemprichi*, respectively. Notably, nearly 70% of the living cover in the Pyramid-AR was contributed by *C. cyatophora*. This species was rarely found on the NR where it barely exceeded 0.1% of the living cover. The contribution of other species, not ranked among the top 10, was considerably higher in the NR than in the Pyramid-AR (45% and 9%, respectively).

3.3.2. Community analyses

Initial statistical analysis indicated no significant differences between the inner and outer pyramids for nearly all parameters examined (one-way ANOVA, $P > 0.05$). The parameters that did differ were those of stony coral diversity and soft coral cover, for which the differences between the two pyramids were much smaller than those from each pyramid to the NR (Scheffe test). Based on this finding, all of the following tests were performed on differences between reef types (AR vs. NR), pooling both pyramids.

3.3.3. Species count

The average species number per transect for both stony and soft corals significantly differed between the Pyramid-AR and NR (Table 4, two-way ANOVA:

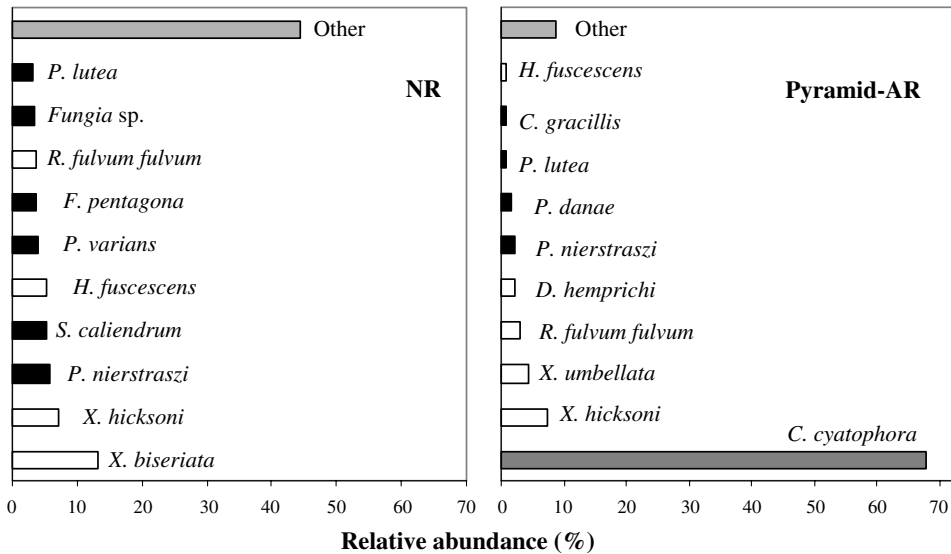


Fig. 3. Relative abundance of the 10 top ranked coral species (stony and soft corals pooled), and the sponge *Crella cyatophora* based on their contribution to living cover on the Pyramid-AR and NR, for stony corals (black bars), soft corals (white bars), *C. cyatophora* (gray bars) and other species not ranked among the top 10 (dotted bars). AR, artificial reef; NR, natural reef.

Table 4
Community features on the Pyramid-AR and NR

		AR (<i>N</i> = 20)	NR (<i>N</i> = 9)	<i>P</i> value
		Avg ± SD	Avg ± SD	
Average species count	Stony corals	5.90 ± 3.32	26.33 ± 5.22	<0.001
	Soft corals	2.25 ± 1.77	5.88 ± 2.26	<0.001
Average living cover	Stony corals	5.70 ± 4.27	35.51 ± 7.99	<0.001
	Soft corals	8.57 ± 11.22	25.51 ± 10.00	<0.01
	Sponge ^a	35.66 ± 13.38	0.08 ± 0.18	<0.001
Average diversity	Stony corals	1.04 ± 0.80	2.91 ± 0.25	<0.001
	Soft corals	0.47 ± 0.54	1.29 ± 0.40	<0.001

N, number of transects.

^a *Crella cyatophora*.

$F_{(df=1,2)} = 104.39$ for stony corals and 45.46 for soft corals; $P < 0.0001$, for both). Average stony coral count on the NR was >4-fold higher than on the Pyramid-AR (26.33 ± 5.22 and 5.90 ± 3.32, respectively). Average soft coral count exhibited a similar but less pronounced pattern (NR: 5.88 ± 2.26, compared to the Pyramid-AR: 2.25 ± 1.77). Stony coral count was not affected by depth on either the Pyramid-AR or the NR (two-way ANOVA: $F_{(df=1,2)} = 0.82$, $P > 0.005$). The effect of depth on the soft coral species count was similar for both the Pyramid-AR and NR (two-way

ANOVA, interaction term: $F_{(df=1,2)} = 0.79$, $P > 0.05$). Soft coral count increased with depth on both reefs, with that of the NR being twice that of the Pyramid-AR (two-way ANOVA: $F_{(df=1,2)} = 14.06$, $P < 0.0001$).

3.3.4. Living cover

Average percent cover per transect for both stony and soft corals was significantly different between the Pyramid-AR and NR (Table 4, two-way ANOVA: $F_{(df=1,2)} = 69.15$ and 10.51 , $P < 0.01$ for both). Average stony coral cover on the NR was nearly 6-fold higher than on the Pyramid-AR ($35.51 \pm 7.99\%$ and $5.70 \pm 4.27\%$, respectively), whereas soft coral cover in the former was twice that of the latter (NR: $25.51 \pm 10.00\%$ compared to Pyramid-AR: $8.57 \pm 11.22\%$). However, a remarkable addition to the living cover on the Pyramid-AR was due to the sponge *C. cyatophora*, which added an average of $35 \pm 13.38\%$ to the total living cover there, in comparison to almost none on the NR. Depth had no effect on the stony or soft coral cover in both reefs (two-way ANOVA: $F_{(df=1,2)} = 1.98$ for stony corals and 1.03 for soft corals, $P > 0.05$ for both).

3.3.5. Living cover diversity

Average diversity significantly differed between the Pyramid-AR and NR for both stony and soft corals (Table 4, two-way ANOVA: $F_{(df=1,2)} = 39.22$ for stony corals and 27.98 for soft corals, $P < 0.001$ for both). Stony coral diversity was threefold higher in the NR than in the Pyramid-AR ($H'_c = 2.91 \pm 0.25$ and 1.04 ± 0.80 , respectively). Soft coral diversity showed the same pattern, although these values for both reefs were much lower than those of the stony coral diversity (NR: $H'_c = 1.29 \pm 0.40$ and for the Pyramid-AR: $H'_c = 0.47 \pm 0.54$). Stony coral diversity was not influenced by depth (two-way ANOVA: $F_{(df=1,2)} = 0.15$, $P > 0.05$). Soft coral diversity in contrast was affected by depth (two-way ANOVA: $F_{(df=1,2)} = 5.17$, $P < 0.05$), with a moderate increase in diversity with depth at both reefs.

3.4. Multivariate analysis

MDS analysis of the complete data set, comprising both stony and soft corals at the Pyramid-AR and NR, including the sponge *C. cyatophora*, revealed a tight clustering of the NR transects, away from those of the Pyramid-AR (Fig. 4(a)). The stress level for this analysis was very low, indicative of a very good representation of the community in the field. However, despite the severe $\log(x + 1)$ transformation used in order to diminish the influence of the most dominant species, the analysis was still greatly skewed by the dominance of *C. cyatophora* in the Pyramid-AR and its near absence from the NR. This is supported by Fig. 4(b), presenting the same analysis but excluding *C. cyatophora*, where the NR transects are still tightly clustered away from those of the Pyramid-AR, although the latter are scattered and the stress level is very high.

Dominance curves for the pooled data set, including *C. cyatophora*, exhibited a distinct separation between the Pyramid-AR and NR curves (Fig. 4(c)). The former

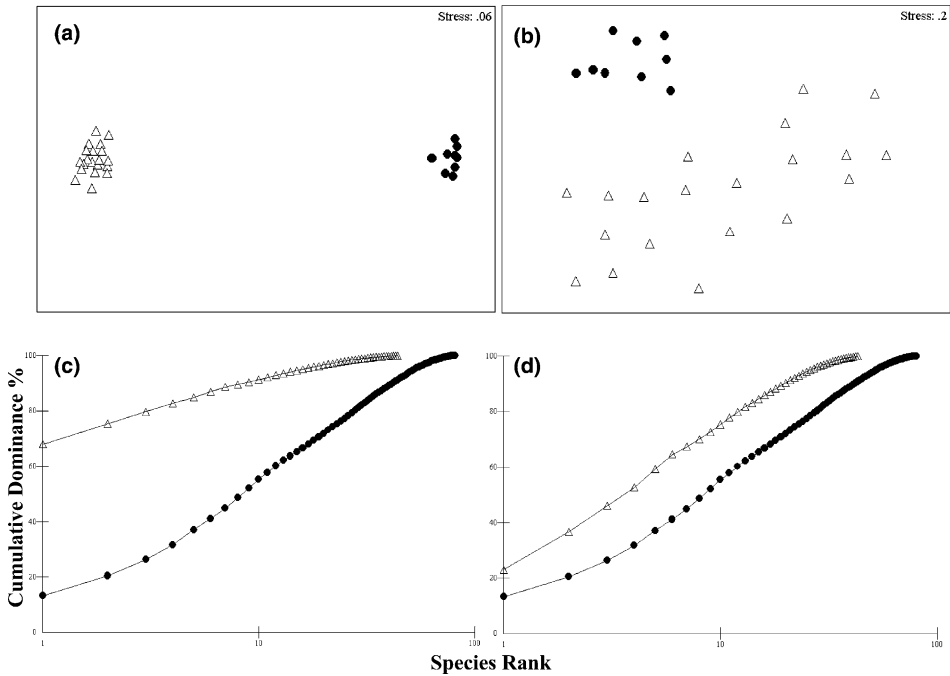


Fig. 4. (a) Two-dimensional MDS for $\log(x + 1)$ transformed living cover data of stony and soft corals at the Pyramid-AR = \triangle and NR = \bullet . (b) MDS excluding the sponge *C. cyatophora*. (c) K -dominance curves living cover data of stony and soft corals for both reefs. (d) K -dominance curves excluding the sponge *C. cyatophora*. AR, artificial reef; NR, natural reef.

curve was completely above the latter, with a very high starting point. With *C. cyatophora* excluded, the starting point of the Pyramid-AR curve was significantly lowered, albeit still entirely above that of the NR, indicating lower diversity at the Pyramid-AR (Fig. 4(d)).

4. Discussion

Despite their close proximity and equivalent depths the community structure and species diversity of the Pyramid-AR were found to differ from those of the neighboring NR. Our findings indicate a community shift from a soft coral dominated community in the initial developmental stages of up to two years past deployment, to a community dominated by the sponge *C. cyatophora* at year 10. Our finding of a lower coral cover and diversity in the Pyramid-AR compared to the adjacent NR indicates that the benthic community of the former may still be undergoing changes and reshaping its features even 10 years after deployment.

Fouling organisms recruited by the time of the initial surveys of the Pyramid-AR consisted mainly of a typical fouling assemblage, including hydrozoans, polychaets,

mollusks, bryozoans, tunicates and sponges, similar to other AR studies describing early colonization stages (Oren & Benayahu, 1997; Palmer-Zwahlen & Aseltine, 1994; Schuhmacher, 1988). Such fouling organisms constitute a minor benthic component on Eilat's NRs (Goren, 1992) yet play an important role in elevating the structural complexity of the ARs' substratum, making it suitable for coral settlement (Schuhmacher, 1988). Recruitment of the soft coral *D. hemprichi* in high numbers was prominent at the initial time points (>1 recruit per 1 m^2 mesh), and these later developed into large colonies (Table 1). This species nevertheless was not recorded at the neighboring NR (Table 3). Dominance of *Dendronephthya* corals may be the result of the Pyramid-AR design that offered mainly inclined flat surfaces (Fig. 1(b)–(f)), which may attract particular coral recruits. For example, it has been found that in the Great Barrier Reef (Australia) some stony corals prefer to settle on horizontal surfaces (Carleton & Sammarco, 1987; Mundy & Babcock, 2000); such surfaces were available on the inner frames of the mesh belts of the Pyramid-AR. These surfaces were included in the visual census and in fact added many stony coral species to the total species list (Table 2). The design of this AR as separate pyramids, one inside the other, did not yield detectable differences in coral communities of the two pyramids, nor did the different levels of the mesh belts. This may be due to the Pyramid-AR's location on a deep sandy bottom, with relatively low radiance levels and high turbidity, which decreased the effect of structural features on recruitment. The Pyramid-AR was designed to favor recruitment by species that flourish in environments exposed to currents that provide a constant supply of food particles (Fabricius, Genin, & Benayahu, 1995a; Goren, 1992). The steep relief of the Pyramid-AR, absent from the NR, may therefore explain the high abundance of *Dendronephthya* corals. The flourishing of this azooxanthellate coral on the inclined surfaces of the Pyramid-AR is derived from exposure to currents, which is typical to such habitats (Fabricius, Genin, & Benayahu, 1995b). As a passive suspension feeder, it depends on ambient currents for the supply of food particles, mainly phytoplankton (Fabricius et al., 1995a) and is found on steep reefs in the southern Gulf of Eilat (Benayahu, 1985). It is able to successfully dominate ARs due to its year-round spawning and a unique mode of clonal propagation (Dahan & Benayahu, 1997a, 1997b). Interestingly, its dominance has been recently documented in other ARs with vertical relief in Eilat (Perkol-Finkel & Benayahu, 2004). The present results reveal a decrease in the number and size of *Dendronephthya* colonies at the 10-year time point (Table 1). Due to a gap of ca. 6 years, when no data were collected at the Pyramid-AR, we could not determine when this decline had commenced. However, 10 years past deployment it was still ranked among the top 10 species contributing to the live cover (Fig. 3) and its size distribution remained similar to that at the initial time points (Fig. 2). Thus, it is likely that the structural features of the Pyramid-AR attract propagules of coral species, rare or even absent from the surrounding NR (see also Perkol-Finkel & Benayahu, 2004). This demonstrates the capability of purpose-designed ARs to elevate species diversity in their surrounding by increasing local habitat heterogeneity.

Although species composition differed between the Pyramid-AR and NR (Tables 2, 3), there were some similarities between the two at the species and generic levels (Fig. 3). The highest ranked stony coral of both reefs was *P. nierstraszi*, and the two

top ranked soft coral species of both reefs were Xenidiidae. However, despite their resemblance at the generic level, there were differences at the species level. Such was the case for the top ranked species of the NR, *X. biseriata*, not recorded in the Pyramid-AR, as well as for *X. umbellata* which ranked third in the latter yet did not appear on the NR. These differences may reflect incidental planulae dispersal from a more remote source, enhanced by a long competence period of Xenidiidae planulae (Ben-David-Zaslow & Benayahu, 1998). Considering the amount of bare substratum offered by the Pyramid-AR, pronounced recruitment is likely. Moreover, the ability of Xenidiidae soft corals to reproduce asexually, together with their rapid growth rate and colony translocation capabilities (Benayahu & Loya, 1985, 1987), contributed to their monopolization of space on some parts of the Pyramid-AR. Thus, in conclusion, the life history traits of Xenidiidae soft corals conduce to their success in both the Pyramid-AR and the NRs of the northern Gulf of Eilat.

Differences between the Pyramid-AR and NR were evident among the community features examined (Table 4). Stony and soft coral species counts in the NR were 2–3-fold higher than those of the adjacent Pyramid-AR, a difference that remained even after accounting for the species added from the visual census. The number of stony coral species recorded in the NR was also high in comparison to other proximate NRs (Loya, 1972; Perkol-Finkel & Benayahu, 2004). This may be due to the depth of the studied NR and its location away from the shoreline, relatively unexposed to the impact of sport divers. The higher soft coral species count in the NR compared to the Pyramid-AR contradicts recent findings for other shallow unplanned ARs in Eilat (Perkol-Finkel & Benayahu, 2004). This may be related to both the depth of the Pyramid-AR (19–32 m) and to its relatively young age. However, similar to the previous findings of Perkol-Finkel and Benayahu (2004), the Pyramid-AR had a higher proportion of soft coral cover and the NR a higher proportion of stony coral cover (Table 4). Einbinder (2003) found a similar ratio in initial recruitment patterns to experimental artificial surfaces placed at the Pyramid-AR and NR, indicating their different impacts on coral settlement through generating different sources of larvae.

The sponge *C. cyatophora* was the main reason for the reduced diversity at the Pyramid-AR compared to the NR, as reflected by the multivariate analyses (Fig. 4(a)–(d)). The pronounced dominance of this sponge greatly influenced the Pyramid-AR's community structure, and subsequently increased the differences between the Pyramid-AR and NR. Sponges and tunicates frequently occur on man-made surfaces submerged in marine waters (Holmstrom & Kjelleberg, 1994; Oren & Benayahu, 1997). In the present study, dominance of *C. cyatophora* on the Pyramid-AR may be the consequence of its extremely rapid growth rate, estimated to be up to 2–3 cm a month, particularly of newly settled individuals, along with a prolonged reproductive period (Burns, 2001). Furthermore, the timing of its larval release in early fall, soon after the major reproductive activity of most of Eilat's corals (Benayahu, 1997; Shlesinger & Loya, 1985), might have enhanced the competitive capabilities of *C. cyatophora* (e.g., Aerts, 1998; McCook, 2001) and reduced competition for space with settling coral larvae. It is suggested that the massive appearance of *C. cyatophora* induced a community shift at the Pyramid-AR, leading to elimination of some coral species and consequently reducing the total living cover and diversity com-

pared to the adjacent NR. Similarly, the reduction in population size of *Dendronephthya* colonies effectively demonstrates ongoing processes of community shift. Future monitoring of the Pyramid-AR will indicate whether the massive cover of certain species is episodic and reveal whether they will be replaced by other species as development there progresses.

The performance of the Pyramid-AR can be measured by comparing its community at the initial and progressed stages of development to that of Eilat's oil jetties that inspired its design (Goren, 1992). During the initial stages of development, the Pyramid-AR showed high resemblance to the community structure of the oil jetties. Ten years after deployment, the species ranking differed between the two ARs, with xeniid species ranking highest and *Dendronephthya* species lowest at the Pyramid-AR, while the opposite was true for the oil jetties. The living cover at the Pyramid-AR was much lower compared to the jetties. Additionally, one decade past deployment diversity values at the oil jetties were more than 2-fold higher than those recorded at the Pyramid-AR (Goren, 1992). Although the sponge *C. cyatophora* was found at the jetties, its contribution to the living cover was minor. On the whole, the design of the Pyramid-AR did result in some similarities in species composition. However, the distinct differences found between the two ARs can be attributed to age differences, and lower structural complexity of the Pyramid-AR compared to that of the oil jetties.

The comparatively recent shift in community structure of the Pyramid-AR may indicate that it is still undergoing successional changes. Wilhelmsson et al. (1998) obtained similar findings when comparing developed communities on three 4–10-year-old shipwrecks and their adjacent NRs in Eilat, finding higher species diversity on the NRs than on the ARs. Undoubtedly, the age of an AR greatly affects its community structure, as some species recruit only after initial settlers have increased the complexity of the surface, making it suitable for secondary settlers (Bohnsack et al., 1991). There is only little information available regarding the time frame of changes in community features, since studies of ARs that apply ecological theories of succession and colonization to their community features are scarce (Cummings, 1994). Wendt et al. (1989), who studied sunken vessels in South Carolina, suggested that AR communities might still be undergoing succession even 10 years following deployment. They further suggested that community differences found between ARs and NRs derive from the fact that the species absent from the ARs, such as sponges and corals, have a slow growth rate on bare substrata. In a long-term study of quarry-rock ARs, Aseltine-Neilson, Bernstein, Palmer-Zwahlen, Riege, & Smith (1999) posited that the development of benthic communities might take as long as 10–15 years in a Pacific temperate environment. Our own findings further support the notion that advanced development of a coral community on ARs takes longer than 10 years, even in tropical ecosystems.

In summary, community development of the experimental Pyramid-AR is suggested to be dependent on various factors, including its structural design, spatial orientation, depth, and age. Each of these may have a critical influence on community features and, therefore, have led to differentiation between the Pyramid-AR and NR communities. These factors should be carefully considered when designing an AR, in order to attract a rich community, elevating diversity in the area. Still

undergoing shifts in its community structure, the Pyramid-AR continues to offer settlement opportunities for coral planulae, contributing to progressive community development and dynamics. A unique structural design such as that of the Pyramid-AR also has strong appeal for recreational divers, from the first moment of its deployment. This trait has great ecological significance, in diverting diving pressure away from NRs and thus contributing to the conservation and restoration of degraded coral reefs (Rilov & Benayahu, 1998; Wilhelmsson et al., 1998). The current study supports the construction of planned ARs, providing their design is appropriate for diverse colonization. Planned ARs will benefit from a more complex and heterogeneous structure offering different habitats, suitable for a rich species assemblage. The addition of high relief habitats to the moderate slope available on the adjacent NR yielded a local increase in species diversity locally; therefore we recommend the construction of ARs that offer niches that are rare in the natural surroundings. The developing communities on an AR must be continuously monitored and compared to adjacent NR communities in order to evaluate the biological and environmental benefit. The time frame within which a biological equilibrium may be reached must be taken into account, including the fact that this may last well over a decade, even in a coral reef ecosystem.

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