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Differential recruitment of benthic communities on neighboring artificial and natural reefs

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Abstract

Shedding light on the ability of benthic artificial reef (AR) communities to resemble those of a natural reef (NR) is of great importance if we are to harness ARs as tools for rehabilitation and restoration of degraded marine habitats. Studying recruitment processes to experimental settlement plates attached to ARs and NRs reveal the factors that shape community structure at the two reef types, and determine the ability of an AR to support communities similar to those found in adjacent natural habitats. In this study, conducted in Eilat (Red Sea), we used settlement plates to test the hypothesis that differences in benthic communities between ARs and NRs are derived from differential recruitment processes. A monitoring period of 18 months revealed great differences in the recruitment of corals and other benthic communities between the studied ARs and adjacent NRs. The ARs were either made of PVC or metal and 10–17 years old when the study commenced. The recruitment of soft corals reflected the species assemblage found in the area, consisting mainly of the family Nephtheidae and Xeniidae, species, while that of stony corals was mostly determined by the life history traits of the recruited taxa, e.g., the opportunistic nature of the family Pocilloporidae. Benthic organisms, mainly filter feeders like bryozoans, bivalves, sponges and tunicates, were more abundant at the ARs than at the NRs, mainly on the underside of the plates. We suggest that this differential recruitment resulted from a synergistic effect of abiotic and biotic factors, including current regime, sedimentation load and larval settlement preferences, which subsequently differentiated the composition of the benthic communities at the ARs and NRs. Thus, in order to construct an AR for restoration purposes, it must offer similar structural features to those found in the natural surrounding, leading to recruitment of local taxa. However, if the AR and NR will differ structurally, the composition of recruits will also differ and eventually the communities at the two reef types will become distinct, hereby increasing the species diversity in the area.

Keywords: Artificial reefs; Coral reefs; Current velocity; Recruitment; Red Sea

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1. Introduction

Artificial reefs (ARs) have been suggested as a tool for rehabilitation and restoration of degraded natural reefs (NRs) (Bohnsack and Sutherland, 1985; Seaman and Jensen, 2000; Seaman, 2002). There are still doubts, however, regarding their performance and their possible effects on the natural surroundings (Svane and Petersen, 2001; Seaman, 2002). A key issue of the ongoing debate is the attraction vs. production hypothesis, i.e., whether ARs merely attract resources away from the natural surrounding, thus depleting them, or whether are they

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capable of producing a biomass that would otherwise have been lost without the AR (Carr and Hixon, 1997; Grossman et al., 1997; Svane and Petersen, 2001). Most studies addressing this question have dealt with fish or motile invertebrates that are capable of migrating as post-larvae or adults from the NR to an adjacent AR, while this aspect has not been examined in relation to benthic communities in general and to coral reefs in particular (Svane and Petersen, 2001). Determining whether ARs merely divert propagules from NRs, or, rather, attract those that would otherwise be lost, is of great ecological importance. However, providing an appropriate answer is hindered by the difficulty of following larval movements in the ocean. Large-scale dispersal patterns of planktonic larvae can be evaluated using satellite-tracked drifters and simulated currents (Lugo-Fernández et al., 2001). Small-scale dispersal of marine organisms has been traditionally studied either by direct observation of their larvae, or by recording their settlement and recruitment (Mariani, 2003); but can be performed only on visible, relatively large larvae, for example certain tunicates (Bingham and Young, 1991). Coral planulae are by nature too small for such observations (e.g., Harrison and Wallace, 1990; Ben-David-Zaslow and Benayahu, 1998; Harii and Kayanne, 2002).

Settlement plates have been widely applied in ecological studies in order to characterize and quantify settlement and recruitment of benthic organisms including corals (e.g., Mundy and Babcock, 2000; Thomason et al., 2002; Glassom et al., 2004; Perkol-Finkel et al., 2006). It has been demonstrated that these processes are affected by abiotic factors related to the structural features of the substratum and the environment, and by biotic factors related to the inhabiting organisms (Table 1). Settlement plates have been extensively used for examining spatial and temporal variations in coral settlement and recruitment to NRs (e.g., Carleton and Sammarco, 1987; Fisk and Harriott, 1990; Mundy and Babcock, 2000; Glassom et al., 2004). However, only a few studies have implemented this approach for investigating these processes on ARs, particularly those that are beyond their initial successional stages (see Mariani, 2003).

The use of settlement plates for examining recruitment of benthic organisms on ARs in comparison to neighboring NRs may help to shed light on the factors that determine community structure at the two reef types. This in turn may enable us to resolve questions regarding the attraction vs. production debate (see above), and whether ARs can mimic NR communities and thus help restore them. Interestingly, most studies have revealed substantial differences in the species composition and abundance of benthic communities found on the two reef types (e.g., Wendt et al., 1989; Wilhelmsson et al., 1998; Perkol-Finkel and Benayahu, 2004). Clark and Edwards (1999) revealed in the Maldives different species assemblage on a 3.5-year-old AR compared to a control NR; i.e., recruitment on the AR consisted mainly of branching corals while slow-growing massive species were less abundant compared to the typical reef-flat communities in the area. Recently, Perkol-Finkel et al. (2005) demonstrated that community differences between ARs and NRs in the Red Sea might still prevail even after >100 years following the AR deployment, depending on the structural differences between the two reef types that can affect both species composition and percentage coral cover. Community differences between the two reef types might be a result of differential recruitment at early successional stages, or alternatively from differential survivorship of the recruits with time (Harrison and Wallace, 1990). Thus, it is suggested here that comparing settlement and recruitment occurring on ARs and NRs is essential in order to determine the grounds for an eventual degree of similarity between the communities of the two reef types.

Table 1
Abiotic and biotic factors affecting settlement and recruitment of benthic organisms

Abiotic
Orientation of the substratum (Harriott and Fisk, 1988; Oren and Benayahu, 1997).
Texture (Carleton and Sammarco, 1987; Thomason et al., 2002).
Current regime (Abelson and Denny, 1997; Eckman and Duggins, 1998).
Sediment load (Birrell et al., 2005).
Light attenuation and depth (Mundy and Babcock, 1998)
Water quality and nutrient levels (e.g., Tsemel et al., 2006 and references therein).
Biotic
Reproduction mode and life history traits (Benayahu and Loya, 1984; 1987).
Chemical attraction/inhibition (Harrison and Wallace, 1990; Morse and Morse, 1996).
Post-settlement predation by fish (Osman and Whitlatch, 2004).
Seasonal reproduction and larval availability (Richmond, 1997; Reyes and Yap, 2001).

Recent studies on benthic communities of ARs and their adjacent NRs at Eilat, Israel (Gulf of Eilat, northern Red Sea) revealed distinct differences between the two (Perkol-Finkel and Benayahu, 2004, 2005), e.g., stony corals were the major component in the NRs, while soft corals, mainly of the family Nephtheidae, dominated the ARs. These differences were evident in the species count, percentage living cover and cover diversity. These community differences were related to the vertical orientation of the ARs as opposed to the horizontal orientation of the NRs, which impose differential current regimes. Intrigued by these findings, we initiated the current study, aimed at testing the hypothesis that differences in benthic community structure between ARs and NRs result from differential recruitment processes, or alternatively from subsequent differential survivorship of the recruits. In order to test this hypothesis, we conducted a comparative study using experimental plates, examining the effects of horizontal vs. vertical orientation and outer vs. inner face of the plates on recruitment processes at the two reef types. The results emphasize the importance of recruitment processes in shaping the features of benthic AR communities, and thus shed new light on the processes determining the degree of similarity between ARs and their neighboring NR communities. The conclusions of the current research are of great significance locally, in light of the poor state of Eilat's reef, which suffers chronically from anthropogenic stressors such as nutrient enrichment, sewage spills and recreational activities such as diving and snorkeling (e.g., Zakai and Chadwick-Furman, 2002; Loya, 2004; Loya et al., 2004).

2. Materials and methods

2.1. Study sites

The research was conducted at two sites in Eilat, Israel (Red Sea), each including an AR and an adjacent NR (Fig. 1). The first study site was the Dolphin Reef of Eilat (for details, see Perkol-Finkel and Benayahu, 2004) and its AR (17 years old when the study was conducted) comprised of a vertical net made of flexible PVC, hanging from the sea surface down to the seabed at 15 m depth. Its adjacent NR has a moderate slope and is nearly horizontal, consisting of scattered knolls located at a range of 4–50 m around the net, at a similar depth. The second study site was the pyramid site located at the northern beach of Eilat, where a pyramid-like AR was submerged on April 1992 (10 years old, see also Perkol-Finkel and Benayahu, 2005). This AR consists of two truncated square metal pyramids, a large outer one and a smaller inner one. Its base lies at 32 m depth on sandy bottom, while its top reaches 12 m below sea surface. The adjacent NR has a moderate slope at a depth of 19–27 m, located at a range of 15–50 m from the base of the pyramid AR. These two sites were chosen for the study since both contain ARs with inclined surfaces, located in close proximity to NRs and thus subjected to similar ambient conditions. The coral communities of the AR and NR in both sites were recently documented and found to be distinct (see Perkol-Finkel and Benayahu, 2004, 2005). Furthermore, both sites are relatively non-degraded with little recreational diving taking place.

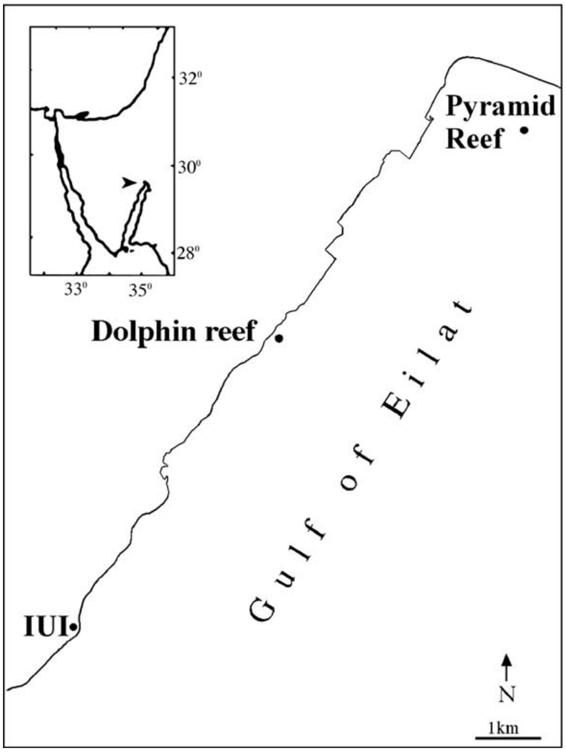

Fig. 1. Map of the study site. Interuniversity Institute = IUI.

2.2. Experimental layout

In order to compare recruitment processes on the ARs and the NRs, we used settlement plates (11.5 × 20.0 × 1.5 cm, total surface area 554.4 cm^2, including both plate faces and their edges) made of recycled PVC (Aviv Recycling Industries LTD), attached by cable ties to a galvanized metal rack (Fig. 2: 400 × 20 × 10 cm). On November 2002, one rack was set at each reef type at the two study sites. Twenty vertical and 20 horizontal plates were attached to each rack. At the Dolphin Reef site, the racks were fastened to the AR and NR at 14 m, and at the pyramid site at 24 m. At both sites, the racks were positioned on the AR and NR in parallel to each other, 15 m apart.

At each site, four vertical and four horizontal plates were removed from the AR and NR 6, 12 and 18 months post-deployment (May, November 2003 and May 2004, respectively). Plates were tagged underwater prior to removal according to site (Dolphin Reef vs. pyramid site), reef type (AR vs. NR), orientation (horizontal vs. vertical) and plate face (outer vs. inner). Plates were sampled in order from the left to right of each rack (four

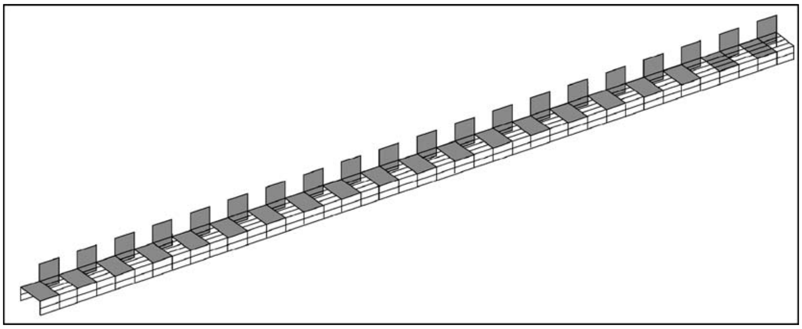

Fig. 2. Schematic illustration of an experimental metal rack (400×20×10 cm) holding 20 vertical and 20 horizontal settlement plates (11.5×20.0×1.5 cm).

plates were spare and were not sampled). After removal, the plates were separately placed underwater in zip-lock bags, transferred to the Interuniversity Institute for Marine Science at Eilat (IUI), placed in a water table supplied with running seawater and examined under a dissecting microscope within 24 h of removal. Both plate faces, the outer (= exposed) and the inner (= oriented towards the reef substratum), were examined, including their edges. We termed the leeward face of vertical plates "outer" and the face directed towards the reef substratum (located in shallower water) "inner". The upper half of the plate's edges was considered as a part of the outer plate face and the lower half as part of the inner one. We recorded the number of stony and soft coral recruits on each face, measured their diameter in mm and identified them to the lowest possible taxonomic level. Due to difficulty in distinguishing between juveniles of the soft corals *Xenia* sp. and *Heteroxenia* sp., they were scored as *Xenia*/*Heteroxenia* sp. and similarly for the stony corals *Pocillopora*/*Stylophora* sp. In cases when the recruits could not be generically assigned, they were scored as unidentified sp., separately for soft and stony corals. We also recorded the taxa composition of other major benthic invertebrates and algae that appeared on the plates in relation to their position (outer vs. inner). By using a 1×1 cm grid of a comparable size to the plate, we recorded the percentage cover of colonial organisms as well as of bare space on each face of the plate and counted the number of the solitary organisms. Taxa that could not be counted as individuals (i.e., serpulid worms), or when their exact percentage cover could not be recorded (turf and coralline algae) due to variations in density, were each scored according to their appearance as follows: 0—absent, 1—sparsely scattered, 2—densely scattered and 3—densely uniform.

After the microscopic examination was complete, all benthic organisms and algae were scraped from the plate's surface using a sharp metal spatula and half (chosen randomly) of the outer face of each plate ($11.5\times10=115$ cm^2) and used for determination of organic weight. We scraped only half of the plate as the quantity of organisms from a whole face was too great for the capacity of the burning furnace we used. We used the outer face for this measurement since preliminary observations had revealed that it had an even distribution of organisms, while the inner face was much less covered and the organisms had a patchy appearance. We compared the biomass of the two faces of the plates only for the first monitoring date (May 2003, 6 months post-submersion). The scraped material was placed in aluminum weighing cups (diameter 70 mm), dried in an oven for 24 h (60 °C), weighed (precision level of 4 decimal points), burned to ash in a furnace for 6 h (450 °C) and then re-weighed. Subtraction of the ash weight from the dry weight divided by the scraped surface area yielded the organic weight in g cm^{-2} (see Shemla, 2002).

2.3. Data analysis

Differences in number of coral recruits between the AR and NR at each site were tested by factorial ANOVA, the factors being: reef type (AR, NR), plate face (outer, inner) and orientation (vertical, horizontal). Data analyses also allowed testing for interactions between these factors. Differences in organic weight were also tested by Factorial ANOVA, the factors being: reef type (AR, NR) and orientation (vertical, horizontal). During May 2003, the factor plate face was also tested (see above). In order to meet ANOVA assumptions, the number of coral recruits was square root transformed, while the organic weight values were log transformed. Data are presented as averaged number of recruits per plate face and for organic weight as g cm^{-2}. All averaged values are presented with standard deviation

(S.D.). Statistical analysis was carried out using Statistica (Version 6, Statsoft, Inc.).

In order to detect possible differences between the AR and NR within each study site, and between the two faces of each plate, we used the Bray-Curtis similarity index based on the percentage cover, abundance and number of individuals (see above: experimental layout) for all community components applying the PRIMER® (V5.2.9) statistical package (Clarke and Warwick, 2001). A square root transformation was applied to all data. As the orientation factor was found to be insignificant according to preliminary analyses, we did not include it in the final ones. The SIMPER (similarity percentage) analysis was used to identify the discriminating community components between the each of the two studied pairs of AR and the NR. The taxa are listed in decreasing order by their contribution to the average dissimilarity between the reef types (Clarke and Warwick, 2001). Two-dimensional non-parametric multidimensional scaling (nMDS) was produced from the similarity matrices of each site, for each sampling date. In order to detect spatial and temporal differences between the two sites, a second stage MDS was done on the similarity matrices of the two sites for each sampling date. The analyses demonstrate the level of similarity between the six matrices (Dolphin Reef site 6, 12 and 18 months, and similarly for the pyramid site).

3. Results

3.1. Recruitment of corals

At both the Dolphin Reef and the pyramid sites throughout the three monitoring dates (May, November 2003 and May 2004), the assemblage of recruited corals differed between the respective NR and AR at each site. This was demonstrated both by differences in the average number of stony and soft coral recruits per plate face

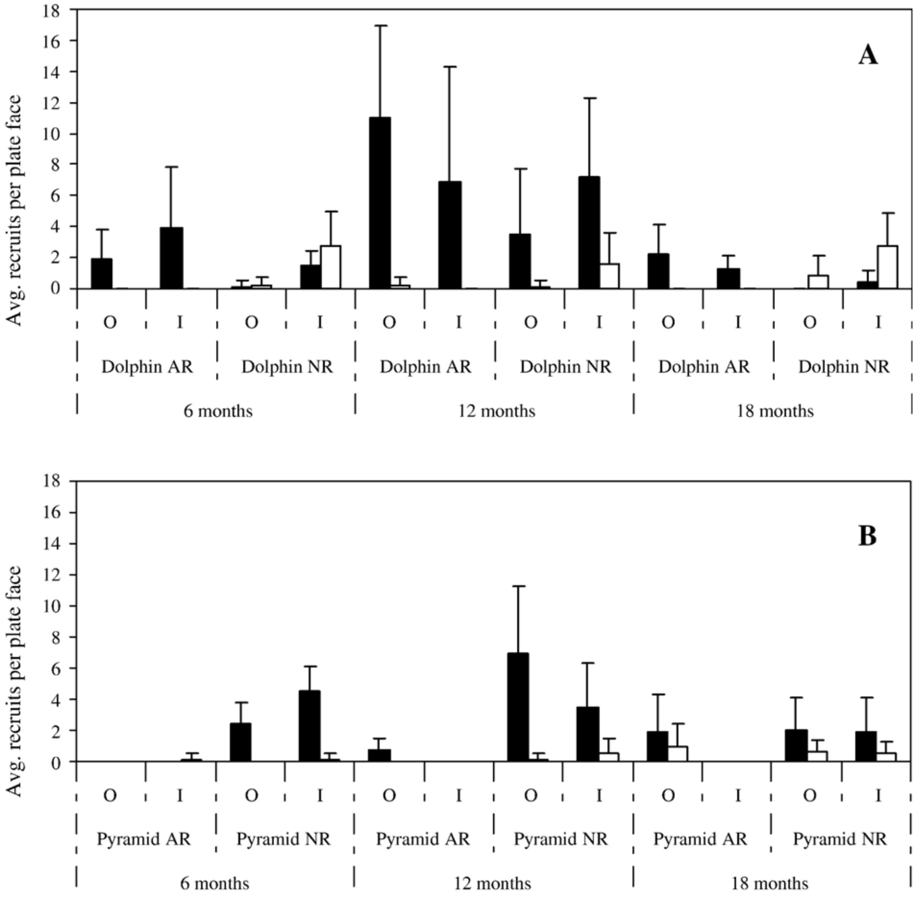

Fig. 3. Average coral spat (+ S.D.) per plate face, 6, 12 and 18 months after deployment (May, November 2003 and May 2004, respectively). (A) Dolphin Reef, (B) pyramid site. Soft corals = black columns, stony corals = white columns. Artificial reef = AR, natural reef = NR. O = outer face of plate, I = inner face. $n = 8$.

Table 2
Number of (A) soft coral and (B) stony coral recruits per plate 6, 12 and 18 months after deployment (May, November 2003 and May 2004, respectively), at the Dolphin Reef and pyramid sites

	Dolphin Reef						Pyramid site					
	6 months		12 months		18 months		6 months		12 months		18 months	
Taxa	AR	NR	AR	NR	AR	NR	AR	NR	AR	NR	AR	NR
A. Soft corals												
Alcyoniidae												
Rhytisma fulvum fulvum	–	–	6	3	5	1	–	–	–	3	12	3
Melithaeidae												
Acabaria sinaica	2	–	–	1	2	–	–	1	–	–	–	–
Nephtheidae												
Dendronephthya hemprichi	8	–	7	–	1	–	–	–	–	1	1	–
Litophyton sp.	–	–	–	2	–	–	–	–	–	–	–	–
Paralemnalia thyrsoides	–	–	–	3	–	–	–	–	–	–	–	–
Scleronephthya corymbosa	2	–	13	–	–	–	–	–	–	–	–	–
Stereonephthya cundabiluensis	–	–	2	–	–	–	–	–	–	–	–	–
Xeniidae												
Xenia/Heteroxenia sp.	34	13	74	76	20	2	–	54	6	80	2	28
Soft corals (unidentified)	–	–	5	1	–	–	–	–	–	–	–	–
Total	46	13	107	86	28	3	0	55	6	84	15	31
B. Stony corals												
Pocilloporidae												
Stylophora/Pocillopora sp.	–	24	2	14	–	28	1	1	–	–	1	1
Oculinidae												
Galaxea fascicularis	–	–	–	–	–	–	–	–	–	1	–	1
Pectiniidae												
Echinophyllia sp.	–	–	–	–	–	–	–	–	–	–	2	1
Dendrophylliidae												
Turbinaria sp.	–	–	–	–	–	–	–	–	–	–	1	–
Faviidae												
Cyphastrea chalcidicum	–	–	–	–	–	1	–	–	–	4	2	1
Favia sp.	–	–	–	–	–	–	–	–	–	–	1	1
Poritidae												
Porites sp.	–	–	–	–	–	–	–	–	–	–	1	–
Stony corals (unidentified)	–	–	–	–	–	–	–	–	–	2	–	4
Total	0	24	2	14	0	29	1	1	0	5	8	9
Grand total	46	37	109	100	28	32	1	56	6	89	23	40

Artificial reef = AR, natural reef = NR.
$n = 8$.

at each reef type (Fig. 3), and by the differences in the respective taxa composition (Table 2). Table 2 lists the number of soft and stony coral recruits of each taxon (upper = A and lower = B parts of the table, respectively), recorded 6, 12 and 18 months post-deployment at the Dolphin Reef site and the pyramid site for the ARs and NRs. The total number of recruits of soft and of stony corals at each reef type per sampling date is presented, as well as the grand total number of soft and stony coral recruits pooled together. Recruitment on the plates attached to the Dolphin Reef site was 1.5 times greater than at the pyramid site, and soft corals were more dominant than stony corals at both sites, with the overall number of soft corals recruited to the Dolphin Reef site being nearly four-fold that of stony corals and nearly eight-fold that at the pyramid site (Fig. 3A–B, Table 2). Soft corals dominated the Dolphin Reef AR, yet recruited in lower numbers to the neighboring NR (Table 2, 181 and 102 recruits, respectively). Stony corals appeared almost only at the Dolphin Reef NR (Table 2: 67 recruits compared to two at the Dolphin Reef AR). This difference was persistent for all three monitoring dates (Table 3: May, November 2003 and May 2004). Table 3 presents the results of the factorial ANOVA tests

Table 3
ANOVA of number of soft and stony coral spat over time at the Dolphin Reef and pyramid sites

Dolphin Reef	6 months			12 months			18 months		
	df	F	P	*df*	F	P	*df*	F	P
Soft corals									
Type (AR, NR)	1	5.44	*	1	1.53	n.s.	1	21.96	****
Face (O, I)	1	6.65	*	1	1.79	n.s.	1	0.17	n.s.
Orientation (V, H)	1	0.76	n.s.	1	0.47	n.s.	1	0.16	n.s.
Type × face	1	0.54	n.s.	1	1.44	n.s.	1	1.67	n.s.
Face × orientation	1	0.247	n.s.	1	3.27	n.s.	1	0.38	n.s.
Type × face × orientation	1	1.433	n.s.	1	4.29	*	1	0.74	n.s.
Stony corals									
Type (AR, NR)	1	32.58	****	1	8.45	**	1	31.53	****
Face (O, I)	1	16.50	****	1	4.44	*	1	5.66	*
Orientation (V, H)	1	0.09	n.s.	1	3.16	n.s.	1	0.04	n.s.
Type × face	1	16.50	****	1	13.74	***	1	5.66	*
Face × orientation	1	3.82	n.s.	1	0.95	n.s.	1	9.15	**
Type × face × orientation	1	3.82	n.s.	1	6.64	*	1	9.15	**

Pyramid site	6 months			12 months			18 months		
	df	F	P	*df*	F	P	*df*	F	P
Soft corals									
Type (AR, NR)	1	157.64	****	1	58.37	****	1	9.15	**
Face (O, I)	1	5.90	*	1	9.02	**	1	6.67	**
Orientation (V, H)	1	0.14	n.s.	1	5.03	*	1	0.24	n.s.
Type × face	1	5.90	*	1	0.00	n.s.	1	3.68	n.s.
Face × orientation	1	1.17	n.s.	1	2.68	n.s.	1	17.84	****
Type × face × orientation	1	1.17	n.s.	1	1.73	n.s.	1	0.07	n.s.
Stony corals									
Type (AR, NR)	1	0.00	n.s.	1	3.99	n.s.	1	0.79	n.s.
Face (O, I)	1	200	n.s.	1	0.91	n.s.	1	5.60	*
Orientation (V, H)	1	0.00	n.s.	1	0.91	n.s.	1	5.60	*
Type × face	1	0.00	n.s.	1	0.91	n.s.	1	2.65	n.s.
Face × orientation	1	0.00	n.s.	1	3.99	n.s.	1	1.75	n.s.
Type × face × orientation	1	2.00	n.s.	1	3.99	n.s.	1	7.14	*

Artificial reef = AR, natural reef = NR.
Outer face of plate = O, inner face = I, vertical = V, horizontal = H.
Probability of significance: ****$P<0.0001$, ****$P<0.001$, **$P<0.01$, *$P<0.05$, n.s. $P>0.05$.

performed for the Dolphin Reef (upper part) and the pyramid site (lower part).

At the Dolphin Reef AR, most soft coral recruits consisted of members of the families Xeniidae and Nephtheidae, while at its adjacent NR only the former was dominant. *Dendronephthya hemprichi* and *Stereonephthya cundabiluensis* (Nephtheidae), which commonly recruited to the Dolphin Reef AR, did not recruit to the NR at all (Table 2, upper left). *Rhytisma fulvum fulvum* of the family Alcyoniidae recruited to both reefs types only 12 months after submersion. The only stony corals recruited to this site were *Pocillopora* and *Stylophora* spp. (family Pocilloporidae). Six months after deployment of the experimental plates, soft corals at the Dolphin Reef site recruited mostly to the underside of the plates, but no longer did so after 12 and 18 months (Fig. 3A, Table. 3). The soft coral recruits did not exhibit any preference for orientation (Table 3: vertical vs. horizontal). Stony corals recruited to the inner face of the plates throughout the experiment, regardless of their orientation; however, this pattern mostly appeared at the NR (Fig. 3A, Table 3).

At the pyramid site, soft corals were the majority of recruits to both the NR and AR, and they were more common on the former compared to the latter (Table 2, 170 and 21, respectively). Recruits were predominantly Xeniidae yet, similarly to the Dolphin Reef, after 12 months of submersion *R. fulvum fulvum* recruited to both reefs types. Only 24 recruits of stony corals were found at this site throughout the study, mainly on the NR

(Table 2). After 6 months, a few recruits of the family Pocilloporidae were recorded, and 18 months following placement additional species appeared, but in low abundance (1–2 recruits per species). We found a significant difference in the recruitment of soft corals to the outer and inner faces of the settlement plate at the pyramid site (Fig. 3B, Table 3); however, this pattern changed from the inner face initially, to the outer one after 12 months.

Table 4
Dissimilarity between the reef types at the Dolphin Reef and pyramid sites pooled over time, based on average abundance (square root transformed) of all community components

Community component	Dolphin AR	Dolphin NR	Average dissimilarity $\bar{\delta}=53.78$		
	Average abundance	Average abundance	Average dissimilarity	$\bar{\delta}_i$%	$\sum\bar{\delta}_i$%
Bare space	21.35	38.72	14.09	26.21	26.21
Bryozoans	19.88	2.64	11.39	21.18	47.39
Bivalves	6.02	5.38	6.92	12.86	60.25
Xenia/*Heteroxenia* sp.	2.67	1.94	4.62	8.59	68.84
Sponges	1.44	1.68	3.13	5.83	74.67
Stylophora/*Pocillopora* sp.	0.04	1.40	2.86	5.32	79.99
Serpulid worms	1.54	0.77	1.60	4.38	84.82
Tunicates-colonial	1.65	0.34	1.89	3.52	88.33
Coralline algae	1.63	1.70	1.58	2.94	91.27
Tunicates-solitary	0.48	0.09	1.29	2.39	93.66
Rhytisma fulvum fulvum	0.23	0.09	1.03	1.91	95.57
Dendronephthya hemprichi	0.33	0.00	0.89	1.66	97.24
Acabaria sinaica	0.08	0.02	0.37	0.68	97.92
Scleronephthya corymbosa	0.31	0.00	0.36	0.66	98.58
Soft corals (unidentified)	0.10	0.02	0.32	0.59	99.17
Stereonephthya cundabiluensis	0.04	0.00	0.15	0.28	99.44
Litophyton sp.	0.00	0.04	0.13	0.24	99.68
Paralemnalia thyrsoides	0.00	0.04	0.10	0.18	99.86
Cyphastrea chalcidicum	0.00	0.02	0.07	0.14	100.00

Community component	Pyramid AR	Pyramid NR	Average dissimilarity $\bar{\delta}=57.61$		
	Average abundance	Average abundance	Average dissimilarity	$\bar{\delta}_i$%	$\sum\bar{\delta}_i$%
Bare space	21.88	8.85	12.95	22.48	22.48
Bryozoans	18.33	11.42	10.87	18.88	41.35
Bivalves	10.25	14.75	9.35	16.23	57.58
Sponges	9.85	4.04	7.27	12.62	70.20
Xenia/*Heteroxenia* sp.	0.17	3.38	5.83	10.12	80.32
Tunicates-colonial	1.00	2.90	2.85	4.94	85.26
Serpulidae	1.35	1.08	2.30	3.99	89.25
Coralline algae	1.96	1.98	1.79	3.12	92.37
Tunicates-solitary	0.63	0.06	1.29	2.25	94.61
Rhytisma fulvum fulvum	0.25	0.13	0.96	1.66	96.27
Cyphastrea chalcidicum	0.04	0.10	0.47	0.82	97.09
Echinophyllia sp.	0.04	0.02	0.30	0.52	97.62
Stylophora/*Pocillopora* sp.	0.04	0.04	0.29	0.50	98.12
Stony corals (unidentified)	0.00	0.08	0.20	0.35	98.46
Dendronephthya hemprichi	0.02	0.02	0.18	0.32	98.78
Favia sp.	0.02	0.02	0.16	0.29	99.07
Galaxea fascicularis	0.00	0.04	0.15	0.26	99.33
Soft corals (unidentified)	0.00	0.04	0.13	0.23	99.56
Turbinaria sp.	0.02	0.00	0.10	0.18	99.74
Porites sp.	0.02	0.00	0.09	0.15	99.89
Acabaria sinaica	0.00	0.02	0.07	0.11	100.00

$\bar{\delta}_i$%=percent contribution of *i*th component to the average Bray-Curtis dissimilarity ($\bar{\delta}$) between the reef types.
$\sum\bar{\delta}_i$%=cumulative percentage.
Community components are listed in decreasing order of importance in contribution to $\bar{\delta}$.
Artificial reef=AR, natural reef=NR.

Orientation significantly affected recruitment of soft corals only 12 months after deployment, with a distinct preference for vertical orientation (Table 3). Stony corals at this site recruited only in very low numbers, which made statistical analyses difficult. Only as late as 18 months post-deployment was no significant difference found in recruitment of stony corals between the reef types, with most recruits being found on the inner face of the plates, mainly the vertical ones (Fig. 3B, Table 3).

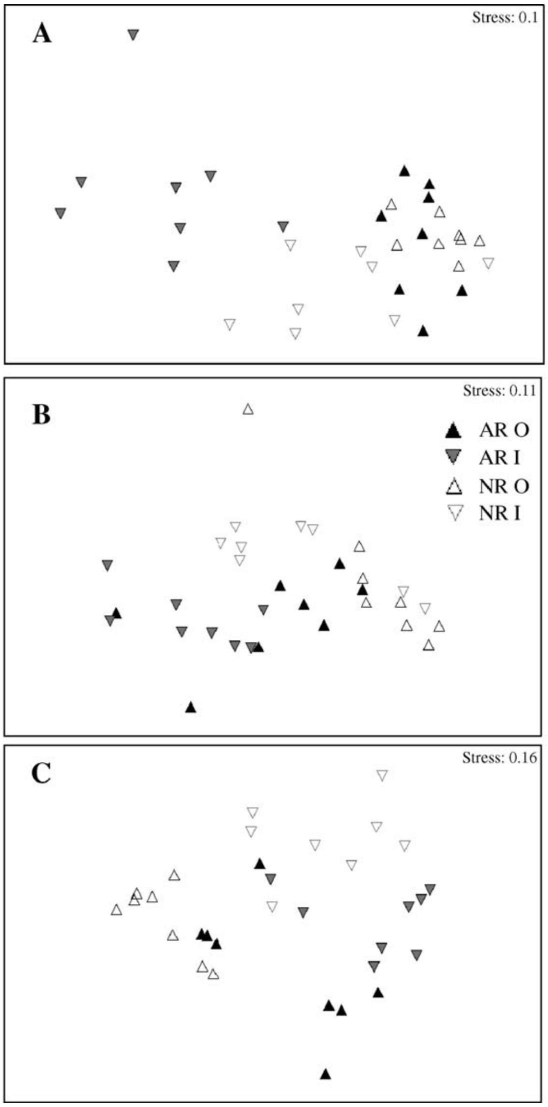

Fig. 4. Two-dimensional MDS based on the abundance of all the community components at the Dolphin Reef according to the type of reef and facing of the settlement plates. (A) 6 months, (B) 12 months, (C) 18 months. Artificial reef = AR, natural reef = NR. O = outer face of plate, I = inner face. $n = 8$.

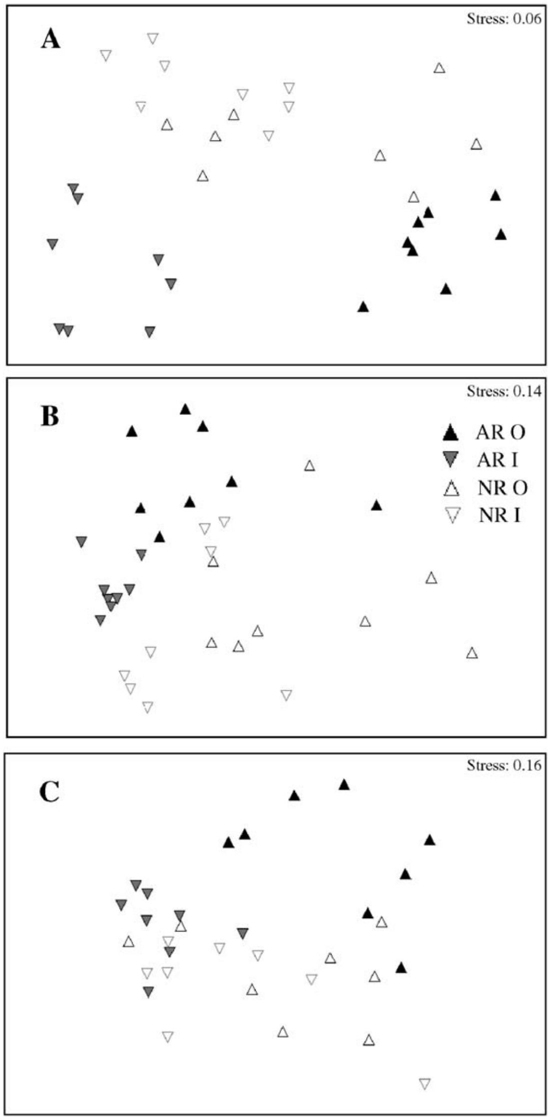

Fig. 5. Two-dimensional MDS based on the abundance of all the community components at the pyramid site according to the type of reef and facing of the settlement plates. (A) 6 months, (B) 12 months, (C) 18 months. Artificial reef = AR, natural reef = NR. O = outer face of plate, I = inner face. $n = 8$.

3.2. Community features

At both the Dolphin Reef and the pyramid sites, dissimilarity between the AR and NR was moderate (Table 4: 53.78% and 57.61%, respectively). Around 75–80% of the cumulative dissimilarity was comprised of the following community categories: (1) percentage of bare space, (2) percentage cover of bryozoans, (3) number of bivalve recruits, (4) number of xeniid recruits and (5) cover of sponges (Table 4). The percentage of bare space was the most dominant factor discriminating

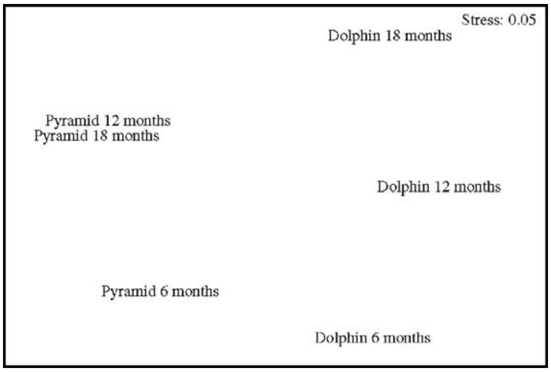

Fig. 6. Second stage MDS based on the similarity matrices of the Dolphin Reef and pyramid site, 6, 12 and 18 months after deployment (May, November 2003 and May 2004, respectively).

between the reef types at both sites, where more bare space was found on the plates of the NR at the Dolphin Reef, while the pyramid site showed an opposite pattern. Percentage coverage of bryozoans and the number of bivalve recruits was higher on the AR than on the NR at both sites, while percentage cover of sponges was greater on both NRs (Table 4). At both the Dolphin Reef and pyramid sites, fouling organisms other than corals contributed more to the dissimilarity between their respective AR and NR than did their coral species composition.

At the Dolphin Reef site, 6 months after deployment a distinct separation appeared between the community structure of the outer and inner faces of the plates for both reef types (Fig. 4A). Taxa assemblages on the outer face of the plates from both AR and NR were highly similar as demonstrated by the overlap of samples (Fig. 4A), while the inner faces of the two reef types were distinct. Twelve months post-deployment, the distinction between the two plate faces of the AR and NR was less clear, but was evident again at month 18 (Fig. 4B and C, respectively). At 12 and 18 months, the difference between AR and NR at the site had increased. At the pyramid site, the difference between the outer and inner faces of the plates of the AR and NR was evident (Fig. 5). There, at month 6, a separation was seen between the reef types, as indicated by the distribution of AR samples in the lower section of the plot and the NR ones in the upper one (Fig. 5A). Such separation also appeared at month 12, although at month 18 some overlap was noted between samples of the outer face of the plates of the pyramid site AR and those of both outer and inner faces of the NR (Fig. 5B,C).

There was a distinct separation between the spatial and temporal features of the two study sites throughout the study, with the matrices of the monitoring dates for each site appearing separately on the plot, i.e., Dolphin Reef site at the right side of the plot and the pyramid site at the left (Fig. 6). The findings from the sampling dates of the Dolphin Reef markedly differed from each other, with the greatest difference between the 6 and 18 months monitoring, positioned at opposite ends of the plot. At the pyramid site, however, whereas the first sampling date differed from the 12 and 18 months samplings, the latter two were similar, almost overlapping (Fig. 6).

The accumulated organic weight on the settlement plates (g cm^{-2}), at months 6, 12 and 18 after deployment are presented in Fig. 7. Differences between the ARs and NRs were only significant 6 months post-deployment

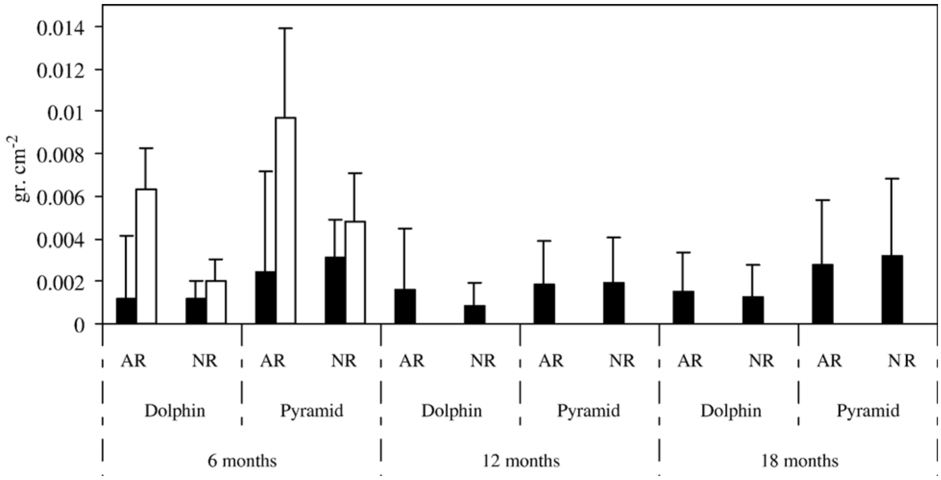

Fig. 7. Average organic weight (g cm^{-2}) at the Dolphin Reef and pyramid site 6, 12 and 18 months after deployment. Outer face of the plate = black columns, inner face = white columns (for the 6 months monitoring only). Artificial reef = AR, natural reef = NR. $n=8$. Probability of significance: 6 months: reef type $P<0.001$, face $P<0.0001$ for both sites, 12 and 18 months: no significant difference between the reef types at both sites.

(factorial ANOVA, $df=1$, $P<0.001$), when we also checked for differences between the two plate faces. At that point, organic weight at both study sites was greater at the AR than at the NR, and more organic weight was found on the inner face of the settlement plates than on their outer one (factorial ANOVA, $df=1$, $P<0.0001$). Later on, no significant difference was found in the amount of organic weight accumulated on plates between the two reef types, at both the Dolphin Reef and pyramid sites.

4. Discussion

Our study has shown that recruitment of stony and soft corals and of other benthic organisms markedly differed between the AR and NR at both the Dolphin Reef and the pyramid sites thus supporting our primary hypothesis that differences in community structure between the two reef types may result from differential recruitment processes. These differences appeared as early as 6 months after deployment and persisted throughout the 18 months of the experiment.

4.1. Recruitment of corals

Coral recruitment at the Dolphin Reef site greatly differed between the AR and NR, as the former recruited almost exclusively soft corals and the latter—mostly stony corals. This pattern corresponds to the resident species assemblage at the site, comprising mainly soft corals at the AR and stony corals at the NR as found by Perkol-Finkel and Benayahu (2004). The dominance of Nephtheidae species at the AR, which were nearly absent from the NR, and the occurrence of Xeniidae species at both reef types at the site (Table 2), also concurs with the findings mentioned in that study. Soft corals recruited to both faces of the plate equally, apart from a weak preference for the inner face 6 months after deployment (Table 3). The latter finding may indicate the mode of reproduction, namely sexual vs. asexual, which led to the recruitment of the soft corals at the site. Sexual recruits tend to settle upside down on undersides of available substrata (e.g., Benayahu and Loya, 1984, 1987), while asexual recruits tend to settle on the upper surface. For example, the soft coral *D. hemprichi* reproduces asexually by autotomized fragments (Dahan and Benayahu, 1997) and *Xenia* spp. by colony fission (Benayahu and Loya, 1985). The former asexually derived recruits are negatively buoyant and thus settle on the outer face of horizontal substratum. Therefore, lack of preference for a particular face (outer vs. inner) indicates that recruits at the site were derived from both modes of reproduction. While differential asexual recruitment may be a function of proximity to adult colonies, differences in recruitment of sexual propagules mostly relates to active searching and preferential settlement behavior of the planula-larvae (Keough, 1998; Harrison and Wallace, 1990). For example, *D. hemprichi* is an azooxanthellate flow-dependant coral, obtaining its food from the ambient current (Fabricius et al., 1995). Thus, the high abundance of Nephtheidae species at the Dolphin Reef AR might be related to the vertical inclination of the substratum, which corresponds to stronger currents compared to those at the adjacent horizontal NR (Perkol-Finkel and Benayahu, in preparation). Similarly, the high abundance of Xeniidae on the vertical AR compared to the nearly horizontal NR at the site may result from their preference to colonize overhangs (Benayahu and Loya, 1987). Therefore, we suggest that recruitment patterns played a key role in structuring coral communities at the site, as the mode of reproduction affected larval distribution on the experimental plates, and reef orientation differentiated the recruitment patterns at the two reef types.

Stony coral recruits at the Dolphin Reef consisted only of Pocilloporidae species, recruited mainly to the NR there. These were mostly *Pocillopora* and *Stylophora*, which are successful colonizers on settlement plates in general (Loya, 1972; Clark and Edwards, 1999; Fairfull and Harriott, 1999) and including the northern Red Sea (Glassom et al., 2004). Both corals are typically regarded as opportunistic species (Loya, 1976; Schuhmacher, 1977). They were the most abundant stony corals at the Dolphin Reef AR in terms of percentage cover, yet were less dominant compared to other slow-growing species such as *Porites lutea* found at the NR there (Perkol-Finkel and Benayahu, 2004). If recruitment of stony corals to the plates were to be consistent with the assemblage of resident colonies at the site, we would have expected recruitment of fast-growing branching corals at the AR, and of massive, slow-growing species at the NR. However, massive stony corals do not recruit to settlement plates as often as branching corals (e.g., Banks and Harriott, 1996; Fairfull and Harriott, 1999; Glassom et al., 2004). Thus, the composition of recruited taxa to settlement plates may, at times, be a poor representative of the overall community assemblage of the site, which is dictated by the life history traits of the taxa, including their larval settlement preferences in early colonization stages.

Recruitment to the pyramid site was much lower than to the Dolphin Reef and consisted mainly of Xeniidae (Fig 2A–B, Table 2), which comprise the majority of resident colonies at the site (Perkol-Finkel and Benayahu, 2005). Surprisingly, *D. hemprichi*, which was one of the most conspicuous species at the pyramid site AR, as reported in the earlier study, hardly recruited to the AR in the present study (Table 2). This finding corresponds to a community shift that took place there, leading to a reduction in the dominance of soft corals and an increased dominance of the sponge *Crella cyatophora* (Perkol-Finkel and Benayahu, 2005). Recruitment of soft corals at the site differed between the two faces of the plates; however the pattern changed over time—from the upper face after 6 months, to its underside at months 12 and 18 (Table 3). Such differential recruitment can indicate the mode of reproduction (see above), i.e., asexual recruitment of Xeniidae to the outer face of the plates, and sexual recruitment of *Xenia* spp. and *R. fulvum fulvum* to the inner one.

Throughout the study stony corals recruited to both the pyramid site AR and NR in very small numbers (Table 3). However, both the number and diversity of the recruits there increased somewhat with time (Table 2), and after 18 months the composition of the stony coral recruits resembled that of the resident community at the site (Perkol-Finkel and Benayahu, 2005). Such a remarkably low recruitment of stony corals may have resulted from the relatively high abundance of fouling organisms (i.e., sponges, tunicates and bryozoans), which appeared on the plates of both reef types, although in greater abundance at the AR (Table 4). Fouling organisms rapidly colonize ARs (Holmstrom and Kjelleberg, 1994; Oren and Benayahu, 1997; Mariani, 2003) and can often inhibit coral settlement (e.g., Kubanek et al., 2002). It is also suggested that the recent degradation of Eilat's reefs due to heavy anthropogenic stresses (e.g., Fishelson, 1995; Glassom et al., 2004; Loya et al., 2004; Loya and Rosefeld, 2005) accounts for the low coral recruitment at the site. It is possible that, given more time, the composition of recruited stony corals on the plates would have born greater resemblance to the resident community at the site, as reaching the carrying capacity of reef-building corals in the Gulf of Eilat (in terms of both species composition and number of colonies) may take several years (Abelson and Shlesinger, 2002). The low recruitment of stony corals made it difficult to detect differential recruitment patterns, although we did find that the facing and orientation of the settlement plates had a certain influence on stony coral recruitment there, as at month 18 a preference for settlement on the inner face of vertical plates was found (Table 3). This result corresponds to other findings that have related high coral abundance on vertical surfaces to increased water motion and lower sedimentation levels (Carleton and Sammarco, 1987; Fisk and Harriott, 1990; Clark and Edwards, 1999).

4.2. Community features

Great differences in the overall structure of the benthic communities were found between the two reef types of the Dolphin Reef and pyramid sites throughout the study (Figs. 4 and 5). These findings were mostly due to differences in the abundance of bare space, bryozoans, serpulid worms and tunicates (Table 4). At both sites, these fouling organisms dominated the ARs, a finding which corresponds to other studies conducted in reefal environments (e.g., Fairfull and Harriott, 1999). High abundance of fouling organisms on ARs may result from strong currents carrying food supply and enhancing larval dispersal, as well as from the sedimentation load (Mariani, 2003). Measurements of current and sediment at the Dolphin Reef site revealed clear differences in these two parameters between the two reef types there, which may account for the high dominance of filter feeders on the AR (Perkol-Finkel and Benayahu, in preparation). Shading may also have differentiated the community structures of the studied ARs and NRs (Maida et al., 1994; Mundy and Babcock, 1998; Glasby, 1999). Both of the ARs in the current study are able to cause shading due to their inclined nature, thus affecting the features of the benthic assemblages in the two reef types. However, this aspect remains for future investigation.

Differences in fouling communities between the outer and inner faces of the settlement plates were evident at the ARs and NRs of both sites (Figs. 4 and 5). The differences resulted from uneven distribution of bryozoans, sponges, serpulid worms and tunicates, which dominated the undersides of the plates at both reef types. The latter finding also affected the average organic weight on the plates, which was significantly greater on the inner face than on the outer one at both reef types (Fig 7). Similar results were found by Fairfull and Harriott (1999) who noted high abundance of these taxa on the inner faces of plates, related to the synergistic effects of low irradiance, sedimentation and predation associated with the lower surfaces of settlement plates. These factors would also apply to our study, equally affecting recruitment on both the reef types.

Differences in recruitment patterns between the Dolphin Reef and pyramid sites were on both spatial and temporal scales (Fig. 6). Such differences might be related to depth (Dolphin Reef 15–18 m vs. pyramid site up to 27–32 m), which may lead to differences in light and current regime as well as sedimentation load (see also Rogers, 1990; Glasby, 1999; Qian et al., 2000). Additionally, water clarity might also have affected the recruitment of fouling organisms at the two sites.

Badalamenti et al. (2002) found that clearer water led to increased diversity of bivalves on concrete ARs in Sicily. Water clarity surrounding the pyramid site is generally lower than at the Dolphin Reef site (personal observations), possibly due to mariculture operations along the north shores of Eilat, near the pyramid site, that affect the water quality in the area (Loya et al., 2004; Loya and Rosefeld, 2005). A recent study by Tsemel et al. (2006) found increased species richness and biomass of biofouling communities near Eilat's fish farms, where the water is rich in organic matter, compared to a control site. The time scale affected both sites: at the Dolphin Reef the similarity in findings between the sampling dates decreased with time; while at the pyramid site, the initial community (6 months post-deployment) greatly differed from the two later samplings (12 and 18 months), which were highly similar (Fig. 6). The amount of bare space on the plates decreased with time at both sites, alongside an increased abundance of corals and other fouling organisms. A similar pattern has been noted in other studies describing a shift from hard-bodied taxa to soft-bodied ones due to competitive overgrowth of tunicates and sponges (Fairfull and Harriott, 1999 and references therein).

4.3. Conclusions

Although there are numerous studies on recruitment of corals or of fouling invertebrates onto settlement plates, only a few have examined both simultaneously (e.g., Fairfull and Harriott, 1999). Examining the wide array of benthic organisms gives a more comprehensive perspective of biological and ecological processes. In our study, coral recruitment was affected in terms of species composition and abundance by both the resident community at the site, and by the presence of bryozoans, bivalves and tunicates that densely covered the plates. Recruitment of corals and fouling invertebrates clearly differed between the AR and NR at the Dolphin Reef and pyramid sites in terms of species composition and/or abundance, which strongly relates to the attraction vs. production issue (see Introduction). We suggest that the vast majority of the taxa that colonized the ARs were not derived from the adjacent NRs, and in all probability would not have recruited to the site if an AR had not been there. Possible sources for the recruits are other nearby artificial structures such as the oil jetties or marinas found in the Gulf of Eilat (Schuhmacher, 1974; Barki, 1992; Perkol-Finkel et al., 2006). This particularly applies to the differential recruitment of Nephtheidae soft corals, which barely recruited to the NR (Table 2), nor were they a part of the resident community there (Perkol-Finkel and Benayahu, 2004, 2005). Furthermore, the fact that most stony corals preferentially recruited to the NRs and not to the ARs, indicates that each reef type offers unique conditions and thus supports different community assemblages.

The findings of the current study can be implemented in the design of ARs for restoration purposes. The results shed new light on the abilities of ARs to resemble NR communities, i.e., if recruitment is different, clearly the communities at the two reef types will remain distinct. The two inclined ARs offered different conditions in terms of current regime and sedimentation load (Perkol-Finkel and Benayahu, in preparation), and therefore recruited larvae that favor these conditions (i.e., azooxanthellate soft corals and fouling filter feeders). Thus, highly inclined “mid water” ARs are not suitable for restoration purposes in low relief reef systems. Such structures may, however, increase the local diversity and raise the abundance of rare species by adding niches otherwise unavailable in the area. Whether such change in diversity is beneficial or not remains controversial (see also Bortone, 2006).

Acknowledging the significance of recruitment processes to ARs is of great importance for applying ARs for restoration purposes. Our results suggest that ARs can be designed to support target species, by taking into account the various abiotic and biotic factors (see Table 1) that shape settlement and recruitment processes. Thus, by gathering more information on differential recruitment to ARs and NRs, we might be able to predict the species composition at the site.

In summary, it is suggested that, in order to construct an AR that will mimic its adjacent NR for restoration or conservation purposes, it is essential that the two reef types will offer similar structural features. Furthermore, as ARs support rich fouling communities comprised mainly of filter feeders, it is possible to use them for improving the water quality and thus reduce the detrimental impact of anthropogenic disturbances in the area (Miller, 2002 and reference therein). This is of particular importance locally in the Gulf of Eilat, in light of the nutrient enrichment from mariculture operations there (Loya, 2004; Loya et al., 2004; Tsemel et al., 2006).

Finally, despite the recent growth of interest in the ecological applications of ARs as a tool for restoring degraded NRs, experimental work on the subject is still lacking (Miller, 2002; Seaman, 2002; Abelson, 2006). Process-oriented research must be undertaken in order to advance ecological engineering goals (Miller, 2002). Our study, as well as others investigating the ecological benefits of ARs in the Gulf of Eilat (e.g., Abelson and Shlesinger, 2002; Tsemel et al., 2006; Perkol-Finkel et al., 2006), yields guidelines for the future design of ARs aimed at achieving specific ecological goals, applicable for restoration purposes with a worldwide significance.

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