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Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea

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ABSTRACT: The semi-enclosed Gulf of Aqaba is under high pressure by urban and industrial pollution, shipping and port activities as well as tourism. Off the Jordanian Red Sea coast, the trophic community structure of shore fishes was determined on coral reefs in front of an industrial area (disturbed), in a marine reserve and site without industry or port activities (undisturbed), as well as in a seagrass-dominated bay. Planktivores were the most abundant feeding guild on coral reefs as well as in the seagrass-dominated bay. The relative abundance of feeding guilds other than planktivores seems to be strongly influenced by the benthic habitat. Multivariate analysis clearly separated disturbed from undisturbed sites, whereas univariate measures, such as species richness, diversity and evenness did not reveal any negative impact of disturbance. The disturbance of the coral reefs led to changes in the fish community through the reduction of total fish abundance by 50%, increased total abundance of herbivorous and detritivorous fishes, decreased total abundance of invertebrate- and fish-feeders, and increased relative abundance of planktivorous fishes.

KEY WORDS: Trophic community structure · Pollution · Shore fishes · Coral reef · Seagrass meadow · Red Sea

INTRODUCTION

The semi-enclosed Gulf of Aqaba is under high pressure by urban and industrial pollution (Mergner 1981, Walker & Ormond 1982, Abu-Hilal 1987, Abu-Hilal & Badran 1990, Abelson et al. 1999), shipping and port activities (Fishelson 1973, Loya 1975, Abu-Hilal 1985, Badran & Foster 1998) as well as tourism (Riegl & Velimirov 1991, Hawkins & Roberts 1994). The Jordanian coastline has a length of about 27 km with a discontinuous series of fringing reefs of 13 km length, interrupted by bays which are mostly covered with seagrass meadows (UNEP/IUCN 1988). During the last 25 yr, 30 to 40% of the Jordanian coastline has been altered from a pristine natural environment to a heavily used port and industrial area (Abu-Hilal 1997). In 2001, Aqaba was declared a Special Economic Zone, and therefore rapid increase in port and industrial activities is to be expected.

Industry and port activities are expected to disturb the coastal ecosystem, which will lead to changes in the fish community. On the one hand, degradation of coral reefs leads to coral death, loss of the complex habitat structure and decrease of associated invertebrates, on the other hand, algal growth is enhanced due to open substrate caused by coral decease and, in some cases, eutrophication. Fishes that depend on corals or associated invertebrates as a source of food are likely to be reduced, whereas planktivores, herbivores and detritivores can increase in relative abundance so long as the dead corals still provide shelter.

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Fig. 1. Gulf of Aqaba, showing study sites along Jordanian coast. 1: cement jetty (29° 28.990' N, 34° 59.010' E); 2: Marine Science Station (29° 27.250' N, 34° 58.359' E; distance from Site 1. = 3.4 km); 3: tourist camp (N 29° 26.351' N, 34° 58.272' E; distance from Site 2 = 1.6 km); 4: Al-Mamlah Bay (29° 24.345' N, 34° 58.549' E; distance from Site 3 = 3.7 km); 5, 6: Jordan Fertiliser Industries and Jordan Fertiliser Industries jetty (29° 22.134' N, 34° 57.667' E; distance from Site 4 = 4.1 km)

Investigations of the impact of coral mining (Shepherd et al. 1992) and coral bleaching (Lindahl et al. 2001) on fish communities have shown that univariate measures, such as species richness and diversity, are not appropriate to reveal changes in the fish community. Therefore, we investigated the trophic community structure of fishes on disturbed as well as undisturbed coral reefs, and in a seagrass-dominated bay along the Jordanian coast. The disturbed reefs are located in front of an industrial area and port, whereas the undisturbed reefs are situated in a marine reserve and at sites with no industry or port activity.

MATERIALS AND METHODS

Study sites. Our investigation of the general trophic community structure of shore fishes in the Gulf of Aqaba is based on 5 coral reefs and the seagrass-dominated Al-Mamlah Bay at the Jordanian coast (Fig. 1). The degree of human-induced disturbance differs greatly along the coastline. The sites regarded as undisturbed are completely closed for human activities (marine reserve) or utilised for small-scale fishing as well as recreational activities. At the disturbed sites, the fringing reef in front of the Jordan Fertiliser Industries (JFI) is under pressure due to port activity, solid waste disposal, spillage during loading and unloading of ships (e.g. sulphur, ammonia), as well as disposal of waste oil from trucks (Gladstone et al. 1999) (see Table 1). In the past, parts of the reef flat were filled in for a parking place and the JFI jetty (Mahasneh & Meinesz 1984). A study on coral diseases revealed a 10-fold higher number of infected coral colonies at the JFI than in the marine reserve (Al-Moghrabi 2001). Values of phosphate concentrations (Badran & Foster 1998), heavy metals (Abu Hilal & Badran 1990), and algal cover (M.A.K. pers. obs.) are higher at the disturbed JFI than in the marine reserve at the Marine Science Station (MSS). Phosphate concentrations at JFI reach the threshold value of 0.1 to 0.2 µM, a level proposed as indicating polluted (Bell 1992). The distance between the disturbed and undisturbed sites is around 8 km.

Visual census. The fish communities in shallow-water habitats along the Jordanian coast were surveyed by the visual census technique using SCUBA, as described by English et al. (1994). Transects of 50 m length and 5 m width (250 m^2) were marked along lines at 6 sites parallel to the shore (Fig. 1, Table 2). At each site, visual censuses were conducted along 3 transects on the shallow reef slope (6 m) and deep reef slope (12 m), respectively. The distance between the transects at each site was 10 to 20 m. After laying the transect line, an observer would wait 5 to 10 min to allow fishes to resume their normal behaviour. Subsequently the diver swam 50 to 60 min along the transect and recorded all fishes encountered 2.5 m on each site of the line and 5 m above the transect. Differences in the skill and technique of the observers are a source of imprecision and/or bias (Thompson & Mapstone 1997). Therefore, the first author (M.A.K.) identified and recorded all fishes of about 30 mm total length or larger on a plastic slate. The visual census technique is widely applied and accepted for ecological fish studies on coral reefs (English et al. 1994). However, all our conclusions are restricted to diurnally active and non-cryptic species (Brock 1982). At 5 sites (cement jetty, Marine Science Station, tourist camp, Jordan Fertiliser

Table 1. Human-induced disturbance on coral reefs along Jordanian Red Sea coast, Gulf of Aqaba

Site	State	Human impact	Activities
Cement jetty	Undisturbed	Medium	Some fishing (hook and line)
Marine Science Station	Undisturbed	Very low	Marine reserve; occasionally illegal fishing
Tourist camp	Undisturbed	Low	Swimming and snorkeling
Jordan Fertiliser Industries	Disturbed	Very high	High port activity; solid waste; phosphate and trace metal pollution, sedimentation
Jordan Fertiliser Industries jetty	Disturbed	Very high	Very high port activity; solid waste; phosphate and trace metal pollution; accidental discharge of sulphur and ammonia, sedimentation

Industries and Jordan Fertiliser Industries jetty) 3 censuses were conducted at each depth in November 1999 and March 2000. In 1997 and 1998, 39 censuses were conducted at Al-Mamlah Bay at 6 m depth and 43 census at 12 m depth (Table 2). A total of 212 349 fishes were counted, representing 198 species belonging to 121 genera and 43 families. Affiliation of species with trophic groups is based on Khalaf & Disi (1997) and on field observations (Table 3).

Statistical analysis. Community indices such as fish abundance, species richness (number of species), Shannon-Wiener diversity (*H'*; ln basis), and Pielou's evenness (*J'*) were compared among sites and depths using 1-way ANOVA. Homogeneity of variances was tested with the *F*-test and, if necessary, data were log(1+*x*)-transformed to obtain homogeneity of variances. If transformation of the data did not lead to homogeneity of variances, no statistical test was conducted. The *F*-test was performed with a spreadsheet analysis programme, and 1-way ANOVA was carried out with STATISTICA 5.1 (StatSoft 1997).

Multivariate analysis of the data such as cluster analysis, MDS (multi-dimensional scaling), ANOSIM (analysis of similarities) significance test, as well as SIMPER (similarity percentages) were performed with PRIMER 5 software (Primer-E 2000). Hierarchical clustering and MDS was based on Bray–Curtis similarities. In contrast to species with very low abundance, highly abundant species can disturb an analysis. Therefore, when necessary, data were standardised (see Fig. 4A,B).

MDS is a 3-dimensional ordination of samples brought down to a 2-dimensional plot. The quality of the MDS plot is indicated by its stress value: values <0.2 give a potentially useful 2-dimensional picture, stress <0.1 corresponds to a good ordination, and stress <0.05 is an excellent representation.

The ANOSIM significance test compares similarities of species compositions between samples and can give evidence of differences. Global R indicates the degree of similarity between the tested groups, with values between –1 and 1. If all replicates within sites are more similar to each other than any replicate from different sites, the value of R is 1, values close to zero indicate that the similarity between sites is very high. A 1-way layout of ANOSIM was performed with the original data, no transformation or standardisation was conducted.

SIMPER is an analytical tool used to reveal the average Bray-Curtis dissimilarity between groups of samples. The aim of the analysis in our study was to calculate the contribution of each feeding guild to the differences between sites (Clarke & Warwick 1994).

RESULTS

Fish community parameters (Fig. 2)

Species richness showed no difference between disturbed and undisturbed coral reefs. Diversity (*H'*) and evenness (*J'*) were higher at the disturbed sites, whereas fish abundance on disturbed reefs was 51.4 % lower than on undisturbed reefs.

Relative species richness and relative abundance of trophic groups (Table 4)

In terms of number of species belonging to different feeding guilds, predators on invertebrates (25.3 %)

Table 2. Sampling sites along Jordanian Red Sea coast, Gulf of Aqaba

Site	n	6 m	n	12 m
Cement jetty	3	Nov 1999	3	Nov 1999
Marine Science Station	3	Nov 1999	3	Nov 1999
Tourist camp	3	Nov 1999	3	Nov 1999
Al-Mamlah Bay	39	Apr 1997–Aug 1999	43	Apr 1997–Aug 1999
Jordan Fertiliser Industries	3	Apr 2000	3	Apr 2000
Jordan Fertiliser Industries jetty	3	Apr 2000	3	Mar 2000

Table 3. Affiliation of fishes from Jordanian Red Sea coast with trophic groups based on Khalaf & Disi (1997) and on field observations. C: corallivore; D: detritivore; H: herbivore (feeds on macroalgae; Scaridae: H/C), IF: invertebrate-feeder; IFF: invertebrate- and fish-feeder; O: omnivore; Pi: piscivore; Pl: planktivore

Species	Trophic Group
Torpedinidae	
Torpedo panthera	IFF
Muraenidae	
Gymnothorax nudivomer	IFF
Siderea sp.	Pi
S. grisea	Pi
Synodontidae	
Saurida gracilis	Pi
Synodus sp.	Pi
S. variegatus	Pi
Atherinidae	
Atherinomorus lacunosus	Pl
Holocentridae	
Myripristis murdjan	Pl
Neoniphon sammara	Pl
Sargocentron caudimaculatum	Pl
S. diadema	Pl
Fistulariidae	
Fistularia commersonii	IFF
Centriscidae	
Aeoliscus punctulatus	Pl
Syngnathidae	
Corythoichthys flavofasciatus	IF
C. nigripectus	IF
C. schultzi	IF
Trachyrhamphus bicoarctatus	Pl
Scorpaenidae	
Dendrochirus brachypterus	IF
Inimicus filamentosus	
Pterois miles	IFF
P. radiata	IF
Scorpaenidae	
Scorpaenopsis sp.	IFF
S. barbata	IFF
Synanceia verrucosa	Pi
Serranidae	
Anthias taeniatus	Pl
Cephalopholis hemistiktos	IFF
C. miniata	IFF
Epinephelus fasciatus	IFF
Grammistes sexlineatus	IFF
Pseudanthias squamipinnis	Pl
Variola louti	IFF

Species	Trophic Group
Carangidae	
Carangoides fulvoguttatus	IFF
Decapterus macrosoma	Pl
Gnathanodon speciosus	IFF
Caesionidae	
Caesio lunaris	Pl
C. suevicus	Pl
C. varilineata	Pl
Nemipteridae	
Scolopsis ghanam	IF
Gerreidae	
Gerres oyena	IF
Haemulidae	
Diagramma pictum	IFF
Lethrinidae	
Lethrinus sp.	IF
Monotaxis grandoculis	IF
Sparidae	
Diplodus noct	O
Mullidae	
Mulloidichthys flavolineatus	IFF
Parupeneus cyclostomus	IFF
P. forsskali	IFF
P. macronema	IFF
P. rubescens	IFF
Pempheridae	
Pempheris vanicolensis	IFF
Chaetodontidae	
Chaetodon auriga	O
C. austriacus	C
C. fasciatus	O
C. melannotus	C
C. paucifasciatus	O
C. trifascialis	C
Heniochus diphreutes	Pl
H. intermedius	O
Pomacanthidae	
Apolemichthys xanthotis	O
Centropyge multispinis	H
Genicanthus caudovittatus	Pl
Pomacanthus imperator	IF
Pygoplites diacanthus	IF

Species	Trophic Group
Pomacentridae	
P. trilineatus	
Mugilidae	
Crenimugil crenilabis	D
Labridae	
Anampses caeruleopunctatus	IF
A. lineatus	IF
A. meleagrides	IF
A. twistii	IF
Bodianus anthioides	IF
B. axillaris	IF
B. diana	IF
Cheilinus sp.	O
C. lunulatus	O
C. mentalis	O
C. trilobatus	O
Cheilio inermis	O
Cirrhilabrus rubriventralis	Pl
Coris aygula	IF
C. caudimacula	IF
C. gaimard gaimard	IF
C. variegata	IF
Gomphosus caeruleus klunzingeri	IF
Halichoeres marginatus	IF
Halichoeres scapularis	IF
Hemigymnus fasciatus	IF
Hologymnosus annulatus	IFF
Labroides dimidiatus	IF
Larabicus quadrilineatus	C
Macropharyngodon bipartitus	IF
Novaculichthys macrolepidotus	IF
Oxycheilinus digrammus	IF
Paracheilinus octotaenia	Pl
Pseudocheilinus evanidus	Pl
P. hexataenia	Pl
Pteragogus cryptus	
P. pelycus	
Stethojulis albovittata	IF
S. interrupta	IF
Thalassoma lunare	IFF
T. rueppellii	IFF
Thalassothia cirrhosa	IFF
Xyrichtys pavo	IF

Species	Trophic Group
Scaridae	
Ecsenius aroni	IF
E. frontalis	IF
E. gravieri	IF
Exallias brevis	C
Meiacanthus nigrolineatus	IF
Plagiotremus tapeinosoma	Pi
Plagiotremus townsendi	Pi
Gobiidae	
Amblyeleotris steinitzi	IF
A. sungami	IF
Amblygobius albimaculatus	IF
Bryaninops natans	Pl
Fusigobius longispinus	IF
Gnatholepis anjerensis	IF
Gobiodon citrinus	
Istigobius decoratus	IF
Lotilia graciliosa	IF
Valenciennea puellaris	IF
Acanthuridae	
Acanthurus nigrofuscus	H
A. sohal	H
Ctenochaetus striatus	D
Naso unicornis	H
Zebrasoma veliferum	O
Z. xanthurum	O
Siganidae	
Siganus argenteus	H
S. luridus	H
S. rivulatus	H
Scombridae	
Euthynnus affinis	IFF
Bothidae	
Bothus pantherinus	IF
Samaridae	
Samaris cristatus	
Soleidae	
Pardachirus marmoratus	IF
Balistidae	
Balistapus undulatus	O
Pseudobalistes fuscus	O
Sufflamen albicaudatus	IF

Table 3. Continued

Species	Trophic Group	Species	Trophic Group	Species	Trophic Group	Species	Trophic Group
Monacanthidae		*C. novemstriatus*	Pl	*Calotomus viridescens*	H	*Cantherhines pardalis*	O
Aluterus scriptus	O	*Abudefduf vaigiensis*	O	*Chlorurus gibbus*	H	*Pervagor randalli*	O
Pseudochromidae		*Amblyglyphidodon flavilatus*	Pl	*C. sordidus*	H	**Ostraciidae**	
Pseudochromis flavivertex	O	*A. leucogaster*	Pl	*Hipposcarus harid*	C	*Pseudomonacanthus pusillus*	
P. fridmani	O	*Amphiprion bicinctus*	Pl	*Leptoscarus vaigiensis*	H	*Ostraccion cubicus*	O
P. olivaceus	O	*Chromis dimidiata*	Pl	*Scarus ferrugineus*	H	*O. cyanurus*	O
P. springeri	O	*C. pelloura*	Pl	*S. fuscopurpureus*	H	*Tetrosomus gibbosus*	O
Priacanthidae		*C. pembae*	Pl	*S. ghobban*	H	**Tetraodontidae**	
Priacanthus hamrur	Pl	*C. ternatensis*	Pl	*S. niger*	H	*Arothron diadematus*	O
Apogonidae		*C. viridis*	Pl	*S. psittacus*	H	*A. hispidus*	O
Apogon sp.	Pl	*C. weberi*	Pl	**Pinguipedidae**		*A. stellatus*	O
A. aureus	Pl	*Dascyllus aruanus*	O	*Parapercis hexophtalma*	IFF	*Canthigaster coronata*	O
A. cyanosoma	Pl	*D. marginatus*	O	**Uranoscopidae**		*C. margaritata*	O
A. exostigma	Pl	*D. trimaculatus*	Pl	*Uranoscopus sulphureus*	IFF	*C. pygmaea*	O
A. fraenatus	Pl	*Neoglyphidodon melas*	C	**Blenniidae**		*Torquigener flavimaculosus*	O
A. nigrofasciatus	Pl	*Neopomacentrus miryae*	Pl	*Aspidontus taeniatus taeniatus*	O	**Diodontidae**	
Cheilodipterus lachneri	Pl	*Pomacentrus sulfureus*	O	*Cirripectes castaneus*		*Cyclichthys spilostylus*	IF
C. macrodon	Pl	*P. trichourus*	IFF	*Amanses scopas*	O		

were the most common feeding guild, followed by planktivores (20.8%) and omnivores (19.2%).

In terms of relative abundance, 58.1% of all fish specimens were planktivorous on coral reefs, and as much as 79.9% in the seagrass-dominated Al Mamlah Bay. Other important trophic groups on coral reefs were invertebrate- and fish-feeders (23.1%), omnivores fishes (11.6%) and herbivores (3.4%). These 3 groups showed a low relative abundance (5 to 6.5%) at Al Mamlah Bay.

Totale abundance of trophic groups (Fig. 3 & Table 5)

The total abundance of the various trophic groups at the different sites revealed patterns connected with the benthic habitat or disturbance at the respective sites. Those patterns were all statistically highly significant.

Corallivores were less abundant at the seagrass-dominated site than on coral reefs. Planktivores were more abundant at 12 m than at 6 m depth on both the coral reefs and at the seagrass-dominated site. The abundance of planktivores at 12 m depth was higher on undisturbed coral reefs than on disturbed reefs, and was higher in the seagrass meadow than on coral reefs.

In the seagrass-dominated Al-Mamlah Bay and on the disturbed coral reefs, herbivores were more abundant at 6 m than at 12 m depth. Comparison of herbivores in 6 m depth between disturbed and undisturbed coral reefs revealed a higher abundance for disturbed reefs.

The number of detritivores was higher on coral reefs than in the seagrass meadow. Disturbed coral reefs tended to have a larger population of detritivores than undisturbed reefs, especially on the shallow reef slope.

Invertebrate- and fish-feeders were more abundant on coral reefs, and their numbers were higher on undisturbed than on disturbed coral reefs, especially on the shallow reef slope.

Invertebrate-feeders had a larger population in the seagrass meadow.

In the seagrass-dominated Al-Mamlah Bay, piscivores were higher in abundance at 12 m than at 6 m. In addition, the population of piscivores at 12 m was larger than on coral reefs.

Omnivores tended to be more abundant on the deep reef slope than on the shallow reef slope, but there was no significant difference between sites.

Multivariate analysis

The cluster analysis and the MDS plot based on abundance of feeding guilds on coral reefs on the shal-

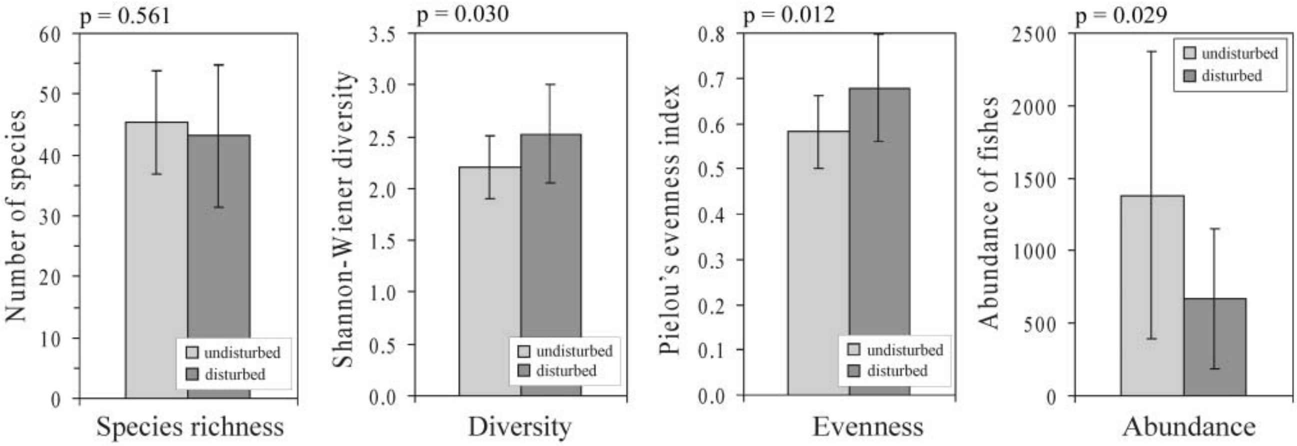

Fig. 2. Fish community parameters (species richness, diversity, eveness, abundance) of undisturbed and disturbed coral reefs at the Jordanian Red Sea coast, Gulf of Aqaba. Bold-face = significant values (1-way ANOVA)

low (6 m) and deep (12 m) reef slope revealed 2 clusters: (1) disturbed, and (2) undisturbed coral reefs (Fig. 4). Analysis of the shallow reef slope showed 2 mismatches (Samples 6a: Fig. 4), but these did not affect the general pattern. A dendrogram and MDS plot of the deep reef slope communities included 2 mismatches at disturbed reefs (Samples 1b and 2b) without affecting the division into the 2 groups. An ANOSIM test confirmed the pattern of both multivariate analyses (Fig. 4). The dendrogram and MDS plot for species abundance were more or less identical to the multivariate analysis of feeding guilds, and are therefore not presented here.

SIMPER analysis revealed that invertebrate- and fish-feeders (48.4%) and planktivores (41.3%) were the main feeding guilds responsible for differences in community structure between disturbed and undisturbed shallow reef slopes. Invertebrate feeders (4.2%), herbivores (3.1%) and omnivores (1.7%) contributed a minor percentage to the dissimilarity between the 2 groups (Table 6). On deep reef slopes, planktivores (64.2%) and invertebrate- and fish-feeders (23.5%) contributed most of the dissimilarity between undisturbed and disturbed sites, whereas omnivores (7.4%), herbivores (2.1%) and invertebrate-feeders (1.2%) played a minor role (Table 6).

Trophic structure of fish fauna on disturbed and undisturbed coral reefs (Fig. 5)

Fish communities on the shallow slope of disturbed coral reefs showed a higher relative abundance of planktivores and herbivores than undisturbed reefs, whereas the relative abundance of omnivores and fish and invertebrate feeders was reduced at the disturbed sites. On the deep reef slope the picture is not so clear. The relative abundance of planktivores and invertebrate- and fish-feeders was reduced at the disturbed coral reef, whereas omnivores and herbivores showed a higher relative abundance.

Table 4. Trophic composition of fish fauna in shallow water habitats along Jordanian Red Sea coast, Gulf of Aqaba

Feeding guilds	Species richness n	Species richness %	Relative abundance (%) Coral reef	Relative abundance (%) Seagrass-dominated bay
Corallivores	7	3.5	0.8	0.1
Herbivores	17	8.6	3.4	6.5
Planktivores	41	20.8	58.1	79.9
Detritivores	2	1.0	0.5	0.1
Invertebrate- and fish-feeders	28	14.1	23.1	5.5
Invertebrate feeder	50	25.3	2.3	2.5
Omnivores	38	19.2	11.6	5.0
Piscivores	8	4.0	0.1	0.2
Unknown	7	3.5	0.0	0.2

DISCUSSION

Fish counts took place at the disturbed site in March and April 2000, and at the undisturbed sites in November 1999. The possibility of the differences detected being due to seasonal changes within the fish community was considered. Our study on the community structure of shore fishes of the Jordanian coast (Khalaf

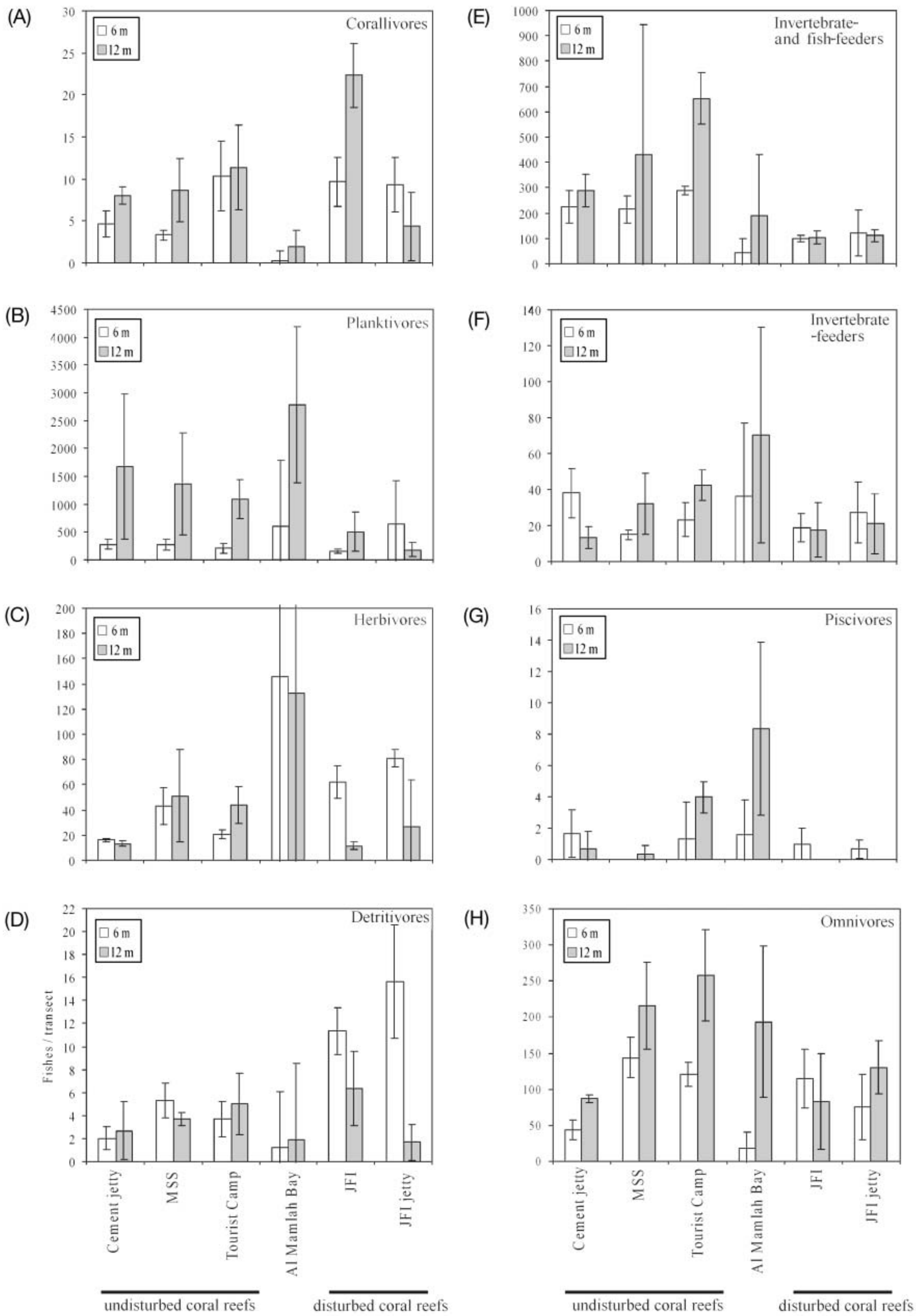

Fig. 3. Abundance of trophic fish groups (mean ± SD) at sites along Jordanian Red Sea coast, Gulf of Aqaba. (A) corallivores; (B) planktivores; (C) herbivores; (D) detritivores; (E) invertebrate- and fish-feeders; (F) invertebrate-feeders; (G) piscivores; (H) omnivores. Note different ordinate scales. JFI: Jordan Fertiliser Industries

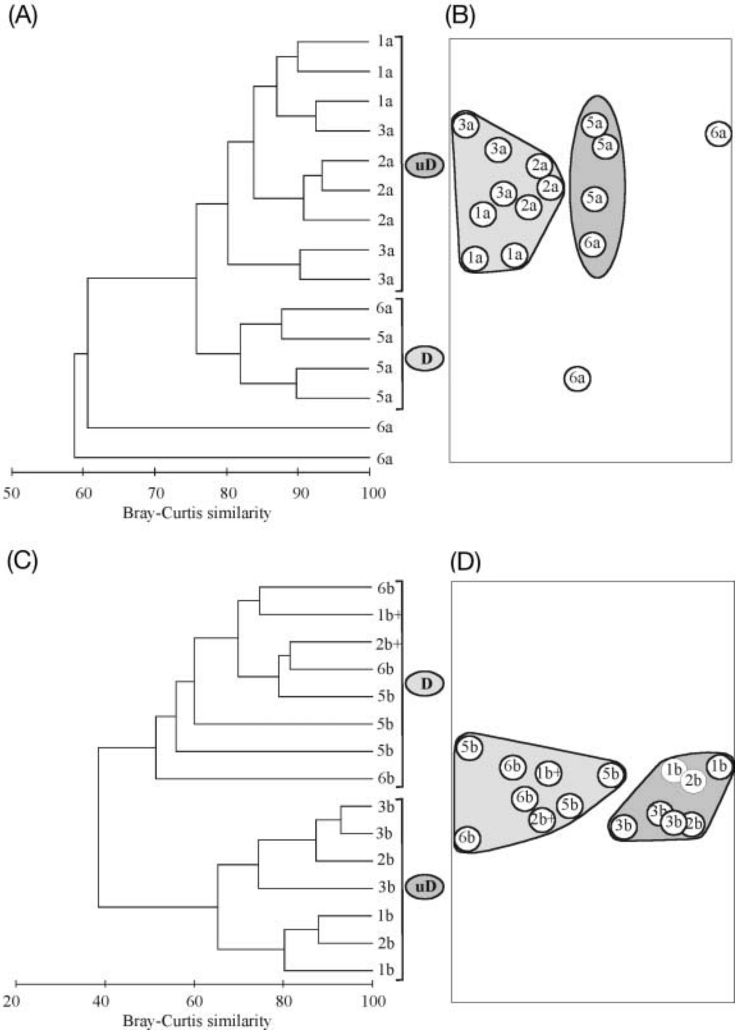

Fig. 4. Fish communities on disturbed and undisturbed coral reefs along Jordanian Red Sea coast, Gulf of Aqaba (based on abundance of feeding guilds—no pelagic or semi-pelagic species). (A, B) Dendrogram (A) and MDS plot (B) of shallow reef slope (6 m, Bray-Curtis similarity, standardisation, group average; stress = 0.05; ANOSIM: global R = 0.0553, p <0.001); (C, D) dendrogram (C) and MDS plot (D) of deep reef slope (12 m, Bray-Curtis similarity, group average; stress = 0.04; ANOSIM: global R = 0.493, p = 0.004). Sites numbered as in Fig. 1 (a = 6 m depth, b = 12 m depth). D: disturbed coral reefs; uD: undisturbed coral reefs; +: mismatch

& Kochzius 2002) revealed a strong spatial influence of habitat composition, but no temporal pattern. Studies on the colonisation of artificial reefs in Eilat (Rilov & Benayahu 1998, Golani & Diamant 1999) indicate that most recruitment takes place between January and May, with lower overall fish abundance in November. In contrast to these findings, total abundance was higher at the undisturbed sites in November than at the disturbed sites in March and April in our study. If temporal changes had been important, an opposite picture would have been expected. Therefore we can assume that temporal effects were not the reason for the observed differences.

Table 5. One-way ANOVA of abundance of feeding guilds at sites along Jordanian Red Sea coast, Gulf of Aqaba. Bold-face: significant p-values; *log(*x*+1)-transformed data; iv: inhomogenous variances; S: seagrass-dominated habitat; CR: coral reef; ud: undisturbed coral reef; d: disturbed coral reef; abbreviations of feeding guilds as in Table 3

Depth (habitat)	Feeding guilds							
	C	Pl	H	D	IFF	IF	Pi	O
S vs CR	**<0.001*** S < CR	iv	iv	**<0.001** S < CR	**0.002** S < CR	**0.020*** S > CR	iv	iv
12 m (S) vs 12 m (CR)	**<0.001*** S < CR	**<0.001** S > CR	0.124*	**<0.001*** S < CR	0.102	**<0.001*** S > CR	**<0.001*** S > CR	0.199
6 m vs 12 m (CR)	0.106	**0.009*** 6 m < 12 m	0.053*	0.885*	0.409	0.879	0.904	**0.035** 6 m < 12 m
6 m vs 12 m (S)	iv	**<0.001** 6 m < 12 m	**<0.001*** 6 m > 12 m	0.616	iv	iv	**<0.001*** 6 m < 12 m	iv
ud vs d	0.091	0.094	0.175	**0.035*** ud < d	**<0.001*** ud > d	0.245	0.164*	0.106
6 m vs 12 m (d)	0.406	0.847	**0.001** 6 m > 12 m	**0.001*** 6 m > 12 m	0.879	0.632	**0.022** 6 m > 12 m	0.691
6 m (ud) vs 6 m (d)	0.090	iv	**<0.001** ud < d	**<0.001** ud < d	**<0.001** ud > d	0.744	0.857	0.763
12 m (ud) vs 12 m (d)	iv	**0.014** ud > d	0.230	0.878	iv	0.242	0.058	0.072

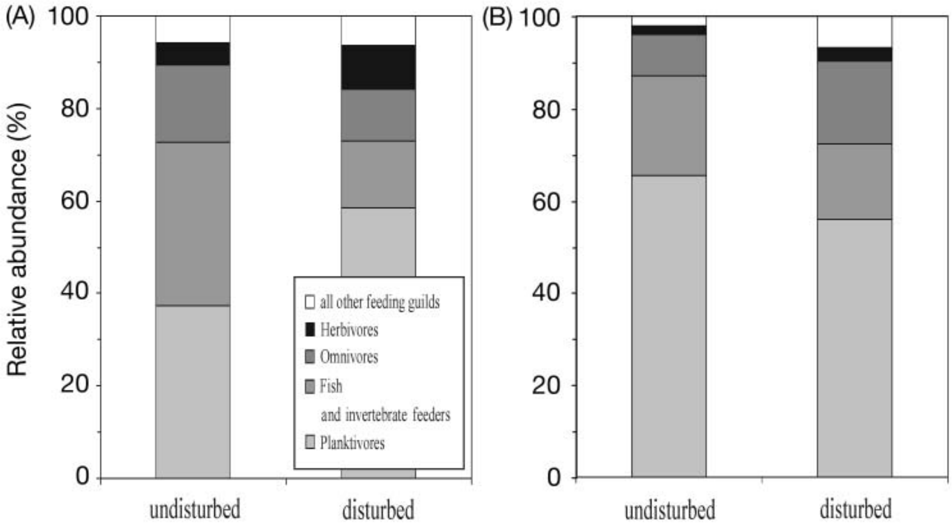

Fig. 5. Trophic composition of the fish fauna on disturbed and undisturbed coral reefs along Jordanian Red Sea coast, Gulf of Aqaba. (A) Shallow reef slope (6 m); (B) deep reef slope (12 m)

Trophic structure of the community

Planktivore fishes dominate the fish community on coral reefs in the Gulf of Aqaba. This finding corresponds with studies in Sri Lanka, the Great Barrier Reef, New Caledonia and the Gulf of Mexico (Williams & Hatcher 1983, Öhman et al. 1997, Pattengill et al. 1997, Rossier & Kulbicki 2000; Table 7). Zooplankton as a source of food, at least for diurnally active fishes, is fairly independent of the benthic habitat composition. Similar pattern of transport of the zooplankton result in a consistent dominance of planktivorous fishes on different coral reefs.

A comparison of our results with those of other studies revealed differences in the ranking and relative abundance of the other feeding guilds (Table 7). In Sri Lanka, New Caledonia, the Great Barrier Reef and the Gulf of Mexico, herbivores contribute a much higher proportion (2 to 7 times higher) to the fish community than they do in the Gulf of Aqaba. The relative abundance of herbivorous fishes was even lower at the seagrass-dominated site in the Gulf of Aqaba (Tables 4 & 7) than on the coral reef sites in other parts of the world.

Table 6. Contribution of feeding guilds to community shift between disturbed and undisturbed coral reefs on the Jordanian Red Sea coast, Gulf of Aqaba (no transformation of data)

Feeding guild	Contribution to dissimilarity (%) at: 6 m depth	12 m depth
Invertebrate- and fish-feeders	48.41	23.45
Planktivores	41.27	64.19
Invertebrate-feeders	4.22	1.13
Herbivores	3.14	2.07
Omnivores	1.72	7.37
Detritivores	0.59	0.21
Unknown	0.40	0.61
Corallivores	0.19	0.68
Piscivores	0.08	0.12

The relative abundance of piscivores is more than 10-fold higher on the coral reefs in Sri Lanka, New Caledonia, the Great Barrier Reef and the Gulf of Mexico than on the Jordanian coast. These differences could be due to various factors such as prey availability, shelter and fishing, but could also be due to

Table 7. Relative abundance (%) of feeding guilds of fishes on coral reefs

Feeding guild	Aqaba[a]	Sri Lanka[b]	Great Barrier Reef[c]	New Caledonia[d]	Gulf of Mexico[e]
Corallivores	0.8	1.3			
Herbivores	3.4	12.0	6.6	14.3	11.7–23.0
Planktivores	58.1	81.0	85.0	65.0	65.0
Omnivores	11.6	1.5			
Piscivores	0.1	2.5	3.6	1.0	1.3–2.8

[a]This study; [b]calculated from Öhman et al. (1997); [c]Williams & Hatcher (1983); [d]Rossier & Kulbicki (2000); [e]Pattengill et al. (1997)

Table 8. Trophic composition (%) of fish assemblages on coral reefs. *: sessile invertebrate browsers. No. of scleractinian coral species is also shown

Feeding guild	Aqaba[a]	Eilat[b]	Sanganeb atoll[c]	Sri Lanka[d]	Great Barrier Reef[e]	Tulear[f]	Moorea[f]	Moorea[g]	Reunion[g]	New Caledonia[g]	Gulf of Mexico[h]
Corallivores	3.5	3.5	7.4	8.1	4.6	6.2*	8.9*	11.0	7.0	8.0	
Herbivores	8.6	10.6	7.4	20.7	14.9	10.1	15.4	3.0	2.5	4.0	15.0
Planktivores	20.8	18.3	24.6	13.3	19.8	10.3	9.6	10.0	8.0	13.0	13.1
Detritivores	1.0	0.7	0.0	3.0				2.5	3.0	3.0	
Invertebrate- and fish-feeders	14.1	10.6	10.7	8.9	52.6	53.8	45.0	40.5	46.0	38.5	18.3
Invertebrate-feeder	25.3	22.5	22.1	20.7							
Piscivores	4.0	5.6	5.7	14.1	8.1	4.0	5.7	7.0	12.5	10.0	28.8
Omnivores	19.2	19.7	18.0	11.1		15.6	15.4	26.0	21.0	23.5	
Unknown	3.5	8.5	4.1								24.8
Scleractinian coral species (n)	138[i]		146[i]	118[j]	212[k]		72[l]		120[m]	108[n]	

[a]This study; [b]Rilov & Benayahu (2000); [c]Krupp et al. (1993); [d]Öhman et al. (1997); [e]Williams & Hatcher (1983); [f]Harmelin-Vivien (1989); [g]Letourneur et al. (1997); [h]Pattengill et al. (1997); [i]Antonius et al. (1990); [j]Rajasuriya et al. (1998); [k]Done (1982), [l]Adjeroud (1997); [m]Bouchon (1981); [n]UNEP/IUCN (1988)

methodological differences. Öhman et al. (1997) restricted their fish counts to 135 species, and Williams & Hatcher (1983) used explosive charges for sampling.

Besides relative abundance, the trophic species composition also reflects the trophic structure of the community (Table 8). Invertebrate feeders are the dominant feeding guild on coral reefs in terms of species richness (Jones et al. 1991), followed by planktivores and omnivores. Detrives comprise only a minor proportion of the ichthyofauna on coral reefs. The number of herbivores varies considerably within the fish communities of different geographical regions, and seems to be much lower around the oceanic islands of Moorea and Réunion and in New Caledonia.

The proportion of species belonging to particular feeding guilds is very similar between the 3 sites in the Red Sea (Aqaba, Eilat, Sanganeb atoll: Table 8), but differs somewhat from sites in the Indian and Pacific Oceans and the Gulf of Mexico (Table 8). The contribution of planktivorous species to fish assemblages in the Red Sea seems to be high in comparison to other coral reefs in the world, whereas piscivores play only a minor role. At the northern tip of the Gulf of Aqaba, the percentage of corallivorous species is only about half that in the central Red Sea and reefs in other parts of the Indo-Pacific. This might be due to lower scleractinian species richness in the Gulf compared to the central Red Sea (Antonius et al. 1990). However, no general correlation between the number of scleractinian corals and percentage of corallivorous species of a fish assamblage could be detected in the present study (Table 8).

Comparing the trophic structure of the ichthyofauna at the Jordanian coast with that of other coral reefs, we can conclude that: (1) the high relative abundance of planktivores is a general feature of the community structure of fishes on coral reefs; (2) most species on coral reefs are invertebrate feeders; (3) the relative abundance of feeding guilds other than planktivores seems to be strongly influenced by the benthic habitat; (4) the trophic species structure of fish communities on Red Sea coral reefs seems to be different from that on reefs in other parts of the Indo-Pacific Ocean.

Comparison between coral reefs and seagrass-dominated site

The reduced abundance of corallivores in the seagrass-dominated site at Al-Mamlah Bay is not surprising, since these fishes are strongly associated with live stony corals (Bouchon-Navaro et al. 1985, Jennings et al. 1996, Öhman & Rajasuriya 1998, Khalaf & Kochzius 2002). Despite the low coral cover and reduced shelter in Al-Mamlah Bay, the abundance of planktivorous fishes at 12 m depth is much higher than at all other study sites. In addition, the rich crustacean fauna of the seagrass meadows can support more invertebrate-feeders than coral reefs. Nocturnal feeding migrations of invertebrate-feeders from coral reefs into seagrasses are documented for the Atlantic as well as the Indo-Pacific (Weinstein & Heck 1979, Bell & Pollard 1989, Kochzius 1999). The higher prey availability at the seagrass-dominated Al-Mamlah correlates with a higher abundance of piscivores in the bay than at the coral reef sites.

Human impact

Univariate measures such as species richness, diversity and evenness were not able to demonstrate a negative impact of the industrial complex on the coral reef ichthyofauna. This situation is not uncommon, and has been reported in studies on the effect of coral mining (Shepherd et al. 1992) and coral bleaching (Lindahl et al. 2001). Investigations into the impact of dredging revealed a significant reduction in species richness on some reefs in French Polynesia, whereas other sites showed no difference from undredged areas (Harmelin-Vivien 1992). However, experimental coral disturbance led to a significant decline in fish species richness on the Great Barrier Reef (Lewis 1997). The higher diversity and evenness at the disturbed sites in the present study could be explained by the intermediate disturbance hypothesis (Connell 1978), i.e. an initial increase in diversity with increasing disturbance followed by a decrease at high levels of disturbance.

The abundance of fishes on disturbed reefs was half that on undisturbed reefs. In other geographical areas, significant declines in fish abundance have been caused by coral mining (Shepherd et al. 1992: the Maldives), turbidity and sedimentation due to dredging (Amesbury 1981: eastern Caroline islands), eutrophication (Chabanet et al. 1995: Indian Ocean) and experimental coral disturbance (Lewis 1997: Great Barrier Reef). However, disturbance by dredging in Moorea and Tahiti led to a decrease in fish abundance at some sites, whereas other reefs showed no significant difference (Harmelin-Vivien 1992). Mass mortality of bleached corals in Tanzania even triggered an increase in fish abundance, due to algal growth which supported a higher standing stock of herbivores (Lindahl et al. 2001).

Analysis of the trophic structure is very important when examining changes in the fish community due to human-induced disturbance. In our study, a higher abundance of detritivores was found on disturbed coral reefs, whereas the number of invertebrate- and fish-feeders was higher on undisturbed reefs. The reduction in invertebrate- and fish-feeders at disturbed sites can be explained by the loss of habitat structure due to degradation. The associated prey fauna of this feeding guild is reduced, and the disturbed reef cannot support a high number of invertebrate- and fish-feeders.

Herbivores were more abundant on the shallow slope of disturbed than undisturbed reefs, indicating a higher biomass of macroalgae on the slope. An increase in abundance of herbivorous fishes was reported after an increase in soft algae on Caribbean coral reefs, due to mass mortality of competing sea urchins (Robertson 1991). An increase in the abundance of some certain herbivorous fish species on degraded coral reefs has been described for bleached reefs by Lindahl et al. (2001) and after experimental coral disturbance by Lewis (1998). In contrast, no change in the abundance and biomass of some herbivores was detected on reefs impacted by the crown-of-thorns starfish *Acanthaster planci* with subsequent algal overgrowth (Hart et al. 1996).

There was a shift in the trophic composition of the ichthyofauna forwards planktivores on the shallow slope of disturbed reefs in our study. This could be due to the independence of planktivores from the benthic substrate in terms of food availability. Onshore transport of zooplankton depends on the oceanographic conditions and not on the condition of the reef. As long as enough shelter is available, these species can survive on a degraded coral reef (Lindahl et al. 2001). On the deep slope of the disturbed reefs in the present study, omnivores increased in relative abundance. This guild of fishes consisted of non-specialised feeders more able to cope with changes in the benthic habitat than invertebrate- and fish-feeders.

Apart from trophic considerations, recruitment to the degraded reef could also be reduced, through decreased settlement due to habitat loss or through higher mortality due to loss of shelter space (Shulman 1985, Schmitt & Holbrook 1999).

In summary, the following changes in the fish community were recorded on the coral reef fronting the industrial complex: (1) 50 % reduction in fish abundance; (2) increased total abundance of herbivorous and detritivorous fishes; (3) decreased total abundance of invertebrate- and fish-feeders; (4) resultant changes in the trophic composition, such as increased relative abundance of planktivores.

These changes are probably the synergetic effects of coastal constructions, sedimentation, nutrient input, algal growth, coral destruction and heavy metal load. In the course of future urbanisation and industrialisation of the Jordanian Red Sea coast, increased coastal pollution is expected. Because of the short (27 km long) coastline, future industrial development should be restricted to already industrialised areas, in order to preserve the remaining coral reefs and seagrass meadows. Marine reserves such as the Red Sea Marine Peace Park and regional co-operation between countries bordering the Gulf of Aqaba are important for the protection of coastal ecosystems.

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