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Fish assemblage on natural versus vertical artificial reefs: the rehabilitation perspective

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Abstract Artificial reefs have been suggested as a potential tool for the restoration of marine habitats. In the present study, the fish assemblage established around the oil jetties of Eilat (northern Red Sea, Israel) was compared to those found in three adjacent natural reef habitats: two in a nature reserve (one shallow and one deep) and a third deep site located near the city. Both species richness and fish abundance were found to be significantly higher around the vertical structures of the jetty's pillars than at all three natural sites, with the lowest values at the site closest to the city. The higher species richness at the jetties may be explained by (1) the vertical relief and high complexity of the jetty which offers a variety of niches for both shallow and deep coral reef species, and (2) by the reduction in available niches at the natural sites as a result of coral destruction due to anthropogenic activity. The pronounced difference in fish abundance is attributed mainly to the high seasonal recruitment at the jetty which was much lower at the natural sites. We therefore suggest that vertical structures are more attractive to fish settlement and recruitment than moderately sloped bottoms such as those found at the fringing reefs of Eilat. High similarity (51 to 56%) was found between fish assemblages at the natural sites while relatively low similarity (27 to 37%) was found between the jetty and the natural reefs. The jetty's complex vertical artificial structures can serve as a model for future construction of artificial reefs designed to restore the fish community in areas where the natural reefs

have been damaged. It should be taken into account, however, that these do not necessarily mimic the natural environment but may rather establish a community of their own, which is influenced by the spatial orientation and complexity of the structure.

Introduction

Artificial reefs have been suggested as a potential tool for the restoration of marine habitats (e.g. Kenchington 1988; Pratt 1994). The creation of new, well-planned, artificial habitats may offer alternative shelters, which are expected to recruit juveniles, and thus enlarge the overall pool of fish (Alevizon and Gorham 1989; Ambrose and Swarbrick 1989). Although most research of artificial reefs has focused primarily on their potential to enhance fishing grounds (e.g. Bohnsack et al. 1991; Liu et al. 1991; Naito 1991; Bombace et al. 1994), a recent approach has been to study their use in mitigation of environmental damage, as examined along temperate Pacific coasts (e.g. Carter et al. 1985; Seaman and Sprague 1991) and in tropical waters (Campos and Gamboa 1989). Size, relief, surface area, complexity and location were all demonstrated to be important factors influencing the success of an artificial reef as an attractor of targeted species, and as a means to enhance the fish community (Bohnsack et al. 1991; Kim et al. 1994). Nevertheless, the question of whether artificial reefs merely redistribute fishes from surrounding areas, or whether they in fact increase production of fish, is still not clear (Bohnsack et al. 1994; Carr and Hixon 1997).

It is well established that many coral reef systems around the world suffer from extensive destruction due to anthropogenic stresses (Richmond 1993; Wilkinson et al. 1997). Evidence for reef damage and subsequent changes in the fish population in the Eilat region (Gulf of Eilat, Israel, northern Red Sea) has already been reported by Fishelson (1977), though no quantitative data were presented. Oil pollution was found to be a major

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anthropogenic stressor for Eilat's reefs (Loya and Rinkevich 1980), but this has been under control since 1979 (Loya 1986). To date, these reefs suffer mainly from extensive urban development and from numerous visitors to the reef (Diamant 1996), who break corals and stir up sediment (Neil 1990), leading to a decrease in reef spatial-complexity. Such negative impacts reduce species richness and diversity of fishes (Sano et al. 1984; Dennis and Bright 1988), since shelter is one of the major limiting factors for settlement of fish on coral reefs (Robertson et al. 1981; Hixon and Beets 1993).

Two oil jetties were constructed in Eilat in the early 1970s to the north of the main natural reef; their support pillars reach 30 m depth. Today these pillars and the barbed wire surrounding them are inhabited by rich macrobenthic communities (Goren 1992; Dahan and Benayahu 1997). Recently we described the features of the diverse fish community at these jetties, listing over 140 species, of which some are found in very high abundance (Rilov and Benayahu 1998). Community indices were affected positively by the depth, proximity to the bottom and spatial complexity of the structures. The vertical pillars differ in structure and inclination from the adjacent natural reefs which have a rather moderate slope (Loya 1972).

Several studies have examined the effectiveness of low-relief artificial reefs (e.g. tire aggregations, quarry rocks and concrete blocks) as alternative habitats for reef fishes in comparison to the adjacent natural reefs. Whereas in temperate seas, fish species richness was higher on the artificial structures (e.g. Ambrose and Swarbrick 1989), in tropical waters species richness on such structures was similar or even lower than on adjacent natural reefs (Randall 1963; Stone et al. 1979; Alevizon et al. 1985; Ambrose and Swarbrick 1989; Brock and Norris 1989; Bohnsack et al. 1994; Carr and Hixon 1997). Fish abundance, however, was higher at the artificial reefs in some of these studies. Intrigued by the recent findings showing diverse fish assemblages at the oil jetties (Rilov and Benayahu 1998), we compared the fish assemblages found around these high-relief pillars at the jetties with those of the adjacent natural reefs. We studied fish species richness, abundance and diversity at these sites, and compared species composition among them using multidimensional scaling and cluster analyses. Thus, the overall purpose of this comparison was to assess the potential use of vertical artificial structures as a management tool for rehabilitation of damaged reefs.

Methods

Study sites

Natural reefs

The continuous fringing reef in the Eilat area is within a nature reserve located ca. 6 km south of the city (Fig. 1a). Two study sites were chosen in the reserve: a shallow fore-reef 4 to 7 m deep

(Shallow) and a coral slope site 18 to 22 m deep known as the "Japanese Gardens" (Garden). These two sites are located at the southern end of the fringing reef of the nature reserve, and are separated by a sandy bottom with scattered coral patches (Loya 1972). A third site at "Dekel Beach" (Dekel) was found on a flat bottom, 20 m deep, located ca. 2 km south of Eilat (Fig. 1a). The hard bottom coverage, including live and dead corals, was assessed at these three natural reef sites within 15 × 3 m belt transects, which were also used for fish censuses (see below). The percent coverage was recorded in 3 × 3 m quadrats delineated within these transects, and averaged for each transect. Hard bottom coverage was as follows: 51 ± 19% for Dekel, 58 ± 8% for Gardens, and 82 ± 11% for Shallow, which was significantly higher (after an arcsine transformation) than both deep sites ($F = 15.7$, $F_c = 3.3$, $p < 0.0001$, ANOVA).

Artificial reef

The southern jetty at the oil terminal is situated ca. 2 km north of the nature reserve study sites (Fig. 1a). It is 250 m long with extensions to the north and south (see Fig. 1b in Rilov and Benayahu 1998) and is supported by pillars 1 m in diameter. Most of the pillars along the jetty are arranged in triplicates: two adjacent pillars (one diagonal) and a third one, based 10 m away (see Fig. 1c in Rilov and Benayahu 1998). The triplicates are arranged 20 m apart, down to 30 m deep. The majority of the pillars are partially encircled by coiled barbed wire. The lower part of the two adjacent pillars in each triplicate are jointly encircled by the wire, forming a single unit, while the third one is encircled separately. One triplicate (Jetty), reaching a depth of 20 m, was selected for comparison with the natural reef. This triplicate was encircled, as described above, by wire from the bottom to ca. 9 m depth. [For an illustration of the different orientations of the Eilat natural reef versus the Jetty see Fig. 1b modified from Loya (1972)].

The barbed wire provides potential shelter space for fish. In order to quantify this space, the wire surrounding the pillar was considered a cylinder. The perimeter of this cylinder was averaged from the perimeters measured at 1-m intervals of depth along the wired section. For the upper 9 m of pillar with no wire, the potential space for fish was regarded as a distance of 1 m around the pillar, and therefore considered as an imaginary cylinder with a radius of 1.5 m. In order to evaluate the total available volume around the entire pillar, we combined the two potential volumes and subtracted the volume of the pillar itself. These calculations resulted in total available space of 130 m³ around the single pillar, and 224 m³ around the two joined ones (mean = 177 ± 66 m³).

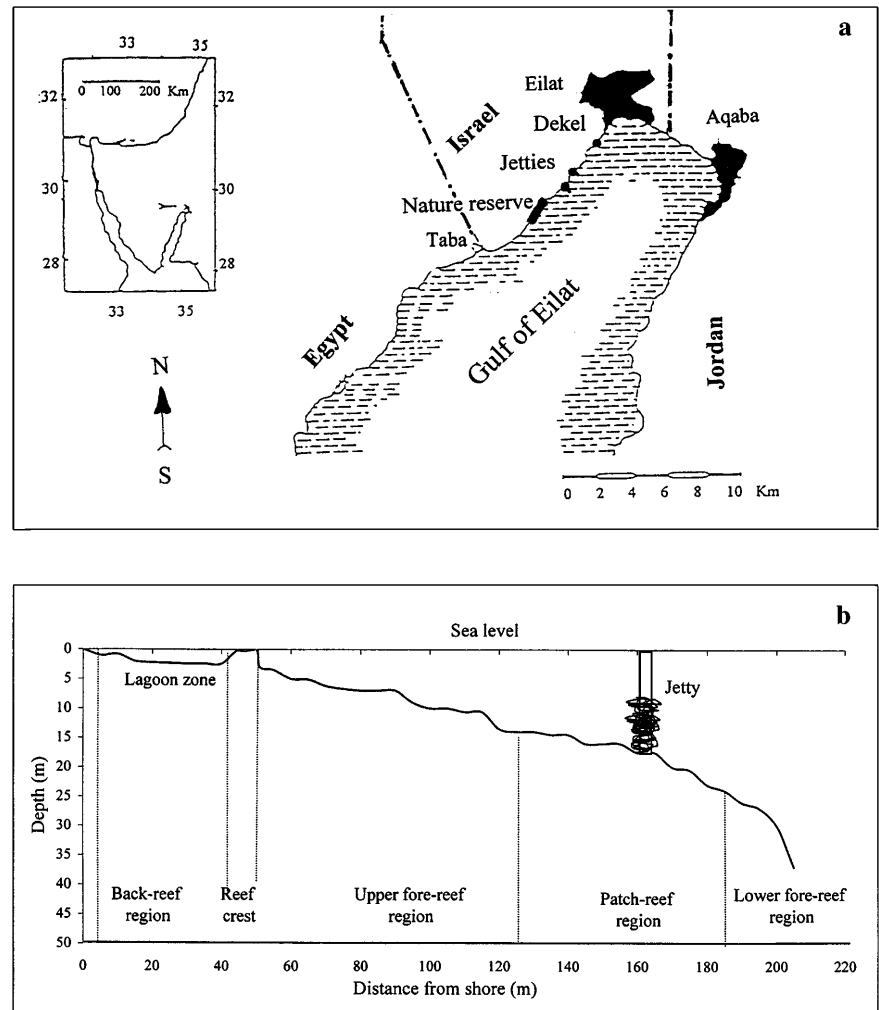
Census technique

The visual census technique was used for the fish counts. It is non-destructive and useful for most fish species, albeit resulting in a certain underestimation of both the cryptic and most abundant species (Brock 1982). At the jetty, the portion of the pillars surrounded by barbed wire was divided into horizontal units (Sale and Sharp 1983; Sale 1997) by circling the wire with nylon lines at intervals of 3 m from the bottom to the top. The upper 9 m of the pillar with no barbed wire were regarded as a single unit. The fish in each of the units were censused separately in order to reveal the vertical distribution of the abundant species and to decrease a possible bias in counts of abundant species by sampling small units (see also Brock 1982).

In the natural reef habitats, the fish censuses were conducted in 3 × 3 m quadrats along belt transects, 15 m long and 3 m wide, placed parallel to the shore-line and marked with nylon lines stretched by lead weights at both ends. All fish were counted up to ca. 4 m above the bottom, therefore forming a total volume of 180 m³ along the transect, which was comparable to the average volume of the available space calculated for the jetty pillars selected for study (see above).

The fish censuses were conducted five times at each study site: at the Jetty in June, September and November 1992, January and

Fig. 1 Description of the study sites. **a** Geographical location of the study sites. **b** Illustration of the Jetty, projected on the profile of the nature reserve (modified from Loya 1972)



April 1993; and at the natural reef sites in November 1992 and in January (twice), February and April 1993. On each sampling date we censused the two pillars at the Jetty or two belt transects at each of the natural sites. During a census, the diver first counted the more conspicuous fish from a distance of 2 to 3 m, and the size of large schools was estimated to the nearest 50 individuals. Next, the diver approached the wires or corals, and closely examined them for the more cryptic species. In most cases, the fish were identified underwater to the species level. Only resident and visitor (transient) species (Bohnsack et al. 1994) with a clear association to the reef or the artificial structures were included in the counts; pelagic species were omitted. Juveniles were included in the counts; they were not recorded separately but their appearance was noted.

Fish community and its indices

The abundance of each species was described in this study by: relative abundance (*RA*), and frequency of appearance (*FA*), calculated as follows: $RA = (\text{the pooled number of individuals of the } i \text{ species from all censuses} / \text{the total number of all individuals in all censuses}) \times 100$ and $FA = (\text{number of censuses in which the } i \text{ species was noted} / \text{total number of censuses}) \times 100$. A census was defined as a single count of fish along a transect or around a pillar at a given date. The resulting values were then transformed into abundance or frequency categories (for details see Table 1 in the "Results" section).

Community indices, including fish abundance, species richness (number of species) and the Shannon–Weaver species diversity index (H'), were calculated for each study site, and then compared among sites using a nonparametric one-way ANOVA (Kruskal–Wallis).

Similarity among sites

A community affinity index *A* (see also Goren 1979), which allowed comparison between pairs of study sites, was calculated using the sum number of individuals of each species from each site, as follows: $G = \sum_{i=1}^S |P_iK - P_iJ|$ and $A_{KJ} = (2 - G_{KJ}) \times 50$, where *K* and *J* are different communities, and P_i is the proportion of species *i* from the total fish number in all censuses. Multidimensional scaling (MDS) and cluster analysis were applied to the data from the individual censuses. These analytical methods were applied in order to reveal the relationships among the fish assemblages at the different study sites. Since in some of the sites a few species were highly abundant (see "Results") and therefore obscured the relationships among the communities at the natural sites, a $\log(x+1)$ transformation was performed on the raw data. A stress coefficient was calculated for the MDS analysis. This coefficient indicates how much of the variation is explained by the dimensions examined in the analysis. The lower the value is the greater the variance explained by the chosen dimensions.

Table 1 Relative abundance (*RA*) and frequency of appearance (*FA*) of all species that occurred in the censuses at the four study sites. The species are listed according to their *RA* at the Jetty site [+ , species that appeared at the oil jetties around other pillars (see Rilov and Benayahu 1998); the number of asterisks represents their

abundance and frequency as follows: for *RA*: * = 0 < *RA* < 0.01, ** = 0.01–0.1, *** = 0.1–1, **** = 1–10, ***** = 10–50, ***** = > 50%; for *FA*: * = 0 < *FA* < 20, ** = 20–39, *** = 40–59, **** = 60–79, ***** = 80–100%

Species	Jetty		Shallow		Garden		Dekel	
	RA	FA	RA	FA	RA	FA	RA	FA
<i>Neopomacentrus miryae</i>	*****	*****	*****	*****	****	**	***	*
<i>Cheilodipterus quinquelineatus</i>	****	*****	****	****	****	**	****	***
<i>Dascyllus trimaculatus</i>	****	*****	**	*	***	*	****	**
<i>Apogon cyanosoma</i>	****	*****	****	**	****	*	***	*
<i>Amblyglyphidodon leucogaster</i>	****	*****	**	*	***	*		
<i>Pomacentrus trichourus</i>	****	**	*****	*****	*****	*****	*****	*****
<i>Pseudanthias squamipinnis</i>	****	*****	****	*****	*****	***	****	*
<i>Apogon aureus</i>	****	**						
<i>Amblyglyphidodon flavilatus</i>	****	*****			****	**		
<i>Paracheilinus octataenia</i>	****	*****	****	****	*****	****	*****	*****
<i>Chromis dimidiata</i>	****	*****	****	*****	****	****	***	*
<i>Sphyraena</i> sp.	***	*						
<i>Chromis pelloura</i>	**	****						
<i>Bodianus anthioides</i>	**	*****			***	*	***	*
<i>Adioryx diadema</i>	**	*****	**	**	*	*		
<i>Pterois miles</i>	**	*****	**	**	***	*	*	*
<i>Holacanthus xanthurus</i>	**	*****			*	*	****	**
<i>Chromis weberi</i>	**	**			****	*		
<i>Abudefduf saxatilis</i>	**	*****	****	****				
<i>Labroides dimidiatus</i>	**	*****	**	**	*	*		
<i>Pteragogus cryptus</i>	**	*****					*	*
<i>Caesio lunaris</i>	**	**	**	*	****	*		
<i>Plagiotremus rhinorhynchus</i>	**	**	**	*			*	*
<i>Siganus rivulatus</i>	**	****	**	**	*	*	*	*
<i>Ostracion cubicus</i>	**	*****	**	**			*	*
<i>Acanthurus nigrofasciatus</i>	**	*****	****	*****	***	*	**	*
<i>Stethojulis</i> sp.	**	**	**	*				
<i>Myripristis murdjan</i>	**	****	**	**	*	*		
<i>Amphiprion bicinctus</i>	**	*****	****	*****	***	**	****	**
<i>Cheilodipterus lachneri</i>	**	**	**	*				
<i>Thalassoma klunzingeri</i>	**	**	****	*****	***	**		
<i>Chaetodon paucifasciatus</i>	**	****	**	*****	****	**	****	**
<i>Heniochus diphreutes</i>	**	**	**	**	*	*	***	*
<i>Chaetodon fasciatus</i>	**	*****	**	**	***	*	**	*
<i>Chromis pembae</i>	**	**			****	*		
<i>Cheilinus digrammus</i>	**	*****			***	*	****	**
<i>Anampses twistii</i>	**	*****	**	****	***	*	***	*
<i>Meiacanthus nigrolineatus</i>	**	**					**	*
<i>Scarus fuscopurpureus</i>	**	**	**	*	***	*		
<i>Scarus ferrugineus</i>	**	****	**	**	**	*	***	*
<i>Ecsenius gravieri</i>	**	****	**	**	**	*	***	*
<i>Pseudochromis springeri</i>	**	**	**	**	****	***	****	**
<i>Centropyge multispinis</i>	**	****	**	*****	***	**	*	*
<i>Anampses meleagrides</i>	**	**	**	*	***	*		
<i>Heniochus intermedius</i>	**	**			***	*		
<i>Fistularia comersonii</i>	**	**						
<i>Priacanthus hamrur</i>	**	**						
<i>Dascyllus marginatus</i>	**	*	****	****	****	***	****	****
<i>Pomacanthus imperator</i>	**	*****			**	*	***	*
<i>Anampses lineatus</i>	**	**						
<i>Parupeneus forsskali</i>	**	**	**	**	***	*	***	*
<i>Canthigaster coronata</i>	**	**					***	*
<i>Cephalopis miniata</i>	**	**	**	*****	***	*		
<i>Bodianus axillaris</i>	**	**	**	**	*	*		
<i>Cheilinus abudjubbe</i>	**	**			***	*		
<i>Bodianus diana</i>	**	**						
<i>Chaetodon austriacus</i>	**	**	****	*****	***	*	*	*
<i>Coris aygula</i>	**	**	**	****	*	*	*	*

Table 1 (contd.)

Species	Jetty		Shallow		Garden		Dekel	
	RA	FA	RA	FA	RA	FA	RA	FA
<i>Scarus sordidus</i>	**	***	***	**	***	*		
<i>Pseudocheilinus evanidus</i>	**	**	***	**	****	***	****	****
<i>Paraglyphidodon melas</i>	**	**	***	**	***	*		
<i>Siderea grisea</i>	**	**	**	**	*	*	***	*
<i>Scarus viridescens</i>	**	**	**	*	*	*		
<i>Pomacanthus maculosus</i>	**	***						
<i>Stethojulis albobittata</i>	**	*	***	**				
<i>Pseudochromis fridmani</i>	**	**	***	**	****	****		
<i>Epinephelus fasciatus</i>	**	**	***	**	***	*	*	*
<i>Canthigaster margaritata</i>	**	**						
<i>Scolopsis ghanam</i>	**	**					**	*
<i>Larabicus quadrilineatus</i>	**	*	****	*****	***	*	***	*
<i>Pseudocheilinus hexataenia</i>	**	**	***	*****	***	*	****	*
<i>Pterois radiata</i>	**	**	***	**	*	*		
<i>Siganus luridus</i>	**	*	***	**	*	*		
<i>Chaetodon auriga</i>	**	*	**	*	***	*		
<i>Istiblennius periophthalmus</i>	**	*						
<i>Zebrasoma xanthurum</i>	*	*	***	****	***	*	***	*
<i>Cephalopholis argus</i>	*	*	***	****	****	***	****	***
<i>Thalassoma lunare</i>	*	*	***	***	***	*		
<i>Parupeneus cyclostomus</i>	*	*	***	*	*	*	*	*
<i>Synodus variegatus</i>	*	*	***	**	*	*	**	*
<i>Ostracion cyanurus</i>	*	*	**	**	*	*		
<i>Naso unicornis</i>	*	*	**	**				
<i>Cheilinus lunulatus</i>	*	*	**	**			*	*
<i>Pseudochromis olivaceus</i>	*	*	**	**				
<i>Dunckerocampus multiannulatus</i>	*	*	**	**			***	*
<i>Chromis ternatensis</i>	*	*			***	*		
<i>Chilomycterus spilostylus</i>	*	*			*	*		
<i>Scorpaenopsis barbatus</i>	*	*			*	*		
<i>Naso brevirostris</i>	*	*						
<i>Cantherhines pardalis</i>	*	*					*	*
<i>Chrysiptera annulata</i>	*	*						
<i>Scarus genazonatus</i>	*	*						
<i>Arothron diadematus</i>	*	*						
<i>Chromis caerulea</i>		+	****	****			**	*
<i>Gomphosus coeruleus</i>			****	*****	***	*		
<i>Scarus juv. sp.</i>			***	****	*	*	***	*
<i>Blenny sp.1</i>			***	***				
<i>Pomacentrus sulfureus</i>			***	**				
<i>Blenny sp. 2</i>		+	***	***				
<i>Dascyllus aruanus</i>		+	***	**	***	*		
<i>Sufflamen albicaudatus</i>		+	***	**	*	*		
<i>Pygoplites diacanthus</i>		+	***	***	*	*		
<i>Zebrasoma veliferum</i>			***	***				
<i>Halichoeres marginatus</i>			***	**				
<i>Siganus stellatus</i>			***	**				
<i>Variola louti</i>			***	**	***	*		
<i>Scarus gibbus</i>		+	***	**				
<i>Coris variegata</i>			**	*	**	*		
<i>Scarus niger</i>			**	*	*	*		
<i>Gobi sp.</i>			**	**				
<i>Epibulus insidiator</i>		+	**	**				
<i>Amanses scopas</i>			**	*				
<i>Tetrosomus gibbosus</i>			**	*			*	*
<i>Amblygobius hectori</i>			**	*	***	*	*	*
<i>Ctenochaetus striatus</i>		+	**	*	***	*		
<i>Plagiotremus tapeinosoma</i>		+	**	*	**	*		
<i>Hologymnosus annulatus</i>			**	*	**	*		
<i>Ecsenius aroni</i>			**	*	*	*	*	*
<i>Ecsenius midas</i>			**	*	*	*	*	*
<i>Labrid sp.</i>		+	**	*	*	*	****	*
<i>Hemigymnus fasciatus</i>			**	*	*	*		
<i>Canthigaster pygmaea</i>			**	*	*	*		
<i>Balistapus undulatus</i>			**	*				

(contd. overleaf)

Table 1 (contd.)

Species	Jetty		Shallow		Garden		Dekel	
	RA	FA	RA	FA	RA	FA	RA	FA
<i>Rhinecantus assasi</i>	+		**	*				
<i>Grammistes sexlineatus</i>			**	*				
<i>Epinephelus malabaricus</i>	+		**	*				
<i>Genicanthus caudovittatus</i>					****	****	****	****
<i>Cirripectes castaneus</i>					***	*	***	*
<i>Pseudanthias taeniatus</i>	+				***	*		
<i>Chaetodon melanotus</i>	+				**	*		
<i>Coris caudimaculata</i>					**	*	***	*
<i>Ecsenius frontalis</i>					*	*	**	*
<i>Echidna nebulosa</i>	+				*	*		
<i>Cephalopholis hemistiktos</i>					*	*		
<i>Cetoscarus bicolor</i>					*	*		
<i>Arothron hispidus</i>					*	*		
<i>Gobiodon citrinus</i>							***	*
<i>Parupeneus macronema</i>	+						***	*
<i>Cirrhitichthys oxycephalus</i>	+						***	*
<i>Pseudochromis flavivertex</i>	+						***	*
<i>Sufflamen albicaudatus</i>							***	*
<i>Trachyrhamphus bicoarctatus</i>							*	*
<i>Naso hexacanthus</i>							*	*
<i>Halichoeres scapularis</i>							*	*
<i>Corythoichthys schultzi</i>							*	*

Results

Fish assemblages

All fish monitored in the four study sites are listed in Table 1 according to their relative abundance and frequency of appearance. The ranking of the ten most abundant species at each site are given in Table 2. A

Table 2 Ranking of the ten most numerically abundant species at each study site (**, species with RA ≥ 1% and/or FA ≥ 80%; *, species present, but with lower abundances)

Species	Jetty	Shallow	Garden	Dekel
<i>Neopomacentrus miryae</i>	1	1	7	*
<i>Cheilodipterus quinquelineatus</i>	2	**	**	5
<i>Dascyllus trimaculatus</i>	3	*	**	6
<i>Apogon cyanosoma</i>	4	**	**	*
<i>Amblyglyphidodon leucogaster</i>	5	*	*	
<i>Pomacentrus trichourus</i>	6	2	2	2
<i>Pseudanthias squamipinnis</i>	7	4	1	9
<i>Apogon aureus</i>	8			
<i>Amblyglyphidodon flavilatus</i>	9		8	
<i>Paracheilinus octataenia</i>	10	5	3	1
<i>Chromis dimidiata</i>	**	3	4	
<i>Acanthurus nigrofuscus</i>	**	6	*	
<i>Abudefduf saxatilis</i>	**	7		
<i>Chromis caerulea</i>		8		
<i>Gomphosus caeruleus</i>		9	*	
<i>Larabicus quadrilineatus</i>	*	10		*
<i>Dascyllus marginatus</i>	*	**	5	3
<i>Genicanthus caudovittatus</i>			6	4
<i>Pseudochromis fridmani</i>	*	*	9	
<i>Chromis pembrae</i>	*		10	
<i>Pseudocheilinus evanidus</i>	*	*	**	7
<i>Chaetodon paucifasciatus</i>	*	**	**	8
<i>Cephalopholis argus</i>	*	*	**	10

total of 93 fish species was counted around the Jetty pillars, 95 at Shallow, 90 at Garden and 65 at Dekel. The damselfish *Neopomacentrus miryae* comprised ca. 50% of all fish at the Jetty, and was also the most abundant at Shallow. It was the seventh most abundant species at Garden, and rare at Dekel (Table 2). *Pseudanthias squamipinnis* was the most abundant in the Garden, the seventh at Jetty, and among the first ten most abundant species at the other two study sites (Table 2). The apogonid *Cheilodipterus quinquelineatus* was abundant at all four study sites (Table 1), but was not among the ten most abundant species at the nature reserve reefs (Table 2). Since this species is nocturnal, it is possible that its numbers are underestimated, especially at the natural reefs, where it can find shelter inside crevices. *Pomacentrus trichourus* comprised 13 to 22% of all fish at the natural sites and was also among the most abundant fish at Jetty. *Pseudocheilinus octataenia* was abundant at all study sites, with greater relative abundance on the deep natural reefs (the most abundant species at Dekel and the third at Garden, with relative abundances of 30 and 11%, respectively). Some species were abundant only at the Jetty (e.g. *Amblyglyphidodon leucogaster*, *Apogon aureus* and *Ostracion cubicus*; Tables 1, 2), and 14 species were recorded only there (Table 1). Other species were abundant only at Shallow (e.g. *Chromis caerulea* and *Acanthurus nigrofuscus*), and some were relatively abundant at both Shallow and Jetty (*Abudefduf saxatilis* and *Labroides dimidiatus*). Some fish were abundant only at the deep sites (e.g. *Genicanthus caudovittatus*), or found at both the deep sites and at Jetty, but not at Shallow (e.g. *Amblyglyphidodon flavilatus* and *Bodianus anthioides*; Tables 1, 2). Thirty-five species, found at the three natural sites, did not appear

at the jetties, when the species reported by Rilov and Benayahu (1998) were included in the list (Table 1).

Some of the abundant species at Jetty showed a clear vertical zonation along the pillars (Fig. 2), and all were rare in the upper 9 m with no barbed wire. *Neopomacentrus miryae* and *Pseudanthias squamipinnis* were concentrated mainly at the upper sections of the wires,

especially during the recruitment period (April 1993, see also Rilov and Benayahu 1998). The three apogonids *Cheilodipterus quinquelineatus*, *Apogon cyanosoma* and *A. aureus* were located mainly near the bottom of the pillars. Juveniles of *C. quinquelineatus* also mainly appeared in April 1993 and those of *A. cyanosoma* during November 1992. *Pomacentrus trichourus* and *Amblyglyphidodon*

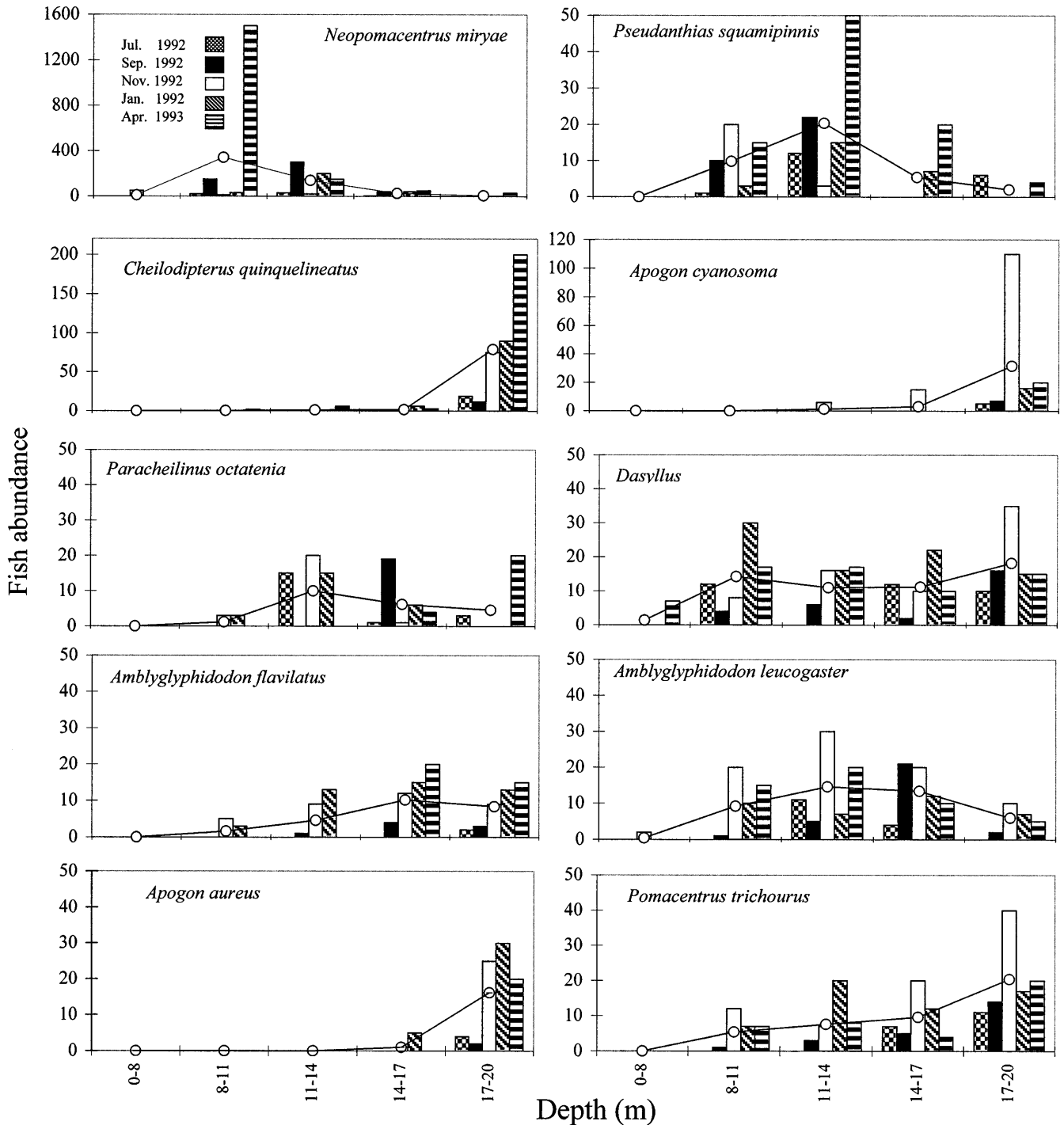


Fig. 2 The vertical distribution of the ten most abundant species at the Jetty on the five census dates. These values were averaged ($n = 5$ dates) for each depth (open circles)

lyphidodon flavilatus similarly demonstrated higher abundances in the lower parts, while the congeneric *A. leucogaster* seemed to concentrate in the middle sections of the wire.

Community indices

The average species richness was significantly higher ($p < 0.0001$, Kruskal–Wallis, $H = 28.2$) at the Jetty as compared to the three natural sites (Fig. 3a). The highest number of species was also found at the Jetty, followed by the Shallow, Garden and Dekel sites (52, 43, 38, 26 species, respectively). Fish abundance was also the highest at Jetty ($p < 0.0001$, $H = 21.9$, Fig. 3b), being ca. 3.5-fold higher than at the two nature reserve sites, and ca. 5 times higher than at the deep Dekel site (Fig. 3b). Maximum fish abundance was found during April 1993, with the highest values at the Jetty, followed by Shallow, Garden and Dekel sites (2380, 622, 478, 285, respectively). Average fish diversity was significantly lower at the Jetty than at the two nature reserve sites ($p = 0.007$, $H = 12$, Fig. 3c). The maximum diversity values at the three sites were similar, and ranged between 2.82 and 2.92, while at Dekel site it was only 2.48. The standard deviations of both fish abundance and diversity

were largest at Jetty (Fig. 3b, c). No correlation was found between coral cover and fish abundance in a regression analysis conducted on the data from the two nature reserve sites (Fig. 4a, b), while a significant positive relationship existed for the Dekel site ($p = 0.02$, $F = 7.9$, Fig. 4c).

Similarity among sites

The highest similarity among sites, expressed by the affinity index A , was found between Garden and Dekel ($A = 56$, Table 3). The two nature reserve sites demonstrated 51% similarity, as compared to only 31% between Shallow and the two deep sites (Table 3). The lowest similarity values were obtained between Jetty and the natural sites. However, when the pomacentrid *Neopomacentrus miryae*, the most abundant fish at Jetty, was excluded from the analysis (see also Caley 1995), this similarity increased (Table 3). The mean similarity between the paired-pillar unit to the separate pillar at Jetty was 57% (± 18 ; $n = 5$), and 51% (± 12 ; $n = 5$) among censuses conducted for the same pillar.

The MDS analysis was applied to the data in order to analyze the relationships between fish assemblages among all sites. The low value of the stress coefficient

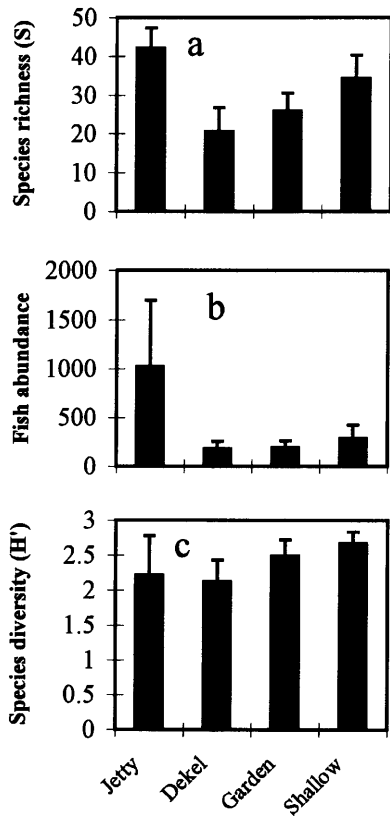


Fig. 3 Species richness (S), fish abundance (number of fish per belt transect or pillar) and species diversity (H') at the four study sites. Error bars represent SD

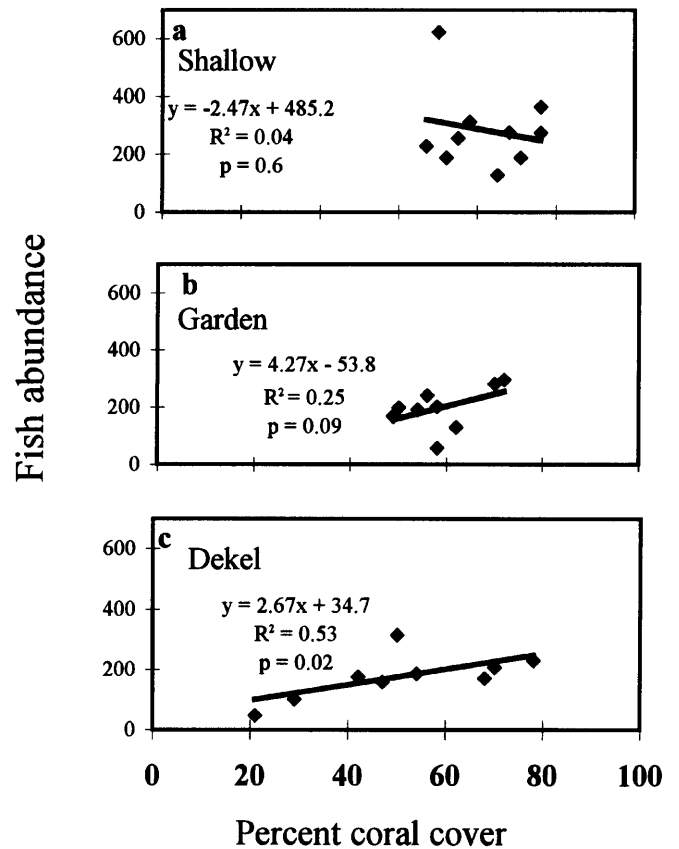


Fig. 4 The relationship between fish abundance (number of fish per belt transect) and percent coral coverage at the three natural study sites

Table 3 Percent similarity index *A* between the study sites. In parentheses: the *A*-value when *Neopomacentrus mirryae* is not included

	Garden	Dekel	Jetty
Shallow	51 (56)	31 (40)	37 (43)
Garden		56 (58)	27 (40)
Dekel			23 (31)

(<0.1) demonstrates that much of the variation is explained by the first two dimensions in this analysis (Fig. 5). Adding dimensions to the analysis did not greatly change the stress value. After we reduced the effect of the most abundant fish species using the $\log(x + 1)$ transformation, a segregation among the three natural sites appeared as a continuum of censuses along the *y*-axis (Fig. 5). The ellipses of the 95% confidence limits overlap considerably, thus revealing a similarity between the two distant deep reefs as well as between the two nature reserve sites. The Jetty is considerably separated from the natural sites, mainly along the *x*-axis (Fig. 5).

Cluster analysis that was conducted on the raw data grouped only the Jetty censuses from the natural sites, however, after $\log(x + 1)$ transformation, a grouping pattern seems to be more apparent also at the natural sites (Fig. 6). Jetty groups separated from the natural sites, except for J10 (census of April 1993), which is also separated from all the others (Fig. 6). At Garden and Shallow only the autumn (November or December) and winter (January and February) counts were paired: at Garden (G3 and G4, G5 and G6, G7 and G8, with 40 to 50% relative dissimilarity) and at Shallow (S1 and S2, S3 and S4, S7 and S8, with 65 to 75% relative dissimilarity). At Dekel, all but one census grouped together with a relatively low dissimilarity of 55%, and no within-date grouping was evident.

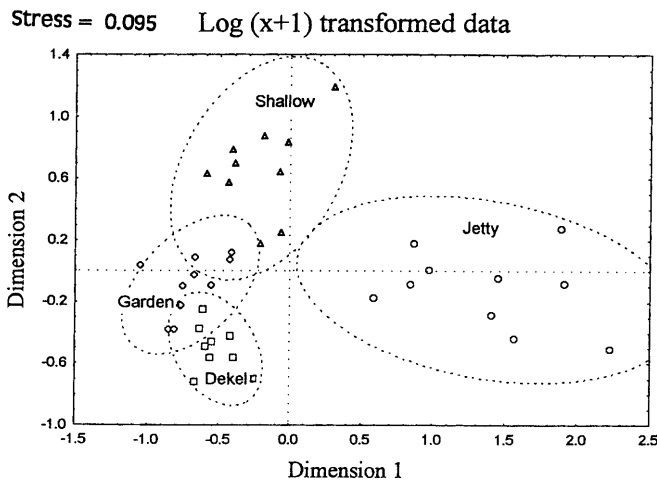


Fig. 5 MDS analysis on the $\log(x + 1)$ transformed data from the four study sites. Ellipses illustrate the 95% confidence limits (circles Jetty; squares Dekel; triangles Shallow; diamonds Garden censuses)

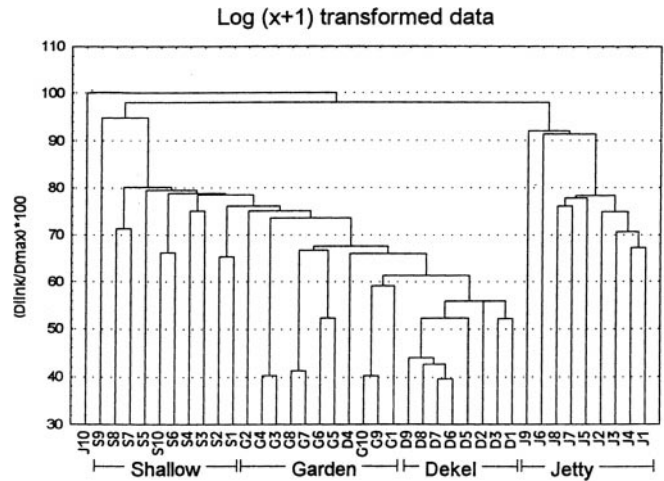


Fig. 6 Cluster analysis on the $\log(x + 1)$ transformed data from the four study sites. Scaling is based on present dissimilarity between censuses expressed as relative dissimilarity: $(D_{link}/D_{max}) \times 100$. Censuses are marked by a letter indicating the site (e.g. *S* = shallow) and numbers indicating the census in progressive chronological order (e.g. *J1*, *J2* = Jetty censuses from June 1992, and *J9*, *J10* = from April 1994)

Discussion

Community indices

The present study demonstrates that the total number of species at the jetties is similar to that of the two relatively rich nature reserve sites, and it is much higher than that of Dekel. Due to its proximity to Eilat, the Dekel site has probably become more exposed to the accelerated urban and recreational development of the last few decades and the adjacent harbor activity. Exposure to these anthropogenic disturbances has damaged the reef there and led to the patchy nature of its coral cover. Hence, a significant correlation between coral cover and fish abundance was found, as opposed to the nature reserve sites, where the hard bottom cover is quite continuous (authors' personal observations). In contrast with the total number of species, the average species richness was significantly higher at the artificial structure than at the nature reserve sites. This contradicts the results found in other studies conducted in tropical waters where low-relief structures were used (e.g. Randall 1963; Alevizon et al. 1985; Brock and Norris 1989). We suggest that the vertical relief of the underwater jetty constructions and the high structural complexity formed by the barbed wire offer niches for reef fish species from various depths, such as the shallow *Abudefduf saxatilis* and *Labroides dimidiatus*, and *Amblyglyphidodon flavilatus* and *Bodianus anthioides* from deeper waters (Fishelson et al. 1974; Allen and Randall 1980; Edwards and Rosewell 1981; present study). The appearance of many species at the jetties and their rarity or even absence from the natural reefs may be a result of habitat loss on the Eilat reefs (see also Sano et al. 1984; Dennis and

Bright 1988; Dawson Shepherd et al. 1992). Other species, however, may be typical on steep vertical habitats, which are not found in the adjacent natural reefs.

Bailey-Brock (1989) stated the importance of the relationship between the sessile organisms found on artificial reefs and the appearance of fish species feeding on them. In the present study, for example, the spongivore angelfish *Holocanthus xanthurus* (see Randall 1983) was abundant at Jetty and absent at the natural reefs. Sponges, indeed, compose a high percentage of the sessile invertebrate cover at the jetties, while on the adjacent natural reefs they are much less abundant (Goren 1992). In contrast, the herbivore *Acanthurus nigrofuscus*, though seen frequently at the jetties (see also Rilov and Benayahu 1998), was less abundant there than at Shallow, probably due to the low algal cover of the former. Thirty-four other species were found only at the natural reefs; of these, some, such as *Dascyllus marginatus* and *Chromis caerulea*, inhabit only branching corals, which are relatively rare at the jetties (Goren 1992).

There was no significant difference in fish numbers between natural reefs and low-relief, tire-constructed artificial reefs in the Florida Keys (Stone et al. 1979). However, other studies have demonstrated higher abundance of fish on low-relief artificial structures than on natural ones (see review by Bohnsack and Sutherland 1985; Ambrose and Swarbrick 1989). Similarly, in the present study, fish abundance was significantly higher at the artificial Jetty site than at all three natural reefs. It has been suggested that the higher abundance of fish on artificial reefs is related to the reefs' relatively small size and isolation, which result in higher fish attraction per unit area than on natural reefs (Randall 1963; Russell 1975; Ambrose and Swarbrick 1989). Nevertheless, the Jetty is part of the larger and complex structure of the oil jetties (see Fig. 1 in Rilov and Benayahu 1998), and therefore this argument seems implausible here. Hence, we suggest that the high-relief and vertical orientation of the pillars offer the first substrate encountered by juveniles of most species as they approach the coastal water for settlement. Two of the most numerous species, *Neopomacentrus miryae* and *Pseudanthias squamipinnis*, demonstrated a distinct zonation pattern at Jetty, and were concentrated mainly around the upper sections of the pillars, especially during the recruitment period (Rilov and Benayahu 1998). Such recruitment episodes were also revealed on the upper units of vertical experimental installations at Eilat (Rilov 1993). However, on the natural reefs of Eilat, *N. miryae* was the most abundant fish in shallow waters (relative abundance of 17% in the fore-reef zone at 3 to 6 m depth, and only 4% at 20 m depth), whereas *P. squamipinnis* was most abundant at deeper sites, with $RA = 16\%$ on the coral slope. Both these species have been described as abundant in the northern Red Sea, and feed on plankton high above the bottom (Fishelson et al. 1974; Allen and Randall 1980; Randall 1983). The similarity in vertical distribution pattern of *N. miryae* between the natural and vertical reefs in Eilat may indicate that it prefers to

aggregate in shallower waters, as also demonstrated for the Great Barrier Reef by Hamner et al. (1988). Doherty et al. (1996) have suggested that pelagic juveniles have excellent sensory and motor capabilities, enabling them to select the habitat before settlement. In contrast to *N. miryae*, the difference in vertical zonation of *P. squamipinnis* between the natural and artificial reefs may indicate that its juveniles are less specific in their settling preferences. Shapiro (1987) speculated that they settle on the first suitable habitats encountered when approaching from the plankton, which are found in the Eilat area in deeper waters.

After settlement, the complex habitat formed by the barbed wire serves as shelter for the recruits, and thus probably allows high survival rates. Beets (1989) and Brock and Kam (1994) demonstrated that floating "Fish Aggregating Devices" (FADs), found high above the bottom, can enhance recruitment of coral reef fishes to benthic low-relief structures. Hence, highly conspicuous structures with shelter, such as Jetty, are probably susceptible to higher recruitment rates than the Eilat natural reefs. Indeed, a substantial increase in fish numbers during April 1993 (Rilov and Benayahu 1998), especially of a few dominant species (present study) was evident at the Jetty, resulting in high standard deviations when the April data were averaged with the data from the other four collection dates, while lower means and small standard deviations were found for the natural reefs, suggesting lower recruitment than at the Jetty. Likewise, considerable fluctuations of fish abundance were demonstrated on artificial reefs, and to a lesser degree on natural reefs, in southeastern Florida, with recruitment episodes occurring in spring and summer (Bohnsack et al. 1994). On La Reunion fringing reefs (west Indian Ocean), some increase in fish abundance was also found in summer, though no distinct seasonal patterns could be detected (Letourneur 1996b). Recruitment episodes may, however, be masked by post-settlement mortality such as predation in "space-limited" rather than "recruitment-limited" habitats, resulting in temporal uniformity in population density for both natural and artificial reefs in Barbados (see Tupper and Hunte 1994).

In contrast with the oil jetties, the Eilat natural reefs today are probably mainly space-limited owing to man-made impact which has reduced habitat complexity, lowered the available shelter for settlement, and thus decreased fish recruitment and abundance (see also Sano et al. 1984; Dennis and Bright 1988). Likewise, Letourneur (1996b) suggested that the decrease in fish abundance, detected at La Reunion reefs, may be related to coral degradation caused by hurricanes and/or eutrophication. In contrast, Doherty et al. (1997) showed high recruitment levels in reef areas with coral cover reduced to lower levels by a catastrophic storm. However, survival rates may be more dependent on shelter availability than the recruitment process itself, and thus be of greater importance for the establishment of a healthy coral reef community. It is clear that further studies are required to determine which of the processes

are of greater importance in the establishment of a diverse reef fish community.

The lower average species diversity (H') at the Jetty than at the two nature reserve sites probably results from high seasonal recruitment rates of a few species which produced a high standard deviation in fish abundance. However, maximum H' values were similar at the nature reserve and the Jetty (2.82 to 2.96), and resembled those found elsewhere in natural coral reef fish communities (northern Red Sea: Ben-Tuvia et al. 1981; Hawaii: Brock 1979; and the Bahamas: Alevizon et al. 1985), although further south in the Red Sea, along the Sudanese shore, fish diversity is lower (Edwards and Rosewell 1981).

Similarity among sites

Letourneur (1996a) has shown that habitats found in analogous zones of reefs at sites in the same area have similar fish assemblages. Likewise, in our study the highest similarity was found between the two deep natural reefs, Garden and Dekel (ca. 56%). Somewhat lower similarity (51%) was found within the same location among depth zones at the nature reserve. However, after log transformation the closely packed natural sites separated into distinctive habitat-related groups of censuses on the MDS plane, which indicates that the high abundance of several species obscured the inherent differences in the presence/absence of other species among habitats.

A within-reef continuum of censuses on the MDS plane was observed by Letourneur (1996a) at Reunion reefs. In the current study, a continuum was found between the two nature reserve sites, and also between the two deep sites along the same axis. These results imply that environmental conditions are similar between these pairs of habitats. However, the Jetty separated from the natural reefs on the second axis, which may reflect differences in the hydrodynamic and in the invertebrate cover between the natural and artificial reefs (Goren 1992; Dahan and Benayahu 1997). Currents were demonstrated to have a profound impact on the benthic sessile community in the Florida Keys, where the highest cover was found on vertical surfaces exposed to the strongest currents (Baynes and Szmant 1989). The vertical structure of the pillars, which extend from the bottom into the water body, probably expose the fish to strong currents, which generated high plankton flux. We suggest that high plankton availability at the upper sections of the pillars leads to high abundance of planktivores, such as *Neopomacentrus miryae* and *Pseudanthias squamipinnis*. The inverse vertical zonation of the nocturnal apogonid planktivores probably does not reflect their distribution during feeding time.

In conclusion, the fish community at the oil jetties demonstrated relatively low similarities to the natural sites. Fish abundance and species richness at this artificial site were higher than on the natural reefs of Eilat,

which can probably be attributed to the unique vertical orientation and spatial complexity of the pillars supporting the jetties. These structural traits no doubt allow for high recruitment and survival rates, and thus for a rapid formation of a rich fish community. Such complex vertical structures can therefore serve as a model for future construction of artificial structures designed to rehabilitate areas where natural reefs have been damaged. Nevertheless, a vertical structure does not necessarily mimic the natural environment, but rather may establish a community of its own. Finally, there is no doubt that the presence of the oil jetties have contributed considerably to the regional production of fish at Eilat since there are no substantial natural reefs in the vicinity of the jetties, which is a prerequisite for a successful artificial reef, as suggested by Carr and Hixon (1997).

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