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Can artificial reefs mimic natural reef communities? The roles of structural features and age

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Abstract

In light of the deteriorating state of coral reefs worldwide, the need to rehabilitate marine environments has greatly increased. Artificial reefs (ARs) have been suggested as a tool for reef conservation and rehabilitation. Although successions of AR communities have been thoroughly studied, current understanding of the interactions between artificial and natural reefs (NRs) is poor and a fundamental question still to be answered is that of whether AR communities can mimic adjacent NR communities. We suggest three alternative hypotheses: Neighboring ARs and NRs will (1) achieve a similar community structure given sufficient time; (2) be similar only if they possess similar structural features; (3) always differ, regardless of age or structural features. We examined these hypotheses by comparing the community structure on a 119-year old shipwreck to a neighboring NR. Fouling organisms, including stony and soft corals, sponges, tunicates, sea anemones and hydrozoans were recorded and measured along belt transects. The ahermatypic stony coral *Tubastrea micrantha* dominated vertical AR regions while the soft corals *Nephthea* sp. and *Xenia* sp. dominated both artificial

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and natural horizontal surfaces. Our results support the second hypothesis, indicating that even after a century an AR will mimic its adjacent NR communities only if it possesses structural features similar to those of the natural surroundings. However, if the two differ structurally, their communities will remain distinct.

Keywords: Shipwreck; Community development; Spatial orientation; Structural complexity; Coral reef; Red Sea

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1. Introduction

Coral reefs worldwide are being continuously disturbed by natural and man-made stresses that severely deteriorate their condition (Wilkinson, 2000). Artificial reefs (ARs) have been suggested as a potential tool for reef restoration and rehabilitation (Clark & Edwards, 1999; Spieler, Gilliam, & Sherman, 2001). Consequently, there is increasing awareness of the importance of understanding the interactions between artificial and natural reef (NR) communities, and thus of the need for a comparison between these communities (Badalamenti, Chemello, D'Anna, Henriquez Ramoz, & Riggio, 2002; Carr & Hixon, 1997; Perkol-Finkel & Benayahu, 2004). Although early development of benthic communities on ARs has been intensively investigated over the past few decades (e.g., Ardizzone, Gravina, & Belluscio, 1989; Aseltine-Neilson, Bernstein, Palmer-Zwahlen, Riege, & Smith, 1999; Cummings, 1994; Qiu, Thiyagarajan, Leung, & Qian, 2003), knowledge of the late developmental stages of AR communities is still lacking. Long-term monitoring of AR communities is essential for the understanding of their ecological processes and for evaluating their performance and possible impact on the natural surroundings (Aseltine-Neilson et al., 1999; Perkol-Finkel & Benayahu, 2005).

A wide array of structural features is known to affect the settlement of benthic invertebrates onto natural and artificial substratum, including spatial orientation, structural complexity, substratum composition and texture. Various settlement substrata and ARs have been widely applied in order to study the settlement preferences of corals and other fouling organisms (Spieler et al., 2001 and references therein). For example, the relief of an AR may greatly influence the species composition and abundance of both its benthic invertebrates (Baynes & Szmant, 1989; Glasby & Connell, 2001) and fish (Rilov & Benayahu, 2000). In a reef environment coral recruitment is usually higher on vertical or inclined surfaces as compared to horizontal ones, mainly due to lower sedimentation levels and increased water circulation on the former (Clark & Edwards, 1999; Wendt, Knott, & Van Dolah, 1989). For example, Baynes and Szmant (1989) found a higher abundance of octocorals on vertical compared to horizontal surfaces of shipwrecks in South Carolina. Likewise, the structural complexity of the reef may greatly affect the species diversity, density and size distribution of both invertebrates and fish, as a more complex and heterogeneous reef structure offers a greater array of niches (Duedall & Champ, 1991; Svane & Petersen, 2001). Many coral species, as well as other invertebrates, will preferably settle on a complex substratum rather than on a simple one (e.g., Carleton & Sammarco, 1987; Guichard, Bourget, & Robert, 2001). Similarly, there is a correlation between the structural complexity of the reef and its species diversity and abundance of the inhabiting fishes (Holbrook, Brooks, & Schmitt, 2002; Rilov & Benayahu, 1998). Additionally, the composition of the substratum, in terms of surface chemistry, toxicity and endurance, can also affect settlement and recruitment of benthic organisms (Baine, 2001; Spieler et al., 2001). This correlates to the AR's performance and long-term resilience (Sheng, 2000), as unsuitable material can lead to breakage and dispersed debris, which may in turn damage the surrounding environment (Brock & Norris, 1989; Waldichuk, 1988). Furthermore, environmental characteristics such as the reef's facing, depth, sedimentation load and water circulation, also play a role in shaping the community structure of the AR (Sheng, 2000; Spieler et al., 2001); however, these also affect the neighboring NRs. Therefore, recognizing the role of the structural features is of prime importance when designing ARs that will be able to meet their goals.

Understanding the relationship between the structural features of an AR and its developing benthic communities thus has a great biological and ecological significance for reef rehabilitation and enhancement (Baine, 2001; Svane & Petersen, 2001 and references therein). However, most studies to date have presented results obtained after a relatively short submersion period, when the AR still has a low coral cover and diversity, yet a high cover of other fouling organisms such as sponges, tunicates and hydrozoans, compared to a NR (Aseltine-Neilson et al., 1999; Clark & Edwards, 1999; Perkol-Finkel & Benayahu, 2005). Such a short time span may be insufficient to assess the development of long-lived organisms such as corals. In a recent study aiming at evaluating the role of time in the long-term development of fouling AR communities, we carried out a survey of seven 17–131-year old shipwrecks in the northern Red Sea and of their adjacent NRs (Perkol-Finkel et al., 2005). In the present study we address the question of whether AR communities can mimic adjacent NRs given sufficient time, despite differences in structural features between the two. We examine three alternative hypotheses, arguing that ARs and NRs will (1) have a similar community structure given sufficient time, (2) be similar only if they possess similar structural features, (3) always differ, regardless of their age and structure. In order to test these hypotheses we compared the benthic community structure of the Kingston AR, a 119-year old shipwreck, to a neighboring NR, taking into account the structural features of both. Our findings suggest that in the long run, the ability of an AR to resemble NR communities will depend mainly on their respective structural features.

2. Materials and methods

2.1. Study site

We compared the benthic communities of the Kingston shipwreck (also known as Sarah H) to those of its adjacent NR. This ship presents a wide variety of structural features in relation to spatial orientation, level of complexity, facings and ship zones (see Section 2.2), which enabled us to examine possible links between these features to long-term patterns in AR community development. The Kingston AR is a steel cargo vessel, sunk in 1881 (119 years old at the time of survey) at Sha'ab Ali (Shag Rock), 27° 46′ 42″ N, 33° 52′ 36″ E (Fig. 1). The ship was 78 m long, 10 m wide, and had a draught of 6 m. It lies starboard side up with its bow smashed into the reef at 5–7 m depth. The stern and hull have remained mostly intact at 15–19 m, comprising mainly vertical surfaces. Large horizontal metal plates, debris of the amidships, are scattered across a coral reef slope. The NR surrounding the Kingston has a moderate slope, at a similar depth range. Highly inclined natural habitats are not common to NRs in the area, which mainly consist of low profile fringing reefs (personal observations). Likewise, the studied NR did not include vertical formations, preventing us from comparing vertical artificial and natural surfaces.

2.2. Data collection

To study the community structure of the benthic organisms of both the Kingston AR and her adjacent NR, using SCUBA we ran a series of belt transects, 2 m long and 0.1 m wide, laid at random on the AR and NR at a comparable depth range (see: Perkol-Finkel et al., 2005). The use of 2 m long transects, shorter than the standard 10 m transects previously used in coral community studies in the Red Sea (e.g., Loya, 1972; Perkol-Finkel & Benayahu, 2004, 2005), was a result of diving safety limitations. However, by making sets of at least five transects with similar structural features in close proximity to each other (Table 1) we overcame this difference in length, as a plateau in species count and diversity was achieved when pooling together 5 × 2 m transects of similar features (see: Perkol-Finkel et al., 2005). The 0.1 m wide

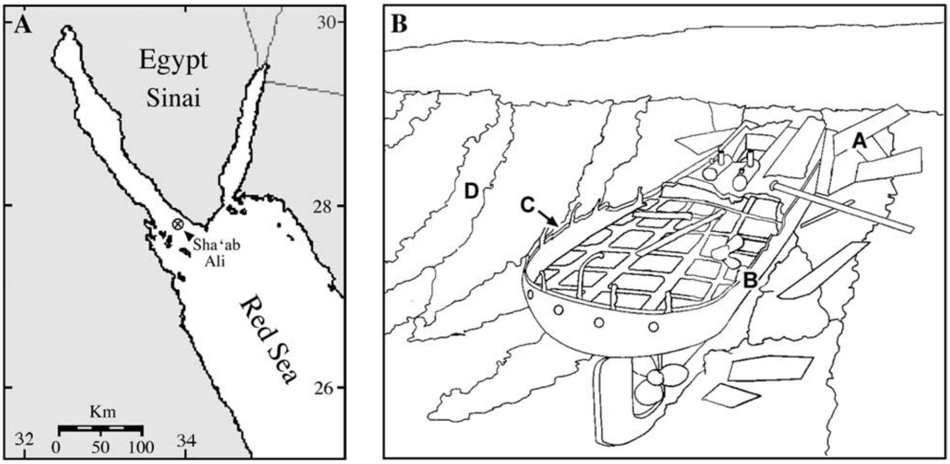

Fig. 1. (A) Geographical location of the study site and (B) Schematic illustration of the Kingston shipwreck partially on top of the adjacent natural reef. Different zones of the shipwreck and natural reef are marked: A. Plates, B. Right hull, C. Left hull, D. Slope of the natural reef.

Table 1
Number of transects (#) conducted for each area with a unique set of structural features on the Kingston artificial reef (AR) and on the adjacent natural reef (NR)

Type	Orientation	Complexity	Facing	Depth (m)	Zone	#
AR	Vertical	Low	North	13–17	Left Hull	10
	Vertical	Medium	North	6–8	Left Hull	9
	Vertical	Low	South	13	Right Hull	6
	Vertical	Medium	South	6–8	Right Hull	7
	Horizontal	Medium–High	South–West	6–8	Plates	18
NR	Horizontal	Medium–High	North–West	8–13	Slope	18

transects were designed to increase the probability of recording data from complex artificial structures that include many gaps as well as protruding appendages. The position of each transect laid on both the AR and the NR was characterized in terms of the following structural features: spatial orientation (scored as vertical, horizontal or other = ca. 45°), level of complexity (low = flat surface, medium = uneven surface or high = irregular with numerous protruding appendices), facing (north, south, east and west), and ship zone (bow, hull, stern, etc. for the shipwreck and reef slope for the NR).

Benthic organisms, including stony and soft corals, sponges, tunicates, sea anemones and hydrozoans, that intercepted the transects were recorded and their projected length along the transects was measured. Due to the frequent appearance of monospecific carpets, mainly of soft corals (Benayahu & Loya, 1977), we did not measure the size of individual colonies, but recorded their respective projected length along the transects. The organisms were identified underwater to the lowest possible taxonomic level.

2.3. Data analysis and statistics

Community parameters of stony and soft corals such as species count, living cover and cover diversity were calculated per 1 m of transect for each reef type and compared between the AR and NR by one-way ANOVA tests. To meet ANOVA assumptions the stony and soft coral cover data were arcsin $\sqrt{X}$ transformed and their respective species counts were $\sqrt{X}$ transformed. The non-parametric Mann–Whitney *U* test (Sokal & Rohlf, 1985) was performed on original cover diversity data, since they did not distribute normally even after transformation.

To detect differences between the Kingston AR and NR and among different spatial orientations within each reef type, we used the Bray–Curtis similarity index based on the percentage living cover for the taxa in each transect using the PRIMER® (V5.2.9) statistical package (Clarke & Warwick, 2001). The analyses were conducted on the full data set including all recorded taxa. Due to the presence of several highly abundant taxa, a $\log(x + 1)$ transformation was applied to reduce their contribution to the similarity and to strengthen that of less common ones. The SIMPER (similarity percentage) analysis was used to identify the discriminating taxa between the AR and the NR and between groups of transects representing areas with different structural features (i.e., spatial orientations, complexity levels, zones and facings). Taxa were listed in decreasing order by their average contribution to the total average dissimilarity, with a cutoff at 50% of $\overline{\delta}$ (Clarke & Warwick, 2001).

One-way ANOSIM (analysis of similarities) tests were applied to assess the significance of differences in species composition between the Kingston AR and NR as well as between different structural features. However, we were unable to apply crossed comparisons as most tested variables in our study were not common to both reef types. The null hypothesis was that there were no differences between the examined groups of transects. The calculated R statistic ranges from -1 to 1, the higher the value, the greater the difference between the groups. The significance of the R statistic was tested using permutation methods on a similarity matrix yielding a standard p value (Clarke & Warwick, 2001). As multiple comparisons were made, we reduced the deciding significance level from $\alpha = 0.05$ to 0.008 to adjust for 6 multiple comparisons (i.e., 0.05/6; Bonferroni procedure).

Non-parametric multidimensional scaling (nMDS) were produced from the similarity matrices for the full data set including stony and soft corals and all other fouling organisms, as well as for the stony coral data set and the soft coral data set separately. To test whether there is a link between the structural features of the two reef types and their species assemblages, bubble plots were created by superimposing key taxa as dictated by the SIMPER analyses on the MDS plot of the full data set. Environmental (ENV) MDS was performed in order to illustrate patterns in the structural features of the reefs and to examine whether these patterns correspond to the community patterns revealed by the MDS analyses. The ENV-MDS was constructed using the following structural features: orientation, complexity, facing, depth and ship's zone of each transect. For this purpose all structural features (excluding depth) were transformed to indices: spatial orientation ($1 = \text{other}$, $2 = \text{horizontal}$ and $3 = \text{vertical}$), complexity ($1 = \text{low}$, $2 = \text{medium}$ and $3 = \text{high}$), facing (assigned numbers from 1 to 8: for example, $1 = \text{east}$, $2 = \text{north}$ and $3 = \text{north-east}$) and ship zone (assigned numbers from 1 to 19: for example, $1 = \text{slope}$, $2 = \text{deck}$ and $3 = \text{left hull}$). These indices were $\log(x + 1)$ transformed and then standardized. All data sets consisted of $n = 68$ transects, apart from the soft coral data set ($n = 50$), as some transects did not have any soft corals.

The level of similarity between the different data sets used (full data, stony corals, soft corals and the environmental data sets) was measured using the RELATE routine, testing whether the different sets of data exhibited similar patterns of community structure or not. The level of similarity was measured by ρ correlation coefficient ranging from $-1 = \text{no similarity}$ to $1 = \text{complete similarity}$ (Clarke & Warwick, 2001).

3. Results

When examining coral communities at the NR and AR as a whole, regardless of structural features within each reef type, most community parameters were higher on the NR surrounding the shipwreck than at the AR itself (Table 2). For example, the

Table 2
Community parameters; total and average species count, average stony and soft coral cover and average cover diversity of the Kingston artificial reef (AR) and of the adjacent natural reef (NR)

Parameter	Stony corals		Soft corals	
	AR	NR	AR	NR
Total species count	38	42	10	14
Avg. species count per m	3.42 ± 1.77	5.43 ± 1.78	0.90 ± 0.83	3.33 ± 1.32
Avg. coral cover (%) per m	46.59 ± 25.18*	47.50 ± 19.05*	18.42 ± 25.24	55.95 ± 21.90
Avg. cover diversity per m	0.90 ± 0.49	1.36 ± 0.43	0.15 ± 0.30	0.97 ± 0.36

Values are presented with ±1 standard deviation. All AR parameters were significantly different from the nearby NR parameters (one-way ANOVA, $p < 0.001$, see Perkol-Finkel et al., 2005) except for the stony coral cover (marked *).

Kingston AR had a total of 38 species of stony corals and 10 of soft corals compared to 42 stony and 14 soft coral species on the NR. Average species count per meter was significantly greater at the NR compared to the AR for both stony and soft corals (Table 2, 3.42 and 5.43 species, respectively, one-way ANOVA, $p < 0.001$). While stony coral cover was similar at both reef types, soft coral cover was greater on the NR compared to the Kingston AR (Table 2). Both stony and soft coral cover diversity were higher at the NR than at the AR. However, when analyzing all of the taxa surveyed and taking into account different areas within each reef type the results differ; for example, horizontal areas of the AR and NR were indistinguishable (see: multivariate analyses below).

All of the multivariate analyses indicated a strong effect of the various structural features, predominantly orientation and complexity, which had a greater effect on the community structure than the effect of the reef type; i.e., AR vs. NR. The greatest difference was found between vertical and horizontal orientation, regardless of the reef type. According to the SIMPER analysis (Table 3), dissimilarity between the AR and NR was lower that the difference between the vertical and horizontal orientations ($\overline{\delta} = 87.93\%$ and 94.06%, respectively). It should be noted that although a dissimilarity of 87.93% between transects of the AR and NR does not signify that they have similar communities, their communities are nonetheless more similar to each other than those of vertical and horizontal orientations. The latter finding was also supported by the ANOSIM tests as the R value for difference between reef types was much lower than that of between orientations ($R = 0.159$, $p = 0.003$ and $R = 0.650$, $p = 0.001$, respectively). Furthermore, groups combining reef type and orientation showed greatest dissimilarity between vertical and horizontal groups, regardless of reef type (AV–AH: $\overline{\delta} = 93.47$, $R = 0.529$, $p = 0.001$ and AV–NH: $\overline{\delta} = 94.51\%$, $R = 0.648$, $p = 0.001$), while the groups of artificial and natural horizontal transects showed higher similarity (AH-NH: $\overline{\delta} = 74.77\%$ with $R = 0.114$, $p = 0.019$).

Stony and soft corals were the most dominant groups at both reef types. Interestingly, fouling organisms such as sponges, tunicates, sea anemones and hydrozoans that appeared in our survey did not contribute much to the dissimilarities between the groups. This is best demonstrated by the fact that only coral species contributed

Table 3
Percentage of average dissimilarities ($\overline{\delta}$) between groups of different structural features of the Kingston artificial reef (AR) and its adjacent natural reef (NR) as calculated by the SIMPER analyses, and value of R statistic as calculated by the one-way ANOSIM test as well as its p value (to account for multiple comparisons, differences with $\alpha > 0.008$ were deemed insignificant and are marked *)

Feature	Levels	Groups	$\overline{\delta}$ (%)	R	p
Type	Artificial reef, natural reef	AR–NR	87.93	0.159	0.003
Orientation	Vertical, horizontal	V–H	94.06	0.650	0.001
Type and orientation	ARV, ARH, NRH	ARV–ARH	93.47	0.529	0.001
		ARV–NRH	94.51	0.648	0.001
		ARH–NRH*	74.77	0.114	0.019*
Complexity	Low, medium, high	L–H	95.93	0.769	0.001
		L–M	90.44	0.297	0.001
		M–H*	82.13	−0.021	0.594*
Zone	Left hull, right hull, plates, NR slope	L. hull–R. hull*	81.12	−0.036	0.714*
		L. hull–plates	92.70	0.428	0.001
		L. hull–slope	93.22	0.599	0.001
		R. hull–plates	94.75	0.687	0.001
		R. hull–slope	96.66	0.877	0.001
		Plates–slope*	74.77	0.114	0.014*
Facing	North, south, west, north-west	N–S*	83.66	0.004	0.399*
		N–W	92.81	0.461	0.001
		N–NW	93.01	0.562	0.001
		W–S	93.18	0.566	0.001
		NW–S	93.54	0.699	0.001
		NW–W*	71.75	0.011	0.341*

The abbreviations are explained in the levels column.

to the top 50% of the dissimilarities among groups combining reef type and orientation (i.e., AR vertical, AR horizontal and NR horizontal, Table 4). Three coral species are primarily responsible for differentiating the reef type and orientation groups (SIMPER analysis, Table 4). The soft corals *Xenia* sp. and *Nephthea* sp. were dominant on both the natural and artificial horizontal groups, yet were nearly absent from the artificial vertical one, while the stony coral *Tubastrea micrantha* dominated the latter and was hardly found on the two former. Since the above-mentioned three taxa also differentiated the other groups examined (complexity levels, zones and facings), we do not present their SIMPER analyses in order to avoid redundancy.

The MDS analysis of the full data set clearly presents the distinct differences in community structure between transects laid on vertical AR surfaces appearing on the left side of the plot, to those of horizontal ones, both artificial and natural that grouped together at the right side of the plot, indicating their similarity (Fig. 2(A)). The MDS plot of the stony coral data set (Fig. 2(B)) resembled that of the full data set (RELATE procedure, $\rho = 0.773$, $p = 0.001$) and the two had similar, and rather high, stress levels (0.16 and 0.17, respectively). The MDS of the soft coral data set revealed a slightly different pattern, in which transects of both reef types and orientations clustered much closer to each other than in the two other plots (Fig. 2(C),

Table 4
Comparison between the Kingston artificial reef vertical surfaces, natural reef horizontal, and artificial reef horizontal surfaces (ARV, NRH and ARH, respectively), on $\log(x+1)$ transformed living cover data of the full taxa data set, averaged for transects of each group

Taxa	ARV	NRH	$\bar{\delta}_i\%$	$\Sigma\bar{\delta}_i\%$
Average dissimilarity between ARV and NRH, $\bar{\delta} = 94.51$				
Xenia sp.	1.56	23.02	8.05	8.05
Nephthea sp.	0.00	15.74	6.95	15.00
Tubastrea micrantha	7.30	0.07	5.97	20.97
Sinularia sp.	0.00	9.98	4.77	25.74
Acropora variabilis	0.08	5.33	3.67	29.40
Acropora eurystoma	0.14	6.98	3.66	33.07
Stylophora wellsi	0.47	4.24	3.14	36.21
Acropora scandens	5.02	3.83	3.09	39.29
Litophyton sp.	0.16	7.93	2.97	42.27
Acropora hemprichi	0.25	5.48	2.87	45.13
Millepora dichotoma	3.41	1.33	2.81	47.94
Cladopsammia gracilis	10.97	0.07	2.78	50.72
Average dissimilarity between ARV and ARH, $\bar{\delta} = 93.47$				
Xenia sp.	1.56	18.72	8.06	8.06
Tubastrea micrantha	7.30	0.16	7.60	15.66
Nephthea sp.	0.00	18.59	7.05	22.71
Acropora variabilis	0.08	13.38	5.45	28.16
Stylophora wellsi	0.47	5.88	5.35	33.51
Acropora hemprichi	0.25	8.31	4.35	37.86
Acropora scandens	5.02	6.69	4.24	42.10
Pocillopora danae	4.55	2.19	3.68	45.78
Acropora sp.	0.00	7.00	3.61	49.39
Cladopsammia gracilis	10.97	0.00	3.49	52.88
Average dissimilarity between ARH and NRH, $\bar{\delta} = 74.77$				
Nephthea sp.	18.59	15.74	7.11	7.11
Xenia sp.	18.72	23.02	6.72	13.83
Sinularia sp.	6.25	9.98	6.22	20.05
Acropora variabilis	13.38	5.33	6.09	26.14
Acropora hemprichi	8.31	5.48	5.17	31.31
Stylophora wellsi	5.88	4.24	5.03	36.33
Acropora eurystoma	3.88	6.98	4.81	41.15
Acropora sp.	7.00	2.43	4.07	45.22
Acropora scandens	6.69	3.83	3.91	49.13

$\bar{\delta}_i\%$ is percentage contribution of *i*th taxa to the average Bray–Curtis dissimilarity ($\bar{\delta}$) between the groups, also expressed as a cumulative percentage ($\Sigma\bar{\delta}_i\%$). Taxa are listed in decreasing order of importance in contribution to $\bar{\delta}$ with a cut-off at 50% of $\bar{\delta}$.

stress = 0.07). Nonetheless, a separation did appear between the vertical AR transects and the horizontal ones of both AR and NR, similar to the trend appearing for the full data set (RELATE procedure, $\rho = 0.823$, $p = 0.001$). However, the latter MDS was based on 50 out of a total of 68 transects as 18 transects did not include any soft corals. ENV-MDS presented a graphical comparison between the three habitats (Fig. 2(D)) which, unlike the pattern of the other data sets, also separated transects of horizontal artificial and natural reef zones. The environmental data

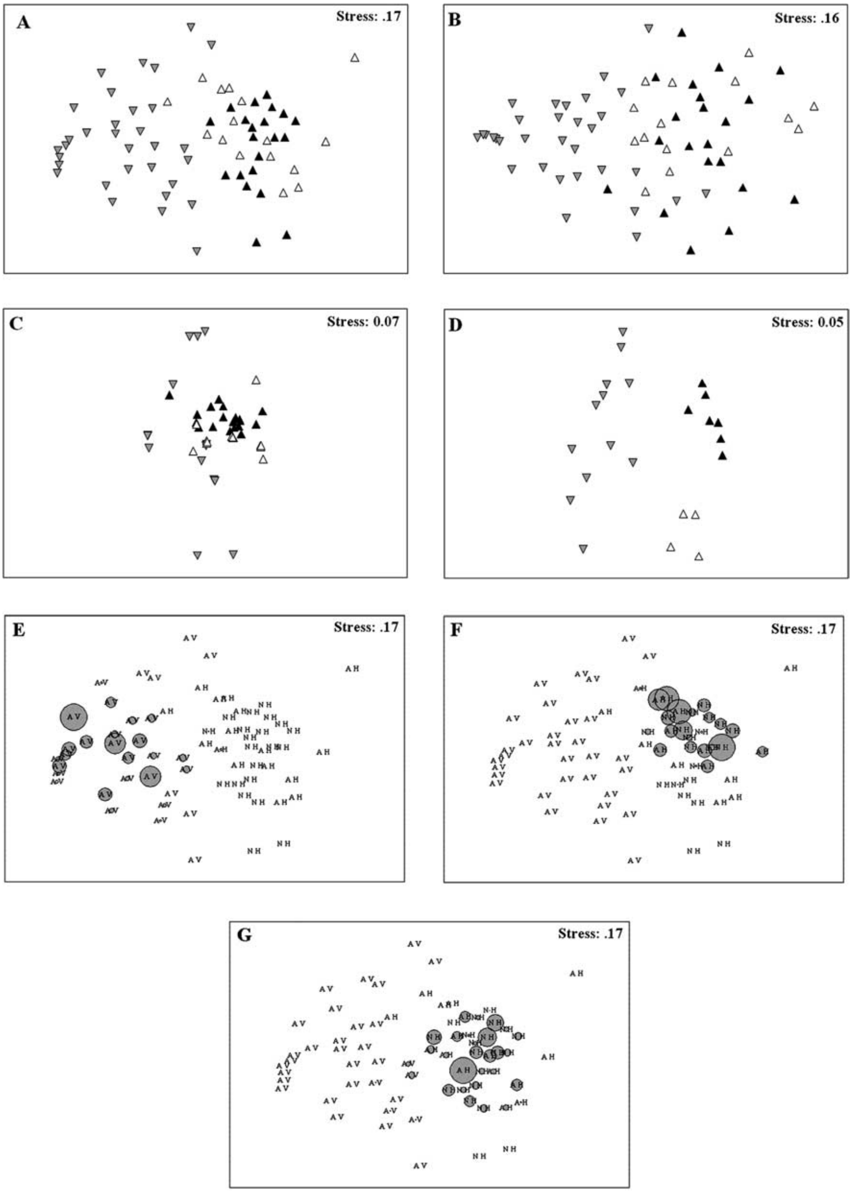

Fig. 2. Two-dimensional MDS for log($x+1$) transformed living cover data for the Kingston artificial reef and its adjacent natural reef [▼ = Artificial-Vertical (AV), △ = Artificial-Horizontal (AH), ▲ = Natural-Horizontal (NH)]: (A) Full taxa data set ($N=68$ transects). (B) Stony coral data set ($N=68$). (C) Soft coral data set ($N=50$). (D) Environmental data set ($N=68$). (E)–(G) Full data set with superimposed taxa: the ahermatypic stony coral *Tubastrea micrantha*, and the soft corals *Nephthea* sp. and *Xenia* sp., respectively. Circle size indicates taxon contribution to live cover; bigger diameter corresponds to a greater contribution of the superimposed taxa to the cover. Transects not including a given species were not assigned a circle.

set was more closely correlated to the full data set (RELATE procedure: $\rho = 0.346$, $p = 0.001$), and less so to the stony and soft data sets ($\rho = 0.260$ and 0.229, respectively, $p = 0.001$ for both). This suggests that the examined environmental features are fairly good predictors for the sessile communities as a whole, yet are poor as predicators of the soft and stony coral community structure. The spatial distribution of these three key species as indicated by the SIMPER analyses (Table 4) concurred with the spatial orientation and reef type clusters (Fig. 2(E)–(G)). The ahermatypic coral *T. micrantha* dominated the vertical AR cluster, while *Nephthea* sp. and *Xenia* sp. dominated the horizontal AR and NR transects.

The level of structural complexity also influenced the community structure. There were great dissimilarities between the two extreme groups, i.e., high and low complexity levels (Table 3: $\overline{\delta} = 95.93\%$ with $R = 0.769$, $p = 0.001$), less difference between the low and medium groups ($\overline{\delta} = 90.44\%$ with $R = 0.297$, $p = 0.001$), and greatest similarity between the high and medium groups ($\overline{\delta} = 82.13\%$ with $R = -0.021$, $p = 0.594$). Transect zone contributed only little dissimilarity between the horizontal metal plates of the shipwreck and the NR slope groups (Table 3: $\overline{\delta} = 74.77\%$), with ANOSIM indicating a non-significant difference between the two ($R = 0.114$, $p = 0.014$). The left and right sides of the hull showed a similar trend ($\overline{\delta} = 81.12\%$, with $R = -0.036$, $p = 0.714$). Interestingly, high levels of dissimilarity were noted for different combinations between these groups (Table 3: left or right hull with plates or slope, $\overline{\delta} = 92.7$–96.60%, $R = 0.429$–0.877, $p = 0.001$ for all). Analyses of the different facings revealed a pattern similar to the above, as the shipwreck was located in such a manner that certain zones corresponded to specific facings (for example, the left hull corresponded to the north facing and the right hull to the south).

4. Discussion

The results of our study suggest that structural features of an AR play a greater role than age in determining its community structure. All multivariate analyses indicated greater dissimilarities between transects of different structural features (i.e., orientation or complexity), than between transects of the AR and NR. Studying a 119-year old shipwreck enabled us to examine the community structure of an AR well beyond its initial developmental stages, and compare it to an adjacent NR. The results support the second hypothesis posited (see Section 1), arguing that given sufficient time, when an AR and its adjacent NR offer similar structural features their community structures will become almost indistinguishable. However, when substrates displaying different structural features are compared, be it within an AR or between an AR and a NR, taxa assemblages will differ even after more than a century.

Multivariate analyses indicate high similarity between horizontal surfaces of both the Kingston AR and NR, while vertical AR surfaces differed from horizontal ones of the two reef types (Fig. 2(A)–(C), Tables 3 and 4). This unique pattern resulted mainly from an uneven distribution of a small number of coral taxa (Table 4). The ahermatypic coral *T. micrantha* dominated the vertical AR cluster (Fig. 2(E)).

Similarly, the species *Tubastrea coccinea* was recently declared an invasive species, successfully colonizing vertical surfaces of shipwrecks and oil jetties in the north-western Gulf of Mexico (Fenner & Banks, 2004). Vertical habitats are able to accommodate specialized species that flourish under the conditions characterizing such habitats. The flourishing of ahermatypic corals on ARs, as opposed to their absence from the adjacent nearly horizontal NRs, was attributed to the current regime and low sedimentation load associated with inclined surfaces as well as to the ample overhangs (Oakley, 1988; Fenner & Banks, 2004; Perkol-Finkel et al., 2005). Natural reefs with extremely steep slopes or wall formation are also inhabited by ahermatypic corals (Loya & Slobodkin, 1971); however such habitats are uncommon in NR systems of the northern Red Sea (Loya, 1972). In fact, none of the other NRs surveyed by Perkol-Finkel et al. (2005) had a steep wall formation, and they did not exhibit a species assemblage similar to that of the Kingston AR. As all the different parts of the studied AR were made of the same material (steel) and had an identical submersion period, it is suggested that spatial orientation was the main cause for the differential taxa composition within the AR. Nonetheless, most horizontal AR surfaces examined were situated directly on the seabed, while vertical ones were usually elevated by 1–5 m. Distance from the seabed may also generate some differences in community structure due to varying sedimentation levels, currents and possibly predations levels (Glasby, 1999). In conclusion, we suggest that particular suits of structural features may correspond to unique taxa composition; and, therefore, in order to obtain high biodiversity on an AR, it should be designed with a variety of niches presenting different structural features.

Horizontal surfaces of both ARs and NRs were characterized by the soft corals *Nephthea* sp. and *Xenia* sp. (Fig. 2(F)–(G) and Table 4). These taxa are characteristic of the Red Sea fauna (Benayahu, 1985), and settle successfully on artificial surfaces there (Benayahu & Loya, 1987; Perkol-Finkel & Benayahu, 2005). Furthermore, these soft corals dominated most of the surveyed shipwrecks and NRs in the area (Perkol-Finkel et al., 2005). Obviously, the horizontal surfaces of the Kingston shipwreck and its nearby NR were of different materials (steel vs. calcareous), and the submersion period of the AR was much shorter than the age of the NR. Nonetheless, despite these differences, their similar spatial orientations and complexity levels had led to similarity in their inhabiting communities. In conclusion, we suggest that areas of an AR that possess unique structural features differing from other AR areas, or from nearby NRs, will ultimately sustain different species assemblages.

The level of similarity between the full taxa MDS and the ENV-MDS according to the RELATE routine was moderate, yet highly significant. Considering the fact that the ENV-MDS related solely to a small number of environmental features, such a level of similarity is reasonably high, supporting the notion that there is a strong link between the environmental features of the substratum and its species assemblages. The fact that the ENV-MDS showed a separation between the horizontal artificial and natural transects, while the full taxa MDS did not, suggests that despite basic differences in structural features, i.e., artificial vs. natural substratum, the community structure of horizontal surfaces remains similar. When comparing the full taxa data set with the stony and soft coral data sets, high levels of similarity were found (RELATE procedure: $\rho = 0.773$ and 0.823, respectively). Therefore, it is possible that in rich coral reef systems, considering stony and soft corals may suffice to obtain a comprehensive and reliable view of the taxa assemblage in a given area. This notion was also supported by the SIMPER results (Table 4).

To the best of our knowledge there are currently no other studies dealing with ARs over 100 years old; however, studies of younger ARs do exist (e.g., Baynes & Szmant, 1989; Perkol-Finkel & Benayahu, 2004, 2005; Wilhelmsson, Ohman, Stahl, & Shlesinger, 1998). Wilhelmsson et al. (1998) have found lower diversity and richness of benthic organisms on ARs than on NRs. Wendt et al. (1989) produced similar findings for 4–10-year old shipwrecks, and suggested that differences between the two reef types may have derived either from the relatively young age of the ARs, still undergoing community changes after 10 years; or, alternatively, from the different abilities of artificial and natural substrata to attract or sustain certain benthic invertebrates. Perkol-Finkel et al. (2005) studied shipwrecks of various ages in comparison to their adjacent NRs and found that young ARs (ca. 20 years) may have similar species composition to that of NRs, while acquiring a similar extent of coral cover may take a full century. The latter study, together with the current results, suggest that both of the above alternative explanations are viable, and thus support the second hypothesis we presented: that given several decades an AR will mimic its adjacent NR communities if it possesses similar structural features to those of the natural surroundings. However, if the two reef types offer different structural features, their communities will remain distinct over time.

We thus conclude that in the long run, the degree of resemblance of AR to NR communities will depend mainly on their respective structural features. Spatial orientation, complexity and facing of the substratum are the most important features to be considered, at least in tropical coral reef systems. Designing a heterogeneous AR will increase diversity and abundance of species and, depending on the level of similarity to the overall composition of the natural surroundings, may also elevate diversity and species abundance in the entire area. These findings are crucial when planning future AR projects, with the aim of long-term rehabilitation and enhancement of denuded marine environments.

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