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Floating and fixed artificial habitats: Spatial and temporal patterns of benthic communities in a coral reef environment

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Abstract

While natural marine habitats with motion capabilities, e.g., kelps and seaweeds, have been studied alongside their associated fouling communities, little is known of the effect of motion on the communities of floating artificial habitats such as buoys, rafts, and pontoons, particularly in tropical systems. Hydrodynamic features greatly differ between floating and fixed artificial substrata, which in turn affect the structure of their associated communities. This study tested the hypothesis that floating and fixed artificial installations in a tropical reef system (Eilat, Red Sea) would support different benthic communities throughout space and time. Specifically, we examined differences in communities recruited onto settlement plates between floating and fixed installations deployed at three different sites, along a two-year monitoring period. The three sites exhibited distinct differences in species assemblages between the monitoring dates (6, 12, 18 and 24 months post deployment), mainly between the first and the last two dates. The average level of dissimilarity between floating and fixed installations increased over time at all sites. Over 50% of the dissimilarity between the floating and fixed installations resulted from five taxonomic groups i.e., bryozoans, bivalves, barnacles, sponges, including the amount of bare space on the settlement plates. The contribution of these groups to the dissimilarity changed both temporally within each site, and spatially among sites. The observed differences were related to the hydrodynamic characteristics of floating and fixed habitats, interacting with biotic features such as predation, successional processes and seasonality; and abiotic features including small-scale spatial changes, light, and position in the water column.

Keywords: artificial reefs; substratum motion; corals; benthic communities; hydrodynamics; coastal structures

1. Introduction

Natural marine habitats with motion capabilities, including kelp forests and seaweed beds, have been studied alongside their associated fouling communities (e.g., Ingolfsson, 1998; Hobday, 2000; Thiel, 2003). Floating artificial habitats can be found in the form of buoys or rafts (Relini et al., 2000), pontoons (Connell and Glasby, 1999; Glasby et al., 2007), docks (Caine, 1987) and FADs (fish aggregation devices, see Dempster and Taquet, 2004). Despite the ongoing proliferation of artificial floating habitats worldwide (Connell, 2000 and references therein), little is known of the effect of their motion capabilities on their species assemblage. For example, studies of epibiotic communities on pontoons in Sydney harbor, Australia, attributed the great differences found between their benthic assemblages and those of the neighboring rocky reefs, mainly to the differences in current regime between the two habitats (Connell and Glasby, 1999; Holloway and Connell, 2002). Similarly, Bulleri (2005), who compared colonization of seawalls constructed against coastal erosion *vs.* rocky reefs in Sydney harbor, found that the two attracted different assemblages of the recruited species. Understanding community development on coastal urban structures, and consequently how to improve their surrogacy for natural reefs (NRs), is thus a subject of major interest in coastal ecology (McDonnell

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and Pickett, 1990; Connell, 2000; Pinn et al., 2005). This particularly applies to benthic communities on floating structures in tropical systems, which have received little attention to date (Perkol-Finkel and Benayahu, 2004).

The motion of a substratum in the water column can greatly influence its surrounding hydrodynamic patterns (Schlichting and Gersten, 2000). Perkol-Finkel et al. (2006b) found substantial differences in current speed and shear stress surrounding floating *vs.* fixed artificial installations in a study conducted in Eilat (northern Red Sea). Differences in hydrodynamic features between floating and fixed habitats can in turn affect the structure of their associated communities (Holloway and Connell, 2002). Current regime has a substantial effect on settlement, recruitment and survival of benthic organisms (reviewed in Abelson and Denny, 1997). The effect of current speed on the ability of marine larvae (such as barnacles, hydroids, bryozoans and polychaete), to encounter and settle on a substratum, may vary from species to species (Mullineaux and Garland, 1993; Qian et al., 2000). Additionally, water flow affects the feeding response of both suspension and filter feeders (e.g., Fabricius et al., 1995; Sebens et al., 1998; Tweddle et al., 2005).

The development of communities on newly-submerged artificial habitats in the marine environment has been investigated mainly on low-profile artificial reefs (ARs) that attempt to mimic the physical and biological characteristics of NR communities (e.g., Bailey-Brock, 1989; Cummings, 1994; Palmer-Zwahlen and Aseltine, 1994). Species turnover in such habitats is thought to be considerably more complex than predicted by succession theories, due to the seasonality of recruitment, growth rate and mortality (Turner and Todd, 1993). Such factors may also influence temporal and spatial variability of AR communities (Butler and Connolly, 1999). To date, only a few studies have investigated species turnover of benthic communities on floating artificial habitats, mainly in temperate environments (e.g., Caine, 1987; Connell and Glasby, 2001; Holloway and Connell, 2002).

In a previous study (Perkol-Finkel et al., 2006b) we found that floating artificial installations were exposed to strong current velocities and shear stress, thus accumulating greater biomass than identical fixed installations which experienced lower current velocities and shear stress. In that study we experimentally demonstrated for the first time in a reefal environment (Eilat, northern Red Sea) the link between flow characteristics of habitats with varying motion capabilities and certain biological parameters of their benthic assemblages (i.e., biomass, chlorophyll concentration and number of coral spat). In light of these findings, in the current study we tested the hypothesis that floating and fixed artificial installations will support different benthic communities throughout space and time. Specifically, we examined differences in the overall benthic species assemblage between floating and fixed installations in Eilat at three sites: two of shallow depth (13 m) and one deep (28 m) along a 2-year monitoring period. Special emphasis was given to examining changes in species composition between and within each of the study sites over time.

2. Materials and methods

2.1. Experimental layout

For this study, conducted at the northern tip of the Gulf of Aqaba (Eilat), Red Sea, Israel, we used the same artificial installations that had recently served us for analysis of the flow regime of floating (movable) *vs.* fixed (motionless) installations deployed during September 2002 (Fig. 1, see also Perkol-Finkel et al., 2006b). There were two shallow sites, with a bottom depth of 13 m: the underwater observatory (observatory) and the north oil jetty (north jetty); and one deeper site with a bottom depth of 28 m: the south oil jetty (south jetty). This experimental array was chosen to allow examination of the developing species assemblages along a wide depth gradient. At each site there were 3 floating and 3 fixed installations, each composed of 3 (shallow sites) or 2 (deep site) identical modules. Each module (60 × 45 × 45 cm in size), made of 8 mm galvanized metal mesh, held 32 settlement plates (11.5 × 20 × 1.5 cm) made of recycled plastic, 16 of which were attached vertically and 16 horizontally, in a step-like formation. Each settlement plate had a total surface area of 554.5 cm^2, comprising both faces of the plate (outer face facing out of the module and inner one facing inward) and its edges. The modules of each installation were suspended at three positions in relation to the water column: seabed (seabed), mid-water (mid), and sea-surface (surface), with a 5 m interval between them (Fig. 1). At the two shallow sites the installations comprised all three positions, set at 12, 6, and 1 m depth respectively, while at the deep site only the seabed and mid positions were set, at 27 and 21 m respectively.

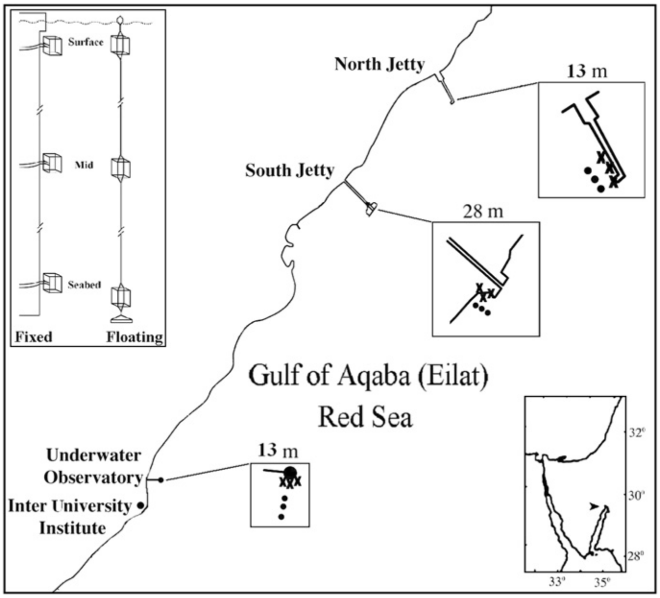

Fig. 1. Map of the study sites and position of the experimental layout (● = floating installations, X = fixed installations). Inset: Schematic illustration of the floating and fixed installations. Modules of fixed installation attached to a firm substratum. Floating installation held by a sinker to the seabed and floated at the sea surface by a buoy; modules connected to each other by rope.

Modules of the floating installations were aligned along a plastic rope (10 mm), anchored by a concrete sinker (160 kg) and floated by two buoys (30 l each). This assembly enabled independent movement for each module, transition, and rotation with six degrees of freedom: three linear velocities (longitudinal, transverse and vertical) and three angular velocities, according to the effects of wind, current, wave motion and tide. Modules of the fixed installations were firmly attached to underwater metal nets or pillars, directly or with a metal band. Since tidal range in Eilat is low (<50 cm between high and low tide, http://isramar.ocean.org.il/TideElat/default.aspx), depth changes of fixed modules along the day were considered negligible.

2.2. Data collection

In order to quantify the abundance of corals and other benthic organisms on the modules, settlement plates were retrieved and examined over a period of two years at months 6, 12, 18 and 24 post deployment (March, September 2003, and March, September 2004 respectively). Due to the extremely high density of organisms at the south jetty, at month 24 we were unable to extract the plates from the modules without detaching and losing most of the biomass on them, and so we did not sample this site at that date. A total of 192 plates were sampled per date: 4 plates per module, (2 vertical and 2 horizontal) × 3 modules per installation (Seabed, Mid and Surface) × 6 installations (3 fixed and 3 floating) × 2 shallow sites (Observatory and North jetty) + 4 plates per module (2 vertical and 2 horizontal) × 2 modules per installation (Seabed and Mid) × 6 installations (3 fixed and 3 floating) × 1 deep site (South jetty). All removed plates were replaced with new ones in order to maintain the structural features of the modules. The removed plates were placed underwater in ziplock bags, immediately transferred to the Interuniversity Institute of Eilat (IUI) and put in running seawater until examination, within 24 h of removal. Both the outer and inner faces of each plate were examined, including their edges. We recorded the number of stony and soft coral recruits on each face, and identified them to the lowest possible taxonomic level. In cases when the recruits could not be generically assigned, they were scored as unidentified sp., separately for soft and stony corals. Due to difficulty in distinguishing between juveniles of *Xenia* sp. and *Heteroxenia* sp., these were scored as *Xenia/Heteroxenia* sp., and similarly for *Pocillopora/Stylophora* sp. The species assemblage of invertebrates and algae that appeared on the plates was recorded using a 1 × 1 cm grid, and included their taxa composition, percentage cover of colonial organisms (bryozoans, tunicates and sponges), as well as of bare space on each face of the plate (outer *vs.* inner), and number of the solitary organisms (solitary tunicates, bivalves and barnacles). Taxonomic groups that could not be counted as individuals (i.e., clusters of serpulid worms), or when their percentage cover could not be recorded (turf and coralline algae) due to variations in density (e.g., 100% coverage of dense turf algae as opposed to 100% coverage of sparsely scattered algae), were each ranked according to their appearance, as follows: 0 – absent, 1 – sparsely scattered, 2 – densely scattered, and 3 – densely uniform (see also Perkol-Finkel and Benayahu, 2007).

2.3. Statistical analyses

To detect spatial and temporal differences between the three sites over the two-year monitoring period, as well as differences between the floating and fixed installations, we calculated the Bray-Curtis similarity index using the PRIMER® (V5.2.9) statistical package (Clarke and Warwick, 2001). The index was calculated for the group average of each type of installation (floating *vs.* fixed) at each site (observatory, north and south jetties) per monitoring date (6, 12, 18 and 24 months post deployment). The calculations were based on the abundance of each taxon (algae, corals and other invertebrates) and on the percentage of bare space on the settlement plates. 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 taxa.

Two-way crossed ANOSIM (analysis of similarities) tests were applied to assess the significance of differences in taxa composition between the four monitoring dates (6, 12, 18 and 24 months post deployment) and between the two types of installations (floating *vs.* fixed) at each site. The null hypotheses were that there were no differences between the monitoring dates, and no differences between the floating and fixed installations. We calculated both the R statistic and its level of significance (Clarke and Warwick, 2001). As multiple comparisons were made for the different monitoring dates at each site (pair-wise analyses), we used the Bonferroni adjustment procedure, in which the alpha level of each individual test is adjusted downwards to ensure that the overall risk for a number of tests remains 0.05. Thus, the deciding significance level was reduced from $\alpha = 0.05$ to 0.008 to adjust for the 6 comparisons (i.e. 0.05/6; Bonferroni adjustment). Similarly, we used two-way crossed ANOSIM tests to assess the significance of differences in taxa composition between the two types of installations (floating *vs.* fixed), and between the three positions of the modules (seabed, mid and surface) at each site, per monitoring date. The null hypotheses were that there were no differences between the floating and fixed installations, and no differences between the three modules. Here too the deciding significance level was reduced from $\alpha = 0.05$ to 0.01 at the two shallow sites due to multiple comparisons for the modules (i.e. 0.05/3; Bonferroni procedure).

Non-parametric multidimensional scaling (nMDS) was produced from the group average similarity matrix in order to reveal any spatial and temporal trends. Additionally, we produced nMDS from the matrices of each site, per monitoring date. Finally, the SIMPER (similarity percentage) analysis was used to identify the discriminating taxonomic groups between the floating and the fixed installations at each site on the different monitoring dates. Taxonomic groups were listed in decreasing order by their average contribution to the total average dissimilarity $\overline{\delta}$ (Clarke and Warwick, 2001).

3. Results

The three study sites demonstrated great differences in taxa composition both spatially and temporally (Fig. 2). The deep site (south jetty) clustered separately from the two shallow ones (observatory and north jetty), indicating its distinct species assemblage; while the two shallow sites exhibited some overlap, indicating their similarity, especially for the floating installations 18 and 24 months post deployment. Table 1 presents results of the two-way crossed ANOSIM tests analyzing differences between monitoring dates and installation types at each site. The three study sites exhibited distinct differences between the monitoring dates (months 6, 12, 18 and 24 post deployment), thus rejecting the null hypothesis of no difference between them (Table 1, $R = 0.220$, 0.268 and 0.314 for the observatory, north and south jetties respectively, $P = 0.001$ for all). According to the pair-wise comparisons, the greatest differences existed between the first and the last dates (months 6 and 24), while only little difference was found between the two last monitoring dates (months 18 and 24) at all sites. This trend is supported by the MDS analysis, presenting a vertical shift along the plot from the first to the last monitoring date at all sites (Fig. 2). Differences between the floating and fixed installations varied among sites. While significant at all sites, the greatest differences between the two types of installations were found at the observatory (Table 1: $R = 0.196$, $P = 0.001$); they were fewer at the south jetty ($R = 0.103$, $P = 0.001$); and distinctively low, yet still significant, at the north jetty ($R = 0.063$, $P = 0.001$).

Table 2 presents the results of the two-way crossed ANOSIM tests analyzing differences between installation types (floating *vs.* fixed) and between the seabed, mid and surface modules at each site per monitoring date. The three study sites revealed different patterns in relation to differences in species assemblage between the floating and fixed installations over the monitoring period, with quite consistent differences between the modules among sites. At the observatory, the level of dissimilarity between floating and fixed installations was the same for the first 12 months (Table 2: $R = 0.482$ and 0.483, $P = 0.001$ for months 6 and 12 respectively), but had greatly increased by month 18 post deployment ($R = 0.606$, $P = 0.001$). Thus, a clear separation existed between the two types of installations at the site, alongside a distinct separation between the modules of the installations, particularly between the seabed and mid-water modules, and the surface ones (Fig. 3). Although the stress level of this plot is relatively high (0.2), its trends are strongly supported by the ANOSIM tests (Table 2). At the north jetty, however, the greatest difference between the two types of installations was found on the first monitoring date (Table 2: $R = 0.185$, $P = 0.001$), decreasing with time to a very low, yet still significant, R value by month 24 (0.084, $P = 0.015$). At that point, the MDS analyses yielded a nearly random distribution of samples (settlement plates) at the site, indicating no visible trend in relation to type of installation or module (Fig. 4). Throughout the experiment, differences between the floating and fixed installations at the north jetty were much lower than at the observatory. At the south jetty, differences between the floating and fixed installations were moderate yet significant at months 6 and 12 post deployment (Table 2: $R = 0.127$, $P = 0.001$ and 0.129, $P = 0.005$ respectively), and by the last monitoring date (month 18) the difference had greatly decreased ($R = 0.087$, $P = 0.022$).

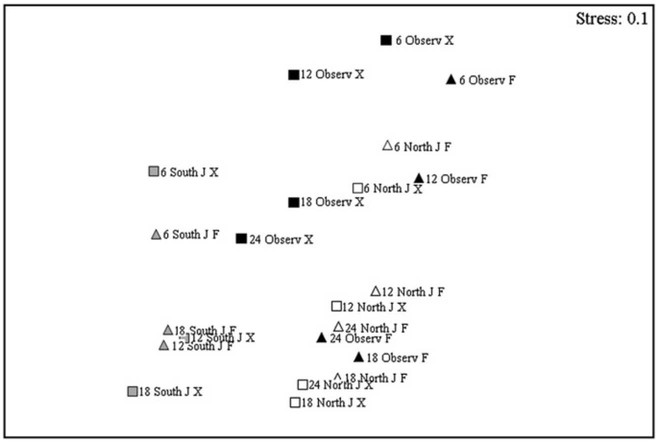

Fig. 2. Non-parametric multidimensional scaling (nMDS) based on the group average similarity matrix of each site (observatory = black symbol; north jetty = white symbol and south jetty = grey symbol), per monitoring date (month 6, 12, 18 and 24 post deployment) and type of installation (F – floating installations = triangle; X – fixed installations = square). $n = 22$ groups.

Table 1
Summary of results, two-way crossed ANOSIM tests for each of the study sites. Examined factors: "Month" (6, 12, 18, and 24 months post deployment) and "Treatment" (F = floating installations, X = fixed ones). Level of significance (P) is given in brackets

Site	Month (6, 12, 18, 24)	Treatment (F, X)
Observatory	Global: 0.220 (0.001)	0.196 (0.001)
	6, 12: 0.085 (0.001)	
	6, 18: 0.492 (0.001)	
	6, 24: 0.365 (0.001)	
	12, 18: 0.201 (0.001)	
	12, 24: 0.151 (0.001)	
	18, 24: 0.047 (0.005)	
North jetty	Global: 0.268 (0.001)	0.063 (0.001)
	6, 12: 0.318 (0.001)	
	6, 18: 0.576 (0.001)	
	6, 24: 0.506 (0.001)	
	12, 18: 0.089 (0.001)	
	12, 24: 0.075 (0.001)	
	18, 24: 0.021 (0.056)	
South jetty	Global: 0.314 (0.001)	0.103 (0.001)
	6, 12: 0.419 (0.001)	
	6, 18: 0.414 (0.001)	
	12, 18: 0.113 (0.001)	

At all sites, results of the global test for differences between the seabed, mid and surface modules were significant, with greatest differences at the shallow sites, particularly at the observatory (Table 2). At both of the shallow sites the greatest difference was between the seabed and the surface modules, with R values reaching as high as 0.727. This separation was also evident from the MDS of the observatory at month 18

Table 2
Summary of results, two-way crossed ANOSIM tests for each of the study sites, for the four monitoring dates (months 6, 12, 18 and 24 post deployment). Examined factors: "Treatment" (F = floating installations, X = fixed ones) and "Module" (seabed, mid, and surface). Level of significance (P) is given in brackets

Site	Month	Treatment (F, X)	Module (seabed, mid, surface)
Observatory	6	0.482 (0.001)	Global: 0.481 (0.001)
			Seabed, Mid: 0.166 (0.001)
			Seabed, Surface: 0.727 (0.001)
			Mid, Surface: 0.584 (0.001)
	12	0.483 (0.001)	Global: 0.482 (0.001)
			Seabed, Mid: 0.175 (0.001)
			Seabed, Surface: 0.674 (0.001)
			Mid, Surface: 0.664 (0.001)
	18	0.606 (0.001)	Global: 0.515 (0.001)
			Seabed, Mid: 0.134 (0.004)
			Seabed, Surface: 0.723 (0.001)
			Mid, Surface: 0.693 (0.001)
	24	0.319 (0.001)	Global: 0.447 (0.001)
			Seabed, Mid: 0.126 (0.004)
			Seabed, Surface: 0.608 (0.001)
			Mid, Surface: 0.586 (0.001)
North jetty	6	0.185 (0.001)	Global: 0.420 (0.001)
			Seabed, Mid: 0.329 (0.001)
			Seabed, Surface: 0.548 (0.001)
			Mid, Surface: 0.378 (0.001)
	12	0.162 (0.001)	Global: 0.320 (0.001)
			Seabed, Mid: 0.296 (0.001)
			Seabed, Surface: 0.407 (0.001)
			Mid, Surface: 0.271 (0.001)
	18	0.095 (0.006)	Global: 0.267 (0.001)
			Seabed, Mid: 0.240 (0.001)
			Seabed, Surface: 0.417 (0.001)
			Mid, Surface: 0.140 (0.004)
	24	0.084 (0.015)	Global: 0.217 (0.001)
			Seabed, Mid: 0.053 (0.099)
			Seabed, Surface: 0.310 (0.001)
			Mid, Surface: 0.289 (0.001)
South jetty	6	0.127 (0.001)	Global: 0.140 (0.003)
	12	0.129 (0.005)	Global: 0.201 (0.001)
	18	0.087 (0.022)	Global: 0.130 (0.002)

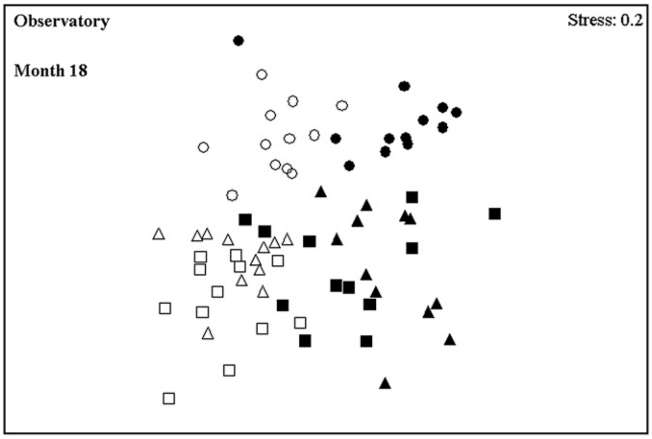

Fig. 3. Non-parametric multidimensional scaling (nMDS) based on the similarity matrix of the observatory site, month 18 post deployment. Floating installations = black symbol; fixed installations = white symbol; seabed module = square symbol; mid-water = triangle; surface = circle. $n = 72$ plates.

(Fig. 3). At the observatory, high R values were also obtained for all of the mid to surface comparisons; while at the north jetty, differences between the seabed and mid modules were usually greater than those between the two upper modules. On the final monitoring date, however, no significant difference was found between the seabed and mid modules at this site (Table 2, Fig. 4).

The SIMPER analyses revealed different patterns in taxa composition along time at the three study sites. Tables 3–5 detail the contribution of individual taxonomic groups to the average dissimilarity ($\bar{\delta}$) between floating and fixed installations at each site, for all monitoring dates. At all three sites the average level of dissimilarity between floating and fixed installations generally increased over time. At the observatory it increased from 33.62 to 43%, while at the north and south jetties the increase was smaller, as were the overall levels of dissimilarity (26.14–31.06% and 24.99–27.84% respectively). At all sites, on all monitoring dates, five taxonomic groups accounted for >50% of the dissimilarity between the two types of installations and included bryozoans, bivalves, barnacles, and sponges as well as the bare space category. Colonial tunicates were also among the taxonomic groups most discriminating between floating and fixed installations, but had slightly less importance at the observatory site, while barnacles appeared only at the two shallow sites. The ranking of these taxonomic groups in terms of their contribution to the average dissimilarity changed temporally within each site, as well as spatially among the three study sites. For example, at the observatory site bryozoans made the greatest contribution to the dissimilarity at months 6 and 12 post deployment (Table 3: 24.51 and 16.23% respectively), yet at months 18 and 24 the amount of bare space was the most dominant factor discriminating between the two types of installations (19.15 and 14.59% respectively). Corals made a much smaller

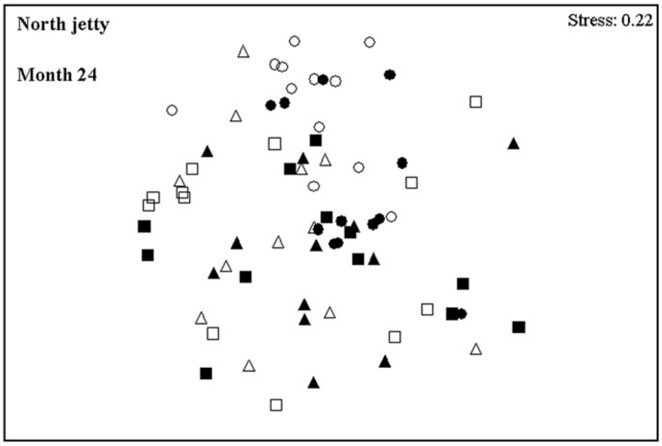

Fig. 4. Non-parametric multidimensional scaling (nMDS) based on the similarity matrix of the north jetty site, month 24 post deployment. Floating installations = black symbol; fixed installations = white symbol; seabed module = square; mid-water = triangle; surface = circle. $n = 72$ plates

Table 3

Comparison between the two types of installations (F = floating and X = fixed) for each monitoring date (months 6, 12, 18 and 24 post deployment) at the observatory site. The average abundance of each taxonomic group is given for each group. $\bar{\delta}_i\%$ is percentage contribution of ith group to the average Bray-Curtis dissimilarity ($\bar{\delta}$) between the groups. Taxonomic groups are listed in decreasing order of importance in contribution to $\bar{\delta}$ as appeared in the first monitoring date

Observatory	Month 6: $\bar{\delta} = 33.62$			Month 12: $\bar{\delta} = 37.89$			Month 18: $\bar{\delta} = 37.35$			Month 24: $\bar{\delta} = 43.00$		
Taxonomic group	F	X	$\bar{\delta}_i\%$	F	X	$\bar{\delta}_i\%$	F	X	$\bar{\delta}_i\%$	F	X	$\bar{\delta}_i\%$
Bryozoans	13.97	21.76	24.51	25.79	23.19	16.23	38.88	15.35	12.24	23.13	15.72	13.62
Bivalves	4.60	2.01	17.5	5.15	1.57	13.69	6.72	3.47	9.83	5.68	2.15	10.86
Bare space	20.28	38.49	14.56	13.75	28.06	15.52	3.85	18.13	19.15	6.60	12.08	14.59
Barnacles	1.79	2.03	11.76	3.32	1.43	10.81	3.81	1.81	10.43	5.42	1.04	9.87
Turf algae	2.11	1.47	4.89	1.94	1.60	3.52	1.69	1.42	2.69	2.07	1.79	3.13
Serpulid worms	1.06	1.10	4.84	0.96	0.97	4.73	1.82	1.50	3.19	1.50	1.11	3.61
Coralline algae	1.65	1.07	4.69	1.25	1.63	3.14	1.61	2.46	3.97	1.75	1.61	4.04
Pocillopora/*Stylophora*	0.25	0.39	4.29	0.33	1.08	6.32	0.22	0.28	2.74	0.14	0.53	3.03
Solitary tunicates	0.04	0.54	3.80	0.22	0.21	2.76	0.46	0.35	3.63	0.51	0.49	4.02
Acabaria sp.	0.64	0.17	3.15	–	0.08	0.65	0.06	0.14	1.33	0.25	0.03	0.89
Sponges	0.13	0.14	2.07	2.38	2.15	9.33	8.29	8.22	13.98	9.25	10.43	14.51
Colonial tunicates	0.08	0.17	1.63	0.07	0.50	2.78	5.35	0.97	9.75	3.06	3.13	8.24
Scleronephthya corymbosa	–	0.14	1.42	–	0.75	2.24	–	2.08	4.38	–	4.31	4.40
Xenia/*Heteroxenia*	–	0.03	0.31	0.11	0.42	3.25	–	0.03	0.20	0.06	0.11	0.95
Unidentified soft corals	–	0.03	0.30	–	0.61	0.91	–	–	–	0.14	–	0.67
Dendronephthya hemprichi	–	–	0.28	0.03	0.42	2.74	0.17	0.28	2.31	2.64	0.17	3.32
Nephthea sp.	–	–	–	0.08	0.03	0.75	–	–	–	–	0.06	0.24
Unidentified stony corals	–	–	–	–	0.03	0.24	0.03	–	0.17	–	–	–
Stereonephthya cundabilensis	–	–	–	–	0.03	0.22	–	–	–	–	–	–
Dendronephthya sinaiensis	–	–	–	–	0.03	0.18	–	–	–	–	–	–

contribution to the overall dissimilarity between floating and fixed installations compared to other benthic invertebrates at all sites. While benthic invertebrates usually accounted for 10–20% of the dissimilarity, the contribution of coral species was much smaller (Tables 3–5: <10% in all cases and <5% in most). Only on the final monitoring date (month 18) at the south jetty, were the soft corals *Scleronephthya corymbosa* and *Dendronephthya hemprichi* among the key taxonomic groups, each contributing ca. 10% to the top 50% of the average dissimilarity.

The relative abundance of the different taxonomic groups varied between the floating and fixed installations at all sites, where the average abundance of most taxonomic groups, including corals, increased with time (Tables 3–5). Corals were less abundant at the shallow sites compared to the deep one, particularly on the later monitoring dates (Tables

Table 4

Comparison between the two types of installations (F = floating and X = fixed) for each monitoring date (months 6, 12, 18 and 24 post deployment) at the North jetty site. The average abundance of each taxonomic group is given for each group. $\bar{\delta}_i\%$ is percentage contribution of ith group to the average Bray-Curtis dissimilarity ($\bar{\delta}$) between the groups. Taxonomic groups are listed in decreasing order of importance in contribution to $\bar{\delta}$ as appeared in the first monitoring date

North jetty	Month 6: $\bar{\delta} = 26.14$			Month 12: $\bar{\delta} = 32.96$			Month 18: $\bar{\delta} = 30.17$			Month 24: $\bar{\delta} = 31.06$		
Taxonomic group	F	X	$\bar{\delta}_i\%$	F	X	$\bar{\delta}_i\%$	F	X	$\bar{\delta}_i\%$	F	X	$\bar{\delta}_i\%$
Bivalves	5.18	4.32	18.03	5.81	5.97	7.89	8.06	6.89	8.95	6.32	5.75	7.09
Bryozoans	17.63	19.13	14.83	33.19	25.82	10.15	33.75	42.04	9.69	27.22	38.10	12.85
Barnacles	1.28	2.88	12.71	1.11	4.24	9.55	0.85	1.99	8.73	0.83	2.11	8.75
Sponges	0.65	2.35	11.97	6.92	13.10	19.15	14.11	16.89	18.19	17.03	20.69	17.50
Colonial tunicates	0.82	1.58	10.11	1.63	3.28	9.58	5.28	7.61	15.91	2.31	8.22	13.92
Bare space	20.14	23.96	8.68	6.60	9.24	17.43	3.82	3.96	14.19	5.42	4.03	15.46
Solitary tunicates	0.13	0.61	6.23	0.13	0.22	2.55	0.25	1.25	4.10	0.22	0.47	3.99
Serpulid worms	1.49	1.83	4.11	1.74	1.92	4.44	1.78	1.79	3.46	1.78	2.28	3.81
Turf algae	1.93	1.47	3.96	1.51	1.49	3.07	1.50	2.07	3.25	1.74	2.00	3.04
Coralline algae	1.46	1.19	3.69	1.68	1.18	4.87	2.56	1.71	4.27	1.75	2.10	4.01
Xenia/*Heteroxenia*	0.19	0.08	2.56	0.64	0.19	4.59	0.06	0.11	1.15	0.06	0.14	1.41
Pocillopora/*Stylophora*	0.11	0.08	1.97	0.11	0.03	1.10	0.03	–	0.28	0.17	0.11	1.95
Dendronephthya hemprichi	0.06	0.06	1.14	0.06	0.36	2.36	0.08	1.97	6.06	0.36	1.06	4.14
Nephthea sp.	–	–	–	0.19	0.19	2.58	–	–	–	–	0.03	0.24
Scleronephthya corymbosa	–	–	–	0.11	–	0.44	–	0.19	1.02	–	0.28	1.38
Acabaria sp.	–	–	–	0.03	–	0.24	–	–	–	–	–	–
Unidentified soft corals	–	–	–	–	–	–	0.03	0.14	0.74	–	–	–
Stereonephthya cundabilensis	–	–	–	–	–	–	–	–	–	0.03	–	0.24
Unidentified stony corals	–	–	–	–	–	–	–	–	–	0.03	–	0.22

Table 5
Comparison between the two types of installations (F = floating and X = fixed) for each monitoring date (months 6, 12, and 18 post deployment) at the South jetty site. The average abundance of each taxonomic group is given for each group. $\bar{\delta}_i\%$ is percentage contribution of ith group to the average Bray-Curtis dissimilarity ($\bar{\delta}$) between the groups. Taxonomic groups are listed in decreasing order of importance in contribution to $\bar{\delta}$ as appeared in the first monitoring date

South jetty	Month 6: $\bar{\delta} = 24.99$			Month 12: $\bar{\delta} = 31.03$			Month 18: $\bar{\delta} = 27.85$		
Taxonomic group	F	X	$\bar{\delta}_i\%$	F	X	$\bar{\delta}_i\%$	F	X	$\bar{\delta}_i\%$
Colonial tunicates	4.48	3.25	14.92	7.23	9.46	12.29	7.63	5.83	13.31
Bryozoans	23.00	18.33	13.40	12.83	22.31	12.10	20.52	36.81	7.88
Bivalves	13.31	8.24	13.32	8.31	8.40	7.60	6.67	9.81	7.65
Sponges	3.19	0.86	11.78	19.88	11.42	13.26	15.79	13.35	11.50
Scleronephthya corymbosa	1.71	0.70	9.57	1.00	2.33	8.68	2.79	5.96	11.54
Dendronephthya hemprichi	0.67	1.52	9.09	0.83	1.79	6.63	3.50	3.00	9.13
Bare space	29.58	36.74	8.00	14.38	11.88	13.42	16.69	16.88	12.46
Solitary tunicates	0.92	0.70	7.15	1.06	0.54	5.24	0.63	0.63	4.48
Serpulid worms	1.69	2.02	3.43	1.00	1.38	3.26	1.25	1.08	4.24
Coralline algae	0.65	0.96	3.17	1.06	1.27	4.35	1.67	1.90	3.37
Turf algae	1.38	1.09	2.51	1.81	1.63	2.74	1.50	1.50	2.33
Xenia/Heteroxenia	0.13	0.17	2.42	0.75	1.04	6.05	0.08	0.29	1.36
Dendronephthya sinaiensis	0.13	0.04	1.41	0.13	0.04	1.05	0.25	2.67	5.19
Stereonephthya cundabilensis	–	0.04	0.43	–	–	–	–	–	–
Acabaria sp.	–	0.04	0.41	0.04	–	0.31	–	0.04	0.35
Nephthea sp.	–	–	–	0.08	0.08	1.06	–	–	–
Unidentified stony corals	–	–	–	0.08	0.04	0.83	0.21	0.58	3.59
Unidentified soft corals	–	–	–	0.04	0.04	0.58	–	0.21	1.05
Pocillopora/Stylophora	–	–	–	–	0.08	0.55	–	0.08	0.57

3–5). Nonetheless, each site had a slightly different temporal pattern of taxa composition. At the observatory, throughout the two monitoring years, the percentage of bare space on the floating installations was always lower than that on the fixed ones (Table 3). The abundance of bryozoans was higher at the fixed installations initially, but from month 12 onwards this trend reversed. Bivalves and barnacles were found in greater numbers at the floating installations compared to the fixed ones, while corals settled more on the latter than on the former, apart from *Dendronephthya hemprichi*, which was significantly more abundant at the floating observatory installations than at the fixed ones at month 24 (Table 3). Taxa composition at the north jetty showed a different trend, with most of the taxonomic groups being more abundant at the fixed installations compared to the floating ones (Table 4). Corals were initially slightly more abundant at the floating installations; however, at months 18 and 24 most coral species were more abundant at the fixed installations. At the south jetty site, no clear trend was found in taxa composition, and the composition of abundant taxonomic groups changed between the floating and fixed installations along time (Table 5). At month 6 post deployment, most taxonomic groups were more abundant at the floating compared to the fixed installations and more bare space was found at the fixed installations. Some coral species were more abundant at the floating, and some at the fixed installations; however, differences were small. At month 12 post deployment, colonial tunicates and bryozoans dominated the fixed installations, while sponges were more abundant at the floating ones, and different coral species compositions were found at the two types of installations. By the final monitoring date at this site (month 18) taxa composition at the floating and fixed installations had shifted again, as had the distribution of corals. On this date all corals, apart from *D. hemprichi*, were more abundant at the fixed than at the floating installations.

4. Discussion

Urban marine habitats such as marinas, coastal defence structures, oil and gas jetties, buoys, rafts and pontoons provide substrata for a variety of benthic communities (e.g., Relini et al., 2007). Studying the developmental processes of fouling communities on such habitats is of prime ecological importance, in light of the growing coastal development processes world-wide (Pinn et al., 2005; Bulleri, 2006; Airoldi and Beck, 2007). The proliferation of coastal man-made habitats has raised the need for studying benthic communities on floating artificial habitats (Connell and Glasby, 1999; Relini et al., 2000; Holloway and Connell, 2002), and for understanding the effects of substratum motion on the development of their benthic assemblages (Perkol-Finkel and Benayahu, 2004). Such knowledge in tropical environments is particularly important in light of the continuous degradation of coral reefs worldwide (Wilkinson, 2000), and in order to advance the ability to harness artificial habitats for ecosystem restoration (Seaman, 2007). The results of the current study demonstrate that in a reefal system there is a link between the motion of a substratum and the structural features of its species assemblage, as the latter was shown to generally differ between floating and fixed installations at all sites regardless of depth. Benthic communities on floating and fixed installations were strongly influenced by spatial (sites) and temporal (months post deployment) factors, as the level of dissimilarity between the two types of habitats varied from site to site and among sampling dates. While studies on floating and fixed structures in temperate environments have demonstrated changes in species abundance between the two habitats (e.g., Glasby, 2001; Holloway and Connell, 2002; Glasby et al., 2007), our current results suggest that in a reefal system the motion of the substratum promotes changes in species assemblages, especially in comparison to natural habitats.

Floating installations, mainly at the observatory site, were fouled in greater abundance by filter feeders compared to the fixed installations (Tables 3–5), thus supporting the findings of Glasby (2001), who recorded greater coverage of filter feeders on movable and rotating panels compared to fixed ones. Filter feeders are strongly affected by water flow, which determines both settlement processes and growth, as flow affects larval availability and food uptake (e.g., Eckman and Duggins, 1998; Qian et al., 2000). In our study, a high abundance of bryozoans, bivalves and barnacles on floating installations appeared mostly at the two shallow sites (Tables 3–5), where current speed and mass transfer rates were higher in comparison to the fixed installations (11–17 cm s^{-1} at the observatory and 7–16 s^{-1} at the north jetty for floating installations, compared to 5–9 s^{-1} and 5–11 s^{-1} for fixed installations at the two sites respectively: see Fig. 4 in Perkol-Finkel et al., 2006b). Thus, based on the community studies presented in the current paper, and on the hydrodynamic analyses (Perkol-Finkel et al., 2006b), it is suggested that the high abundance of filter feeders on floating installations is a result of the motion capabilities of the substratum that are associated with strong shear stress and greater flow velocity. In a high current environment, floating installations will experience increased motion that will lead in turn to greater amplitude and frequency of movement accompanied by stronger current velocities on their surface area (Perkol-Finkel et al., 2006b). Under such conditions larval supply may increase and cause massive settlement of fouling organisms (Pawlik and Butman, 1993). Moreover, once settled, recruits on floating installations will benefit from an elevated supply of food that could enhance their growth rate (e.g., Eckman et al., 1989). Similarly, Glasby (2001) found distinct community differences between floating and fixed habitats in sites exposed to strong currents.

The position of the modules in the water column (seabed, mid or surface) significantly affected the species assemblage at all sites (Table 2, Fig. 2). These differences existed at both types of installations and were probably derived from differential larval availability in the water column as well as from light intensity, sedimentation levels or depth. Certain larvae, such as of barnacles, tend to concentrate near the water surface and settle on shallow substrata (Holloway and Connell, 2002), as was also observed in our study. Although in the current study we did not measure light intensities at the different models, irradiance is generally higher near the surface than at greater depths. For example, Zeevi Ben-Yosef et al. (2006) measured radiation levels along a depth gradient (0–20 m) in close proximity to the observatory site, and found a steep decline in irradiance at 5 m depth, and again at 20 m depth. Such gradient in light intensities can influence the survival of certain fouling organisms, including corals (see Oren and Benayahu, 1997). Additionally, light is an important determinant of larval behavior and the distribution of recruits (Mundy and Babcock, 1998 and references therein) and also affects algal development (Glasby, 1999), thus influencing the species assemblage of the fouled surfaces. The locations of the modules in the water column exposed them to different current velocities, which increased closer to the sea surface (Perkol-Finkel et al., 2006b), thus leading to differences in taxa composition between the modules as more filter feeders fouled the surface and mid modules (Perkol-Finkel et al., 2006b; this study). High turbulence, as observed for the surface modules, can cause enhanced settlement of large-sized larvae such as those of barnacles (Mullineaux and Garland, 1993), and can thus inhibit settlement of the smaller coral planulae. We do not rule out an interaction between the motion capabilities of the modules, the ambient current regime, and the biotic and abiotic factors mentioned above, all of which contributed to the observed community differences between the modules. Undoubtedly, this matter calls for further examination in future studies.

The level of dissimilarity between the floating and fixed installations increased with time at all sites (Tables 3–5). Temporal differences can be related to both successional processes and seasonality larval supply (Pinn et al., 2005). We found that while a small number of taxonomic groups dominated the installations throughout the study, their abundance changed over time (Tables 3–5). Moreover, the proportion of the key taxonomic groups, i.e., bryozoans, bivalves, barnacles, and sponges, as well as the bare space category, changed over time between the floating and fixed installations, indicating temporal changes in the species assemblage. The number of taxa increased from month 6 to month 12, and then fluctuated. Similar temporal patterns have been recorded in other studies describing a shift from early successional stages dominated by one or a few taxa to later ones with a more diverse and complex community (e.g., Ardizzone et al., 1989; Palmer-Zwahlen and Aseltine, 1994). Since in our study it was mostly coral species that were added with time (Tables 3–5), seasonality should be considered. The first monitoring date was March (month 6), immediately after the winter when most Eilat corals do not reproduce; while the second monitoring date was September (month 12), following the summer, which is the main coral reproduction season there (Benayahu et al., 1990; Shlesinger et al., 1998). In the following year the difference in the number of taxa between winter and summer (months 18 and 24 respectively) was much smaller, as taxa recruited during the first year had already established themselves, allowing the addition of only a few new species. These findings emphasize the importance of long-term monitoring, especially in a reefal environment, as coral recruitment processes might take longer than those of other benthic invertebrates. Therefore, we suggest that temporal changes in species assemblages at both floating and fixed installations are derived from early successional processes, possibly the inhibition of settlement by the early key taxonomic groups (i.e., bryozoans, bivalves, barnacles, and sponges), followed by an increase in diversity subsequent to the main coral reproductive season.

Taxa composition of the experimental installations, consisting mainly of filter feeding organisms, differed between the floating and fixed installations, while both types differed from the typical taxa composition of Eilat NRs, which consist predominantly of stony and soft corals (e.g., Loya, 1972; Perkol-Finkel and Benayahu, 2004). Recently, Perkol-Finkel et al. (2006a) demonstrated that fouling organisms, such as sponges, tunicates, sea anemones and hydrozoans, had only a minor contribution to the taxa assemblage on Red Sea NRs, as well as on mature ARs (shipwrecks 20 to >100-years-old) in the area. The results of the current study thus demonstrate that submerged man-made structures protruding from the seabed attract a taxa assemblage different from that of low profile NRs in the same surroundings. As these fouling organisms obviously do not constitute the major component of live coverage in most tropical NRs, it is very likely that the majority of the taxonomic groups recruited to these habitats, whether they have motion capabilities or not, would not have recruited to the area if the ARs had not existed. The latter finding is supported by Perkol-Finkel and Benayahu (2007), who experimentally examined recruitment of corals and other benthic invertebrates on neighboring ARs and NRs and found greater coverage of bryozoans, sponges and tunicates on settlement plates attached to ARs than to NRs. Species diversity has become a major global issue in recent years and has been closely linked with habitat complexity (Pinn et al., 2005). High profile artificial structures, both floating and fixed, deployed in a flat reef area or in an area with a moderate slope, can increase the complexity of the habitat and thus locally elevate species diversity. Nonetheless, the ecological implications of this kind of man-made intervention must be carefully considered, as these man-made environments could promote the invasion of non-indigenous species to the ecosystem (Glasby et al., 2007).

Taxa composition on both the floating and the fixed installations also differed from that found on the supporting pilings of the oil jetties and on the underwater observatory to which the fixed installations were attached (personal observations). Despite their vertical inclination, these pilings, already deployed for several decades in a reefal environment, have accumulated a rich and diverse coral community, while other benthic invertebrates, such as the key taxa characterizing our experimental installations, are less dominant there. Therefore, it is possible that given sufficient time, fixed installations would accumulate more coral recruits and eventually support a typical reefal assemblage. This also suggests that, in a coral reef environment, a monitoring period of two years still represents a relatively early successional stage, and is not necessarily an indication of the more advanced stages of a community's development. This is in contrast to temperate environments where, for example, taxa composition on floating *vs.* fixed experimental panels demonstrated similar community patterns to those found on pontoons *vs.* rocky reefs in the same area after a period of seven months (Connell, 2000; Glasby, 2001; Glasby and Connell, 2001).

In summary, the current study demonstrates that the motion capabilities of artificial habitats greatly influence their taxa composition, as floating and fixed installations developed different benthic assemblages. Moreover, these differences increased in high flow environments, enhancing hydrodynamic differences between the two types of habitats, which consequently developed unique taxa assemblages. Spatial and temporal variations played a major role in shaping the benthic communities of both floating and fixed habitats, influencing successional changes in terms of species composition and abundance throughout the study. Finally, communities on both types of installations differed from those of NRs in the area, with the former consisting mainly of filter feeders, with a relatively low recruitment of corals. Thus, high profile structures with varying motion capabilities can elevate the species diversity in a reefal environment, and can be used as a successful tool for ecosystem management in coastal waters (see also: Relini et al., 2007). The results of the current study offer a first step towards understanding the effects of coastal development that incorporates the deployment of both floating and fixed artificial structures on benthic assemblages in a tropical environment.

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