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REPORT

Shimrit Perkol-Finkel · Yehuda Benayahu

Community structure of stony and soft corals on vertical unplanned artificial reefs in Eilat (Red Sea): comparison to natural reefs

Abstract In many reef ecosystems, artificial reefs (AR) have become permanent additions to the area, sustaining well-developed benthic communities. Long-term studies on the development of AR coral communities are scarce, and comparisons with their natural surroundings are limited. The present study describes the stony and soft coral community structure of unplanned vertical AR in Eilat (Red Sea) that have progressed beyond the initial successional phases, and compares these to the adjacent natural reefs (NR). Coral communities were characterized using belt transects, conducted on 34- and 14-year-old unplanned AR, and on two proximate NR. Stony corals were the major component in the NR, while soft corals, mainly Nephtheidae, accounted for up to 90% of the total living coverage in the AR. This was attributed to physical and biological features associated with the AR's vertical orientation, which was absent in the NR, and to the life history traits of these soft corals. Community differences between the two AR were related to structural stability and age. The results suggest that AR may increase local heterogeneity and space availability by adding novel habitats, increasing production and elevating species diversity in the surroundings.

Keywords Artificial reefs · Coral reefs · Biodiversity · Multivariate analysis · Red Sea

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Introduction

Coral reefs worldwide are experiencing substantial degradation (Wilkinson 2000). Extensive coral mortality can be attributed to natural stresses such as coral bleaching, catastrophic low tide events, and storms (Done 1999; Brown et al 2000). The growing world population contributes additional stresses in the form of terrestrial runoff, pollution, overfishing, coral mining, and recreational activities, which threaten the very existence of coral reefs (Clark and Edwards 1995; Hawkins et al 1999). These latter factors reduce the reef's resilience and ability to recover in the face of further natural or man-made catastrophes (Hughes and Connell 1999).

Artificial reefs (AR) have been suggested as a potential tool for the restoration of disturbed marine habitats, by enhancing the recruitment and reproduction of marine organisms (Bohnsack and Sutherland 1985; Carr and Hixon 1997; Seaman and Jensen 2000). The definition of AR has successively been widened to include submerged man-made structures susceptible to fouling (Svane and Petersen 2001). Recently, various objects already deployed for other purposes have been classified, secondarily, as AR (Seaman and Jensen 2000). These unplanned AR include shipwrecks, and structures like oil jetties and gas platforms (Bohnsack and Sutherland 1985). The traditional use of AR to create habitats for fishes and invertebrates has increased in recent years throughout the world (reviewed in Baine 2001; Seaman 2002). They have been used for a variety of purposes, such as aquaculture, as breakwaters, to support conservation of biodiversity, and to test ecological theories (Seaman and Jensen 2000; Seaman 2002). It has also been suggested that properly managed AR, made available to the public as alternative diving sites, may reduce human pressure on nearby natural reefs (NR) and therefore facilitate their rehabilitation (Rilov and Benayahu 1998; Wilhelmsson et al 1998).

The relatively narrow spatial and temporal scales of most studies dealing with the development of AR communities are insufficient to document the complete progression of the communities, making it difficult to provide statistical distinction between actual biological effects and natural variability (Bohnsack et al 1997; Aseltine-Neilson et al 1999). A few long-term studies have monitored species turnover on AR and noted their faunistic differences from NR communities (Aseltine-Neilson et al 1999; Clark and Edwards 1999; Relini et al 2000). The majority of such studies have dealt with fish communities, especially in regard to the attraction versus production issue (Bohnsack et al 1997; Grossman et al 1997; Rilov and Benayahu 1998). Only a few studies have compared stony coral communities of AR and NR (Chou and Lim 1986; Wilhelmsson et al 1998), and similar studies regarding soft corals are scarce.

In the reef ecosystem of the northern Red Sea, various unplanned AR have become permanent additions to the area, sustaining well-developed benthic communities. The location and, more importantly, date of construction of these are known. The goal of the present study is to describe the stony and soft coral community structure of unplanned vertical AR that have progressed beyond the initial successional phases, and to compare them with their surrounding NR systems. The widespread concept in AR construction is the use of low-profile structures, aiming to mimic NR (Seaman and Jensen 2000). The current study demonstrates a contrasting approach: the introduction of vertical AR to low-profile natural environments to increase local heterogeneity and elevate biodiversity. The results are discussed in relation to the physical and biological differences between the two types of habitats. We suggest that these differences are responsible for generating the unique community structure found in the studied AR. The conclusions drawn from the current study are expected to contribute to the planning of future AR design, aimed at creating structures that do not attempt to mimic the natural surroundings, but instead add novel habitats to the surroundings.

Materials and methods

Study sites

The study was carried out on two unplanned AR and two NR (Fig. 1) along the coast of Eilat. The Navy-AR constitutes a rigid vertical metal net (1 cm thick, mesh size 40×40 cm), placed under water 34 years ago (1968) on a sandy bottom off the naval port. The surveyed area was 80 m along the net, which hangs from the sea surface down to the seabed at 15 m. The Dolphin-AR is a 14-year-old vertical net made of relatively flexible PVC (0.5 cm thick, mesh size 10×15 cm), which surrounds the "Dolphin Reef", a recreational facility with dolphins kept in a fenced area. The surveyed area was 60 m along the net, from the sea surface down to 10 m. The
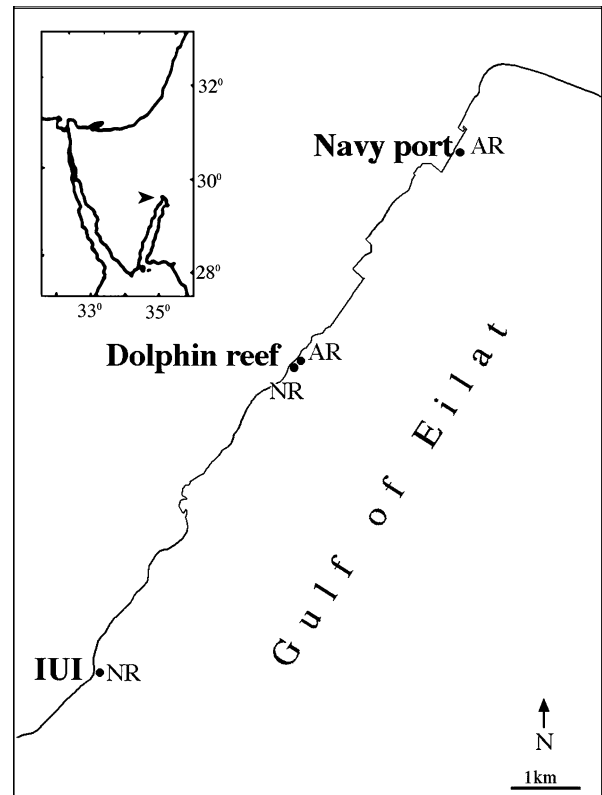
Fig. 1 Geographical location of the study sites; Navy port, Dolphin reef, and Interuniversity Institute (IUI): Navy-AR and Dolphin-AR. AR: Artificial reef; NR: natural reef

Dolphin-NR consists of scattered knolls, located 4–50 m around the net. The Interuniversity Institute NR (IUI-NR) was chosen as a second reference reef, since there is no NR in the vicinity of the Navy-AR. The reef area surveyed there was 80 m wide, at a depth of 4–14 m.

Sampling method

The community structure of stony and soft corals was studied through a series of belt transects, using SCUBA, following the technique developed by Loya (1972). On both AR, three replicate 10 m transects were placed at 2 m depth intervals running up from the base of the net (3–15 m depth in the Navy-AR and 2–10 m in the Dolphin-AR). Transects in the NR were set at respective depths to the AR transects. The transects, placed randomly on the reefs, ran parallel to the shore and to each other at fixed intervals of 2 m depth, with three replicates at each depth. The surveyed area along a transect consisted of a 5 cm belt on each side of the line, forming a belt transect of 10×0.1 m. This modification of Loya's line transect increased the probability of recording data from the net-made AR. All stony and soft corals intercepted by the transect were recorded, and their maximal projected length was measured. An individual colony of a stony coral was defined as any colony growing independently of its neighbors (Loya 1972). This definition

was not always applicable to soft corals, since many of them produce monospecific carpets where individual colonies are indistinguishable; therefore their intercepted length was measured without recording the number of colonies. The hermatypic hydrozoan *Millepora dichotoma* was also included in this study (see Loya 1972). In order to obtain a complete coral species list of the AR, comparable to reference lists for Eilat's NR coral communities (Loya 1972; Benayahu and Loya 1977), a thorough visual census was conducted. When necessary for identification, the colonies were sampled and identified with the aid of the reference collection from the Zoological Museum of Tel Aviv University. The fieldwork was carried out during July 1999–March 2000, totaling 60 dives.

Community analysis

The relative abundance (RA) of each species (see Rilov and Benayahu, 1998) was calculated according to its contribution to living cover:

$$RA = \frac{P_i}{P_{total}} \times 100$$

where P_i = pooled living coverage of the ith species from all transects at a given site and P_{total} = pooled total living coverage 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), dominant (RA > 20). RA was also calculated for stony and soft corals pooled together, termed here as total living coverage. Species coverage diversity (H'_c) was calculated using the Shannon-Weaver function (Shannon and Weaver 1964), applied separately for stony and soft corals by using values of species contribution to living coverage (Loya 1972). All averaged values of community features are presented with 95% confidence intervals (CI).

Univariate analysis

Comparisons of living coral coverage and species counts among the different sites were performed by two-way ANOVA (using the STATISTICA program), run separately for stony and soft corals. The main effects were "reef type" with two levels (NR versus AR), and "depth" divided into three zones (shallow = 0–5 m, intermediate = 6–10 m, and deep = 11–15 m). In order to meet ANOVA assumptions, the living coverage and species count analyses were performed on transformed data (arcsine $\sqrt{x}$ and $\sqrt{x}$, respectively). Whenever transformed data did not meet ANOVA assumptions, the non-parametric Mann-Whitney U-test and Kruskal-Wallis tests were used (Sokal and Rohlf 1985). A Pearson correlation analysis between community features

and depth was performed separately for stony and soft corals, using raw data.

Multivariate analysis

Multidimensional scaling and ordination were used to detect community patterns, using the PRIMER (v 5.1.2) software program (Clarke and Warwick 1994). Data sets included percent coverage for the stony and soft coral species (rows) in each of the transects (columns).

A two-dimensional non-metric Multidimensional Scaling (MDS), based on the rank order of the Bray-Curtis similarities (Bray and Curtis 1957), was used to define and visualize community patterns. The adequacy of the MDS is assessed through a stress coefficient: the lower the value, the greater the variance explained by the chosen dimensions. The coefficient should be < 0.15 in order to minimize misinterpretations (Clarke and Warwick 1994). Since both AR had a small number of highly abundant soft coral species, a $\log(x+1)$ transformation was applied to reduce their contribution to similarity and strengthen that of less common species. All MDS analyses were performed separately on stony coral, soft coral, and pooled data sets. Ordinations incorporated transect depth by superimposing circles of increasing size within a depth range of 2 (smallest diameter) to 15 m (largest diameter). K-dominance curves (Lambshead et al 1983) present the different species ranked in order of dominance according to their contribution to living coverage on the x-axis (logarithmic scale) with percentage dominance on the y-axis (cumulative scale). The starting point of the curve and its inclination are indicative of the diversity profile of the examined community; for example, a steep slope with a high starting point reflects low diversity. K-dominance curves were constructed on the above-mentioned data sets.

Results

Species number and composition

A total of 64 stony coral species and 19 soft coral species were found on the transects (Tables 1 and 2). Additional species were added from the visual surveys, as indicated in Tables 1 and 2, raising the total stony coral species count to 73, and that of the soft coral to 25. The total number of stony coral species was distinctly different in the two AR (Fig. 2A). Forty-six stony coral species were recorded in the Navy-AR compared to 14 species in the Dolphin-AR. The former site resembled the NR in this respect (Dolphin-NR, 46 species; and IUI-NR, 52 species). *Stylophora pistillata* was the most abundant species in the IUI-NR, contributing 16% of the stony coral cover. It was also common in the Dolphin-NR and in the Navy-AR (9 and 2%, respectively), and dominated the Dolphin-AR, accounting for 25% of the cover (Table 1). In the latter site, the most dominant

Table 1 Relative abundance (RA: see *Materials and methods* section) of stony corals occurring in the transects at each of the study sites, according to their contribution to living coverage

Species	AR		NR	
	Navy	Dolphin	Dolphin	IUI
Acroporidae				
Acropora eurystoma	***	***	***	**
Acropora hemprichi	-	-	***	***
Acropora humilis	**	-	**	**
Acropora nasuta	+	+	-	-
Acropora scandens	+	-	***	***
Acropora sp.	*	-	-	-
Acropora variabilis	*	-	***	***
Astreopora myriophthalma	**	-	**	***
Montipora danae	**	***	***	***
Montipora erythraea	***	-	***	***
Montipora granulata	**	-	***	***
Montipora meandrina	+	-	***	-
Montipora sp.	-	-	-	**
Pocilloporidae				
Pocillopora danae	***	*****	***	***
Seriatopora caliendrum	**	-	***	-
Seriatopora sp.	-	-	-	*
Stylophora pistillata	***	*****	***	****
Oculinidae				
Galaxea fascicularis	-	-	***	*
Siderastreidae				
Coscinaraea monile	***	-	**	***
Psammocora nierstraszi	****	+	**	**
Siderastrea lilacea	-	-	-	***
Agariciidae				
Leptoseris fragilis	+	-	-	-
Leptoseris tubulifera	+	-	-	-
Pavona clavus	**	-	**	*
Pavona decussata	**	+	***	**
Pavona gardineri	***	+	**	-
Pavona varians	**	+	****	**
Fungiidae				
Fungia fungites	**	-	**	-
Fungia sp.	+	-	**	**
Pectiniidae				
Echinophyllia aspera	+	-	**	*
Mycedium tubifex	+	-	-	-
Merulinidae				
Hydnophora contignatio	+	-	**	**
Dendrophylliidae				
Cladopsamia gracillis	**	+	-	-
Tubastrea micrantha	+	-	-	-
Turbinaria sp.	**	-	**	**
Caryophylliidae				
Gyrosmilia interrupta	**	-	**	***
Plerogyra sinuosa	+	-	-	-
Mussidae				
Acanthastrea echinata	***	***	**	***
Balastomusa merleti	**	-	-	-
Cynarina sp.	**	+	**	***
Lobophyllia corymbosa	-	-	-	**
Lobophyllia hemprichii	+	-	-	-
Faviidae				
Cyphastrea chalcidicum	***	***	**	***
Cyphastrea microphthalma	***	***	-	***
Cyphastrea serailia	-	***	**	*
Echinopora gemmacea	+	+	**	**
Echinopora lamellosa	**	-	***	**
Favia doreyensis	**	+	-	**
Favia favus	***	+	***	****
Favia speciosa	***	**	-	**
Favia stelligera	**	-	-	*

Table 1 (Contd.)

Species	AR		NR	
	Navy	Dolphin	Dolphin	IUI
Favia sp.	*	-	*	**
Favites abdita	***	**	-	***
Favites halicora	***	***	-	*
Favites pentagona	**	+	**	***
Favites virens	***	+	**	-
Goniastrea retiformis	*	-	-	***
Goniastrea pectinata	**	-	-	***
Leptastrea bottae	**	-	-	***
Leptastrea purpurea	**	-	**	**
Leptastrea transversa	***	+	***	***
Platygyra lamellina	****	***	***	***
Platygyra subdentata	**	-	**	*
Plesiastrea laxa	-	-	**	**
Plesiastrea mammillosa	+	-	-	-
Poritidae				
Alveopora daedalea	-	-	-	**
Goniopora sp. 1	-	-	*	-
Goniopora sp. 2	-	-	**	-
Goniopora sp. 3	-	-	**	-
Porites lutea	***	***	****	***
Porites mayri	***	-	-	-
Porites sp.	+	+	-	-
Milleporidae				
Millepora dichotoma	***	****	***	***

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), and ***** dominant (RA > 20). Species recorded in visual census are marked with +. AR: Artificial reefs; NR: natural reefs

species, comprising 43% of the stony coral cover, was *Pocillopora danae*. The most abundant stony coral species in the Navy-AR was *Psammocora nierstraszi* (14%). *Porites lutea* comprised 10% of the coverage in the Navy-AR and was also abundant in the Dolphin-NR (14%). *Acropora* species were mostly common in the NR, but *A. eurystoma* was common in both AR. *Millepora dichotoma* was common in both NR, as well as in the Navy-AR, and was abundant in the Dolphin-AR.

The visual census added 15 stony coral species to the Navy-AR species list, including new records for the families Pectiniidae and Merulinidae. Seven of the species were new records that did not appear in the transects at any of the four sites (Table 1). Visual surveys added a similar number of new species to the Dolphin-AR species list (14 species) from the families Siderastreidae, Dendrophylliidae, and Agariciidae.

The total number of soft coral species was slightly higher in the AR than in the NR (Fig. 2A, Navy-AR, 15 species, and Dolphin-AR, 12, compared to Dolphin-NR, 10, and IUI-NR, 9). The majority of the abundant and dominant soft corals at both NR were Xeniidae (Table 2). *Heteroxenia fuscescens* ranked first in the IUI-NR, contributing 30% to the soft coral cover there, and was also abundant at the Dolphin-NR (16%). *Ovabunda macrospiculata* ranked first in the Dolphin-NR (32%) and *Xenia umbellata* ranked second in the IUI-

Table 2 Relative abundance (RA: see materials and methods) of soft corals occurring in the transects at each of the study sites, according to their contribution to living coverage (symbols and abbreviations as in Table 1)

Species	AR		NR	
	Navy	Dolphin	Dolphin	IUI
Tubiporidae				
Tubipora musica	-	-	-	**
Alcyoniidae				
Cladiella pachyclados	-	-	****	-
Klyxum sp.	-	+	-	-
Rhytisma fulvum fulvum	***	***	***	*****
Sarcophyton glaucum	***	*	-	****
Sinularia humesi	+	-	-	-
Sinularia leptoclados	*	-	***	-
Sinularia loyai	+	+	-	-
Sinularia polydactyla	+	+	-	-
Melithaeidae				
Acabaria sinaica	+	+	-	-
Nephtheidae				
Dendronephthya hemprichi	***	*****	-	-
Dendronephthya sinaiensis	*	**	-	-
Litophyton sp.	*****	*****	***	-
Paralemnalia thyrsoides	***	**	-	***
Scleronephthya corymbosa	****	**	-	-
Stereonephthya cundabiluensis	-	+	-	-
Xeniidae				
Heteroxenia fuscescens	**	***	****	*****
Ovabunda biseriata	***	**	***	-
Ovabunda macrospiculata	**	-	***	***
Ovabunda verseveldti	**	**	-	-
Xenia hicksoni	**	-	*****	-
Xenia impulsatilla	-	-	-	***
Xenia ternatana	***	***	****	*****
Xenia umbellata	**	-	-	-
Xenia sp.	-	*	***	*

NR (24%) and Dolphin-NR (16%). In contrast, at both AR the dominant species were from the Nephtheidae, such as *Litophyton* sp., which ranked first in the Navy-AR, comprising 71% of the soft coral cover, and second in the Dolphin-AR (38%). *Dendronephthya hemprichi* ranked first in the Dolphin-AR, accounting for almost half of the soft coral coverage.

The visual census added six soft coral species to the AR that had not appeared in the transects at any of the four reefs (Table 2). Most of the new records were Alcyoniidae. Three of the additional species were common to both AR, including two *Sinularia* species and *Acabaria sinaica*.

The top ten ranked species in each study site, based on their relative contribution to total living cover, are presented in Fig. 3. There was variation in species composition and ranking among the sites. Stony corals dominated the NR, while soft corals were poorly represented there. A high abundance of *Porites lutea*, *Stylophora pistillata,* and *Millepora dichotoma* was noted in both NR (Figs. 3A,B). *S. pistillata* and *M. dichotoma* were highly ranked in the Dolphin-AR, and *P. lutea* in the Navy-AR. *Acropora* species were also among the most common species in both NR, having 2–3 of the top ten rankings. *Acropora* spp. were not found among the top ten species in the AR. There were no stony corals
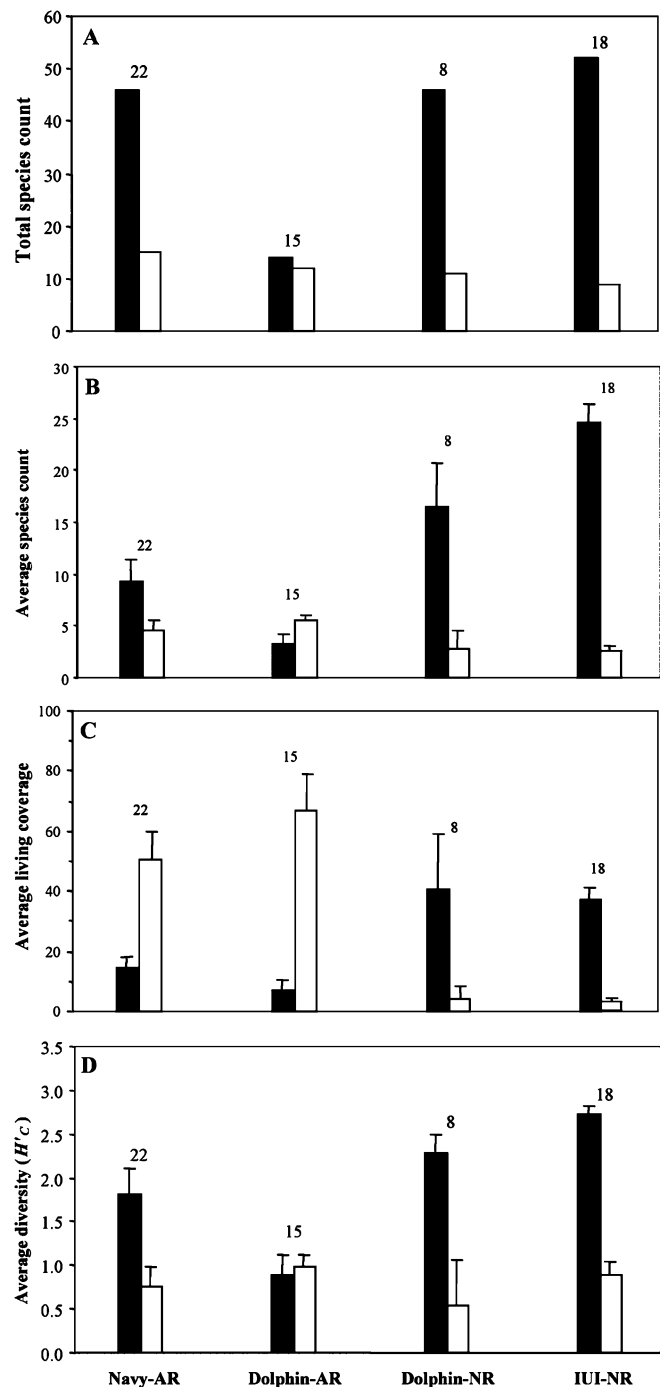

Fig. 2 Community features of stony (black columns) and soft (white columns) corals, per 10 m transect, on the artificial and natural reefs. **A** Total species count; **B** average species count ($\pm$95% confidence intervals); **C** average % living coverage ($\pm$CI); **D** average coverage diversity ($\pm$CI). Number of transects is indicated for each site. AR: Artificial reef; NR: natural reef

common to both AR among the top ten species. Pocilloporidae and Milleporidae were present in the Dolphin-AR, while Faviidae, Poritidae, and Siderastreidae appeared in the Navy-AR (Fig. 3C,D).

Soft corals dominated both AR and accounted for 74–91% of the cover contributed by the top ten species,

Fig. 3 Relative abundance of the ten top-ranked coral species, and of other species (stony and soft corals pooled), according to their contribution to living cover at each site. Stony corals: white bars; soft corals: black bars; other species (not ranked among the top ten): dotted bars. AR: Artificial reef; NR: natural reef
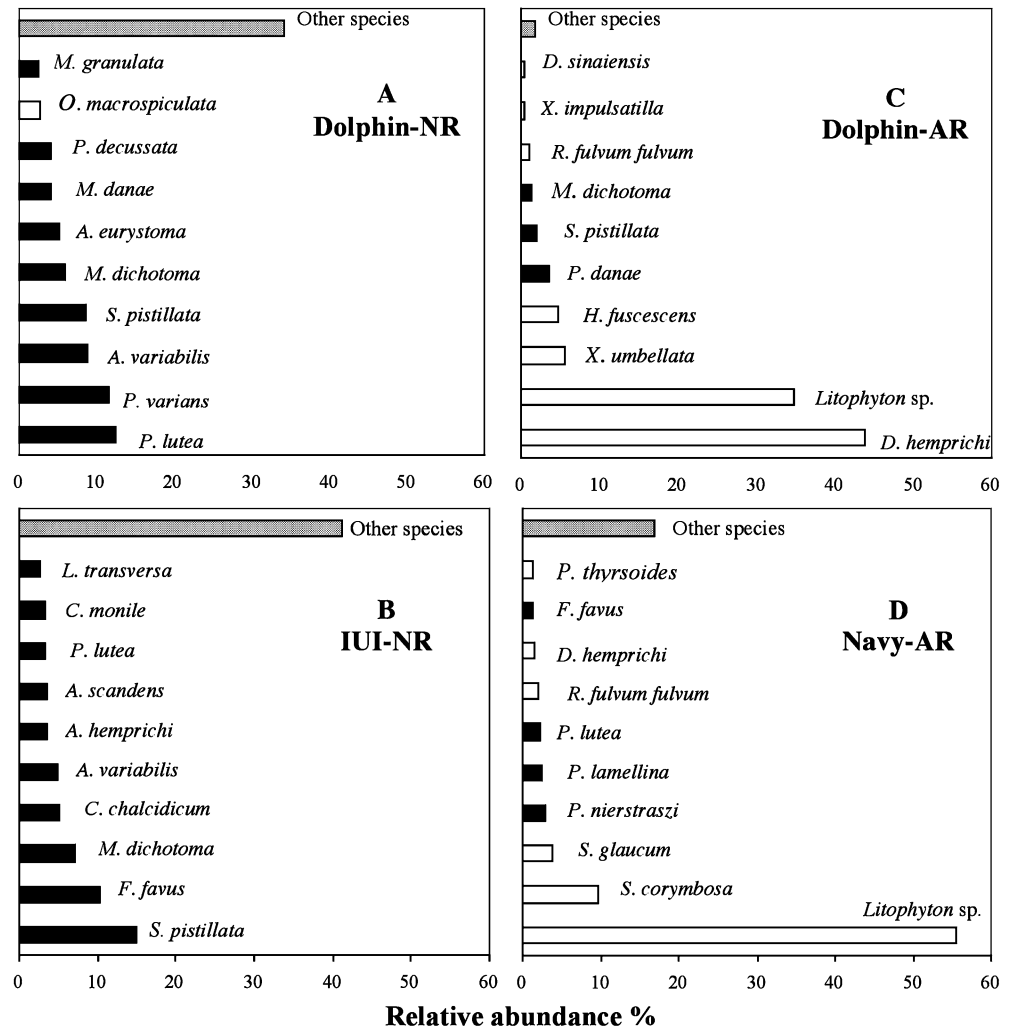
while on the NR their coverage was only 3% (Fig. 3A,B). Nephtheidae, such as *Dendronephthya,Scleronephthya,* and *Litophyton,* were the most abundant taxa in both AR (Fig. 3C,D), yet were negligible in the NR (Fig. 3A,B). *Litophyton* sp. was conspicuous in both AR, and *D. hemprichi* was highly dominant in the Dolphin-AR, while in the Navy-AR its contribution was lower. Furthermore, *D. hemprichi* and *S. corymbosa*, both prominent on the AR, were not observed at either of the NR. These colorful species were highly impressive on the exterior of the AR, contributing greatly to their aesthetics.

Univariate analysis

Species count

The average species number per transect for both stony and soft corals differed significantly between the AR and NR (Fig. 2B, two-way ANOVA:$F_{(df=1,2)}=111.75$ for stony corals and 32.33 for soft corals; $P<0.0001$ for both). Average stony coral count on the AR was lower than on the NR (Navy-AR, 9.32 ± 2.07, Dolphin-AR, 3.20 ± 1.01, compared to Dolphin-NR, 16.05 ± 4.17, and

IUI-NR, 24.56 ± 1.84). The opposite pattern was found for the soft coral counts, which were higher on the AR than on the NR (Navy-AR, 4.55 ± 0.96, Dolphin-AR, 5.47 ± 0.62 compared to Dolphin-NR, 2.75 ± 1.88, and IUI-NR, 2.67 ± 0.48). Stony coral count was affected differently by depth on the two reef types (two-way ANOVA, interaction term:$F_{(df=1,2)}=7.29,P<0.005$), increasing with depth on the ARs (Table 3) but not correlated with depth on the NRs ($r_p=0$, $P>0.05$). The effect of depth on the soft coral species count was similar between reef types (two-way ANOVA, interaction term: $F_{(df=1,2)}=0.25,P=0.78$), increasing with depth on both AR and NR ($r_p=0.44$, $P<0.01$ and $r_p=0.48,P<0.05$, respectively).

Living cover

Average percent cover per transect for both stony and soft corals was significantly different among artificial and natural reefs (Fig. 2C, two-way ANOVA:$F_{(df=1,2)}=98.59$ for stony corals and 446.43 for soft corals; $P<0.0001$ for both). Stony coral cover on the AR was more than 4-fold lower than on the NR

Table 3 Pearson correlation analysis (r_p) between depth and community features, for stony and soft corals on artificial and natural reefs

Parameter	Artificial reefs		Natural reefs	
	Stony corals	Soft corals	Stony corals	Soft corals
Species count	0.65****	0.44**	0.00	0.48*
Living coverage	0.63****	−0.72****	−0.74****	0.41*
Coverage diversity	0.57***	0.45**	0.17	0.22

$N = 37$ for artificial reefs, $N = 26$ for natural reefs. Significance level of the Pearson coefficient is marked as follows: - not significant; **** P < 0.0001; *** P < 0.001; ** P < 0.01; * P < 0.05

(Navy-AR, 16.61 ± 3.68%, Dolphin-AR, 7.14 ± 3.30%, compared to Dolphin-NR, 40.50 ± 18.26%, and IUI-NR, 37.39 ± 4.06%). Soft coral cover demonstrated an opposite pattern, being as much as 22-fold greater on the AR than on the NR (Navy-AR, 50.86 ± 9.10%, Dolphin-AR, 66.62 ± 12.48%, compared to Dolphin-NR, 4.08 ± 3.79%, and IUI-NR, 2.98 ± 0.89%), reaching a maximum value of nearly 90% on the AR, compared to a maximum of only 8% on the NR. Living cover was differently affected by depth on the two reef types (two-way ANOVA, interaction term: $F_{(df=1,2)} = 19.30$ for stony corals and 12.83 for soft corals; $P < 0.0001$ for both). Stony coral cover on the AR was positively correlated with depth, whereas on the NR their cover decreased with depth (Table 3). Soft coral cover had an opposite trend, showing decrease in cover with depth on the AR, and an increase on the NR (Table 3).

Living cover diversity

Average stony coral diversity differed between the four sites (Kruskal-Wallis test, $P < 0.0001$), and was higher in the NR than in the AR. Significantly higher diversity was found at Navy-AR than at Dolphin-AR (Fig. 2D, Mann-Whitney test, $P < 0.0001$, $H'_c = 1.82 ± 0.28$ and $0.90 ± 0.22$, respectively), resembling the results obtained in the NR (Dolphin-NR, 2.28 ± 0.22, and IUI-NR, 2.72 ± 0.09). Furthermore, the stony coral coverage diversity in the Navy-AR did not differ from that of the Dolphin-NR (Mann-Whitney test, $P > 0.05$), while diversity was significantly different between the two NR (Mann-Whitney test, $P < 0.005$). No significant differences in soft coral diversity were revealed among sites (Fig. 2D, Kruskal-Wallis test, $P > 0.05$) and H'_c values were < 1 for all locations. Table 3 shows stony coral diversity to be positively correlated with depth on the AR, while no such correlation was revealed for the NRs, and H'_c values there were > 1.50. Soft coral diversity showed a similar trend of increase with depth on the AR, while no such correlation was found on the NR (Table 3).

Multivariate analysis

Multidimensional Scaling (MDS)

MDS analysis of the stony coral data set (Fig. 4A) revealed a relatively high stress level (0.19), making the display of the relationships among sites less certain. No overlap between the NR and AR appeared. Dolphin-AR transects were scattered on the right side of the x-axis, opposite those from the NR and overlapping some of the shallow Navy-AR transects. Deep Navy-AR transects were located in a different cluster near the NR, away from the Dolphin-AR transects.

MDS analysis conducted on the soft coral data set (Fig. 4B, stress = 0.15) indicated a distinct separation between the AR and the NR on the x-axis, whereas depth distribution appeared on the y-axis. NR transects overlapped on the left side of the x-axis, while AR aggregated into separate clusters on its right side. Dolphin-AR created a distinct cluster, separate from the Navy-AR which was distributed similarly to the stony coral data set.

MDS analysis for the pooled stony and soft coral data set (Fig. 4C, stress = 0.14) exhibited distinct clustering for each of the four sites. The NR appeared on the left side of the x-axis, while the AR featured on its right side. All sites apart from the Navy-AR exhibited a depth-related pattern, in which deeper transects were spread out higher on the y-axis and the shallower ones on its lower side (Fig. 4C). In contrast, the deeper transects of the Navy-AR spread towards the lower part of the y-axis.

K-dominance curves

Dominance curves for the stony coral data set (Fig. 5A) exhibited a distinct separation between the Dolphin-AR curve and the Navy-AR, and the Dolphin and IUI-NR ones, indicating lower species diversity in the Dolphin-AR. Dominance curves for the soft corals data set (Fig. 5B) revealed a different pattern, separating the two NR curves from the AR curves, which started much above them. However only the Navy-AR curve rose moderately, indicating a greater soft coral diversity there than for the other three reefs. Dominance curves for the pooled stony and soft corals data set (Fig. 5C) showed a similar trend to the soft coral data set but had a more moderate slope for all reefs.
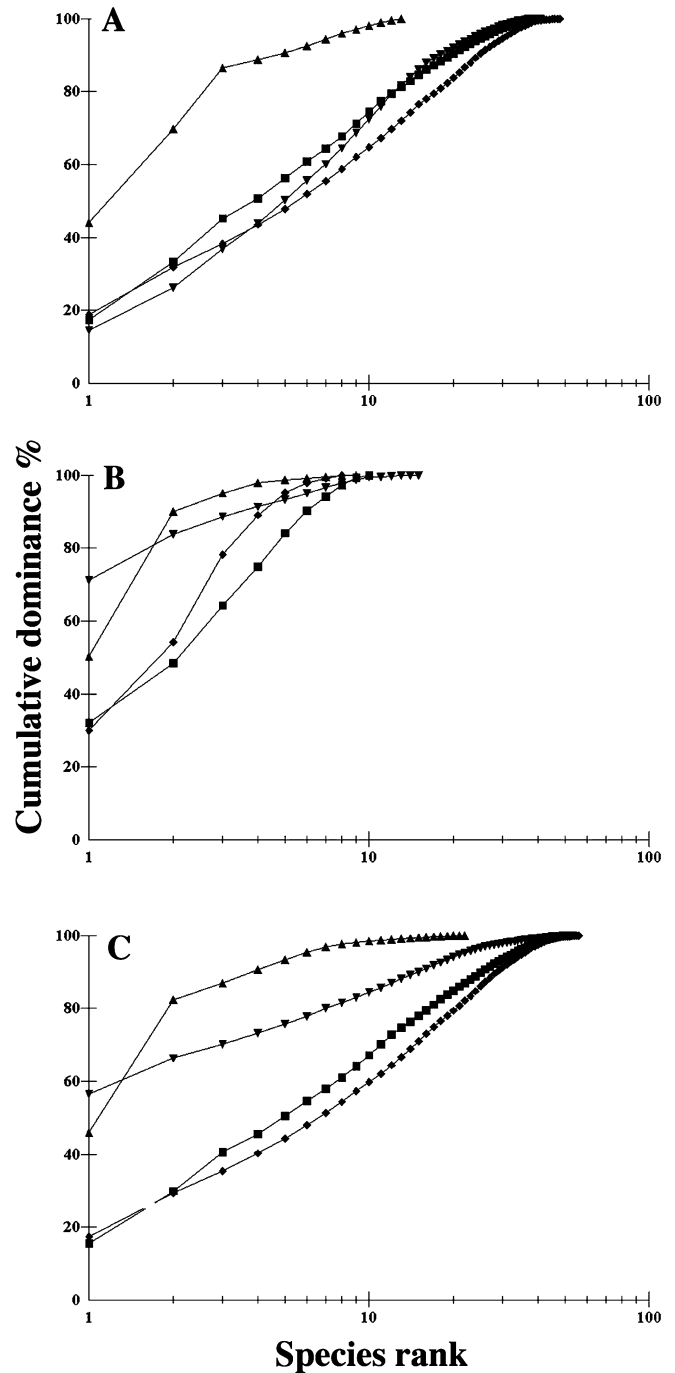
Discussion

AR are susceptible to colonization and will successively recruit benthic communities, which may or may not
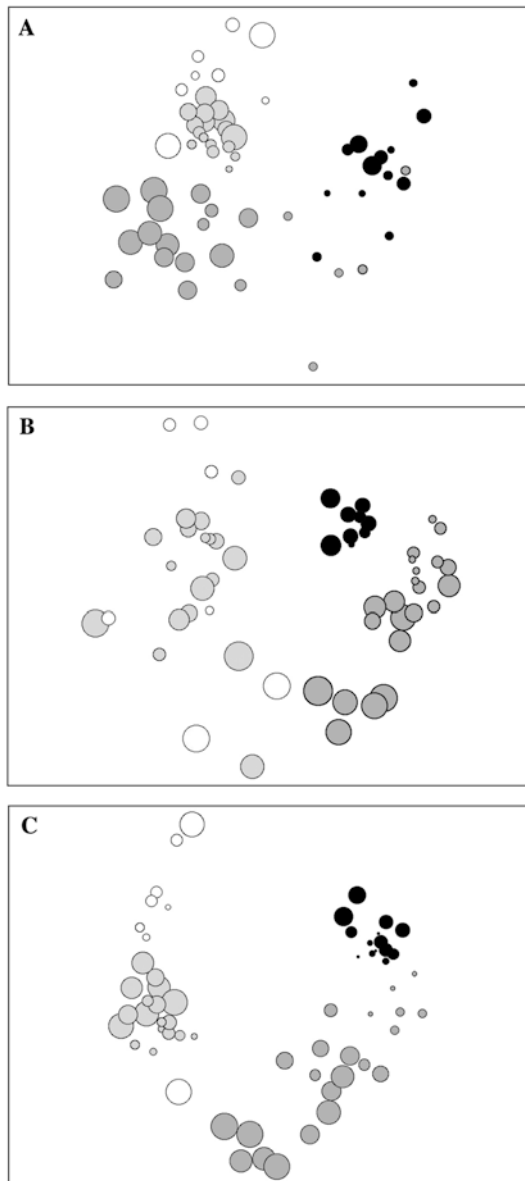
Fig. 4 Two-dimensional MDS for [log(x + 1)]-transformed living coverage data at each site (Navy-AR: dark gray circles, Dolphin-AR: black circles, Dolphin-NR: unfilled circles, IUI-NR: light gray circles), for: **A** stony coral data set (stress = 0.19); **B** soft coral data set (stress = 0.15); **C** pooled stony and soft coral data set (stress = 0.14). Circle size indicates transect's depth, where a larger diameter corresponds to deeper water (depth range = 2–15 m). AR: Artificial reef; NR: natural reef

Fig. 5 *K*-dominance curves for all sites (Navy-AR: inverted triangles; Dolphin-AR: triangles; Dolphin-NR: squares; IUI-NR: diamonds), for: **A** stony coral data set; **B** soft coral data set; **C** pooled stony and soft coral data set. AR: Artificial reef; NR: natural reef

resemble epibiosis on natural communities (see also Svane and Petersen 2001). Carr and Hixon (1997) pointed out the need for detailed comparisons of species assemblages of AR and NR, in order to evaluate the impact of AR on their surroundings. They also discussed the need to determine the spatial scales along which AR act to attract or produce NR species. Our study revealed distinct differences between the community features of the vertical AR and adjacent NR. Although the studied AR and NR occupied the same depth range and were located only a few kilometers apart (Fig. 1), species

composition differed between the two reeftypes. The majority of the top ten ranked species found on both NR were stony corals, with a species composition typical to that of the northern Gulf of Eilat (see Benayahu and Loya 1977). In contrast, the community structure of the unplanned AR was different, because stony corals were less dominant, particularly in comparison to the

remarkable dominance of soft corals. Soft corals accounted for up to 90% of their total living coverage, in comparison to only 8% in the NR. Soft corals of the family Nephtheidae dominated the AR, yet had only a minor contribution in the NR. We suggest that the vertical AR surveyed, as opposed to the nearly horizontal NR, are exposed to currents that enhance development of the fast-growing herbivorous colonies of *Dendronephthya hemprichi* and *Scleronephthya corymbosa* (see Fabricius et al 1995). Notably, the scarcity of these species in other northern Gulf of Eilat reefs has been previously documented, yet they are commonly found on reefs in the southern Gulf of Eilat, on steep slopes, and on inclined man-made structures that are routinely exposed to strong currents (Benayahu 1985; Fabricius et al 1995). The zooxanthellate *Litophyton* sp. was also abundant on the AR (Table 2). Schuhmacher (1974) found that this species was first to appear on Eilat's AR, specifically on vertical substrata. It grows in clumps at depths of 3–18 m on Eilat's NR (Benayahu 1985), yet is found mostly in shallow sections of AR (this study; Goren 1992). The depth-related distribution of *Litophyton* sp. may be linked to light attenuation along high-relief surfaces. Light intensity is a dominant ecological factor that affects the depth distribution of different reef species (Schuhmacher 1974; Mundy and Babcock 2000). Many corals exhibit a species-specific, light-dependent settlement, usually with a preference for vertical or underside surfaces (Mundy and Babcock 1998), since direct radiation has a negative effect on some coral species (Kuffner 2001). The vertical AR studied increased the local heterogeneity, resulting in a depth-related recruitment of species in relation to light penetration, and consequently increased the overall diversity in the area.

We suggest that the proliferation of soft corals on the studied AR can be attributed to their life history traits. These include an extended breeding season, and various modes of asexual propagation (Weil 1990; Dahan and Benayahu 1997a, 1997b; Lutzky 1997). Sexual reproduction results in expansion of the population to new sites, and asexual propagation contributes to their local abundance (Lasker and Coffroth 1999). Both *Litophyton* sp. and *D. hemprichi* exhibit a rapid growth rate that further enhances their exploitation of available space (Weil 1990; Fabricius et al 1995; Dahan and Benayahu 1997b).

Coverage diversity (H'_c) varied between the two AR, with the Navy-AR being double that of the Dolphin-AR (1.82 and 0.90, respectively). Furthermore, H'_c values in the Navy-AR resembled those obtained in the NR (Fig. 2D), which fall within the diversity range given for Eilat's NR at a comparable depth range (Loya 1972). This was supported by the MDS ordinations, as well as by the *K*-dominance curves, which distinguished between the Navy-AR transects adjoining the NR ones and the Dolphin-AR transects (Figs. 4, 5A). These differences between the two AR may be attributed to differences in their structural stability. The Navy-AR comprises a relatively firm metal net, suitable for the development of a NR community, while the flexible PVC net of the Dolphin-AR apparently favors the development of soft corals. Firmness of substrata is particularly relevant for encrusting organisms, which may become detached under strong currents or storms (Chou 1997). Although the physical characteristics of an AR, including size, complexity, texture, and relief have been long considered important for recruitment (Bohnsack and Sutherland 1985), its firmness and stability have only recently been addressed (Glasby 2001; Holloway and Connell 2002). The detailed significance of the latter factors for coral recruitment remains to be determined (work in progress).

Differences in community features between the two studied AR can also be attributed to their respective submersion period. Aseltine-Neilson et al (1999) suggested that the development of turf community on AR may take 10–15 yrs in Pacific temperate environments, and even longer than that in the tropics (Clark and Edwards 1999). Wendt et al (1989), in a study of sunken vessels in South Carolina, found that stony and soft corals comprised a much greater proportion of the total biomass on older AR (8–10 yrs) than on younger ones (3.5–4.5 yrs), and that species composition of even the oldest AR differed from that of the nearby NR. In our study, visual censuses of the AR increased the total number of species by 1.5- to 2-fold, mainly through the presence of juveniles or rare species. Therefore, the relative contribution of stony corals in the AR and their resemblance to NR communities will increase over time. Nonetheless, differences will most probably continue if the structure of the AR markedly differs from that of the surrounding NR, and offers novel niches not found in the latter. Further research on AR of various ages is required in order to document temporal changes in community features and to delineate the expected timeframe for achieving a well-developed community.

The vertical relief of the studied AR provided a steep depth gradient, which does not exist in Eilat's NR. Apart from a decrease in soft coral cover, all other community features increased with depth on the AR (Table 3). A similar pattern for stony corals occurs in Eilat's reefs and has been related to environmental stability at deeper reef zones (Loya 1972). Therefore, depth is suggested to be of greater influence on community features of vertical AR than on NR with moderate slopes. Increasing depth on the AR also corresponds to proximity to the bottom, which may result in increased sedimentation and affect coral distribution (Riegl 1995). Baynes and Szmant (1989), who worked on benthic communities recruited to shipwrecks, found high living cover and species diversity under conditions of low sedimentation and strong currents. Such conditions are found on vertical surfaces, and are preferable for coral settlement (Fisk and Harriott 1990). Stony corals are able to withstand applied sediment through their own ability to secrete mucus, whereas soft corals rely mainly on water motion or inclined substrata; consequently,

continuous sedimentation may more rapidly affect the latter (Riegl 1995). This fits our findings of opposite depth-related coverage patterns in stony and soft corals on the AR.

A consequence of depth and the proximity of hard bottom is the proximity to a source of larvae (Wendt et al 1989). Recruitment, and the resulting space utilization are strongly affected by the presence of propagules (Benayahu and Loya 1987). Areas of AR that are close to the bottom encounter different physical and biological conditions to those encountered by elevated or mid-water ones, which affect species count and diversity. Therefore, vertical AR can provide a wide array of conditions on a relatively narrow spatial scale. In cases such as presented in our study, where a pronounced depth gradient does not exist in the NR, vertical AR offer conditions for the development of an ecosystem different to the surrounding one.

The current study demonstrates a good agreement between the univariate and multivariate methodologies. Their dual application contributes a thorough comprehension of the reefs' community features and of differences between AR and NR. Multivariate analyses provide a powerful graphical representation of the data, capable of linking community patterns to environmental variables such as depth. However, univariate analyses, such as species count and living coverage, are required for determining abundance and diversity and for comparisons to previous studies (Loya 1972; Benayahu and Loya 1977). Therefore, we recommend the use of both measures when applicable, in order to produce a complete community profile.

There is a synergistic effect of a wide array of biotic and abiotic parameters that contribute to the observed differences between AR and NR, and among AR. These include abiotic factors such as spatial orientation, light intensity, substrata stability, submersion period, sedimentation levels, and biotic factors, including life history traits of the recruited organisms and larval availability. Undoubtedly, additional parameters are involved in shaping the community structure of AR (such as type of material, structural complexity, position in relation to a NR), that immensely complicate the comparisons between AR and NR and therefore raise the need for further research on the role played by each of them. Careful manipulation of AR design can create novel habitats, increasing local heterogeneity and space availability by attracting species that are rare or even absent in the surrounding NR. Furthermore, when such targeted colonizers do not occur on the adjacent NR, it is safe to predict that competition for recruited larvae of these species between the two reef types is limited, or even may not occur at all. Therefore, the AR recruit larvae that would otherwise be lost, increasing production and elevating species diversity in the area.

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