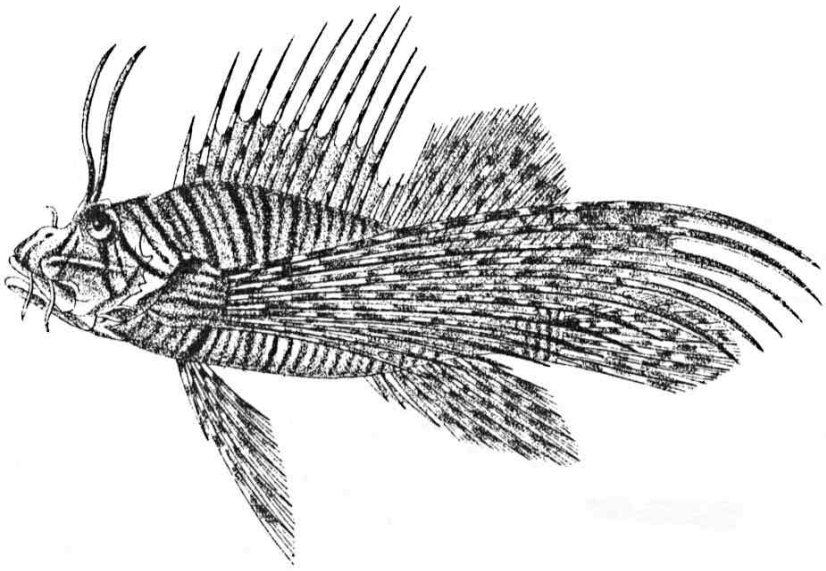
Zentrum für Marine Tropenökologie - Centre for Tropical Marine Ecology

Ecology, genetic population structure, and molecular phylogeny of fishes on coral reefs in the Gulf of Aqaba and northern Red Sea

Marc Kochzius



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to Uli and our child

Drawing on cover: the lionfish *Pterois miles*, taken from Klunzinger CB (1884) Die Fische des Rothen Meeres. 1. Theil. Schweizbart'sche Verlaghandlung, Stuttgart

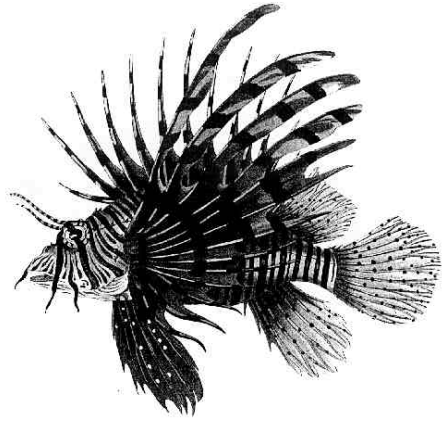
Drawing on next page: the lionfish *Pterois volitans* (*miles*?)*, taken from Bennett JWB (1830) Selection from the most remarkable and interesting fishes found on the coast of Ceylon. Longman, Rees, Orme, Brown, and Green, London [*see chapter 5]

…more than 150 years of fascination…

"As humming-birds sport around the plants of the tropics, so also small fishes, scarcely an inch in length and never growing larger, but resplendent with gold, silver, purple and azure, sport around the flower-like corals."
Christian Ehrenberg 1832

"In splender of colour and diversity of forms the fishes of the coral region do not yield to the most brilliant birds."
Carl B. Klunzinger 1878

"I am gliding like a bird. The world around me is blue and limitless. Far below me are bizarre, beautifully decorated towers. Colourful birds – or perhaps fishes – circle about these mysterious buildings."
Hans Hass 1987



"Some of the most delightful hours of my scientific career have been spent studying reef fishes. To a biologist, scuba diving over a coral reef is roughly like being able to fly through a tropical rain forest."
Paul R. Ehrlich 1991

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ABSTRACT

Tropical coral reefs, such as the reefs in the Red Sea, harbour the most diverse fish communities on earth. The Gulf of Aqaba is part of the tropical Indo-West Pacific that extends longitudinally more than half around the world from the Red Sea to Polynesia. The centre of diversity is Southeast Asia, but the Red Sea is regarded as a secondary centre of diversity. To date more than 1,280 fish species are known from the Red Sea and many are endemic.

Aim of this thesis is the study of (1) biogeography and ecology, (2) genetic population structure, and (3) molecular phylogeny of fishes on coral reefs in the Gulf of Aqaba and northern Red Sea. Ecological and genetic pattern are compared on different spatial scales: Gulf of Aqaba, Red Sea, Indian Ocean, and finally Indo-West Pacific. Molecular markers add a temporal scale and facilitate the study of evolutionary processes.

Biogeographic analysis supported the differentiation of the Arabian sub-province from the Indian Ocean, but the affiliation of the Arabian Gulf is not clear. The difference between Red Sea and Indian Ocean is also suggested by some differences in the trophic community structure, which might be induced by unfavourable environmental conditions during the last glacial maximum. Due to the lowered sea level by 120 m, water exchange between the Red Sea and Indian Ocean was limited. Salinity of the Red Sea increased and temperature decreased. This severe ecological conditions lead to partial extinction of ichthyofauna in the Red Sea. After the glacial maximum the environmental conditions improved. However, it seems that the relatively short period of a few thousand years since then was not sufficient for the Red Sea ichthyofauna to reach the same trophic community structure than its counterpart in the Indian Ocean. However, high genetic diversity of the lionfish *Pterois miles* in the northern Red Sea suggest that this species survived the last glacial maximum with a stable population.

The analysis of the genetic population structure based on the mitochondrial control region revealed homogenity between populations of *P. miles* in the Gulf of Aqaba and northern Red Sea. Consideration of high genetic diversity, paleoceanography of the Red Sea, and life history of *P. miles* indicate high gene flow and panmixia.

Investigations on interrupted gene flow in the evolutionary history of lionfishes (Scorpaenidae, Pteroinae) revealed a differentiation between the Indian Ocean and Western Pacific. Phylogenetic analysis of mitochondrial DNA sequences of the

siblings *P. miles* and *P. volitans* and molecular clock estimates suggest a divergence time of 2.4-8.3 million years. This coincide with tectonic events and sea level changes in Southeast Asia during the glacial maxima that partly separated populations of the Indian Ocean and Western Pacific. Additionally, this genetic study suggested that morphological definition is unprecise for the genera *Pterois* and *Dendrochirus*, and gave indications for taxonomic revision.

Ecological studies on the shore fishes off the Jordanian coast showed that fish species richness was positively correlated with hard substrate cover and benthic diversity. Especially abundance of corallivores was positively linked to live coral cover. The multivariate analysis of the fish community has revealed several associations of fishes in different habitats, such as deep and shallow reef slope.

The northern tip of the Gulf of Aqaba and its western shores are particularly subject to human disturbances by urban and industrial pollution, shipping and port activities, as well as tourism. The studies on ecology and gene flow gave some implications for marine conservation in the Gulf of Aqaba and off the Jordanian coast in particular. Fish abundance at an industrial site was 50% lower than on an undisturbed reef and the trophic community structure was different. Structural complexity of the coral reef habitat supports high species diversity due to shelter holes and prey availability. Seagrass meadows are important for many fishes on coral reefs as a feeding ground. High levels of gene flow in *P. miles* implicate re-colonisation of restored habitats and replenishment of depleted stocks from the Red Sea proper. However, it is not clear how fast depleted populations will be replenished or restored habitats will be re-colonised. Therefore, coastal zone management in the Gulf of Aqaba has to follow the precautionary principle and should not rely upon fast replenishment or re-colonisation.

ZUSAMMENFASSUNG

Tropische Korallenriffe, wie die des Roten Meeres, beherbergen Fischgemeinschaften mit der höchsten Artenvielfalt. Der Golf von Aqaba ist Teil des tropischen Indo-West-Pazifik, der sich vom Roten Meer bis Polynesien über mehr als die Hälfte des Globus erstreckt. Das Zentrum der marinen Artenvielfalt liegt in Südostasien, aber das Rote Meer wird als sekundäres Zentrum der Artenvielfalt gesehen. Im Moment sind mehr als 1.280 Fischarten aus dem Roten Meer bekannt, von denen viel endemisch sind.

Ziel dieser Doktorarbeit ist die Untersuchung von (1) Biogeographie und Ökologie, (2) genetischer Populationsstruktur und (3) molekularer Phylogenie von Fischen der Korallenriffe des Golfes von Aqaba und nördlichen Roten Meeres. Ökologische und genetische Muster werden auf unterschiedlichen räumlichen Skalen betrachtet: Golf von Aqaba, Rotes Meer, Indischer Ozean, und letztendlich Indo-West-Pazifik. Molekulare Marker fügen eine zeitliche Skala hinzu und ermöglichen die Untersuchung von evolutiven Prozessen.

Die biogeographische Analyse unterstützt die Abtrennung der arabischen Unterprovinz vom Indischen Ozean, aber die Zugehörigkeit des Persischen Golfes kann nicht abschließend geklärt werden. Der Unterschied zwischen dem Roten Meer und dem Indischen Ozean wird auch durch Differenzierung in der trophischen Fischgemeinschaftsstruktur nahegelegt. Dieses könnten durch ungünstige Umweltbedingungen während des Höhepunktes der letzten Eiszeit bedingt sein. Durch die Absenkung des Meeresspiegels um 120 m war der Wasseraustausch zwischen dem Roten Meer und dem Indischen Ozean stark eingeschränkt, was zu einem Anstieg des Salzgehaltes im Roten Meer führte. Aufgrund klimatischer Veränderungen sank zudem die Wassertemperatur. Diese schwierigen ökologischen Bedingungen führten zu einem teilweisen Aussterben der Fischfauna. Nach dem Ende der Eiszeit verbesserten sich die Umweltbedingungen wieder, doch es scheint, daß die seitdem vergangene Zeitspanne von einigen tausend Jahren nicht ausgereicht hat, die gleiche trophische Fischgemeinschaftsstruktur wie im Indischen Ozean zu erreichen. Die hohe genetische Diversität des Rotfeuerfisches *Pterois miles* läßt hingegen vermuten, daß diese Art die letzte Eiszeit im Roten Meer als stabile Population überdauert hat.

Die Analyse der genetischen Populationsstruktur basiert auf der mitochondrialen Kontrollregion und zeigt eine Homogenität der Populationen von *P. miles* im Golf

von Aqaba und nördlichen Roten Meer. Unter Berücksichtigung der hohen genetischen Diversität, der Paläoozeanograpie des Roten Meeres und des Lebenszykluses von *P. miles* kann man auf einen hohen Genfluß und eine einzige große Population schließen.

Die Studie über unterbrochenen Genfluß in der evolutiven Vergangenheit der Rotfeuerfische (Scorpaenidae, Pteroinae) zeigte eine Differenzierung zwischen dem Indischen Ozean und westlichen Pazifik. Die phylogenetische Analyse von mitochondrialen DNS Sequenzen der Schwesterarten *P. miles* und *P. volitans*, sowie zeitliche Abschätzungen mit Hilfe der molekularen Uhr, legen eine Auftrennung vor 2,4 bis 8,3 Millionen Jahren nahe. Dieses stimmt mit tektonischen Ereignissen in Südostasien und Meeresspiegelschwankungen während der Eiszeiten überein, die zu einer teilweisen Trennung von Populationen im Indischen Ozean und westlichen Pazifik führten. Außerdem weist diese phylogenetische Studie darauf hin, daß die morphologische Beschreibung der Gattungen *Pterois* und *Dendrochirus* ungenau ist und eine taxonomische Überarbeitung durchgeführt werden müßte.

Die ökologischen Untersuchungen von Küstenfischen entlang der Jordanischen Küste zeigte, daß die Artenzahl positiv mit der Hartsubstratbedeckung und bentischen Diversität korreliert. Besonders die Abundanz von korallenfressenden Fischen war auf positive Weise von der Bedeckung mit lebenden Korallen abhängig. Die multivariate Analyse der Fischgemeinschaften konnte verschiedene Fischgruppen aufzeigen, die mit unterschiedlichen Habitaten assoziert waren, wie z.B. oberer und unterer Riffhang.

Besonders der nördliche Teil des Golfes von Aqaba und seine westliche Küste sind vielfältigen anthropogenen Einflüssen ausgesetzt, zu denen städtische und industrielle Verschmutzung, Schiffsverkehr und Häfen sowie Tourismus zählen. Die Untersuchungen zur Ökologie und Genfluß können wichtige Informationen für den marinen Umweltschutz im Golf von Aqaba zur Verfügung stellen. Die Untersuchungen haben gezeigt, daß die Abundanz von Fischen in der unmittelbaren Nähe eines Industriekomplexes 50% niedriger war als in einem nicht unmittelbar beinflußten Korallenriff. Es zeigte sich auch, daß die trophische Fischgemeinschafts-struktur große Unterschiede aufwies. Die strukturelle Komplexität eines Korallenriffes ermöglicht eine hohe Artenzahl von Fischen, da diese Versteck und Nahrung finden. Seegraswiesen sind zudem ein wichtiger Nahrungsgrund für viele Fische der Korallenriffe. Der hohe Genfluß zwischen Populationen von *P. miles*

impliziert, daß eine Besiedlung von wiederhergestellten Habitaten und eine Erholung von ausgebeuteten Beständen möglich ist. Leider ist es aber nicht möglich Aussagen darüber zu treffen, wie schnell diese Prozesse ablaufen. Deshalb sollte man sich bei einem Küstenmanagement im Golf von Aqaba nicht auf eine schnelle Wiederbesiedlung verlassen, sondern nach dem Vorsorge-Prinzip handeln.

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I would like to thank my doctoral thesis supervisor Prof. Hempel (former director of the Centre for Tropical Marine Ecology, ZMT) for the chance to study the colourful fishes on coral reefs. Since my MSc on tropical shore fishes in the Philippines I am crazy on these beautiful animals and work in the Red Sea made a dream come true. I learned a lot from his straightforward and constructive comments on my manuscripts. He gave me a lot of scientific freedom and backed me up when necessary.

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My time in the Middle East gave me the great opportunity to get to know friendly people of all nations that have to share this beautiful region: Jordanians, Palestinians, Egyptians, and Israelis. What did John Lennon say? “Give peace a chance!”
Ariel Chaouat (Interuniversity Institute, Eilat) helped me a lot during my time in Israel and gave me the chance to celebrate Jewish New Year with his family. Thank you very much for this beautiful experience.

Last but not least many thanks to my family: My parents Irene and Ulrich Kochzius have always encouraged me to learn throughout the last 25 years of school and university. I thank them for their “investment” in my education.
Finally I would like to thank Uli for her support during all the years of work for the present thesis. Especially her tolerance of my absence during field work at the Red Sea and her faith made this work possible. Sometimes it might have been not so easy for her to live with someone that has only fishes in his mind and took over some “Middle Eastern” attitudes. Thank you so much for your patience and love.

Ecology, genetic population structure, and molecular phylogeny of fishes on coral reefs in the Gulf of Aqaba and northern Red Sea

Marc Kochzius

Centre for Tropical Marine Ecology, Bremen, Germany

Review of PhD Thesis

1. Introduction

Tropical coral reefs harbour the most diverse fish communities on earth (Harmelin-Vivien 1989). The coral reefs of the Red Sea are the closest to Europe and therefore research on the ichthyofauna started already more than 200 years ago by the collections and descriptions of Peter Forsskål.

The Gulf of Aqaba is part of the tropical Indo-West Pacific that extends longitudinally more than half around the world from the Red Sea to Polynesia (Fig. 1). The shelf waters of the Indo-West Pacific cover a huge area of approximately 6.6 million km^2 and show an incredible diversity of biota with more than 4,000 species of fishes, 6,000 species of molluscs, 800 species of echinoderms, and 500 species of hermatypic corals. The Southeast Asian triangle between the Philippines, Indonesia and New Guinea hosts the world's greatest diversity of marine species (Briggs 1995). Besides the Southeast Asian triangle of outstanding biodiversity, the Red Sea is considered as an important centre of evolution (Marshall 1952, Botros 1971, Klausewitz 1989, Roberts et al. 2002). To date more than 1,280 fish species are known from the Red Sea (Baranes and Golani 1993, Goren and Dor 1994, Randall 1994, Khalaf et al.

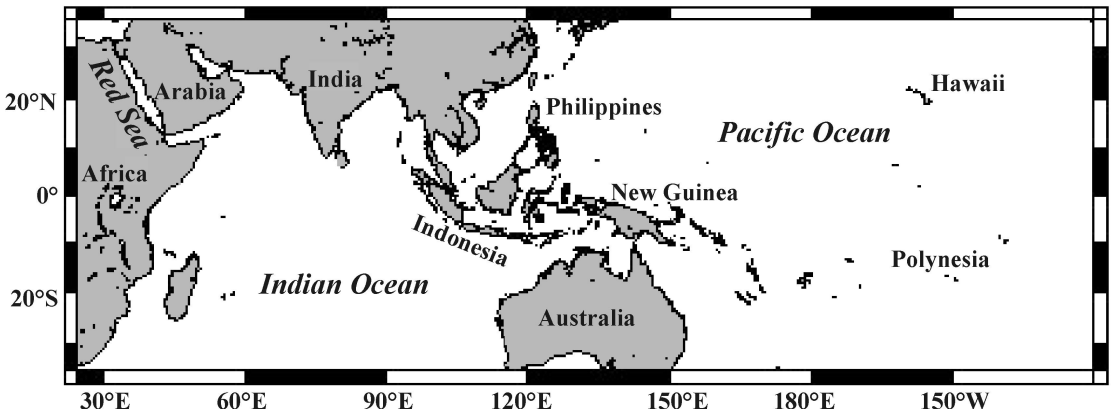

Fig. 1 Map of the tropical Indo-West Pacific

1996). The ichthyofauna of the Red Sea has a high rate of endemism (13.7%) and a high species diversity of corals. Therefore, this ocean basin is regarded as a secondary centre of diversity (Goren and Dor 1994, Veron 2000).

Biodiversity in the Red Sea can be observed on different spatial scales: (1) differences between Red Sea and Indian Ocean, (2) north-south differences within the Red Sea, (3) differences between the Gulf of Aqaba and northern Red Sea, and possibly within the Gulf (Fig. 2).

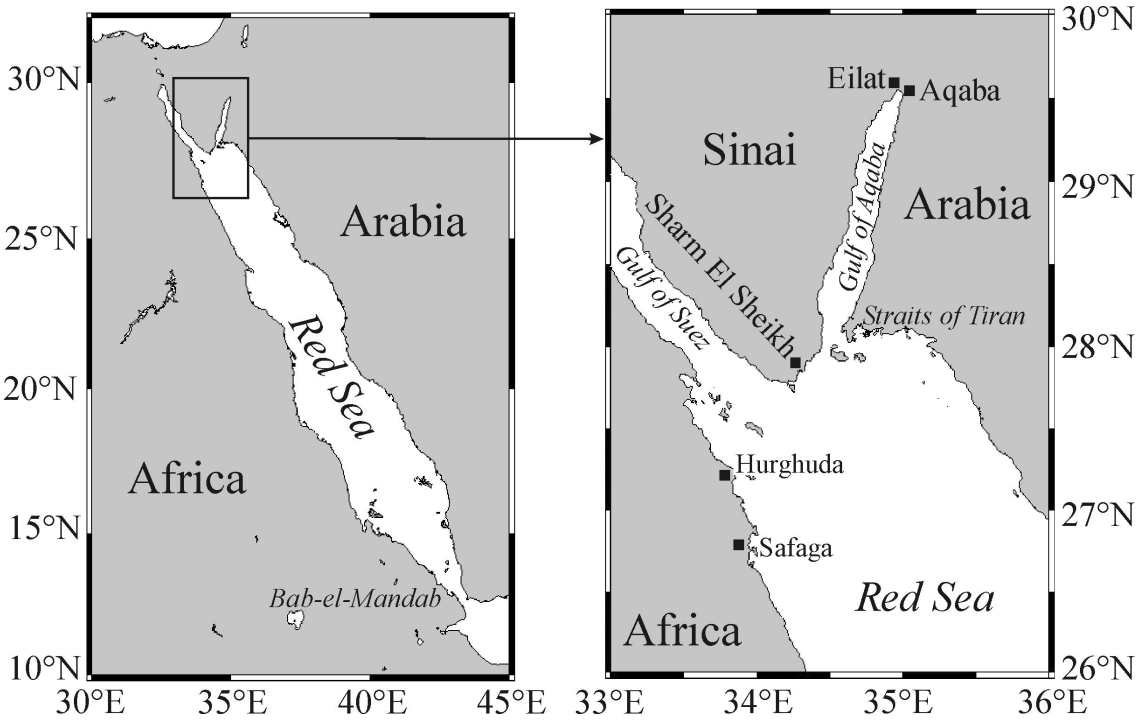

Fig. 2 Map of the Red Sea and Gulf of Aqaba

1.1 Relationship between Red Sea and Indian Ocean ichthyofauna

The Red Sea is the product of sea-floor spreading between the African and Arabian plate, and therefore regarded as an ocean by the geologist (Braithwaite 1987). It is 1932 km long, on average 280 km wide and over 2,500 m deep. The shallow sill of Bab-el-Mandab, which is 26 km wide and 130 m deep, separates the Red Sea from the Indian Ocean (Morcos 1970) (Fig. 2). There is a north-south gradient in sea surface temperature with higher values in the south. Annual minimum/maximum temperatures are 17.5°C/26°C for the north, and 27°C/32°C for the south. Salinity shows a north-south gradient as well, with an annual mean of 40.5‰ in the north and 36.5‰ in the

south. It is remarkable that the Red Sea has a constant temperature of about 21.5°C and constant salinity of 40.5‰ below a depth of 250-300 m (with the exception of the hot brine pools in the deep sea) (Edwards 1987).

Biogeographic studies on butterflyfishes (Chaetodontidae) and angelfishes (Pomacanthidae) revealed differences between the Red Sea and Indian Ocean. These faunal differences justified the establishment of the Arabian sub-province, that includes the Red Sea, Gulf of Aden, Southern Arabia, and the Arabian Gulf (Klausewitz 1978, Kemp 1998). This biogeographic pattern was verified by the analysis of scleractinian corals (Sheppard and Sheppard 1991).

1.2 North-south differences within the Red Sea

Within the Red Sea, differences in the structure of fish communities on northern and southern Red Sea coral reefs are shown for several families, such as Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), Pomacentridae (damselfishes), Acanthuridae (surgeonfishes), Scaridae (parrotfishes), Labridae (wrasses), Lethrinidae (emperors), and Lutjanidae (snappers) (Sheppard et al. 1992). Some species, such as the damselfishes *Chromis dimidiata* (Plate 5) and *Neopomacentrus miryae* (Plate 6), or the wrasse *Paracheilinus octotaenia* (Plate 7) are abundant in the northern Red Sea, but virtually absent in the southern part (Ormond and Edwards 1987, Sheppard et al. 1992).

Scleractinian corals show distinct changes in species richness from north to south as well, with a higher number of species in the central Red Sea (Roberts et al. 1992), and north-south differences in the community structure (Sheppard and Sheppard 1991).

These differences in the community structure of fishes and corals within the Red Sea might be due to north-south differences in habitat as well as an abrupt increase in turbidity south of 20°N (Sheppard et al. 1992, Roberts et al. 1992).

1.3 Differences between the Gulf of Aqaba and northern Red Sea

Faunal differences can also be detected between the Gulf of Aqaba and Red Sea proper (Fig. 2). The fjord-like Gulf of Aqaba is a deep, narrow northern extension of the Red Sea. It has a length of 180 km and is 6-25 km wide. The depth can reach over 1,800 m, but averages 800 m. The Gulf of Aqaba is separated from the Red Sea by a shallow sill of 242-270 m depth at the Straits of Tiran. Desert and mountains, with a hot

and dry climate flank the semi-enclosed basin. A high evaporation rate results in a high salinity of 41‰ and a thermohaline circulation that drives water exchange with the Red Sea proper (Reiss and Hottinger 1984). Calculations of the residence time of the upper 300 m vary from four month to one or two years. The inflow of Red Sea water reaching the northern tip of the gulf is estimated to 1% of that at the Straits of Tiran (Wolf-Vecht et al. 1992 and references therein).

The vertical distribution of some fishes on coral reefs in the Gulf of Aqaba differs from the Red Sea proper. Several species commonly occur shallowly in the Gulf of Aqaba, e.g. *Chaetodon paucifasciatus* (butterflyfishes; Plate 4), *Apolemichthys xanthotis* (angelfishes; Plate 4), *Genicanthus caudovittatus* (anglefishes; Plate 4), *Chromis pembae* (damselfishes; Plate 5), *Pseudochromis fridmani* (dottybacks), and *Canthigaster coronata* (tobies; Plate 8). This pattern might be due to lower surface temperatures in the Gulf of Aqaba (Edwards and Rosewell 1981, Ormond and Edwards 1987, Sheppard et al. 1992). However, this hypothesis remains conjectural and other explanations such as niche expansion in the absence of certain competitor species are possible (Sheppard et al 1992).

In addition to the difference in vertical zonation, the Gulf of Aqba harbours two endemic shore fish species: *Pseudochromis pesi* and *Chromis pelloura* (Plate 5) (Randall 1983, Sheppard et al 1992). The deep-sea fishes show such distinct differences, that Klausewitz (1989) suggests a “isolated development of the secondary deep-sea ichthyofauna in the Gulf of Aqaba”. Therefore, some authors consider the Gulf of Aqaba as a distinctive zoogeographic region within the Red Sea (Klausewitz 1964, Klausewitz 1989, Sheppard et al. 1992).

2. Objectives and studies

These special biogeographic and oceanographic settings in the Gulf of Aqaba and Red Sea are very interesting for comparative studies as described below on (1) biogeography and ecology, (2) genetic population structure, and (3) molecular phylogeny of fishes on coral reefs. The nested hierarchy of the biogeographic and oceanographic compartments Gulf of Aqaba, Red Sea, Indian Ocean, and finally Indo-West Pacific allows to compare differentiation in ecological and genetic pattern on

different spatial scales. As described later, molecular markers add a temporal scale and facilitate the study of evolutionary processes.

In addition, the studies on the ecology and genetic population structure can provide important baseline data for marine conservation of coral reef fishes in the Gulf of Aqaba.

Such an approach of an ecological and evolutionary study on fishes of the Red Sea is only possible by close co-operation with taxonomists and molecular biologists. Field work at the Red Sea, especially in Jordan, was conducted in close contact with the ichthyologist Dr. M.A. Khalaf (Marine Science Station, Aqaba, Jordan). I collected tissue samples and specimens of the lionfish *Pterois miles* (Plate 1) and other scorpionfishes for genetic studies during three field trips in 1998, 1999, and 2000. The basis was the Marine Science Station in Aqaba (Jordan), but field work was also conducted in Israel (Interuniversity Institute, Eilat) and Egypt (Sinai, Hurghada, Safaga).

Molecular genetic analysis was carried out in co-operation with Prof. Blohm and Dr. Söller (Department for Biotechnology and Molecular Genetics, University of Bremen, Germany). Complete processing of the samples (DNA extraction, PCR, sequencing, and data analysis) was conducted by myself in the laboratory of the Department for Biotechnology and Molecular Genetics, University of Bremen.

This co-operation generated four joint German-Jordanian papers on ecological and evolutionary aspects of fishes on Red Sea coral reefs.

2.1 Biogeography and ecology (Chapters 1-3)

The biogeographic and ecological researches focus on shore fish communities off the Jordanian coast at the northern tip of the Gulf of Aqaba (Fig. 2 and map in chapter 1). Aim of these investigations is the study of (1) biodiversity, (2) community structure and habitat preferences, as well as (3) trophic community structure of shore fishes. Due to the described oceanographic and biogeographic pattern it is expected that shore fishes in the Gulf of Aqaba exhibit differences compared to other parts of the Indo-West Pacific.

Biodiversity (Chapter 1 and 2)

This part of the research investigates (1) the number of shore fish species, (2) the taxonomic composition of the shore fish communities, and (3) the biogeography of shore fish assemblages in the Arabian sub-province and Indian Ocean province.

Community structure and habitat preferences (Chapter 1)

These ecological investigations are conducted (1) to reveal the influence of environmental factors, such as benthic habitat and depth, and (2) to determine fish assemblages associated to certain habitats. Such ecological information can give indications for marine conservation measures in the Gulf of Aqaba.

Trophic community structure (Chapter 3)

The study of the trophic community structure includes two aspects: (1) changes in trophic community structure can indicate environmental stress including the effects of fishing, and (2) comparison to other regions of the Indo-West Pacific can provide implications on evolutionary aspects of the ichthyofauna in the Red Sea.

2.2 Genetic population structure and molecular phylogeny (Chapters 4 and 5)

Mitochondrial DNA (mtDNA) sequences can be used to study gene flow on different time scales. Genetic population structure and recent gene flow are microevolutionary processes, whereas speciation reflected in molecular phylogenies is a macroevolutionary process and result of interrupted gene flow in the past. "*Thus, the branches in macroevolutionary trees have a substructure that consists of smaller branches and twigs, ultimately resolved as generation-to-generation pedigrees. It is through these pedigrees that genes have been transmitted, tracing the stream of heredity that is phylogeny"* (Avise et al. 1987; Fig 3).

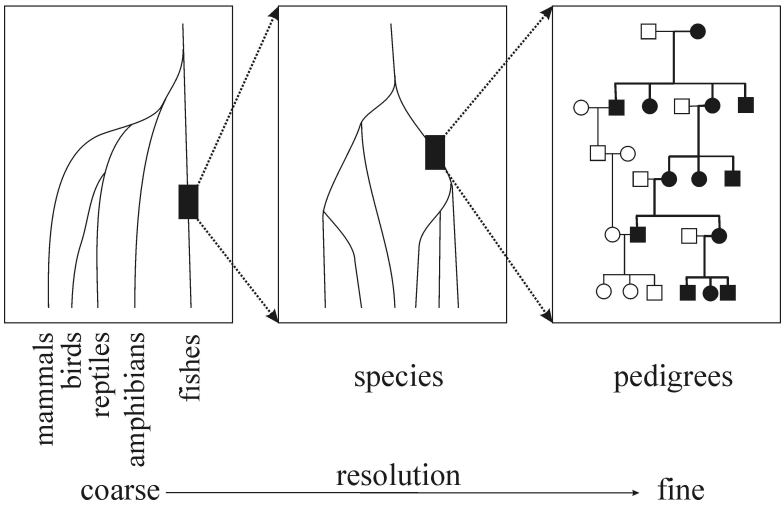

Fig. 3 Macroevolutionary trees (e.g. the one on the left representing the relationships among some invertebrate classes) have a substructure of smaller branches that are ultimately resolvable as family pedigrees. Darkened branches in the pedigree indicate the transmission path of the maternal inherited mtDNA (after Avise et al. 1987)

The mitochondrial genome in higher Metazoa is a circular (linear in *Paramecium* and *Hydra*), double-stranded DNA molecule contained in multiple copies in mitochondria. The typical size of the mitochondrial genome in animals is 16,500 ± 500 basepairs (bp) and up to several thousand identical mitochondrial genomes are found per cell. The animal mtDNA is haploid (Moritz et al. 1987, Meyer 1993), generally considered as non-recombining (but see Eyre-Walker et al. 1999, Hagelberg et al. 1999) and the signal from genetic drift is therefore stronger than for nuclear loci (Waples 1998). The mitochondrial genome of fishes follows the vertebrate gene order and contains 13 protein genes which code for subunits of enzymes (ATP synthesis or electron transport), 2 ribosomal RNA (rDNA) genes, and 22 transfer RNA (tRNA) genes (Fig. 4).

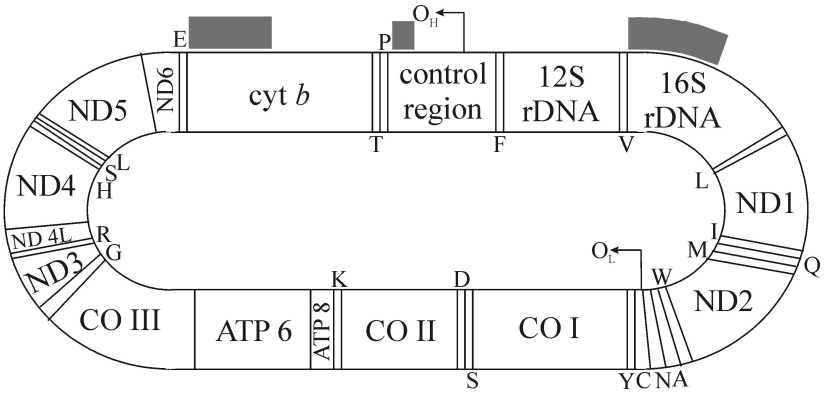

Fig. 4 Mitochondrial functional map of fish; O_H=origin of H-strand replication; O_L=origin of L-strand replication; The majority of tRNA-genes and coding sequences for all proteins are on the H-strand (except ND6); tRNA genes coded for by H-strand are labelled inside the circle, tRNA genes coded for by L-strand ouside; grey bars indicate regions sequenced in this study (after Meyer 1993, Thomas and Beckenbach 1989)

Mitochondrial genes show different rates of evolution, which determine their applicability as molecular markers. On the one hand, slow evolving protein coding sequences, such as cytochrome *b* (cyt *b*) and 16S rDNA, are useful markers for evolutionary relationships between closely related species that diverged within the last few million years (Avise et al. 1987). On the other hand, the rate of evolution of the control region is 2-5 times higher than in the protein coding genes in fishes (Meyer 1993), and therefore a suitable marker for investigations on the genetic structure of populations (Avise et al. 1987, Moritz 1994, Parker et al. 1998, Féral 2002).

Genetic population structure (Chapter 4)

The study on the genetic population structure focuses on the lionfish *Pterois miles* (Plate 1) in the northern Red Sea and Gulf of Aqaba. Due to the described oceanographic settings and faunal differences, restricted gene flow might be possible between the gulf and Red Sea proper. This research investigates (1) gene flow between *P. miles* populations in the Gulf of Aqaba and northern Red Sea, and (2) genetic diversity which can give indications on the population history of a species.

Molecular phylogeny (Chapter 5)

Mitochondrial DNA markers are the bridges between population genetics (recent gene flow) and evolution (past gene flow). Research on the molecular phylogeny of lionfishes (Pteroinae) has a spatial and temporal scale. On the spatial scale, the phylogeographic analysis of the occurrence of the lionfish *P. miles* in the Indian Ocean and Arabian sub-province provides information on its biogeography. On the temporal scale, comparison to its sibling species *P. volitans* (Plate 2) and other members of the subfamily Pteroinae gives indications for evolutionary processes.

3. Abstracts of papers

Chapter 1

Khalaf MA, Kochzius M (2002) ***Community structure of shore fishes in the Gulf of Aqaba, Red Sea****. Helgoland Marine Research 55: 252-284*

Shore fish community structure off the Jordanian Red Sea coast was determined on fringing coral reefs and in a seagrass-dominated bay in 6 m and 12 m depth. A total of 198 fish species belonging to 121 genera and 43 families was recorded. Labridae and Pomacentridae dominated the ichthyofauna in terms of species richness and Pomacentridae were most abundant. Neither diversity nor species richness was correlated to depth. The abundance of fishes was higher at the deep reef slope, due to schooling planktivorous fishes. In 12 m depth abundance of fishes at the seagrass-dominated site was higher than on the coral reefs. Multivariate analysis demonstrated a strong influence on the fish assemblages by depth and benthic habitat. Fish species richness was positively correlated to hard substrate cover and habitat diversity. Abundance of corallivores was positively linked to live hard coral cover. The

assemblages of fishes were different on the shallow reef slope, deep reef slope as well as on seagrass meadows. An analysis of the fish fauna showed that the Gulf of Aqaba harbours a higher species richness than previously reported. The comparison with fish communities on other reefs around the Arabian Peninsula and Indian Ocean supported the recognition of an Arabian subprovince within the Indian Ocean. The affinity of the Arabian Gulf ichthyofauna to the Red Sea is not clear.

Chapter 2

Kochzius M (submitted) ***Threatened fishes of the world: Chromis pelloura Randall and Allen, 1982 (Pomacentridae)****. Environmental Biology of Fishes*

Chromis pelloura is currently not listed in the IUCN 2000 Red List of Threatened Species (http://www.redlist.org), but considered as threatened. It is only known from the coasts off Israel and Jordan in the Gulf of Aqaba, Red Sea. Utilised habitats are deep reef slopes at the Israeli coast from 30 m down to 150 m depth, and above 30 m at the artificial structures of the oil jetty. In Jordanian coastal waters C. pelloura is usually found below 20 m depth, but also present at 6 m to 12 m depth at the seagrass-dominated Al-Mamlah Bay. The species is not commercially fished, but habitat destruction is a severe problem. The northern Gulf of Aqaba is under high pressure by (1) urban and industrial pollution, (2) shipping and port activities, and (3) tourism. The only known areas of occupancy of this species are under high human impact at the Israeli and Jordanian coast. Therefore C. pelloura should be protected in the countries bordering the Gulf of Aqaba. Size of the known populations needs to be investigated and joint conservation plans should be established for the known Israeli and Jordanian populations. In addition, this species might be recorded in the IUCN Red List of Threatened Species as vulnerable (VU D2), because the population is characterised by a restriction in its area of occupancy (< 100 km^2) and in the number of locations (< 5).

Chapter 3

Khalaf MA, Kochzius M (in press) ***Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea****. Marine Ecology Progress Series*

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 an marine reserve and sites without industry or port (undisturbed), as well as in a seagrass-dominated bay. Planktivores were the most abundant feeding guild on coral reefs as well as at 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 of the fish community by reduction of total fish abundance by 50%, increased total abundance of herbivorous and detritivorous fishes, decreased total abundance of invertebrate & fish feeders, as well as increased relative abundance of planktivorous fishes.

Chapter 4

Kochzius M, Söller R, Khalaf MA, Blohm D (manuscript) ***Genetic population structure of the lionfish Pterois miles (Scorpaenidae, Pteroinae) in the Gulf of Aqaba and northern Red Sea****. Prepared for Marine Biology*

Fishes on coral reefs, such as the lionfish Pterois miles, have a life history with two totally different phases: adults are relatively strongly side-attached, whereas larvae of virtually all species are planktonic. Therefore, large-scale dispersal and high gene flow could be expected. However, due to the fjord-like hydrography and topology of the Gulf of Aqaba isolation of populations might be possible. The gulf is a 180 km long and 6-25 km wide northern extension of the Red Sea and separated by a shallow sill. The aim of this study is to reveal genetic population structure, genetic diversity, and gene flow between populations of the lionfish P. miles in the Gulf of Aqaba and northern Red Sea.

The applied molecular marker is a 166 bp sequence of the 5' mitochondrial control region. It is the most variable mitochondrial gene in fishes and a suitable marker to investigate genetic population structure. Among 94 P. miles specimens 32 polymorphic sites were detected, yielding 38 haplotypes. Sequence divergence among haplotypes ranged from 0.6% to 9.9% and genetic diversity was high (h=0.85, π=1.9%). AMOVA indicates no restriction of gene flow between the Gulf of Aqaba and northern Red Sea (Φ_{ct} = 0.05258). Consideration of observed high genetic diversity, paleoceanography of the Red Sea, and life history of P. miles indicate that the revealed genetic population structure reflects high gene flow and panmixia. However, it is not possible to estimate on which time-scale gene flow operate. Therefore, coastal zone management in the Gulf of Aqaba has to follow the precautionary principle and should not rely upon fast replenishment or re-colonisation.

Chapter 5

Kochzius M, Söller R, Khalaf MA, Blohm D (submitted) ***Molecular phylogeny and biogeography of lionfishes (Scorpaenidae, Pteroinae) based on mitochondrial DNA sequences****. Molecular Phylogenetics and Evolution*

This study investigates the molecular phylogeny of 7 lionfishes of the genera Dendrochirus and Pterois, as well as the evolution of the sibling species Pterois miles and P. volitans. Phylogenetic analysis based on 964 bp of partial mitochondrial DNA sequences (cytochrome b and 16S rDNA) revealed two main clades: (1) "Pterois" clade (Pterois miles and P. volitans), and (2) "Pteropterus-Dendrochirus" clade (remainder of the species). Neither Pterois nor Dendrochirus were monophyletic. This result is not congruent to the current taxonomy and questions the recognition of separate genera. However, the molecular phylogeny corresponds with the morphological character of cycloid and ctenoid scales. Therefore we suggest merging the species of the "Pteropterus-Dendrochirus" clade into a single genus. Molecular clock estimates for P. miles and P. volitans suggest a divergence time of 2.4-8.3 my, which coincide with tectonic uplift and sea level changes during the ice ages that separated populations of the Indian and Pacific Ocean. The importance of Pleistocene environmental changes for speciation processes in the Indo-Malayan Archipelago is underlined by these findings.

4. Synoptic discussion

4.1 Biogeography and evolution of fishes on Red Sea coral reefs

Taxonomic and ecological aspects (Chapters 1 and 3)

Biogeographic analysis of ichthyofauna that led to the recognition of the Arabian sub-province was based only on butterflyfishes (Chaetodontidae) and angelfishes (Pomacanthidae) (Klauswitz 1978, 1989, Blum 1989, Kemp 1998). Aim of this study was the evaluation of these findings with a larger data set of 712 species from 14 families (including Chaetodontidae and Pomacanthidae). The results confirm the differentiation of the Arabian sub-province from the Indian Ocean, but in contrast to the studies mentioned above the affiliation of the Arabian Gulf is not clear. Dependent on the analytical tool (Bray-Curtis similarity or Euclidean distance), the Arabian Gulf is either closer related to the Indian Ocean or to the Red Sea.

Comparison of the Red Sea ichthyofauna with several fish assemblages of the Indo-West Pacific showed a general dominance in species richness of wrasses (Labridae) and damselfishes (Pomacentridae).

Trophic analysis suggests also some difference between fish assemblages in the Red Sea and Indo-West Pacific. Relative abundance of herbivores (2-4 times) and piscivores (>10 times) was higher on Indo-West Pacific coral reefs (Sri Lanka, New Caledonia, Great Barrier Reef) than in the Gulf of Aqaba. It seems that the trophic species composition (percentage of species per feeding guild) also show some differences between the Red Sea and other parts of the Indo-West Pacific. Planktivores contribute relatively more species to the fish assemblages in the Red Sea than on other Indo-West Pacific reefs, while the percentage of piscivorous species seems to be lower in the Red Sea. Differences within the Red Sea have been revealed for corallivorous species. The percentage of corallivores at the northern tip of the Gulf of Aqaba was only half of that in the Central Red Sea. This pattern might be due to lower scleractinian species richness in the gulf (Antonius et al. 1990).

These differences in trophic community structure of Red Sea fish assemblages might be the result of unfavourable environmental conditions due to lowered sea level and restricted water exchange with the Indian Ocean during the last glacial maximum (Braithwaite 1987, Klausewitz 1989). Unfavourable environmental conditions led to partial extinction of ichthyofauna in the Red Sea (Goren 1986, Klausewitz 1989),

whereas environmental conditions were more stable in the Indian Ocean proper. Rise of sea level after the last glacial maximum adjusted the environmental conditions in the Red Sea to that of the Indian Ocean, and present day condition were established about 4,000 years BC in the Gulf of Aqaba (Reiss and Hottinger 1984). Rising sea level and improvement of environmental conditions was associated with a penetration of fauna from the Indian Ocean (Goren 1986). It seems that the relatively short period of a few thousand years was not sufficient for the Red Sea ichthyofauna to reach the same trophic community structure than its counterpart in the Indian Ocean.

Genetic aspects (Chapter 4 and 5)

The investigations on the genetic population structure of *P. miles* in the Gulf of Aqaba and northern Red Sea (1) revealed a high genetic diversity and (2) suggest high levels of gene flow due to genetic homogenity.

The observed high genetic diversity indicates a large, stable population. This supports the view of partial persistence of the Red Sea ichthyofauna during the last glacial, which was important for the evolution of the Red Sea ichthyofauna (Goren 1986, Klauswitz 1989).

High gene flow indicates that the oceanographic settings in the Gulf of Aqaba do not restrict exchange with the Red Sea proper. Genetic homogenity is observed in several fishes on coral reefs (Shaklee 1984, Lacson 1992, Lacson and Morizot 1991, Planes et al. 1993, Doherty et al. 1995, Lacson and Clark 1995, Shulman and Bermingham 1995, Bernardi et al. 2001) and is conditional on their life history. As most fishes on coral reefs, *P. miles* has pelagic eggs and a planktonic larval stage (Fishelson 1975), and hence a high potential of dispersal.

Investigations on interrupted gene flow in the evolutionary history of lionfishes (Scorpaenidae, Pteroinae) did not reveal a differentiation between the Red Sea and Indian Ocean, but between Indian Ocean and Western Pacific. Phylogenetic analysis of the siblings *P. miles* and *P. volitans* supported their species status and distribution suggested by Schultz (1986). Molecular clock estimates suggest a divergence time of 2.4-8.3 million years, which coincide with tectonic events (Hall, 1998) and sea level changes during the glacial maxima (Voris 2000) that partly separated populations of the Indian and Pacific Ocean. These processes are major forces that facilitated allopatric

speciation in the Southeast Asian centre of biodiversity (McManus 1985, Pandolfi 1992, Benzie 1998, Randall 1998).

Additionally, this genetic study suggested that morphological definition is unprecise for the genera *Pterois* and *Dendrochirus*, and gave indications for taxonomic revision.

4.2 Ecology of fish assemblages in the Gulf of Aqaba (Chapters 1 and 3)

Ecological studies on the shore fishes off the Jordanian coast showed that fish species richness was positively correlated with hard substrate cover and benthic diversity. Especially abundance of corallivores was positively linked to live coral cover. This shows the importance of the three-dimensional structure of coral reefs that provides shelter and food for fishes (Roberts and Ormond 1987, Friedlander and Parrish 1998, Bouchon-Navaro and Bouchon 1989). Investigations on the trophic community structure at disturbed and undisturbed reefs showed a shift towards planktivores on the shallow slope of disturbed reefs. The reason might be 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 health 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 disturbed reefs omnivorous fishes increased in their relative abundance. This guild of fishes consists of non-specialised feeders that can more easily cope with changes in the benthic habitat.

A significant higher fish abundance was observed at 12 m depth than at 6 m depth in shallow water habitats off the Jordanian coast. The deeper reef slope is more exposed to currents bringing zooplankton from offshore waters into the reef. Therefore, large schools of planktivorous fishes utilise this habitat (Chapter 3). A similar positive correlation of abundance as well as biomass of planktivores and depth was reported from a coral reef in Hawaii (Friedlander and Parrish 1998).

The seagrass-dominated site showed at 12 m depth a significant higher abundance and species richness than coral reefs. The higher species richness and abundance at the seagrass-dominated site can be explained by the high productivity of the seagrass meadows and by feeding migrations of fishes from the coral reef to the seagrass beds (Ogden 1980, Robblee and Ziemann 1984, Quinn and Ogden 1984, Kochzius 1999). Invertebrate feeders are significantly more abundant at the seagrass-dominated site

(Chapter 3), where they can utilise the rich crustacean fauna. This findings underline the importance of seagrass meadows for fishes on adjacent coral reefs.

Multivariate analysis revealed that fish communities of shallow water habitats along the Jordanian Red Sea coast are strongly influenced by the composition of the benthic habitat and depth. These habitat and depth specific differences in fish communities on tropical shallow-water habitats are supported by other studies, e.g. Öhman and Rajasuriya (1998) for coral and sandstone reefs, as well as Friedlander and Parrish (1998) for a coral reef.

The multivariate analysis of the fish community has revealed several associations of fishes in different habitats. The fish communities of shallow-water habitats along the Jordanian Red Sea coast showed different assemblages of fishes (1) on the deep reef slope (12 m depth), (2) on the shallow reef slope (6 m depth) and (3) on seagrass meadows and sand flats. In addition the analysis revealed ecological groups such as schooling herbivores, schooling planktivores and reef-associated apogonids.

4.3. Marine conservation in the Gulf of Aqaba

The Red Sea is regarded as a marine biodiversity hotspot with conservation priority, because it harbours a high number of endemics. Species with a restricted range are vulnerable to extinction and are mainly found in centres of endemism (Roberts et al. 2002). The northern tip of the Gulf of Aqaba and its western shores are particularly subject to human disturbances by urban and industrial pollution, shipping and port activities, as well as tourism (Hawkins and Roberts 1994, Badran and Foster 1998, Abelson et al. 1999), while the eastern side is controlled by Saudi-Arabia and seems little disturbed so far. Habitat loss might lead to extinction of the damselfish *Chromis pelloura*, which is only known from northern tip of the Gulf of Aqaba (Chapter 2).

Destruction and disturbance of the marine environment in the northern gulf is observed for almost three decades (Fishelson 1995), but investigation of community structure and response to disturbance of shore fishes assemblages in the gulf is deficient. Therefore, the results presented in chapters 1 and 3 can give some implications for the protection of coral reefs in the Gulf of Aqaba and off the Jordanian coast in particular.

(1) Fish abundance at an industrial site was 50% lower than on an undisturbed reef and the trophic community structure was different. (2) Structural complexity of the coral reef habitat supports high species diversity due to shelter holes and prey availability. (3) Seagrass meadows are important for many fishes on coral reefs as a feeding ground and other studies have shown their importance as nursery area (Kochzius 1999).

High levels of gene flow in *P. miles* implicate re-colonisation of restored habitats and replenishment of depleted stocks from the Red Sea proper. However, it is not clear how fast depleted populations will be replenished or restored habitats will be re-colonised. Therefore, coastal zone management in the Gulf of Aqaba has to follow the precautionary principle and should not rely upon fast replenishment or re-colonisation.

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Chapter 1

[1]Khalaf MA, [2]Kochzius M

[1]Marine Science Station, Aqaba, Jordan

[2]Centre for Tropical Marine Ecology, Bremen, Germany

Community structure of shore fishes in the Gulf of Aqaba, Red Sea

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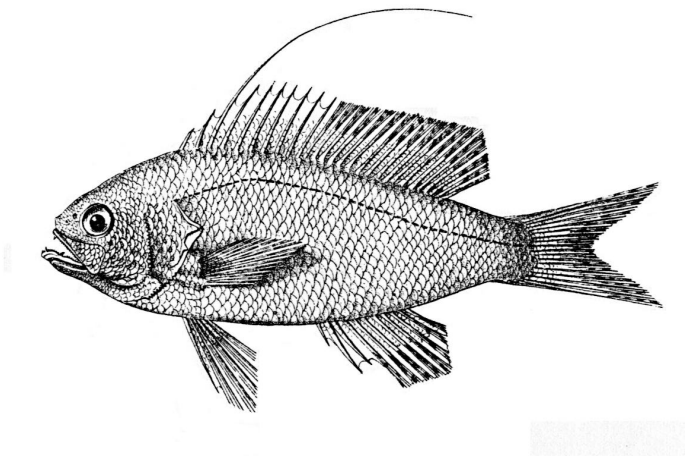

Pseudanthias squamipinnis, taken from Klunzinger CB (1884) Die Fische des Rothen Meeres. 1. Theil. Schweizbart’sche Verlaghandlung, Stuttgart

ABSTRACT

Shore fish community structure off the Jordanian Red Sea coast was determined on fringing coral reefs and in a seagrass-dominated bay in 6 m and 12 m depth. A total of 198 fish species belonging to 121 genera and 43 families was recorded. Labridae and Pomacentridae dominated the ichthyofauna in terms of species richness and Pomacentridae were most abundant. Neither diversity nor species richness was correlated to depth. The abundance of fishes was higher at the deep reef slope, due to schooling planktivorous fishes. In 12 m depth abundance of fishes at the seagrass-dominated site was higher than on the coral reefs. Multivariate analysis demonstrated a strong influence on the fish assemblages by depth and benthic habitat. Fish species richness was positively correlated to hard substrate cover and habitat diversity. Abundance of corallivores was positively linked to live hard coral cover. The assemblages of fishes were different on the shallow reef slope, deep reef slope as well as on seagrass meadows. An analysis of the fish fauna showed that the Gulf of Aqaba harbours a higher species richness than previously reported. The comparison with fish communities on other reefs around the Arabian Peninsula and Indian Ocean supported the recognition of an Arabian subprovince within the Indian Ocean. The affinity of the Arabian Gulf ichthyofauna to the Red Sea is not clear.

KEYWORDS

Community structure, Coral Reef, Red Sea, Seagrass meadow, Shore fishes

INTRODUCTION

Coral reefs are one of the most complex marine ecosystems in which fish communities reach their highest degree of diversity (Harmelin-Vivien 1989). Morphological properties and the geographical region of the coral reef determine the structure of the fish assemblages (Sale 1980, Thresher 1991, Williams 1991). The ichthyofauna of coral reefs can be linked in different degree to adjacent habitats (Parrish 1989) such as seagrass meadows (Ogden 1980, Quinn and Ogden 1984, Roblee and Ziemann 1984, Kochzius 1999), algal beds (Rossier and Kulbicki 2000) and mangroves (Birkeland 1985, Thollot 1992).

Although the Red Sea ichthyofauna is taxonomically quite well known compared to other parts of the tropical Indo-Pacific Ocean, the community structure of shore fishes has been less well investigated. To date more than 1,280 fish species are known from the Red Sea (Baranes and Golani 1993, Goren and Dor 1994, Randall 1994, Khalaf et al. 1996). Ichthyological research in the Red Sea dates back more than 200 years to the collections and descriptions of fishes by Peter Forsskål (Klausewitz 1964, Nielsen 1993). Despite a long tradition of taxonomic work since then (e.g. Forsskål 1775 and Klunzinger 1884), as well as biosociological and ecological studies on certain families, such as damselfishes (Pomacentridae) (e.g. Fishelson et al. 1974, Fricke 1977, Ormond et al. 1996) and butterflyfishes (Chaetodontidae) (e.g. Bouchon-Navaro 1980, Bouchon-Navaro and Bouchon 1989, Roberts et al. 1992), surprisingly few studies are published on the general community structure of Red Sea shore fishes (Ben-Tuvia et al. 1983, Rilov and Benayahu 2000). Other investigation deal with fish communities on artificial reefs (Rilov and Benayahu 1998, Golani and Diamant 1999) or give species lists for certain areas (Clark et al. 1968, Tortonese 1983).

Shallow-water habitats along the Jordanian Red Sea coast are fringing coral reefs and seagrass meadows. The coral reefs of the Jordanian coast have been studied in detail by Mergner and Schuhmacher (Mergner and Schuhmacher 1974, Mergner 1979, Mergner and Schuhmacher 1981, Mergner 2001). Several studies on the autecology (e.g. Harmelin-Vivien and Bouchon-Navaro 1981, Wahbeh and Ajiad 1985a, 1985b) and population ecology (e.g. Bouchon-Navaro and Harmelin-Vivien 1981, Bouchon-Navaro 1986) of fishes were conducted along the Jordanian coastline of the Gulf of Aqaba, but no synecological approach has been conducted to date.

Coral reefs are under threat on a global scale (Bryant et al. 1998, Hoeg-Guldberg 1999, Souter and Lindén 2000) and under high human impact in the Gulf of Aqaba, caused by pollution (Walker and Ormond 1982, Abu-Hilal 1987, Abu-Hilal and Badran 1990, Abelson et al. 1999), shipping and port activities (Abu-Hilal 1985, Badran and Foster 1998) as well as tourism (Riegl and Velimirov 1991, Hawkins and Roberts 1994).

Detailed ecological information of reef organisms is needed for conservation and for proper management of coral reef ecosystems. This study investigates for the first time the fish communities of shallow-water habitats along the Jordanian coast to obtain ecological information to facilitate a proper management of the Red Sea Marine Peace Park and adjacent waters of the Jordanian coast. The main objectives of the study are: (1) to investigate the community structure of fishes on coral reefs and seagrass meadows, (2) to reveal the ecological parameters which influence the community structure, (3) to detect general features of fish communities on coral reefs, (4) to describe the biodiversity of the ichthyofauna, and (5) to assign the biogeographic affinity of the shore fishes in the Gulf of Aqaba.

METHODS

Study area

This study was conducted at five coral reefs (sites 1-3, 5, 6) and one seagrass meadow (site 4) along the 27 km Jordanian coast, Gulf of Aqaba, Red Sea (Fig. 1). Fringing reefs are discontinuously distributed over a length of 13 km along the coast, separated by bays that are usually covered by seagras meadows (UNEP/IUCN 1988). Studies of a 25 m^2 quadrat on the reef slope in the reserve at the Marine Science Station (Fig. 1) recorded 78 scleractinian coral species (Mergner and Schuhmacher 1981). Reef morphology and zonation is described in detail by Mergner and Schuhmacher (1974). The largest seagrass meadow along the coast is located at Al-Mamlah Bay (site 4) (UNEP/IUCN 1988). The meadows are composed of the seagrass species *Halophilia ovalis*, *H. stipulacea* and *Halodule universis*, which is the dominand species at Al-Mamlah Bay (Wahbeh 1981).

Fig. 1 Map of the Gulf of Aqaba with study sites at the Jordanian coast (*inset*): *1* Cement jetty (N 29°28.990'; E 34°59.010'), *2* Marine Science Station (N 29°27.250'; E 34°58.359'), *3* Tourist Camp (N 29°26.351'; E 34°58.272'), *4* Al-Mamlah Bay (N 29°24.345'; E 34°58.549'), *5* and *6* Jordan Fertiliser Industries and Jordan Fertiliser Industries jetty (N 29°22.134'; E 34°57.667')

Visual census

The fish communities in shallow-water habitats (fringing coral reef and seagrass meadow) along the Jordanian Red Sea coast were surveyed by the visual census technique using SCUBA as described in English et al. (1994). Transects of 50 m length and 5 m width (250 m^2) were marked at the study sites (Fig. 1). At each site visual censuses were conducted along three transects at the shallow slope (6 m) and deep slope (12 m), respectively. The distance between the transects at one site was 10 to 20 m. The observer waited five to ten minutes after laying the transect line to allow fishes to resume their normal behaviour. Subsequently the diver swam along the transect and recorded all fishes encountered 2.5 m on each site of the line and 5 m above the transect. All observed fishes of 30 mm total length or longer were identified by the first author (M.A. Khalaf) and recorded on a plastic slate. The duration for the count of each transect was 50-60 minutes. At five sites (Cement jetty, Marine Science Station, Tourist Camp, Jordan Fertiliser Industries and Jordan Fertiliser Industries jetty) three censuses were conducted at each depth in November 1999 and March 2000. At Al-Mamlah Bay 39 censuses were conducted in 6 m and 43 census in 12 m depth in 1997 and 1998 (Table 1). The survey of the benthic habitat at each visual census transect was conducted by the line-intercept method, recording percentage cover

of live hard coral, live soft coral, dead coral and rock, sand, and seagrass (English et al. 1994).

Table 1 Sampling at sites along the Jordanian Red Sea coast, Gulf of Aqaba

Site	n	6 m	n	12 m
Cement jetty	3	November 1999	3	November 1999
Marine Science Station (MSS)	3	November 1999	3	November 1999
Tourist Camp	3	November 1999	3	November 1999
Al-Mamlah Bay	39	April 1997–August 1999	43	April 1997–August 1999
Jordan Fertilizer Industries (JFI)	3	April 2000	3	April 2000
Jordan Fertilizer Industries jetty (JFI jetty)	3	April 2000	3	March 2000

Statistical analysis

Abundance of fishes was described by relative abundance (RA) and frequency of appearance (FA), calculated as follows: RA = (the pooled average abundance of species *i* from each depth and site/the pooled average abundance of all species from each depth and site) x 100 and FA = (number of transects in which species *i* was present/total number of all transects) x 100. Calculation of RA with average values was necessary to prevent overvaluation of Al-Mamlah Bay.

Community indices such as fish abundance, species richness (number of species) and Shannon-Wiener diversity (*H’*; ln basis) were compared among sites and depths using one-way ANOVA. Homogeneity of variances was tested with *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. *F*-test was performed with a spreadsheet analysis programme and one-way ANOVA was carried out with STATISTICA 5.1 (StatSoft 1997).

Regression analysis (power and linear regression) was performed with a spreadsheet analysis programme and the significance level of the correlation was obtained from statistical tables after calculating the empirical *F*-value with the following formula: $F_{emp}=(r^2\text{-}J)/((1\text{-}r^2)/K\text{-}J\text{-}1))$; where r^2=coefficient of determination; *J*=number of regressors; *K*=sample size (Backhaus et al. 1994).

Multivariate analysis of the data such as cluster analysis, MDS (multi-dimensional scaling), RELATE, BIO-ENV, as well as ANOSIM (analysis of similarities) significance test were performed with PRIMER-5 software (Primer-E 2000).

Hierarchical clustering and MDS was based on Bray–Curtis similarities of abundance data. Highly abundant species in contrast to species with very low abundance can disturb the analysis. Therefore, if necessary, data were transformed and standardised as indicated at the figures. MDS is a 3-dimensional ordination of samples brought down to a 2-dimensional plot. The quality of the MDS plot is indicated by the stress value. Values <0.2 give a potentially useful 2-dimensional picture, stress <0.1 corresponds to a good ordination and stress <0.05 gives an excellent representation.

ANOSIM significance test compares similarities of species compositions between the samples and can give evidence for differences. A one-way layout of ANOSIM was performed with the original data, no transformation or standardisation was conducted. Two terms are important in an ANOSIM significance test: *p* (significance level) and Global *R*. 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, showing a low difference between them (Clarke and Warwick 1994).

BIO-ENV analysis was performed with PRIMER-5; this correlates environmental variables to the multivariate analysis of the fish community based on a weighted Spearman rank correlation. RELATE compares the multivariate analysis of the fish community to the benthic habitat and reveals the degree of correlation between the two data sets (Clarke and Warwick 1994).

Biogeographic comparison was performed on the basis of species lists from 21 sites (Fig. 7) in the Red Sea (Vine & Vine 1980, Krupp et al. 1993, Schraut 1995, Rilov and Benayahu 2000, W. Gladstone unpublished report, M.A. Khalaf and F. Krupp unpublished data, U. Zajonz et al. unpublished report), Arabian Gulf (Coles and Tarr 1990, Krupp et al. 1994, Krupp and Almarri 1996, Carpenter et al. 1997), Gulf of Aden (Kemp 1998, 2000), Oman (Randall 1995) and Indian Ocean (Smith & Heemstra 1991, Randall and Anderson 1993, Letourneur 1996, Pittman 1996, Öhman et al. 1997, Winterbottom and Anderson 1997, Anderson et al. 1998, Kunzmann et al. 1999). Presence/absence data of 712 species from the following families have been considered for the biogeographic comparison: Acanthuridae, Balistidae, Caesionidae, Chaetodontidae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Nemipteridae,

Pomacanthidae, Pomacentridae, Scaridae, Serranidae and Siganidae. All species names were checked for synonyms with FishBase 99 (FishBase 1999) to prevent double counts of species. Multivariate statistics for the biogeographic analysis was based on Bray-Curtis similarity and Euclidean distance.

RESULTS

Benthic habitat

Along the Jordanian Red Sea coast the highest live coral cover was 35% and the average 19%. Five of the study sites were coral reefs, whereas Al-Mamlah Bay was dominated by seagrasses (59% cover). At all coral reefs dead coral and rock as well as sand made up most of the cover (Table 2).

Table 2 Benthic habitat at sites along the Jordanian Red Sea coast, Gulf of Aqaba. Average percentage of cover at the study sites

Site	Average percentage					
	Live stony coral	Live soft coral	Dead coral and rock	Seagrass	Sand	
Cement jetty	17	7	26	0	50	coral reef
MSS	22	3	30	0	45	coral reef
Tourist Camp	23	6	47	0	24	coral reef
Al-Mamlah Bay	3	3	8	59	27	seagrass meadow
JFI	22	4	21	0	53	coral reef
JFI jetty	13	5	25	0	57	coral reef

Fish assemblages and community indices

In this study a total of 212,349 fishes were counted, representing 198 shallow-water species belonging to 121 genera and 43 families (Table 4). Most individuals belonged to the families Pomacentridae (44.1%, 18 species), Anthininae (25.3%, 2 species, subfamily of Serranidae), Labridae (9.7%, 38 species), Atherinidae (3.9%, 1 species), Caesionidae (2.7%, 3 species), Acanthuridae (2.2%, 6 species) and Apogonidae (2.1%, 9 species) (Fig. 2). In terms of species richness per family the ichthyofauna showed the following ranking: Labridae (19.2%), Pomacentridae (9.1%), Gobiidae (5.1%), Scaridae (5.1%), Blenniidae (4.5%), Apogonidae (4.0%), Chaetodontidae (4.0%), Scorpaenidae

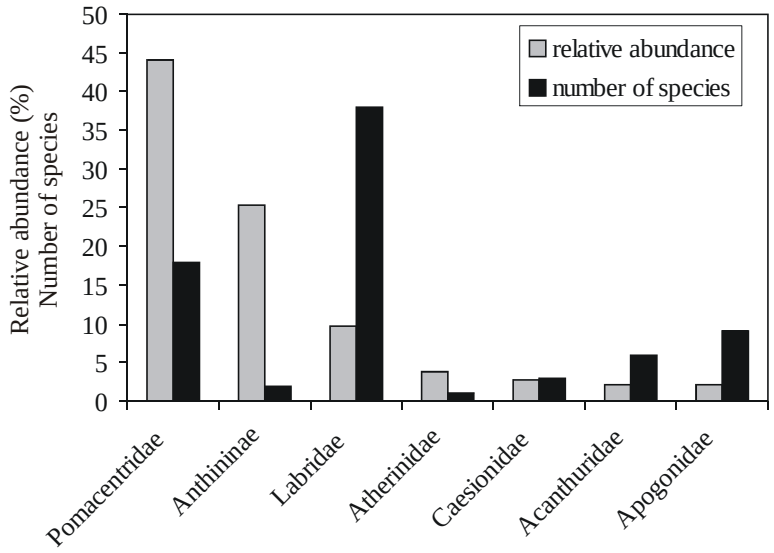

Fig. 2 Dominant families of the ichthyofauna on visual census transects (250 m^2) at the Jordanian Red Sea coast, Gulf of Aqaba

(4.5%) and Serranidae (3.5%) (Table 3). The most abundant species were *Pseudanthias squamipinnis* (24.1%; Plate 3), *Pomacentrus trichourus* (16.1%; Plate 6), *Paracheilinus octotaenia* (6.4%; Plate 7), *Neopomacentrus miryae* (6.2%, Plate 6), *Chromis dimidiata* (5.6%; Plate 5) *Dascyllus marginatus* (5.0%; Plate 6) and *Atherinomorus lacunosus* (3.9%; Plate 1). Those seven species made up for two thirds of all individuals. In terms of frequency of appearance the most common species were *Pomacentrus trichourus* (87.3%), *Amphiprion bicinctus* (79.7%; Plate 5), *Pseudanthias squamipinnis* (79.7%) and *Coris caudimacula* (78.8%; Plate 6), as well as *Chaetodon paucifasciatus (Plate 4)*, *Chromis dimidiata* and *Dascyllus marginatus* (all 72.9%) (Table 4).

Average Shannon-Wiener diversity (ln basis) ranged from 1.3 at Al-Mamlah Bay at 6 m depth to 2.8 at Jordan Fertilizer Industries at 12 m depth (Fig. 3), but no significant difference was detected (Table 5).

Average species richness ranged from 17.9 species at Al-Mamlah Bay at 6 m depth to 58.5 species at Al-Mamlah Bay at 12 m depth (Fig. 6). The seagrass-dominated site Al-Mamlah Bay showed more species at 12 m compared to 6 m depth. At 6 m depth species richness was higher on coral reefs than on the seagrass meadow. The picture for 12 m depth was reverse with a higher species richness at the seagrass-dominated site. All differences were evidenced on a significance level of $p<0.001$. No significant difference in species richness was detected between other sites (Table 5).

Table 3 Percentage of species of the most abundant fish families at the Jordanian Red Sea coast, Gulf of Aqaba in comparison to other fish assemblages on coral reefs. [1]this study (VC), [2]Rilov and Benayahu 2000 (VC), [3]Zajonz et al. unpubl. report (VC), [4]Schraut 1995 (VC), [5]Krupp et al. 1993 (VC+F), [6]Kemp 1998 (VC), [7]Kemp 2000 (VC), [8]Coles and Tarr 1990 (VC), [9]Krupp et al. 1994 (VC+F+R), [10]Pittman 1996 (VC), [11]Harmelin-Vivien 1989(?), [12]Letourneur 1996 (VC), [13]Letourneur et al. 1997 (VC+R), [14]Williams and Hatcher 1983 (E), [15]Gladfelter et al. 1980 (VC), [16]Pattengill et al. 1997 (VC). *VC* visual census, *F* fishing, *R* rotenone, *E* explosive charges

Location	Region	Labridae	Pomacentridae	Gobiidae	Scaridae	Blenniidae	Apogonidae	Chaetodontidae	Scorpaenidae	Serranidae
Aqaba[1]	Red Sea	19.2	9.1	5.1	5.1	4.5	4.0	4.0	4.0	3.5
Eilat[2]	Red Sea	20.4	12.7	2.1	5.6	7.7	2.1	4.9	2.1	6.3
Dahab[3]	Red Sea	13.7	11.9	1.2	3.6	3.0	4.2	5.4	2.4	7.7
Sharm El Sheikh[4]	Red Sea	14.8	10.2	2.3	4.0	5.1	2.3	5.1	2.3	6.3
Sanganeb[5]	Red Sea	12.4	9.6	7.2	3.6	3.6	4.8	4.8	2.0	5.2
Socrota[6]	Gulf of Aden	11.1	7.9	1.4	1.9	0.9	2.8	6.0	1.4	6.9
Yemen[7]	Gulf of Aden	12.5	7.6	4.5	3.0	3.0	2.7	6.8	1.5	4.9
Jubail[8]	Arabian Gulf	7.9	9.9	4.0	5.9	5.0	5.0	3.0	-	5.0
Jubail[9]	Arabian Gulf	4.3	4.8	9.1	2.1	2.2	3.2	1.6	2.7	4.3
Seychelles[10]	Western Indian Ocean	11.8	7.5	0.4	5.9	0.8	1.3	6.7	2.5	5.4
Tulear[11]	Western Indian Ocean	11.2	7.4	9.1	2.5	4.5	4.3	3.8	4.0	4.3
Réunion[12]	Western Indian Ocean	14.3	11.5	1.8	4.1	3.2	1.4	7.4	3.7	3.7
Réunion[13]	Western Indian Ocean	13.5	11.2	1.2	3.2	2.4	1.7	7.0	-	3.2
Great Barrier Reef[14]	Western Pacific	14.2	17.6	6.5	4.3	-	5.3	8.7	-	6.8
New Caledonia[13]	Western Pacific	15.0	16.5	1.5	5.8	0.5	3.0	9.5	-	6.1
Moorea[11]	Central Pacific	13.6	8.9	3.9	4.3	2.1	5.0	6.8	2.1	3.6
Moorea[13]	Central Pacific	15.8	9.5	3.2	1.1	-	5.7	10.1	-	1.1
Enewetak[15]	Central Pacific	22.5	12.4	0.6	5.6	2.2	2.8	11.2	1.1	7.3
St. Croix[15]	Caribbean	6.0	9.5	2.6	7.8	2.6	5.2	4.3	1.7	12.1
Gulf of Mexico[16]	Caribbean	5.9	7.8	3.9	4.6	-	2.6	3.3	1.3	11.1

Table 4 Average fish abundance (AA) and relative abundance (RA) per transect (250 m^2) at sites along the Jordanian Red Sea coast, Gulf of Aqaba. Nomenclature is according to FishBase 99 (FishBase 1999)

	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty					
Depth	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		**Total**	
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Torpedinidae																									**<0.01**	
Torpedo panthera Olfers, 1831													0.03	<0.01	0.02	<0.01									<0.01	1.69
Muraenidae																									**0.02**	
Gymnothorax nudivomer (Günther, 1867)					0.33	0.05	0.33	0.02							0.09	<0.01									<0.01	5.08
Siderea sp.													0.05	0.01											<0.01	1.69
Siderea grisea (Lacepède, 1803)													0.13	0.01	1.84	0.05	0.33	0.07							0.02	25.42
Synodontidae																									**0.11**	
Saurida gracilis (Quoy and Gaimard, 1824)	1.00	0.16									0.33	0.02	0.08	0.01	1.53	0.05	0.33	0.07							0.02	29.66
Synodus sp.							0.33	0.02																	<0.01	0.85
Synodus variegatus (Lacepède, 1803)	0.67	0.11	0.67	0.03					1.33	0.20	3.33	0.16	1.33	0.16	4.79	0.14	0.33	0.07			0.67	0.07			0.09	56.78
Atherinidae																									**3.88**	
Atherinomorus lacunosus (Forster, 1801)													256.41	29.94							333.33	34.44			3.88	2.54
Holocentridae																									**0.76**	
Myripristis murdjan (Forsskål, 1775)					1.00	0.14	1.67	0.08	3.00	0.45	2.67	0.13			0.19	0.01	2.00	0.42	4.00	0.53	0.33	0.03			0.10	13.56
Neoniphon sammara (Forsskål, 1775)													0.08	0.01	0.95	0.03									0.01	17.80
Sargocentron caudimaculatum (Rüppell, 1838)					0.33	0.05	0.67	0.03																	0.01	4.24
Sargocentron diadema (Lacepède, 1802)	2.33	0.38	2.67	0.13	1.67	0.24	2.67	0.13	2.00	0.30	1.00	0.05	0.10	0.01	71.26	2.10	1.67	0.35	4.33	0.58	2.33	0.24	7.00	1.43	0.65	54.24
Fistulariidae																									**0.07**	
Fistularia commersonii Rüppell, 1838									0.67	0.10	0.67	0.03	2.95	0.34	2.44	0.07					3.33	0.34			0.07	16.95
Centriscidae																									**0.01**	
Aeoliscus punctulatus (Bianconi, 1855-59)													0.41	0.05	1.49	0.04									0.01	7.63
Syngnathidae																									**0.26**	
Corythoichthys flavofasciatus (Rüppell, 1838)											0.33	0.02	0.62	0.07	1.30	0.04					3.67	0.38			0.04	14.41
Corythoichthys nigripectus Herald, 1953									0.33	0.05															<0.01	0.85

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Corythoichthys schultzi Herald, 1953	7.00	1.15	1.00	0.05			1.33	0.06	5.33	0.79	5.00	0.24	1.26	0.15	3.49	0.10	1.00	0.21	1.67	0.22			1.00	0.20	0.18	33.90
Trachyrhamphus bicoarctatus					0.33	0.05	1.00	0.05					0.97	0.11	1.63	0.05	0.67	0.14							0.03	26.27
(Bleeker, 1857)																										
Scorpaenidae																									**0.16**	
Dendrochirus brachypterus													1.38	0.16	0.81	0.02									0.01	27.97
(Cuvier, 1829)																										
Inimicus filamentosus (Cuvier, 1829)													0.15	0.02	0.14	<0.01									<0.01	6.78
Pterois miles (Bennett, 1828)					1.00	0.14	1.00	0.05	1.00	0.15	0.33	0.02	0.74	0.09	7.02	0.21	0.67	0.14	2.33	0.31	1.00	0.10	0.33	0.07	0.10	46.61
Pterois radiata Cuvier, 1829	0.33	0.05					0.33	0.02					0.03	<0.01	0.58	0.02			1.33	0.18	0.67	0.07	1.67	0.34	0.03	19.49
Scorpaenidae													0.13	0.01	0.81	0.02									0.01	16.10
Scorpaenopsis barbata (Rüppell, 1838)															0.02	<0.01									<0.01	0.85
Scorpaenopsis sp.			0.33	0.02																					<0.01	0.85
Synanceia verrucosa															0.02	<0.01									<0.01	0.85
Bloch and Schneider, 1801																										
Serranidae																									**25.47**	
Anthias taeniatus Klunzinger, 1884							183.33	8.71																	1.21	4.24
Cephalopholis hemistiktos							0.67	0.03			0.67	0.03							0.33	0.04					0.01	5.08
(Rüppell, 1830)																										
Cephalopholis miniata (Forsskål, 1775)															0.07	<0.01	0.33	0.07					0.33	0.07	<0.01	5.08
Epinephelus fasciatus (Forsskål, 1775)	2.33	0.38	1.00	0.05	1.67	0.24	0.67	0.03	3.00	0.45	2.00	0.09	0.87	0.10	2.91	0.09	1.33	0.28	1.33	0.18	1.33	0.14	1.00	0.20	0.13	61.86
Grammistes sexlineatus									0.33	0.05					0.16	<0.01			0.33	0.04					0.01	6.78
(Thunberg, 1792)																										
Pseudanthias squamipinnis	121.67	19.98	966.67	46.39	110.00	15.80	283.33	13.47	32.33	4.80	195.00	9.22	158.97	18.56	1566.5	46.11	21.67	4.59	81.67	10.89	41.67	4.30	80.00	16.33	24.05	79.66
(Peters, 1855)															1											
Variola louti (Forsskål, 1775)	0.67	0.11	1.00	0.05			2.67	0.13	0.67	0.10	1.67	0.08			0.14	<0.01	0.33	0.07	2.00	0.27			0.33	0.07	0.06	18.64
Pseudochromidae																									**0.41**	
Pseudochromis flavivertex Rüppell, 1835							0.33	0.02							0.05	<0.01	0.33	0.07	0.33	0.04			0.33	0.07	0.01	5.93
Pseudochromis fridmani	0.67	0.11	3.67	0.18			8.33	0.40	16.67	2.48	5.33	0.25	0.21	0.02	6.77	0.20	1.00	0.21	1.67	0.22	1.67	0.17	0.67	0.14	0.31	53.39
Klausewitz, 1968																										
Pseudochromis olivaceus Rüppell, 1835					0.33	0.05	0.33	0.02			1.00	0.05	0.05	0.01	0.74	0.02									0.02	22.88
Pseudochromis springeri Lubbock, 1975	0.67	0.11	0.67	0.03	0.67	0.10	1.33	0.06	0.67	0.10	2.67	0.13	0.08	0.01	3.79	0.11			0.33	0.04	0.33	0.03			0.07	44.07

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Priacanthidae																									**0.01**	
Priacanthus hamrur (Forsskål, 1775)															1.74	0.05									0.01	1.69
Apogonidae																									**2.14**	
Apogon aureus (Lacepède, 1802)															16.23	0.48									0.11	19.49
Apogon cyanosoma Bleeker, 1853							3.33	0.16					10.92	1.28	91.67	2.70			1.00	0.13					0.70	34.75
Apogon exostigma (Jordan and Starks, 1906)													0.03	<0.01	1.74	0.05									0.01	6.78
Apogon fraenatus Valenciennes, 1832															0.28	0.01									<0.01	5.08
Apogon nigrofasciatus Lachner, 1953															0.23	0.01									<0.01	5.93
Apogon sp.									0.33	0.05			0.05	0.01											<0.01	1.69
Cheilodipterus lachneri Klausewitz, 1959					1.00	0.14							3.15	0.37	143.98	4.24	0.33	0.07			0.67	0.07			0.98	31.36
Cheilodipterus macrodon (Lacepède, 1802)					1.33	0.19	1.00	0.05							8.26	0.24	0.33	0.07			0.33	0.03	0.67	0.14	0.08	28.81
Cheilodipterus novemstriatus (Rüppell, 1838)	0.67	0.11							1.33	0.20			0.33	0.04	33.72	0.99					2.00	0.21			0.25	36.44
Carangidae																									**0.35**	
Carangoides fulvoguttatus (Forsskål, 1775)													0.03	<0.01											<0.01	0.85
Decapterus macrosoma Bleeker, 1851													6.41	0.75	46.51	1.37									0.35	3.39
Gnathanodon speciosus (Forsskål, 1775)															0.02	<0.01									<0.01	0.85
Caesionidae																									**2.65**	
Caesio lunaris Cuvier, 1830													61.28	7.16	104.42	3.07					0.33	0.03	3.33	0.68	1.11	16.95
Caesio suevicus Klunzinger, 1884							0.67	0.03					53.85	6.29	11.63	0.34	16.67	3.53	25.00	3.33	26.67	2.75			0.88	10.17
Caesio varilineata Carpenter, 1987			0.67	0.03					10.00	1.49			32.05	3.74	52.79	1.55	3.33	0.71							0.65	14.41
Nemipteridae																									**0.04**	
Scolopsis ghanam (Forsskål, 1775)													0.62	0.07	1.53	0.05					1.00	0.10	2.33	0.48	0.04	28.81
Gerreidae																									**<0.01**	
Gerres oyena (Forsskål, 1775)													0.13	0.01											<0.01	0.85
Haemulidae																									**<0.01**	
Diagramma pictum (Thunberg, 1792)															0.12	<0.01									<0.01	1.69

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Lethrinidae																									**0.08**	
Lethrinus sp.													0.05	0.01	6.51	0.19									0.04	13.56
Monotaxis grandoculis (Forsskål, 1775)													0.08	0.01	0.30	0.01	3.33	0.71			1.00	0.10	1.33	0.27	0.04	13.56
Sparidae																									**0.01**	
Diplodus noct (Valenciennes, 1830)													0.77	0.09	0.23	0.01									0.01	2.54
Mullidae																									**0.78**	
Mulloidichthys flavolineatus (Lacepède, 1801)			10.00	0.48	0.67	0.10							1.28	0.15											0.08	3.39
Parupeneus cyclostomus (Lacepède, 1801)					0.33	0.05			0.33	0.05	0.33	0.02			0.67	0.02									0.01	15.25
Parupeneus forsskali (Fourmanoir and Guézé, 1976)	0.67	0.11	1.00	0.05			2.00	0.10	0.33	0.05	1.00	0.05	1.82	0.21	16.74	0.49	2.33	0.49	1.67	0.22	1.00	0.10	1.67	0.34	0.20	62.71
Parupeneus macronema (Lacepède, 1801)	1.00	0.16	0.67	0.03			1.00	0.05	0.33	0.05	0.67	0.03	3.00	0.35	59.81	1.76	1.33	0.28	0.67	0.09					0.45	53.39
Parupeneus rubescens (Lacepède, 1801)															5.79	0.17									0.04	12.71
Pempheridae																									**<0.01**	
Pempheris vanicolensis Cuvier, 1831													0.08	0.01											<0.01	0.85
Chaetodontidae																									**1.89**	
Chaetodon auriga Forsskål, 1775	0.33	0.05					0.67	0.03					0.05	0.01	0.28	0.01	0.33	0.07	2.00	0.27	1.33	0.14			0.03	14.41
Chaetodon austriacus Rüppell, 1836	4.00	0.66	4.33	0.21	3.00	0.43	4.00	0.19	6.67	0.99	8.00	0.38	0.23	0.03	0.40	0.01	6.67	1.41	12.33	1.65	7.00	0.72	3.00	0.61	0.39	39.83
Chaetodon fasciatus Forsskål, 1775	0.33	0.05	0.67	0.03	1.33	0.19	1.33	0.06	0.67	0.10			0.18	0.02	0.35	0.01	0.67	0.14	0.67	0.09	2.33	0.24	1.00	0.20	0.06	22.03
Chaetodon melannotus Bloch and Schneider, 1801													0.05	0.01	0.26	0.01			6.67	0.89	0.33	0.03			0.05	7.63
Chaetodon paucifasciatus Ahl, 1923	9.33	1.53	10.00	0.48	12.00	1.72	15.67	0.74	12.00	1.78	21.67	1.02	2.51	0.29	8.09	0.24	11.00	2.33	11.00	1.47	5.33	0.55	2.33	0.48	0.79	72.88
Chaetodon trifascialis Quoy and Gaimard, 1825																	1.67	0.35	1.33	0.18	1.33	0.14	0.33	0.07	0.03	5.93
Heniochus diphreutes Jordan, 1903													5.51	0.64	51.44	1.51			1.67	0.22					0.39	12.71
Heniochus intermedius Steindachner, 1893	2.00	0.33	1.67	0.08	2.00	0.29			1.00	0.15					0.28	0.01	3.33	0.71	7.33	0.98	1.67	0.17	3.00	0.61	0.15	25.42

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Pomacanthidae																									**0.55**	
Apolemichthys xanthotis (Fraser-Brunner, 1951)													0.03	<0.01	0.14	<0.01			0.67	0.09			0.33	0.07	0.01	9.32
Centropyge multispinis (Playfair, 1867)	2.33	0.38	2.67	0.13	3.33	0.48	5.67	0.27	2.67	0.40	9.00	0.43	0.38	0.04	2.21	0.07	2.67	0.56	3.67	0.49	3.33	0.34	2.67	0.54	0.27	60.17
Genicanthus caudovittatus (Günther, 1860)	1.00	0.16	10.67	0.51			10.00	0.48			12.67	0.60			0.12	<0.01			0.67	0.09			1.00	0.20	0.24	18.64
Pomacanthus imperator (Bloch, 1787)									0.33	0.05			0.03	<0.01	0.33	0.01			1.00	0.13			0.67	0.14	0.02	17.80
Pygoplites diacanthus (Boddaert, 1772)			0.33	0.02	0.33	0.05					0.67	0.03			0.02	<0.01			1.33	0.18	0.33	0.03	0.67	0.14	0.02	11.02
Pomacentridae																									**44.11**	
Abudefduf vaigiensis (Quoy and Gaimard, 1825)					2.67	0.38							0.51	0.06	0.81	0.02									0.03	3.39
Amblyglyphidodon flavilatus Allen and Randall, 1980	3.67	0.60	6.33	0.30	14.67	2.11	13.33	0.63	7.33	1.09	12.67	0.60					20.00	4.24	55.00	7.34	8.67	0.90	2.33	0.48	0.95	26.27
Amblyglyphidodon leucogaster (Bleeker, 1847)	1.00	0.16	1.33	0.06	10.00	1.44			10.67	1.58	3.67	0.17	0.51	0.06	8.21	0.24	34.67	7.34	2.00	0.27	7.67	0.79	1.67	0.34	0.53	38.98
Amphiprion bicinctus Rüppell, 1830	19.00	3.12	18.00	0.86	11.67	1.68	15.67	0.74	19.00	2.82	16.00	0.76	2.77	0.32	9.47	0.28	13.00	2.75	12.33	1.65	9.33	0.96	8.33	1.70	1.02	79.66
Chromis dimidiata (Klunzinger, 1871)	32.33	5.31	36.67	1.76	92.33	13.26	218.33	10.38	95.00	14.12	173.33	8.20	2.41	0.28	13.65	0.40	28.00	5.93	30.33	4.05	102.67	10.61	25.00	5.10	5.59	72.88
Chromis pelloura Randall and Allen, 1982													1.03	0.12	163.93	4.83									1.08	36.44
Chromis pembae Smith, 1960													0.13	0.01	39.53	1.16									0.26	12.71
Chromis ternatensis (Bleeker, 1856)							111.00	5.28	3.33	0.50	63.33	3.00	0.26	0.03	66.28	1.95							6.67	1.36	1.65	43.22
Chromis viridis (Cuvier, 1830)					16.67	2.39	26.67	1.27	5.00	0.74	326.67	15.45			3.37	0.10					26.67	2.75			2.66	12.71
Chromis weberi Fowler and Bean, 1928													0.03	<0.01	5.33	0.16									0.04	24.58
Dascyllus aruanus (Linnaeus, 1758)	7.00	1.15	4.00	0.19	71.33	10.24	80.00	3.80	17.00	2.53	46.67	2.21			10.49	0.31	76.67	16.24	11.67	1.56	15.67	1.62	4.33	0.88	2.27	38.98
Dascyllus marginatus (Rüppell, 1829)	18.00	2.96	57.67	2.77	46.67	6.70	96.67	4.59	66.33	9.86	168.33	7.96	4.62	0.54	129.49	3.81	8.00	1.69	40.00	5.34	9.00	0.93	111.00	22.65	4.97	72.88
Dascyllus trimaculatus (Rüppell, 1829)	2.33	0.38			8.33	1.20	4.00	0.19	0.67	0.10			3.23	0.38	31.33	0.92	10.33	2.19	10.00	1.33	1.67	0.17	16.67	3.40	0.58	61.02
Neoglyphidodon melas (Cuvier, 1830)			0.67	0.03			1.33	0.06	0.67	0.10					0.33	0.01	1.00	0.21	1.67	0.22					0.04	9.32
Neopomacentrus miryae Dor and Allen, 1977	86.67	14.23	500.00	24.00					3.33	0.50	16.67	0.79	2.05	0.24	30.00	0.88			233.33	31.12	68.67	7.09	8.33	1.70	6.24	25.42
Pomacentrus sulfureus Klunzinger, 1871					0.67	0.10			1.00	0.15											13.00	1.34			0.10	3.39
Pomacentrus trichourus Günther, 1867	212.33	34.87	268.33	12.88	192.33	27.62	395.00	18.77	268.67	39.92	633.33	29.96	28.74	3.36	82.33	2.42	81.67	17.30	90.00	12.01	96.00	9.92	103.33	21.09	16.12	87.29

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Pomacentrus trilineatus Cuvier, 1830																	0.33	0.07							<0.01	0.85
Mugilidae																									**0.01**	
Crenimugil crenilabis (Forsskål, 1775)													0.90	0.10	0.28	0.01									0.01	3.39
Labridae																									**9.71**	
Anampses caeruleopunctatus Rüppell, 1829					0.67	0.10			0.67	0.10	0.33	0.02	0.08	0.01	0.28	0.01									0.01	8.47
Anampses lineatus Randall, 1972													0.38	0.04	1.70	0.05									0.01	22.03
Anampses meleagrides Valenciennes, 1840							0.33	0.02	0.33	0.05	0.67	0.03	0.44	0.05	0.12	<0.01	0.33	0.07			1.67	0.17			0.03	12.71
Anampses twistii Bleeker, 1856	4.00	0.66	2.67	0.13	0.67	0.10	6.00	0.29	4.67	0.69	11.00	0.52	0.64	0.07	1.88	0.06	5.33	1.13	2.33	0.31	3.00	0.31	1.67	0.34	0.29	59.32
Bodianus anthioides (Bennett, 1832)	0.67	0.11			0.33	0.05	2.67	0.13	0.33	0.05	1.67	0.08	0.26	0.03	0.81	0.02	0.67	0.14	2.00	0.27	1.00	0.10	3.67	0.75	0.09	40.68
Bodianus axillaris (Bennett, 1832)	0.33	0.05					0.33	0.02							0.02	<0.01	1.00	0.21			1.00	0.10			0.02	4.24
Bodianus diana (Lacepède, 1801)																							0.33	0.07	<0.01	2.54
Cheilinus lunulatus (Forsskål, 1775)			0.33	0.02									0.03	<0.01	0.42	0.01							0.33	0.07	0.01	10.17
Cheilinus mentalis Rüppell, 1828	1.00	0.16	3.67	0.18	1.33	0.19	5.33	0.25	2.00	0.30	4.67	0.22	0.08	0.01	1.86	0.05	0.33	0.07	2.33	0.31	1.00	0.10	0.33	0.07	0.16	45.76
Cheilinus sp.													0.13	0.01	5.12	0.15									0.03	11.02
Cheilinus trilobatus Lacepède, 1801			0.33	0.02			1.33	0.06			0.33	0.02	0.15	0.02	1.19	0.03			2.33	0.31	1.33	0.14	2.67	0.54	0.06	38.98
Cheilio inermis (Forsskål, 1775)									0.33	0.05			0.44	0.05	1.51	0.04			0.67	0.09					0.02	30.51
Cirrhilabrus rubriventralis Springer and Randall, 1974	2.67	0.44							1.67	0.25	1.00	0.05	2.31	0.27	93.14	2.74					1.67	0.17			0.67	27.97
Coris aygula Lacepède, 1801	0.33	0.05			0.33	0.05	1.33	0.06			0.33	0.02	0.21	0.02	0.70	0.02	3.00	0.64			0.33	0.03			0.04	18.64
Coris caudimacula (Quoy and Gaimard, 1834)	4.33	0.71	2.33	0.11	0.33	0.05	4.33	0.21			3.00	0.14	18.74	2.19	27.56	0.81			1.33	0.18	1.00	0.10	0.67	0.14	0.42	78.81
Coris gaimard gaimard (Quoy and Gaimard, 1824)							0.67	0.03	0.33	0.05															0.01	1.69
Coris variegata (Rüppell, 1835)	1.00	0.16	1.00	0.05	0.33	0.05			1.33	0.20	0.33	0.02	0.26	0.03	0.53	0.02	0.67	0.14	0.33	0.04			1.33	0.27	0.05	23.73
Gomphosus caeruleus klunzingeri Klausewitz , 1962	0.67	0.11	0.33	0.02	1.00	0.14	2.67	0.13	1.33	0.20	1.67	0.08	0.10	0.01	0.23	0.01			1.67	0.22	3.33	0.34	0.67	0.14	0.09	24.58
Halichoeres marginatus Rüppell, 1835															0.16	<0.01									<0.01	1.69
Halichoeres scapularis (Bennett, 1832)															0.02	<0.01									<0.01	0.85
Hemigymnus fasciatus (Bloch, 1792)											0.33	0.02			0.07	<0.01			0.67	0.09	1.00	0.10			0.01	6.78

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Hologymnosus annulatus (Lacepède, 1801)							1.00	0.05					0.03	<0.01	0.33	0.01			0.33	0.04					0.01	11.02
Labroides dimidiatus (Valenciennes, 1839)			0.67	0.03	0.33	0.05	0.67	0.03	0.33	0.05			0.74	0.09	2.74	0.08			1.33	0.18					0.04	40.68
Larabicus quadrilineatus (Valenciennes, 1839)	0.67	0.11	3.00	0.14	0.33	0.05	3.33	0.16	3.00	0.45	3.33	0.16	0.03	<0.01	0.81	0.02	0.33	0.07	0.33	0.04			1.00	0.20	0.11	33.05
Macropharyngodon bipartitus bipartitus Smith, 1957							1.33	0.06			0.33	0.02			0.09	<0.01					0.33	0.03			0.01	7.63
Novaculichthys macrolepidotus (Bloch, 1791)													0.03	<0.01											<0.01	0.85
Oxycheilinus digrammus (Lacepède, 1801)					0.33	0.05	2.33	0.11	0.33	0.05	0.67	0.03	0.05	0.01	0.26	0.01									0.03	12.71
Paracheilinus octotaenia Fourmanoir, 1955	4.00	0.66	126.67	6.08			476.67	22.66			180.00	8.51	0.59	0.07	115.88	3.41			41.67	5.56			20.00	4.08	6.35	50.85
Pseudocheilinus evanidus Jordan and Evermann, 1903			0.67	0.03			3.33	0.16			4.00	0.19	0.05	0.01	1.95	0.06			0.33	0.04					0.07	36.44
Pseudocheilinus hexataenia (Bleeker, 1857)	1.33	0.22			1.33	0.19	6.33	0.30	3.00	0.45	2.00	0.09	0.26	0.03	3.19	0.09	0.67	0.14	1.00	0.13	1.33	0.14	1.00	0.20	0.14	55.08
Pteragogus cryptus Randall, 1981							0.33	0.02							0.09	<0.01	0.33	0.07	0.33	0.04			0.67	0.14	0.01	5.93
Pteragogus pelycus Randall, 1981													2.51	0.29	5.47	0.16									0.05	32.20
Stethojulis albovittata (Bonnaterre, 1788)					0.33	0.05			0.33	0.05	2.67	0.13	0.23	0.03	0.91	0.03					2.00	0.21	0.33	0.07	0.04	19.49
Stethojulis interrupta (Bleeker, 1851)					0.33	0.05							0.08	0.01	0.23	0.01									<0.01	5.08
Thalassoma lunare (Linnaeus, 1758)			0.67	0.03	0.33	0.05	3.00	0.14			0.33	0.02	0.31	0.04	5.70	0.17							1.00	0.20	0.07	42.37
Thalassoma rueppellii (Klunzinger, 1871)	6.00	0.99	5.33	0.26	14.33	2.06	21.33	1.01	12.33	1.83	11.00	0.52	3.33	0.39	3.19	0.09	11.67	2.47	4.00	0.53	18.67	1.93	1.00	0.20	0.74	65.25
Thalassothia cirrhosa (Klunzinger, 1871)															0.05	<0.01									<0.01	1.69
Xyrichtys pavo Valenciennes, 1840															0.02	<0.01									<0.01	0.85
Scaridae																									**0.56**	
Calotomus viridescens (Rüppell, 1835)	1.00	0.16	0.33	0.02			0.67	0.03	1.33	0.20			1.46	0.17	8.33	0.25									0.09	38.14

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Chlorurus gibbus (Rüppell, 1829)			1.33	0.06			0.33	0.02			1.33	0.06	0.08	0.01	0.16	<0.01			0.33	0.04					0.02	10.17
Chlorurus sordidus (Forsskål, 1775)					5.33	0.77	5.67	0.27	2.00	0.30	9.33	0.44			0.47	0.01	3.33	0.71	0.67	0.09	6.00	0.62			0.22	16.95
Hipposcarus harid (Forsskål, 1775)															0.16	<0.01									<0.01	3.39
Leptoscarus vaigiensis (Quoy and Gaimard, 1824)													4.90	0.57	17.51	0.52									0.15	27.12
Scarus ferrugineus Forsskål, 1775							1.67	0.08							1.65	0.05									0.02	3.39
Scarus fuscopurpureus (Klunzinger, 1871)													0.13	0.01	2.84	0.08									0.02	11.86
Scarus ghobban Forsskål, 1775															0.79	0.02							0.33	0.07	0.01	12.71
Scarus niger Forsskål, 1775							1.67	0.08			0.67	0.03			0.12	<0.01					1.33	0.14	0.33	0.07	0.03	7.63
Scarus psittacus Forsskål, 1775											1.33	0.06			0.49	0.01									0.01	5.93
Pinguipedidae																									**0.06**	
Parapercis hexophtalma (Cuvier, 1829)	1.33	0.22			2.67	0.38	0.67	0.03	1.00	0.15			0.08	0.01	0.91	0.03					0.67	0.07	1.67	0.34	0.06	29.66
Uranoscopidae																									**<0.01**	
Uranoscopus sulphureus Valenciennes, 1832													0.03	<0.01											<0.01	0.85
Blenniidae																									**0.40**	
Aspidontus taeniatus taeniatus Quoy and Gaimard, 1834													0.08	0.01	0.91	0.03									0.01	12.71
Cirripectes castaneus (Valenciennes, 1836)	0.33	0.05							0.33	0.05															<0.01	1.69
Ecsenius aroni Springer, 1971	1.00	0.16	0.67	0.03					0.33	0.05															0.01	5.08
Ecsenius frontalis (Valenciennes, 1836)	1.00	0.16	0.33	0.02	0.33	0.05	1.33	0.06	0.67	0.10	1.33	0.06			0.14	<0.01			0.33	0.04	2.33	0.24			0.05	16.10
Ecsenius gravieri (Pellegrin, 1906)	0.67	0.11			1.33	0.19					1.33	0.06	0.26	0.03	1.05	0.03			0.33	0.04	0.67	0.07			0.04	22.88
Exallias brevis (Kner, 1868)																					0.67	0.07			<0.01	0.85
Meiacanthus nigrolineatus Smith-Vaniz, 1969	7.67	1.26	2.67	0.13	3.67	0.53	3.00	0.14	4.33	0.64	5.33	0.25	6.10	0.71	5.67	0.17	0.67	0.14	0.67	0.09	0.67	0.07	2.00	0.41	0.28	55.08
Plagiotremus tapeinosoma (Bleeker, 1857)													0.03	<0.01	0.14	<0.01									<0.01	4.24
Plagiotremus townsendi (Regan, 1905)											0.33	0.02													<0.01	0.85

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Gobiidae																									**0.95**	
Amblyeleotris steinitzi (Klausewitz, 1974)					3.00	0.43	1.67	0.08	0.67	0.10	3.33	0.16			0.07	<0.01					0.33	0.03	1.00	0.20	0.07	8.47
Amblyeleotris sungami (Klausewitz, 1969)							0.67	0.03			0.33	0.02	0.05	0.01	0.05	<0.01									0.01	3.39
Amblygobius albimaculatus (Rüppell, 1830)													0.56	0.07	2.60	0.08									0.02	17.80
Bryaninops natans Larson, 1985									6.67	0.99	86.67	4.10													0.61	3.39
Fusigobius longispinus Goren, 1978															0.05	<0.01									<0.01	1.69
Gnatholepis anjerensis (Bleeker, 1851)	5.00	0.82					1.00	0.05					1.62	0.19	4.40	0.13							0.67	0.14	0.08	22.03
Gobiodon citrinus (Rüppell, 1838)					1.33	0.19											1.00	0.21	1.00	0.13			12.67	2.59	0.11	6.78
Istigobius decoratus (Herre, 1927)	2.33	0.38	0.33	0.02					1.00	0.15							1.33	0.28			1.33	0.14	0.67	0.14	0.05	9.32
Lotilia graciliosa Klausewitz, 1960															0.07	<0.01									<0.01	2.54
Valenciennea puellaris (Tomiyama, 1956)											0.33	0.02	0.03	<0.01	0.05	<0.01									<0.01	2.54
Acanthuridae																									**2.19**	
Acanthurus nigrofuscus (Forsskål, 1775)	12.33	2.03	8.33	0.40	28.33	4.07	35.33	1.68	14.00	2.08	22.67	1.07	1.44	0.17	2.74	0.08	46.67	9.89	6.67	0.89	62.67	6.47	10.00	2.04	1.65	57.63
Acanthurus sohal (Forsskål, 1775)															0.16	<0.01									<0.01	2.54
Ctenochaetus striatus (Quoy and Gaimard, 1825)	2.00	0.33	2.67	0.13	5.33	0.77	3.67	0.17	3.67	0.54	5.00	0.24	0.31	0.04	1.58	0.05	11.33	2.40	6.33	0.84	15.67	1.62	1.67	0.34	0.39	39.83
Naso unicornis (Forsskål, 1775)													0.26	0.03	0.84	0.02									0.01	7.63
Zebrasoma veliferum (Bloch, 1795)							0.33	0.02			0.33	0.02	0.08	0.01	0.33	0.01	0.33	0.07	0.67	0.09	3.67	0.38	1.00	0.20	0.04	11.86
Zebrasoma xanthurum (Blyth, 1852)	0.33	0.05	0.67	0.03	1.67	0.24	0.67	0.03	1.00	0.15	1.67	0.08	0.10	0.01	0.72	0.02	5.33	1.13			1.67	0.17	0.33	0.07	0.09	31.36
Siganidae																									**1.76**	
Siganus argenteus (Quoy and Gaimard, 1825)													0.31	0.04	1.07	0.03									0.01	7.63
Siganus luridus (Rüppell, 1829)			0.67	0.03	6.00	0.86							67.38	7.87	27.30	0.80	2.00	0.42			1.33	0.14			0.69	31.36
Siganus rivulatus Forsskål, 1775													69.10	8.07	65.88	1.94	7.33	1.55			6.33	0.65	13.33	2.72	1.06	32.20
Scombridae																									**<0.01**	
Euthynnus affinis (Cantor, 1849)															0.58	0.02									<0.01	0.85

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Bothidae																									**<0.01**	
Bothus pantherinus (Rüppell, 1830)													0.21	0.02	0.09	<0.01									<0.01	5.93
Samaridae																									**<0.01**	
Samaris cristatus Gray, 1831													0.03	<0.01											<0.01	0.85
Soleidae																									**<0.01**	
Pardachirus marmoratus (Lacepède, 1802)					0.33	0.05									0.05	<0.01	0.33	0.07							<0.01	2.54
Balistidae																									**0.07**	
Balistapus undulatus (Park, 1797)																							0.33	0.07	<0.01	0.85
Pseudobalistes fuscus (Bloch and Schneider, 1801)					0.33	0.05							0.31	0.04	0.02	<0.01									<0.01	5.93
Sufflamen albicaudatus (Rüppell, 1829)	1.00	0.16	0.67	0.03	1.00	0.14	0.33	0.02	0.33	0.05	1.00	0.05	1.21	0.14	1.93	0.06	0.33	0.07	1.00	0.13	0.67	0.07	0.33	0.07	0.06	54.24
Monacanthidae																									**0.10**	
Aluterus scriptus (Osbeck, 1765)															0.02	<0.01									<0.01	0.85
Amanses scopas (Cuvier, 1829)					0.33	0.05	0.33	0.02			1.33	0.06			0.09	<0.01			0.33	0.04	1.00	0.10			0.02	11.02
Cantherhines pardalis (Rüppell, 1837)			0.33	0.02			0.33	0.02	0.33	0.05	0.33	0.02	0.05	0.01	0.28	0.01					1.00	0.10			0.02	14.41
Pervagor randalli Hutchins, 1986	1.33	0.22					1.33	0.06					0.18	0.02	1.02	0.03	1.67	0.35			2.00	0.21	0.33	0.07	0.05	29.66
Pseudomonacanthus pusillus (Rüppell, 1829)													0.36	0.04	0.65	0.02									0.01	17.80
Ostraciidae																									**0.10**	
Ostraccion cubicus (Bloch, 1791)	0.33	0.05	1.00	0.05	1.33	0.19	0.33	0.02			0.67	0.03	0.46	0.05	1.74	0.05	1.33	0.28	0.33	0.04	2.00	0.21			0.06	41.53
Ostracion cyanurus Rüppell, 1828	0.33	0.05	0.33	0.02	0.67	0.10	0.33	0.02	0.33	0.05	0.33	0.02	0.21	0.02	0.42	0.01	0.67	0.14			1.67	0.17	0.33	0.07	0.04	24.58
Tetrosomus gibbosus (Linnaeus, 1758)	0.33	0.05													0.21	0.01									<0.01	8.47
Tetraodontidae																									**0.32**	
Arothron diadematus (Rüppell, 1829)			0.33	0.02									0.03	<0.01							0.33	0.03			<0.01	3.39
Arothron hispidus (Linnaeus, 1758)					0.33	0.05							0.23	0.03	0.44	0.01									0.01	19.49
Arothron stellatus (Bloch and Schneider, 1801)	0.33	0.05	0.33	0.02									0.03	<0.01	0.05	<0.01									<0.01	4.24
Canthigaster coronata (Vaillant and Sauvage, 1875)			1.00	0.05	0.33	0.05	0.33	0.02	1.00	0.15	2.33	0.11	1.13	0.13	3.00	0.09	1.67	0.35	0.33	0.04	0.67	0.07	1.00	0.20	0.08	68.64

Table 4 continued

Depth	Cement jetty				Marine Science Station				Tourist camp				Al-Mamlah Bay				Jordan Fertilizer Industries				Jordan Fertilizer Industries jetty				**Total**	
	6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m		6 m		12 m			
	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	AA	RA	RA	FA
Canthigaster margaritata (Rüppell, 1829)	1.33	0.22	0.33	0.02					0.33	0.05			3.05	0.36	5.65	0.17	1.67	0.35	0.67	0.09	9.33	0.96	0.67	0.14	0.15	65.25
Canthigaster pygmaea Allen and Randall, 1977															0.02	<0.01									<0.01	0.85
Torquigener flavimaculosus Hardy and Randall, 1983													2.85	0.33	7.26	0.21									0.07	25.42
Diodontidae																									**0.02**	
Cyclichthys spilostylus (Leis and Randall, 1982)	0.67	0.11	0.33	0.02					0.33	0.02			0.10	0.01	0.79	0.02	1.00	0.21	0.33	0.04					0.02	22.88

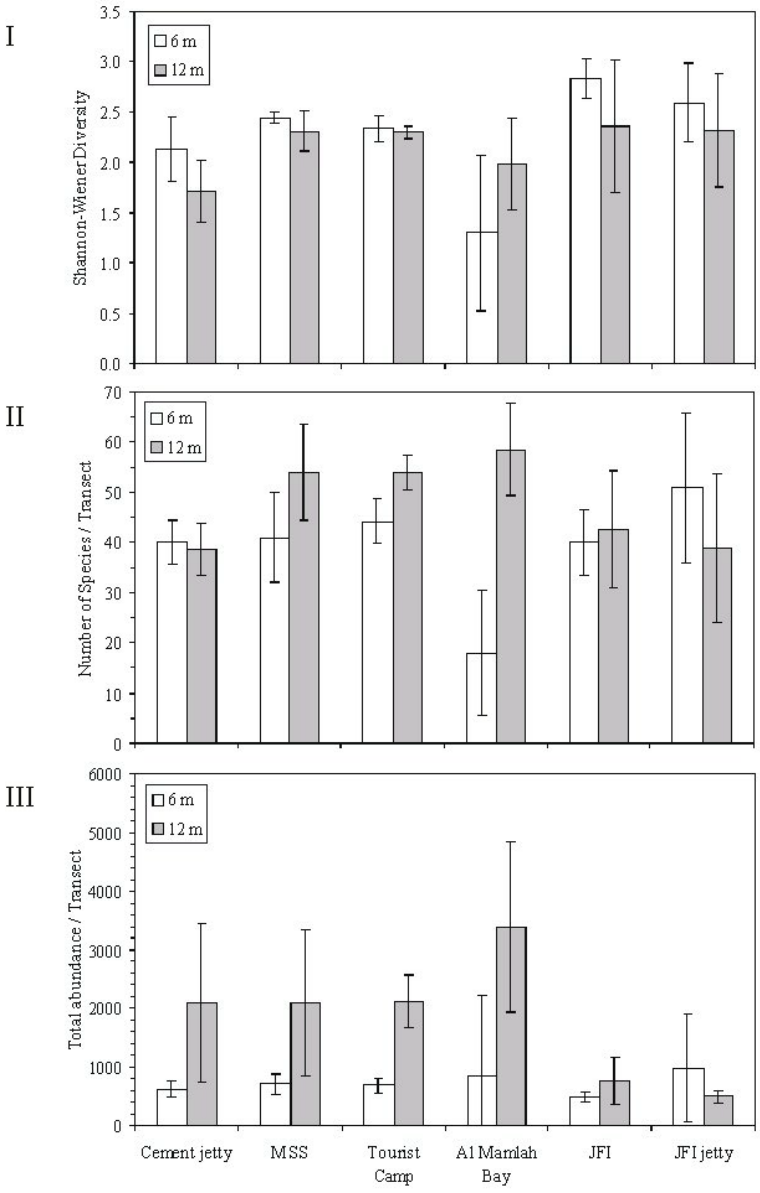

Fig. 3 I Diversity (Shannon-Wiener Index; ln basis), **II** species richness, and **III** abundance for 6 m and 12 m depths (average and ±SD) of fish assemblages at sites along the Jordanian Red Sea coast, Gulf of Aqaba

Average abundance ranged from 472 fishes per transect at Jordan Fertiliser Industries at 6 m depth to 3,397 fishes per transect at Al-Mamlah Bay at 12 m depth (Fig. 3). Higher fish abundance was observed at 12 m compared to 6 m depth covering all sites (p<0.001), at the seagrass-dominated site Al-Mamlah Bay (p<0.001) as well as on coral reefs (p=0.015). There were more fishes at 12 m depth at Al-Mamlah Bay compared to 12 m depth of coral-dominated sites (p<0.001). Due to inhomogenous variances no significant differences in abundance were detected at 6 m depth between coral reef and seagrass meadow (Table 5).

Table 5 Significance tests for diversity, species richness and abundance of fish assemblages at sites along the Jordanian Red Sea coast, Gulf of Aqaba (*0.05≥p≥0.01, **0.01>p≥0.001, ***p<0.001, *log(1+x)* represents log(1+x) transformed data, *i.v.* inhomogenous variances, *n.s.* not significant, *coral* coral reef, *seagrass* seagrass meadow)

	6 m vs 12 m	6 m vs 12 m (seagrass)	6 m vs 12 m (coral)	6 m (seagrass) vs 6 m (coral)	12 m (seagrass) vs 12 m (coral)
Diversity					
F-Test	i.v.	i.v.		i.v.	
F-Test PV			1.831		1.085
F-Test CV P 99%			3.910		3.420
ANOVA	i.v.	i.v.		i.v.	
F			3.643		2.521
p			0.067		0.118
Significance level			n.s.		n.s.
Species richness					
F-Test	i.v.				
F-Test PV		1.863	1.639	2.123	1.438
F-Test CV P 99%		2.120	3.910	3.450	2.600
ANOVA	i.v.				
F		285.488	0.445	52.113	19.706
p		< 0.001	0.510	< 0.001	< 0.001
Significance level		*******	n.s.	*******	*******
Abundance			log(1+x)		
F-Test				i.v.	
F-Test PV	1.843	1.149	2.865		1.920
F-Test CV P 99%	1.910	2.150	3.910		3.420
ANOVA				i.v.	
F	97.409	21.211	6.719		20.839
p	< 0.001	< 0.001	0.015		< 0.001
Significance level	*******	*******	*****		*******

Multivariate analysis of the shore fish communities along the Jordanian Red Sea coast

Cluster analysis and MDS plot based on percentage of benthic cover revealed two main groups (Fig. 4): (A) the seagrass-dominated Al-Mamlah Bay and (B) the coral reefs with two subgroups (B.1) 6 m and (B.2) 12 m depth. Two samples (3a and 6b) did not match the clusters in the dendrogram, but 6b did fit into the groups of the MDS plot. Coral reef sites at 6 m and 12 m depth were grouped together with a 1.5 times higher

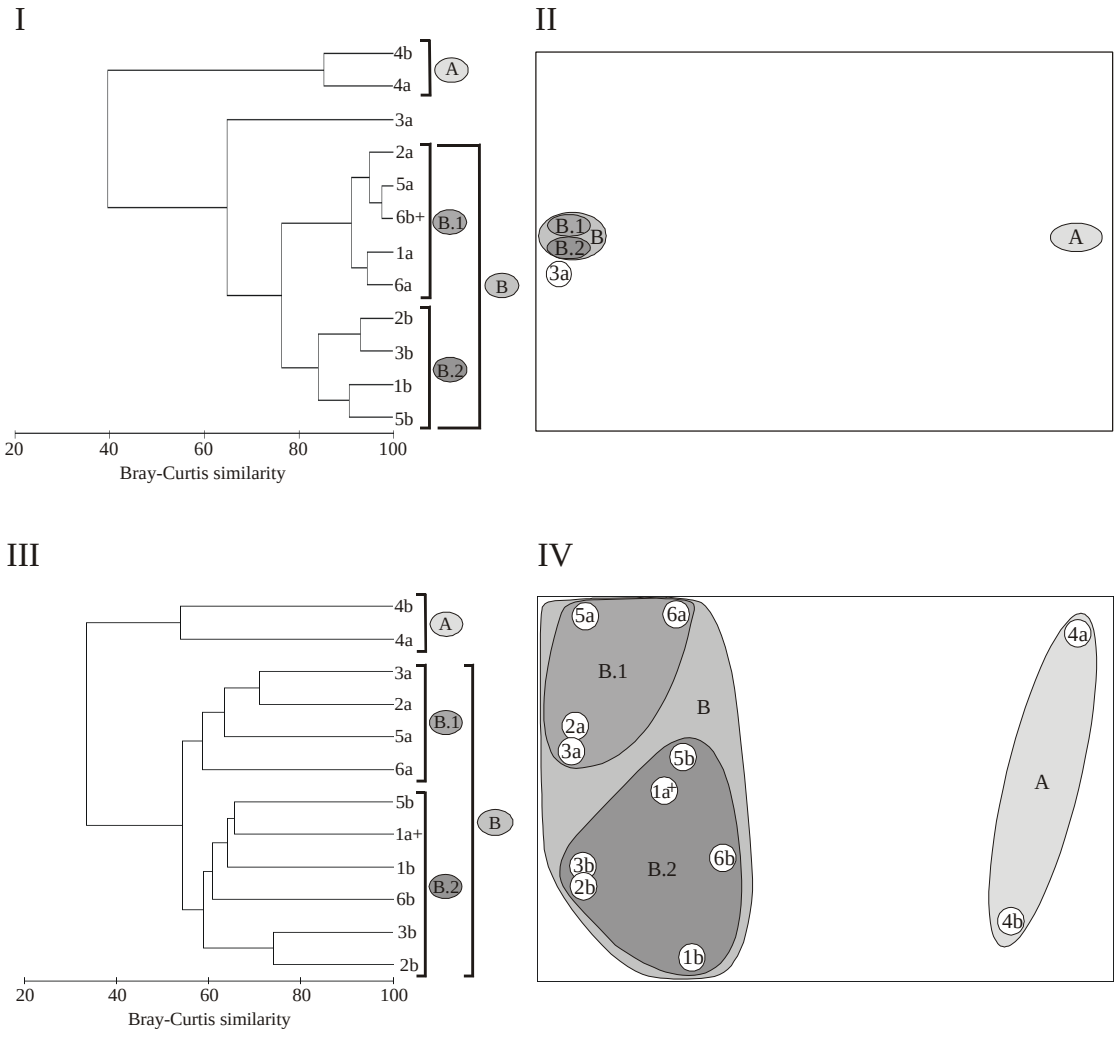

Fig. 4 Dendrogram **I** and MDS plot **II** of relationships between benthic habitats (Bray-Curtis similarity, group average; stress = 0), and dendrogram **III** and MDS plot **IV** of relationships between fish assemblages (Bray-Curtis similarity, log(1+x) transformation of data, standardisation, group average, stress = 0.05) at sites along the Jordanian Red Sea coast, Gulf of Aqaba. RELATE test for similarities between the multivariate pattern: Global ρ=0.638, p=0.006. For site labels see Fig. 1 (*a* 6 m depth, *b* 12 m depth). *A* seagrass-dominated site, *B* coral-dominated sites (*B.1* 6 m depth, *B.2* 12 m depth). $^{+}$ indictes mismatch

similarity than coral reefs to the seagrass meadow. This grouping was correlated with cluster analysis as well as MDS plot based on average fish species abundance (Fig. 4). The mismatch of sample 1a in the dendrogram and MDS plot did not disturb the general division into three groups. The RELATE test for similarities between the multivariate pattern revealed a significant correlation (Global ρ=0.638, p=0.006).

An ANOSIM significance test confirmed the difference in the benthic habitat between 6 m and 12 m depths of coral reefs (p=0.021) as well as between reefs and the seagrass meadow (p<0.001) (Table 6). There were no significant differences between 6 m and 12 m depths regarding all sites (coral and seagrass) and the seagrass-dominated site. All identified groups of the fish assemblages were evidenced by an ANOSIM significance test with p<0.001 (Table 6).

Table 6 ANOSIM significance test on Bray-Curtis similarities of relationships between benthic habitats and between fish assemblages at sites along the Jordanien Red Sea coast, Gulf of Aqaba (no transformation or standardisation of data, *coral* coral-dominated sites, *seagrass* seagrass-dominated site, *0.05≥p≥0.01, **0.01>p≥0.001, ***p<0.001, *n.s.* not significant)

	6 m vs 12 m	6 m vs 12 m (coral)	6 m vs 12 m (seagrass)	coral vs seagrass
Benthic habitat				
Global R	0.053	0.123	-0.185	0.754
p	0.064	0.021	0.6	<0.001
Significance level	n.s.	*	n.s.	***
Fish assemblages				
Global R	0.345	0.255	0.455	0.144
p	<0.001	<0.001	<0.001	<0.001
Significance level	***	***	***	***

Species analysis by dendrogram and MDS plot revealed four main groups (Fig. 5): (A) fishes of coral reefs, with the subgroups (A.1) Apogonidae, (A.2) higher relative abundance at the shallow reef slope (6 m) and (A.3) higher relative abundance at the deep reef slope (12 m); (B) fishes of seagrass meadows and sand flats; (C) Siganidae; and (D) Caesionidae. Five species were not assigned to any group identified above. In addition, four species showed a mismatch in the correlation to the main groups. These minor mismatches are due to uneven distribution of these species and did not disturb the

overall picture. Species analysis by dendrogram and MDS is an exploratory tool for the identification of typical fish communities of a certain habitat. Due to the high number of species and abundance it was difficult to distinguish these groups a priori. Therefore, an

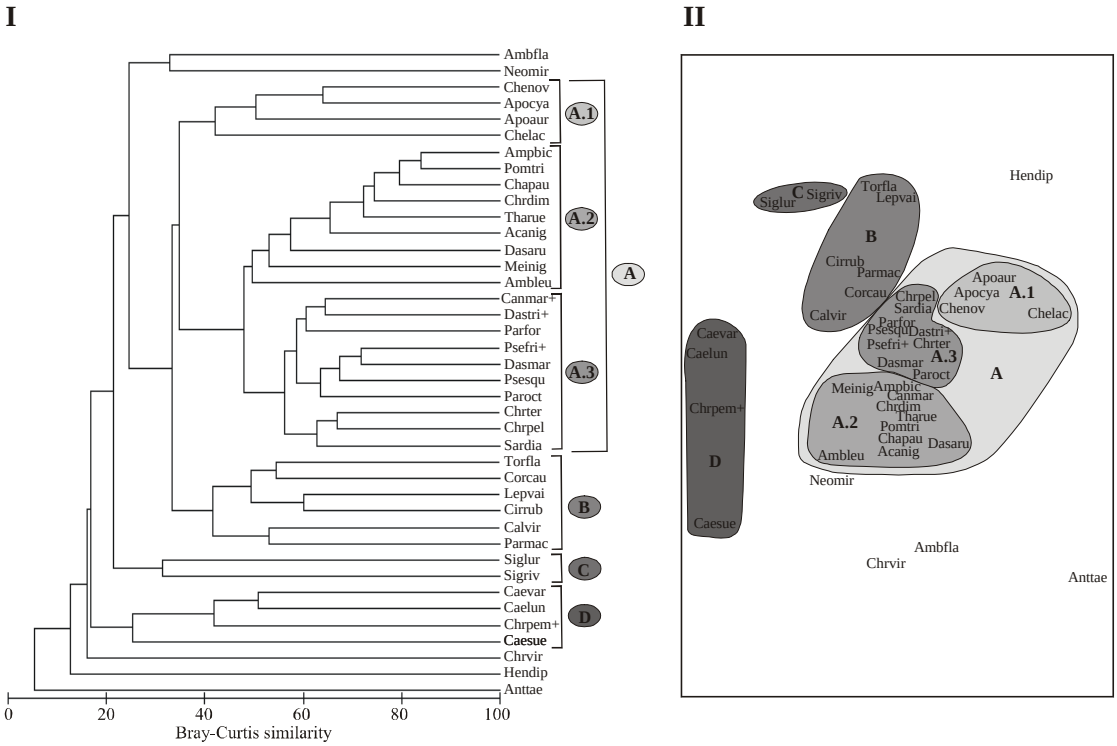

Fig. 5 Dendrogram **I** and MDS plot **II** of fish communities at the Jordanian Red Sea coast, Gulf of Aqaba. This analysis considers species with at least 0.2% of total abundance (no pelagic species, square root transformation of data, standardisation, group average, stress=0.16). *A* Fishes of coral reefs (*A.1* Apogonidae, *A.2* 6 m depth, *A.3* 12 m depth). *B* Fishes of seagrass meadows and sand flats. *C* Siganidae. *D* Caesionidae. Assignment of species to different depth reflects a higher relative abundance in this depth. $^{+}$indictes mismatch. *Species key*: Acanig *Acanthurus nigrofuscus*, Ambfla *Amblyglyphidodon flavilatus*, Ambleu *Amblyglyphidodon leucogaster*, Ampbic *Amphiprion bicinctus*, Anttae *Anthias taeniatus*, Apoaur *Apogon aureus*, Apocya *Apogon cyanosoma*, Caelun *Caesio lunaris*, Caesue *Caesio suevicus*, Caevar *Caesio varilineata*, Calvir *Calotomus viridescens*, Canmar *Canthigaster margaritata*, Chapau *Chaetodon paucifasciatus*, Chelac *Cheilodipterus lachneri*, Chenov *Cheilodipterus novemstriatus*, Chrdim *Chromis dimidiata*, Chrpel *Chromis pelloura*, Chrpem *Chromis pembae*, Chrter *Chromis ternatensis*, Chrvir *Chromis viridis*, Cirrub *Cirrhilabrus rubriventralis*, Corcau *Coris caudimacula*, Dasaru *Dascyllus aruanus*, Dasmar *Dascyllus marginatus*, Dastri *Dascyllus trimaculatus*, Hendip *Heniochus diphreutes*, Lepvai *Leptoscarus vaigiensis*, Meinig *Meiacanthus nigrolineatus*, Neomir *Neopomacentrus miryae*, Parfor *Parupeneus forsskali*, Parmac *Parupeneus macronema*, Paroct *Paracheilinus octotaenia*, Pomtri *Pomacentrus trichourus*, Psefri *Pseudochromis fridmani*, Psesqu *Pseudanthias squamipinnis*, Sardia *Sargocentron diadema*, Siglur *Siganus luridus*, Sigriv *Siganus rivulatus*, Tharue *Thalassoma rueppellii*, Torfla *Torquigener flavimaculosus* (see Plates 1-8)

ANOSIM significance test was not conducted, because it only applies to groups of samples specified prior to seeing or collecting the data.

Correlation of fish community pattern to the benthic habitat

The BIO-ENV procedure of the PRIMER 5 software was used to correlate the fish community pattern to the benthic habitat (Table 7). The maximum correlation (r=0.703, weighted Spearman rank correlation) was obtained with the seagrass cover, followed by the combination of seagrass cover and depth (r=0.677), and the combination of seagrass, depth and live coral cover (r=0.579).

Fish species richness was positively linked to hard substrate cover by a power regression (r=0.6742, p<0.005) (Fig. 6). The coefficient of determination (r^2) indicates that 45.5% of variation can be attributed to hard substrate cover. The relationship of fish species richness to habitat diversity showed a positive correlation in a power regression (r=0.7064, p<0.005) as well (Fig. 6). The analysis revealed that r^2 can assign 49.9% of variation to habitat diversity. A linear regression of abundance of corallivores in relation to live coral cover resulted in a positive correlation (r=0.6956, p<0.005). In this case the r^2 indicates that 48.4% of variation can be attributed to live hard coral cover.

Table 7 Correlation of fish community pattern to the benthic habitat (BIO-ENV, weighted Spearman rank correlation); *LC* live hard coral, *SC* live soft coral, *DC* dead coral and rock, *SG* seagrass, *S* sand, *D* depth, *k* number of variables combined

k	Best variable combinations (weighted Spearman rank correlation)					
1	SG	LC	DC	D	S	SC
	(**0.703**)	(0.280)	(0.241)	(0.224)	(0.035)	(-0.094)
2	SG+D	SG+LC	SG+S	SG+DC	SG+SC	LC+D
	(**0.677**)	(0.506)	(0.488)	(0.459)	(0.385)	(0.286)
3	SG+D+LC	SG+D+DC	SG+D+S	SG+T+SC	SG+LC+S	SG+LC+DC
	(**0.579**)	(0.528)	(0.507)	(0.491)	(0.458)	(0.439)

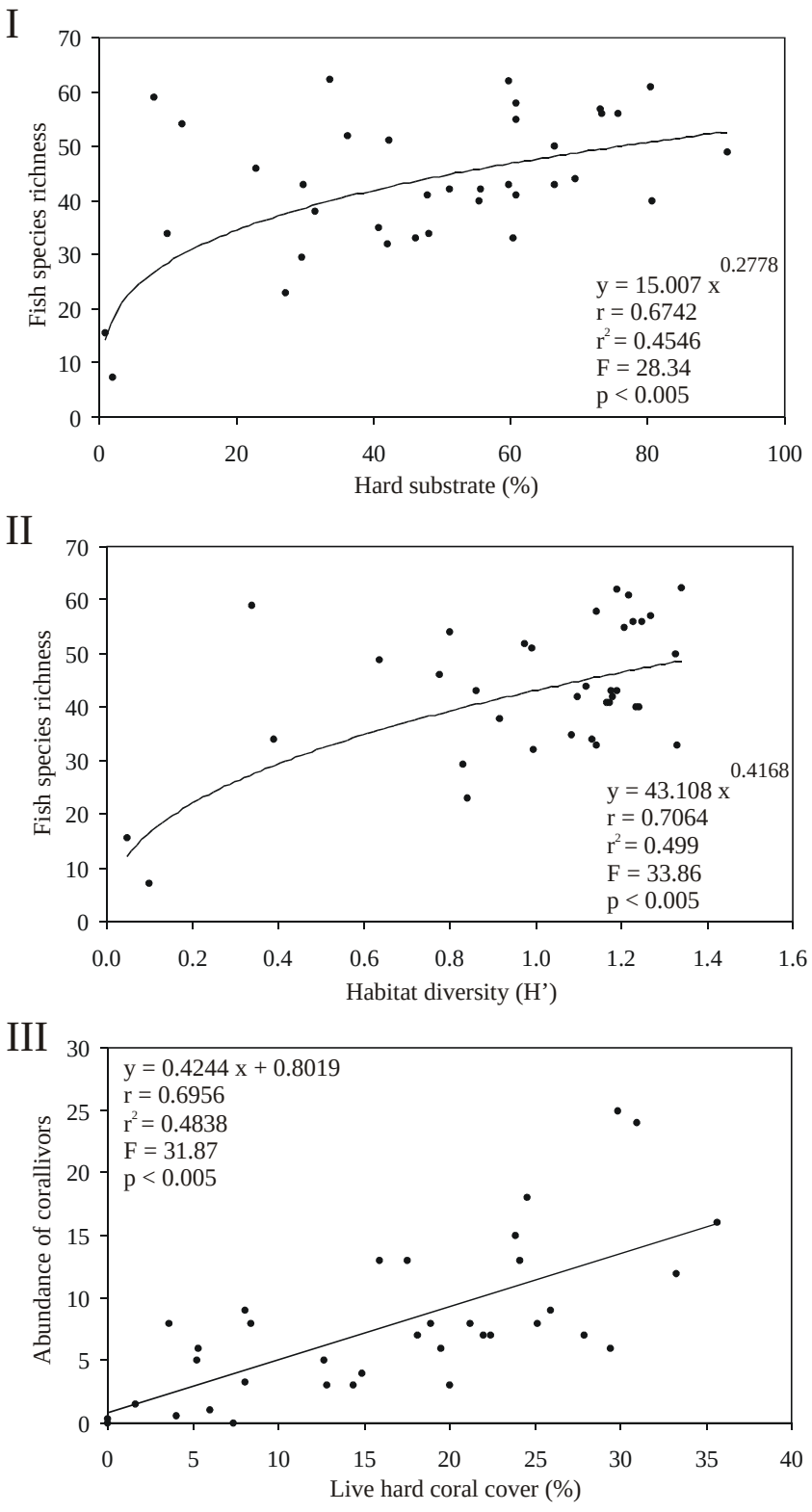

Fig. 6 Relationship of **I** fish species richness to benthic hard substrate cover and **II** to habitat diversity, as well as **III** abundance of corallivores to live hard coral cover at the Jordanian Red Sea coast, Gulf of Aqaba

Biogeography

Cluster analysis and MDS plot revealed four main groups (Fig. 7): (1) Arabian Gulf, (2) Indian Ocean, (3) Red Sea, and (4) Southern Arabia. Differences in the grouping of the Southern Arabian cluster can be observed between the multivariate methods used in this analysis. On the one hand the Southern Arabia cluster shows the lowest similarity to all other sites in the analysis based on Bray-Curtis similarity. On the other hand the Euclidian distance revealed a high similarity to the Red Sea cluster. However, both MDS plots show a very similar pattern, where the Red Sea and Southern Arabian sites are situated between the Arabian Gulf and Indian Ocean sites.

The dendrogram suggested subgroups within the Red Sea, but neither MDS plot nor ANOSIM significance test confirmed this pattern, but ANOSIM gave evidence for the main groups (Table 8). However, ANOSIM based on Bray-Curtis similarity showed a significant difference between the Arabian Gulf and all other sites, whereas analysis based on Euclidian distance was not significant. On the one hand the Arabian Gulf shares 55.3% of its species with the Indian Ocean, whereas only 45.6% of its species occure in the Red Sea. On the other hand 75.4% of the Red Sea species have an Indian Ocean distribution, but the Red Sea shares only 22.7% of its species with the Arabian Gulf.

Table 8 ANOSIM significance test on Bray-Curtis similarities (*BCS*) and Euclidean distance (*ED*) for biogeographic relationships. (*$0.05 \geq p \geq 0.01$, **$0.01 > p \geq 0.001$, ***$p < 0.001$, *n.s.* not significant)

	Red Sea vs Southern Arabia	Red Sea vs Indian Ocean	Red Sea vs Arabian Gulf	Gulf of Aqaba vs Red Sea proper	Arabian Gulf vs Red Sea, Southern Arabia and Indian Ocean
BCS					
Global R	0.992	0.993	1.000	0.323	0.787
p	0.006	0.001	0.006	0.125	0.001
Significance level	**	**	**	n.s.	**
ED					
Global R	0.914	0.616	0.987	0.169	-0.037
p	0.006	0.001	0.006	0.161	0.548
Significance level	**	**	**	n.s.	n.s.

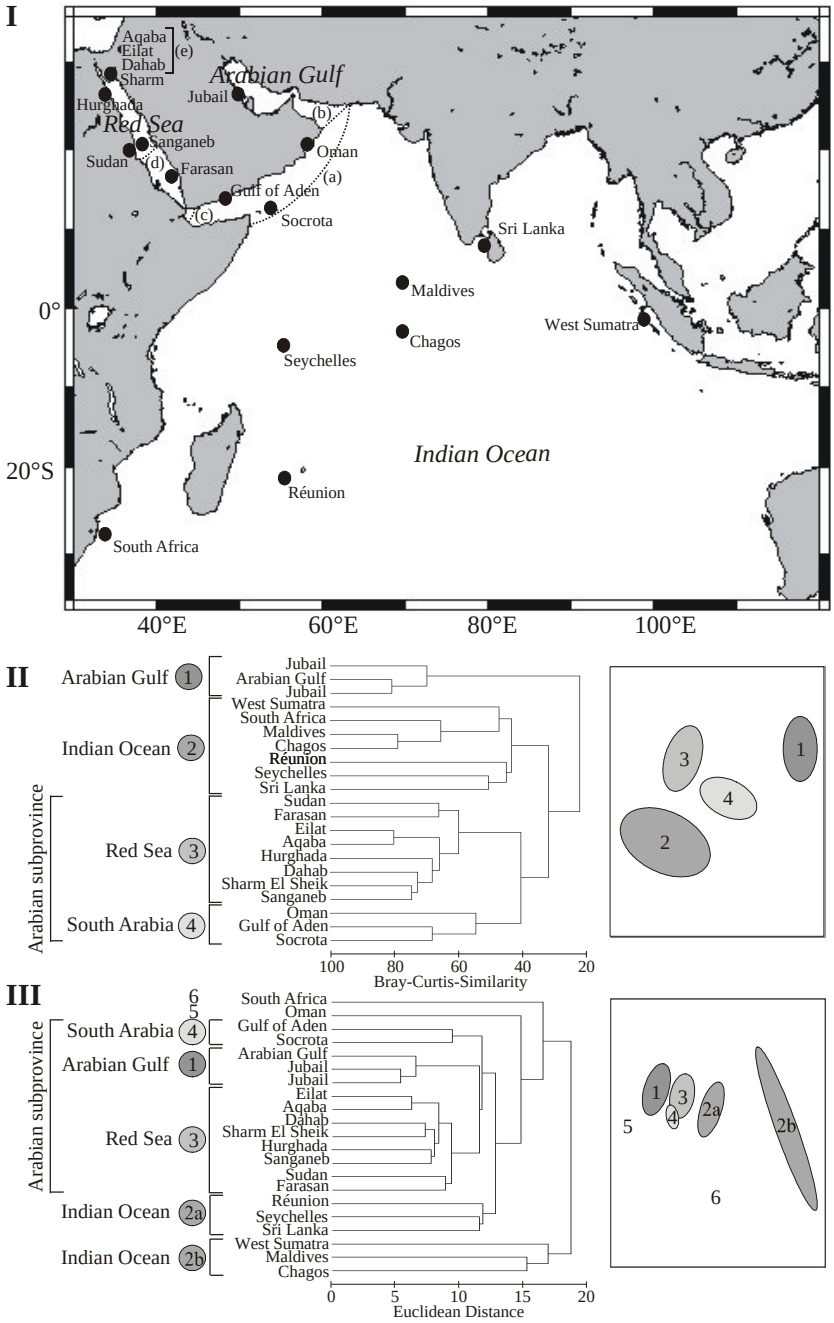

Fig. 7 Map **I**, dendrogram and MDS plot based on Bray-Curtis similarity (stress=0.09) **II** and Euclidean distance (stress=0.06) **III** of biogeographic relationships between coastal fish assemblages of the Red Sea, Gulf of Aden, Indian Ocean and Arabian Gulf (Bray-Curtis similarity and Euclidean distance based on presence/absence of 712 species); proposed biogeographic borders after Klausewitz (1978, 1989) and (Kemp 1998): *a* border between Indian Ocean and Gulf of Aden/Southern Arabia, *b* border between Arabian Gulf and southern Arabia, *c* border between Gulf of Aden and Red Sea (please see discussion about location), *d* barrier in the southern Red Sea at 20°N, *e* Gulf of Aqaba (see Fig. 1)

DISCUSSION

All our conclusions are restricted to day active and non-cryptic species. As discussed by Brock (1982) dwarf, cryptic and nocturnal species are underestimated by the visual census technique. The visual census technique is widely applied and accepted for fish ecological studies on coral reefs (English et al. 1994), although differences in skill and technique of observers are a source of imprecision and/or bias (Thompson and Mapstone 1997). Therefore, the first author (M.A. Khalaf) conducted all censuses himself to avoid this problem. In the Jordanian waters of the Gulf of Aqaba 348 species of fish have been recorded to date, with around 294 species occurring in shallow-water habitats such as coral reefs, seagrass meadows and sand flats (Khalaf and Disi 1997). In this study, approximately two thirds (198 species) of the ichthyofauna at the Jordanian coast are considered for the analysis of shallow-water fish communities. In many other studies the investigations are restricted to certain families or subsets of the fish community, and the percentage of species considered for the analysis is not known.

Shore fish communities at the Jordanian Red Sea coast

Dominant taxa and fish community parameters

Pseudanthias squamipinnis (Plate 3) is the most abundant species on Jordanian coral reefs as well as in the “Japanese gardens”, off Eilat (Rilov and Benayahu 2000), at Nuweiba (Ben-Tuvia et al. 1983) and at Sanganeb atoll (Krupp et al. 1993). Other species making up more than 1% of total abundance in Jordan as well as at Sanganeb atoll are *Chromis dimidiata* (Plate 5) and *Chromis ternatensis*. The following species belong to the ten most abundant species at both sides of the northern end of the Gulf of Aqaba (“Japanese gardens” and sites in Jordan): *Pomacentrus trichourus* (Plate 6), *Paracheilinus octotaenia* (Plate 7), *Chromis dimidiata* (Plate 5), *Dascyllus marginatus* (Plate 6) and *Neopomacentrus miryae* (Plate 6) (Table 4). As expected, the fish assemblages at the Jordanian and Israeli coasts are very similar.

On Indo-Pacific coral reefs, labrid and pomacentrid species are the dominant fishes (Table 3). Labridae (wrasses) contribute the highest percentage of species, followed by Pomacentridae (damselfishes). The fish fauna on coral reefs in the Arabian Gulf shows a different composition, probably due to unfavourable environmental conditions for many tropical fishes. Two studies in the Caribbean revealed two main differences to the

Indo-Pacific: a lower percentage of Labridae and a very high percentage of Serranidae (Table 3). However, comparisons have to be taken with caution, especially for rather cryptic families such as Gobiidae, Blenniidae and Scorpaenidae.

In terms of relative abundance of families, the ichthyofauna of the Jordanian coast is dominated by Pomacentridae, followed by Anthininae (subfamily of Serranidae) and Labridae. Visual censuses of fish assemblages on coral reefs in New Caledonia (Rossier and Kulbicki 2000) and on the Great Barrier Reef (Ackerman and Bellwood 2000) revealed the dominance of Pomacentridae as well. In New Caledonia the second most abundant family was Lutjanidae, followed by Chaetodontidae, Labridae and Apogonidae (Rossier and Kulbicki 2000). On the Great Barrier Reef the ranking after the dominant pomacentrids was Gobiidae, Caesionidae, Apogonidae, Labridae and Chaetodontidae (Ackerman and Bellwood 2000). Several families, such as Lutjanidae (3 species), Haemulidae (4 species) and Ephippidae (1 species) are very rare along the Jordanian Red Sea (Khalaf and Disi 1997), but can be frequently observed in the Red Sea proper and other parts of the Indo-Pacific.

Shannon-Wiener diversity (*H’*) did not differ significantly between depths as well as coral- and seagrass-dominated sites (Fig. 3). Comparison to other studies does not give a clear picture of an influence of depth on diversity (*H’*). On the one hand Friedlander and Parrish (1998) pointed out a weak positive correlation between diversity (*H’*) and depth which explained around 20% of the variation. On the other hand Öhman and Rajasuriya (1998) did not find a significant correlation between diversity (*H’*) and depth.

On the one hand species richness was rather similar in the two depths on the coral reefs. This picture is in contrast to the general trend of species richness increasing with depth, shown for the Red Sea (Edwards and Rosewell 1981, Roberts and Ormond 1987), in Sri Lanka (Öhman and Rajasuriya 1998) and Hawaii (Friedlander and Parrish 1998). However, this trend is most pronounced between 1 m and 6 m depth, with a smaller or no difference between 6 m and 12 m depth (Roberts and Ormond 1987). One or the other of our study sites might show this difference as well (e.g. Tourist Camp), but the overall pattern does not support a significant difference between 6 m and 12 m depth. On the other hand the seagrass-dominated site showed a significantly higher species richness at 12 m depth. This pattern might be generated by a higher percentage

of hard substrate at 12 m depth, which provides more three-dimensional structures with holes for shelter. In a study of Roberts and Ormond (1987) the number of holes in a coral reef accounted for 77% of the variance in fish abundance and Friedlander and Parrish (1998) accounted 73% of the variance in fish biomass to the mean hole volume. Due to the lack of shelter in 6 m depth at Al-Mamlah Bay, the species richness is reduced relative to coral reefs at the same depth. Comparison of seagrass meadow and coral reefs in 12 m depth revealed the opposite picture, with a higher number of species and higher abundance in the seagrass.

The higher species richness and abundance in 12 m depth can be explained by the high productivity of the seagrass meadows and by feeding migrations of fishes from the coral reef to the seagrass beds (Ogden 1980, Robblee and Ziemann 1984, Quinn and Ogden, 1984, Kochzius 1999). Invertebrate feeders are significantly more abundant at the seagrass-dominated site (Khalaf and Kochzius in press), where they can utilise the rich crustacean fauna. Nocturnal feeding migrations of invertebrate feeders from coral reefs into seagrasses are documented for the Atlantic as well as Indo-Pacific (Weinstein and Heck 1979, Bell and Pollard 1989, Kochzius 1999). Studies in the Caribbean have shown that the biomass of fishes in coral reefs adjacent to seagrass meadows is higher than in reefs without seagrass beds (Birkeland 1985). Comparison of fisheries from different coral reef regions suggested that coral reefs bounded by extended shallow-water habitats, such as seagrass meadows or mangroves, yield the highest catch. Reefs with a ratio of shallow-water habitat to coral reef of 1:1 or more are very productive (Marshall 1985). Despite the lack of biomass data in this study, the high abundance of fishes in Al-Mamlah Bay supports these findings. Before the recent closing of this area, it was the favourite fishing ground for local fishermen, indicating a high standing stock and high productivity of fish. These results support the importance of Al-Mamlah Bay as a high productive area along the Jordanian Red Sea coast. A comparison of six seagrass meadows along the Jordanian coast revealed the highest seagrass biomass (g/m^3) at Al-Mamlah Bay (Wahbeh 1981).

The overall picture shows a significantly lower abundance of fishes at 6 m depth than at 12 m depth (Fig. 3, Table 5). At the seagrass-dominated Al-Mamlah Bay this pattern can be explained by the lack of shelter at 6 m depth. At the coral-dominated sites, this difference is due to the high abundance of *Pseudanthias squamipinnis* (Plate 3) and

other planktivores in 12 m depth at all sites (Table 4). *P. squamipinnis* accounts for 24.1% of the total abundance and feeds in large schools on zooplankton at sites exposed to current. At the Jordanian coast planktivorous fishes are significantly more abundant at 12 m depth than at 6 m depth (Khalaf and Kochzius in press). The 12 m transects are more exposed to currents bringing zooplankton from offshore waters into the reef. A positive correlation of abundance as well as biomass of planktivores and depth was reported by Friedlander and Parrish (1998), but total fish abundance did not reveal a connection to depth as well. Investigations on herbivorous fishes, such as Acanthuridae (surgeonfishes), Scaridae (parrotfishes), and Siganidae (rabbitfishes) on a coral reef in Aqaba suggests a higher abundance of these families in 10 m depth than in 5 m depth (Bouchon-Navaro and Harmelin-Vivien 1981).

The analysis of the dominant taxa and fish community parameters revealed the following pattern: (1) Labridae and Pomacentridae dominated the ichthyofauna in terms of species richness in the Gulf of Aqaba as well as on other Indo-Pacific coral reefs, (2) Pomacentridae was the dominant family in terms of relative abundance, (3) in the observed range of 6 m and 12 m depth fish diversity and species richness on coral reefs in Aqaba were not correlated to depth, (4) abundance of fishes was significantly higher at 12 m depth than at 6 m depth along the Jordanian Red Sea coast, and (5) the seagrass-dominated site showed a significantly higher species richness and abundance at 12 m depth than the coral-dominated sites, probably due to the high productivity of the seagrass meadows.

Multivariate analysis of the fish community

Cluster analysis, MDS plot and ANOSIM indicate significant differences between the fish communities of the two different depths as well as the two different habitats (Fig. 4, Table 6). This pattern of the fish communities is correlated to the composition of the benthic habitat (Global ρ=0.638, p=0.006), supporting that habitat composition as well as depth are the main factors that influence the composition of the fish assemblages. The multivariate BIO-ENV procedure reveals the best correlation of the fish community pattern to habitat parameters in seagrass cover (r=0.70) and combinations of the parameters seagrass cover and depth (r=0.68) as well as seagrass cover, depth and live hard coral (r=0.58). ANOSIM indicate that the overall benthic

habitat composition does not show a significant difference between 6 m and 12 m depth, whereas fish communities are significantly different. This pattern implies that fish community changes with depth are not caused by changes in habitat composition. However, coral reefs show a significant difference in benthic habitat composition at the two depths, suggesting that differences in fish assemblages between depths were connected to changes in the benthic habitat. Results from this study indicate that the fish communities of the shallow-water habitats along the Jordanian Red Sea coast are strongly influenced (1) by the composition of the benthic habitat and (2) by depth. These habitat and depth specific differences in fish communities on tropical shallow-water habitats are supported by other studies, e.g. Öhman and Rajasuriya (1998) for coral and sandstone reefs, as well as Friedlander and Parrish (1998) for a coral reef.

Correlation of the fish community parameters and benthic habitat

Regression analysis of benthic habitat and fish community parameters has revealed significant linear and curvilinear correlation. Species richness of fishes is positively correlated to hard substrate cover (live hard coral, dead coral and rock) as well as to habitat diversity (*H’*) in a power regression. Hard substrate cover is a measure of habitat complexity. A high hard substrate cover provides more shelter and food than a low hard substrate cover. A positive relationship of three-dimensional structure of the coral reef to fish community parameters was demonstrated in many studies (Risk 1972, Talbot and Goldman 1972, Luckhurst and Luckhurst 1978, Gladfelter et al. 1980, Carpenter et al. 1981, Roberts and Ormond 1987, McClanahan 1994, Ormond et al. 1996, Chabanet et al. 1997, Friedlander and Parrish 1998, Lindahl et al. 2001) and accounts to 45% of the variance in fish species richness on coral reefs in the Gulf of Aqaba. Species richness is also positively correlated with habitat diversity (*H’*) (Roberts and Ormond 1987), and can explain nearly 50% of the variance in fish species richness. Habitat diversity (*H’*) is a measure for the heterogenity as well as patchiness of the habitat and higher values of *H’* indicate a higher herterogenity or patchiness. The architectural property of heterogene or patchy habitats fosters diversity by allowing coexistance through microhabitat diversification and by increasing survivorship through provision of refuge from predation (Heck and Orth 1980, Salita 2001).

Live hard coral cover was positively correlated to the abundance of corallivorous fishes and accounted for 48% of the variance in abundance. This strong relationship was shown in several studies for corallivorous fishes (Bouchon-Navaro et al. 1985, Jennings et al. 1996, Öhman and Rajasuriya 1998), Chaetodontidae in general (Bell et al. 1985, Bouchon-Navaro and Bouchon 1989) and the complete fish community in regard to abundance, species richness and diversity (Bell and Galzin 1984, Carpenter et al. 1981, Harmelin-Vivien 1989, Cabanet et al. 1997, Adjeroud et al. 1998). An experimental disturbance of hard corals resulted in a significant reduction in abundance of chaetodontid fishes (Lewis 1997). However, there are also studies that found only weak correlation of live coral cover for corallivores (Friedlander and Parrish 1998) and Chaetodontidae (Roberts et al. 1988) or even no correlation at all (Luckhurst and Luckhurst 1978, Roberts and Ormond 1987). The discrepancy between the different studies may have several reasons. Jennings at al (1996) stated that “resident obligate corallivores will be absent if sites without coral cover are included, but this does not suggest that coral cover limits abundance in areas where coral is present”. Jones and Syms (1998) discussed this problem more detailed and conclude that these discrepancy between studies is due to different ranges of observed coral cover. None of the studies examined the whole range of coral cover from 0% to 100% and therefore the nature, e.g. linear, curvilinear or unimodal, of the relationship is not known. The assumed linear relationships in the studies mentioned above are likely to be subsets of a more complex pattern, because very few ecological parameters follow linear patterns indefinitely (Jones and Syms 1998). In our study we analysed the relationship of abundance of corallivores to live hard coral cover in a range of 0% to 35% and a linear regression revealed the best fit. It is likely that the availability of hard corals as a source of food is the limiting factor for the abundance of corallivores in this particular range of live hard coral cover. However, on the one hand it is possible that above a certain percentage of live hard coral cover this is not the main limiting factor any longer and other factors, such as competition between corallivorous fishes, may govern their abundance. Coral-feeding Chaetodontidae defend their territories against competitors, in some species intraspecific, in others also interspecific (Kosaki 1991, Wrathall et al. 1992, Righton et al. 1998). On the other hand Connell (1978) has demonstrated that species richness of hard coral assemblages decreases with increasing live hard coral cover and Aronson and

Precht (1995) showed that at sites with low levels of disturbance only a few coral species dominate the community. Therefore, corallivorous fishes might be limited in their food source, because some chaetodontid species prefer or even feed only on a few species of coral (Reese 1977, Bouchon-Navaro 1986).

Another limitation, and possibly reason for the differences in the studies on relation of fishes to habitat, is the assumption of the regression models that the habitat parameters are independent of the fish community. Corallivores and herbivores have an influence on the habitat by their feeding activity and there are as well inter- and intraspecific interactions within the fish community (Roberts and Ormond 1987, Öhman and Rajasuriya 1998).

In summary our analysis of the correlation between fish community and benthic habitat revealed that (1) fish species richness is positively linked to hard substrate cover as well as habitat diversity, and (2) the abundance of corallivorous fishes is positively linked to live hard coral cover in our range of observation from 0% to 35%.

Fish associations of shallow-water habitats

The multivariate analysis of the fish community has revealed several associations of fishes in different habitats. Within the large group of mainly coral reef associated fishes we can distinguish (1) a group of species that occur mainly at 6 m depth at the shallow reef slope, (2) a group that has a higher relative abundance at 12 m depth at the deep reef slope and (3) the Apogonidae (cardinalfishes). Within the first group it is interesting to note that *Chaetodon paucifasciatus* (Plate 4) is assigned to the upper reef slope, whereas in the Red Sea proper this species occurs in deeper water. Also several other species commonly occur shallowly in the Gulf of Aqaba, e.g. *Apolemichthys xanthotis* (angelfishes; Plate 4), *Genicanthus caudovittatus* (anglefishes; Plate 4), *Chromis pembae* (damselfishes; Plate 5), *Pseudochromis fridmani* (dottybacks), and *Canthigaster coronata* (tobies; Plate 8). It is suggested that this pattern be due to lower surface temperatures in the Gulf of Aqaba (Edwards and Rosewell 1981, Ormond and Edwards 1987, Sheppard et al. 1992). However, this hypothesis remains conjectural and other explanations such as niche expansion in the absence of certain competitor species are possible (Sheppard et al. 1992).

Other studies revealed similar pattern of a different species composition at the shallow and deep slope (McGehee 1994, Friedlander and Parrish 1998). McGehee (1994) assigned the difference to higher water movement in the shallow reef slope, but that study compared 2-4 m depth to a maximum of 10 m depth and is therefore difficult to compare with our results. At the Jordanian coast it seems more likely that the onshore transport of zooplankton is a factor that triggers the differences in occupation between the shallow and deep reef slope. The species group at the shallow reef slope contains only two planktivorous species, the non-schooling pomacentrids *Chromis dimidiata* (Plate 5) and *Amblyglyphidodon leucogaster* (Plate 4). In contrast, the fish group at the deep reef slope comprises four planktivores, the solitary *Chromis ternatensis* (Pomacentridae) as well as the schooling species *Pseudanthias squamipinnis* (Serranidae; Plate 3), *Paracheilinus octotaenia* (Labridae; Plate 7) and *Chromis pelloura* (Pomacentridae; Plate 5). As discussed earlier, *Pseudanthias squamipinnis* showed a higher abundance at the current exposed deeper reef slope. In general, the abundance of planktivorous fish was significantly higher at 12 m depth than at 6 m depth (Khalaf and Kochzius in press). It has to be mentioned that *Chromis pelloura* was recorded only at the seagrass-dominated site and therefore is an exception in the fish group regarded as typical for deep reef slope sites. However, this species showed the highest abundance at 12 m depth and is therefore assigned to this group of deep reef slope species.

The third group of coral reef associated fishes are apogonid species. Members of the family Apogonidae are nocturnally active species that hide in day time e.g. in crevices or between spines of sea urchins. A study in the Philippines has shown that apogonid species, such as *Apogon aureus* (Plate 2) and *Apogon cyanosoma* (Plate 2), seek for shelter in the coral reef during day and migrate at night into adjacent seagrass meadows to forage (Kochzius 1999). Members of this family utilise the same habitat for shelter and are therefore grouped together.

Another association of fishes are species of seagrass meadows and sandflats, such as the scarid *Leptoscarus vaigiensis* which is known as a resident species in seagrass meadows (Randall 1983, Kochzius 1999). The scarid *Calotomus viridescens* (Plate 7) is most commonly seen on seagrass meadows, but also occurs on coral reefs or rocky substrate (Randall 1983). *C. viridescens* is endemic to the Red Sea and in the Indo-West

Pacific the niche of this species seems to be occupied by *Calotomus spinidens* (Kochzius 1999). The labrids *Cirrhilabrus rubriventralis* (Plate 6) and *Coris caudimacula* (Plate 6) are inhabitants of seagrass meadows as well as areas of mixed sand, rubble, rocks and corals (Randall 1983, Khalaf and Disi 1997). The mullid *Parupeneus macronema* (Plate 4) is a feeder on benthic invertebrates of sandy areas and juveniles are associated with seagrass meadows (Khalaf and Disi 1997). *Torquigener flavimaculosus* (Tetraodontidae; Plate 8) is a typical species of shallow sand flat and rubble habitats (Khalaf and Disi 1997).

Two smaller groups of fish associations are the two siganid species, both of them feeding on benthic algae, and the three planktivorous species of the family Caesionidae, which usually school in mid-water (Khalaf and Disi 1997).

The fish communities of shallow-water habitats along the Jordanian Red Sea coast showed different assemblages of fishes (1) on the deep reef slope, (2) on the shallow reef slope and (3) on seagrass meadows and sand flats. In addition the analysis revealed ecological groups such as schooling herbivores, schooling planktivores and reef-associated apogonids.

Biogeography

The number of shore fishe species in the Gulf of Aqaba is higher than previously reported. Sheppard et al. (1992) examined the species richness of the families Chaetodontidae (butterflyfishes), Pomacentridae (damselfishes), Labridae (wrasses), Acanthuridae (surgeonfishes), Serranidae (groupers) and Scaridae (parrotfishes) in different areas of the northern Red Sea, Gulf of Suez and Gulf of Aqaba. Their study showed a decrease of species richness from 100 species at the southern coast of Egypt in the Red Sea proper to 75 species in the northern Gulf of Aqaba. The results of our study and additional species lists from literature (Khalaf and Disi 1997, Rilov and Benayahu 2000) demonstrate that the species richness of these families in the northern Gulf of Aqaba is much higher and reaches 104 species. A compiled list from different sources indicates a total of 362 species of shore fishes for the Gulf of Aqaba (Ben-Tuvia et al. 1983, Khalaf and Disi 1997, Rilov and Benayahu 2000, Kochzius personal observation, Zajonz et al. unpublished report, this study).

In terms of shore fish species composition there are significant differences between the Red Sea, Gulf of Aden, Arabian Gulf and Indian Ocean. The relationships of the ichthyofaunal composition based on presence/absence data from these localities showed a pattern of decreasing similarity of fish communities in the dendrogram from the northern Gulf of Aqaba through the Red Sea proper into the Indian Ocean (Fig. 7). This pattern could indicate a generalised track between the northern Red Sea and the southern Red Sea plus Indian Ocean (Winterbottom 1985).

Differences in the structure of fish communities on northern and southern Red Sea coral reefs are shown for several families, such as Chaetodontidae (butterflyfishes), Pomacanthidae (angelfishes), Pomacentridae (damselfishes), Acanthuridae (surgeonfishes), Scaridae (parrotfishes), Labridae (wrasses), Lethrinidae (emperors), and Lutjanidae (snappers). Scleractinian corals as well show distinct changes in species richness from north to south, with a higher number of species in the central Red Sea (Sheppard et al. 1992), and north-south differences in the community structure (Sheppard and Sheppard 1991). These differences in the community structure of fishes and corals within the Red Sea might be due to north-south differences in habitat as well as an abrupt increase in turbidity south of 20°N (Sheppard et al. 1992, Roberts et al. 1992).

Differences between Red Sea fish communities and fish assemblages of the Indian Ocean are caused by two barriers: On the one hand there is a barrier at the connection of the Red Sea to the Indian Ocean. Some authors regard the shallow sill of the Bab El Mandab strait as the barrier (Klausewitz 1989, Roberts et al. 1992), others locate it in the southern Red Sea (Blum 1989, Righton et al. 1996) or in the western Gulf of Aden (Kemp, 1998). On the other hand there is the reef-free section between Somalia and India, separating the Red Sea from the Indian Ocean (Klausewitz 1978, Roberts et al. 1992). This lack of coral reefs is connected to a ‘pseudo-high latitude effect’, which results from seasonal cold water upwelling along the southern coast of the Arabian peninsula and the Indian Ocean coast of Somalia (Klausewitz 1989, Sheppard and Sheppard 1991, Kemp 1998).

Klausewitz (1978, 1989) regarded the ichthyofauna of the Arabian seas as a biogeographical sub-province, including Red Sea, Gulf of Aden and Arabian Gulf. Further studies of chaetodontid species assemblages by cluster analysis support this

view, grouping assemblages from Oman, Socrota and Arabian Gulf together in one cluster, more closely related to the Red Sea than to the Indian Ocean (Kemp 1998). An analysis of the Indian Ocean coral fauna based on presence/absence of species revealed a biogeographic Arabian sub-province as well (Sheppard and Sheppard 1991). However, our biogeographic analysis revealed a clear pattern of the faunal relationships between Red Sea, Southern Arabia and the Indian Ocean, but the biogeographic affinity of the Arabian Gulf is not clear. The two dendrograms based on different coefficients revealed conflictive results and one dendrogram does not support the close affinity of the Arabian Gulf to the Red Sea.

There is no doubt that not all of the species lists used in this analysis are comprehensive and taxonomic error can not be excluded. Nevertheless, multivariate statistics are very robust in regard to completeness of the data sets and clusters are stable up to an error of 10-20% (Sheppard 1998). Re-examination of the chaetodontid distribution data presented by Kemp (1998) using Bray-Curtis analysis revealed the same pattern than our more comprehensive analysis based on Bray-Curtis similarity: the Arabian Gulf shows the lowest similarity to all other sites. Therefore the oppositional results are due to methodological problems of the cluster analysis, rather than to incomplete species lists or taxonomic error. There are gradual changes between the different areas, but cluster analysis forces gradual into stepwise changes. MDS plots are able to represent gradual differences and therefore the MDS plots based on Bray-Curtis similarity and Euclidean distance are very similar (Fig. 7). However, there are other arguments that support the view of a low similarity of the Arabian Gulf to the Red Sea. The Arabian Gulf shares more fish species of our data set with the Indian Ocean than with the Red Sea. Cluster analysis and MDS plot of absence/presence data of hermatypic corals revealed a closer relationship of the Red Sea to islands from the Central Indian Ocean than to the Arabian Gulf and Southern Arabia (Sheppard 1998). Studies on the zoogeographic relationships of grapsid and ocypodid crabs have revealed that most of the Arabian Gulf species are of an “eastern” Indian Ocean origin. In addition species of an “western” Indian Ocean origin (East Africa and Red Sea) are absent from the northern and western Gulf (Kuwait and Saudi Arabia) (Apel and Türkay 1999). Reasons for these differences might be more ecological rather than historical, because the Arabian Gulf and Red Sea have been recolonised from the same area after

transgression of sea level about 17,000 years ago. The unfavourable oceanographic conditions for tropical species explain the relatively low species richness (Coles and Tarr 1990, Krupp and Almarri 1996).

Summarising the arguments mentioned above, the biogeographic analysis revealed the following pattern: (1) the species richness of fishes on coral reefs in the Gulf of Aqaba is much higher than previously reported, and (2) the Red Sea and southern Arabia are significant different from other sites of the Indian Ocean, but the affiliation of the Arabian Gulf is not clear.

Our study has demonstrated that the shore fishes in the Gulf of Aqaba show a relative high biodiversity. Due to urbanisation, industrialisation, shipping activities and tourism in the Gulf of Aqaba, the environment is under growing pressure. Management for the protection of the marine resources is therefore needed. Scientific programmes such as the Red Sea Program on Marine Sciences (RSP) and the Red Sea Marine Peace Park Project provide important baseline data for multinational research and conservation of the Gulf of Aqaba. Our results on the ecological parameters which structure the shore fish communities give valuable information for the establishment of marine reserves at the Jordanian Red Sea coast. Beside the highly important coral reefs, adjacent habitats such as seagrass meadows should be considered as well in the establishment of marine reserves.

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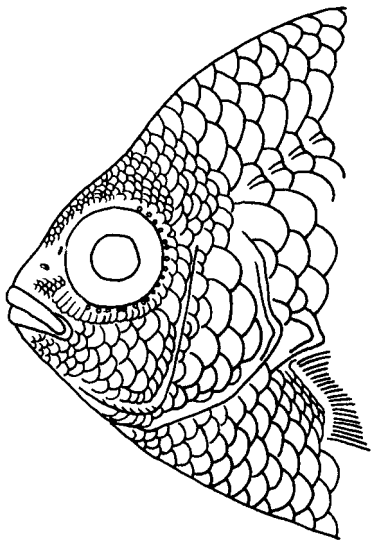
Chapter 2

Kochzius M

Centre for Tropical Marine Ecology, Bremen, Germany

Threatened fishes of the world: *Chromis pelloura* Randall and Allen, 1982 (Pomacentridae)

Environmental Biology of Fishes (accepted)



Chromis pelloura, drawing by A.Y. Suzumoto; taken from Randall and Allen, 1982

Common name: Duskytail chromis (Plate 5).

Conservation status: Currently not listed in the IUCN 2000 Red List of Threatened Species (http://www.redlist.org), but considered as threatened (Hawkins et al. 2000).

Identification: A small size damselfish of around 10 cm TL. It has a light grey to bluish coloration with a black spot at the axil base of the pectoral fin, and a broad black bar at the base of the dusky caudal fin. D XIV, 13 or 14; A II, 12 or 13; P 18 or 19; Lateral line scales 15-17; gill rakers 7-9 + 19-22; body depth 1.85-2.0 in SL (Randall and Allen 1982). Photograph by the author.

Distribution: Currently only known from the coasts off Israel (Randall and Allen 1982) and Jordan (Khalaf and Kochzius 2002) in the Gulf of Aqaba, Red Sea.

Abundance: Observed rarely (1% relative abundance) in small aggregations or solitary (Khalaf and Kochzius 2002).

Habitat and ecology: Occurs at deep reef slopes at the Israeli coast from 30 m (Randall and Allen 1982) down to 150 m depth (Baranes and Golani 1993) and above 30 m at the oil jetty (Rilov and Benayahu 2000). In Jordanian coastal waters usually found below 20 m depth, but also present at 6 m to 12 m depth at the seagrass-dominated Al-Mamlah Bay (Khalaf and Kochzius 2002). This species seems to feed primarily upon zooplankton, but no study on feeding habits has been conducted.

Reproduction: The reproduction biology of this species is not known.

Threats: The species is not commercially fished, but habitat destruction is a severe problem. The northern Gulf of Aqaba is under high pressure by (1) urban and industrial pollution (Abelson et al. 1999), (2) shipping and port activities (Badran and Foster 1998), as well as (3) tourism (Hawkins and Roberts 1994). A study at the Jordanian coast has shown a reduction of fish abundance by 50% at an industrial site (Khalaf and Kochzius in press).

Conservation action: This species is not protected in any of the countries bordering the Gulf of Aqaba, but in Egypt, Israel and Jordan marine protected areas have been established. However, to date the only known areas of occupancy of this species are under high human impact at the Israeli and Jordanian coast.

Conservation recommendations: This species should be protected in the countries bordering the Gulf of Aqaba. Size of the known populations should be investigated and joint conservation plans should be established for the known Israeli and Jordanian populations. In addition, this species might be recorded in the IUCN Red List of

Threatened Species as vulnerable (VU D2), because the population is characterised by a restriction in its area of occupancy (< 100 km^2) and in the number of locations (< 5).

Remarks: It might be possible that this species is not endemic to the Gulf of Aqaba and occurs in much deeper waters elsewhere in the Red Sea. However, despite numerous fish collections and surveys in the Red Sea this species is not recorded from any location outside the Gulf of Aqaba.

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Chapter 3

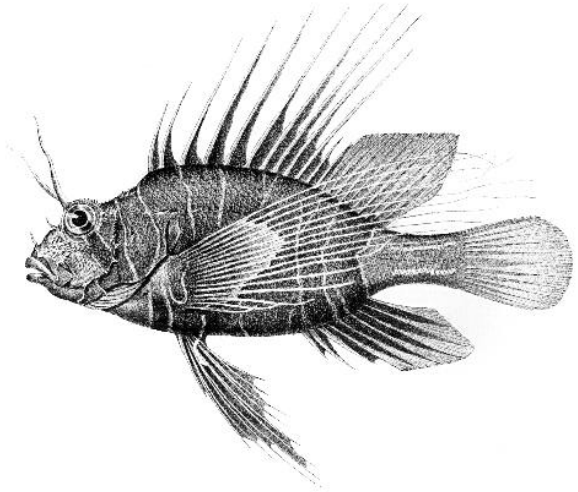
[1]Khalaf MA, [2]Kochzius M

[1]Marine Science Station, Aqaba, Jordan

[2]Centre for Tropical Marine Ecology, Bremen, Germany

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

Marine Ecology Progress Series (in press)



Pterois radiata, taken from Rüppell E (1835-38) Neue Wirbeltiere zu der Fauna Abyssiniens gehörig. Fische des rothen Meeres, Frankfurt a.M.

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 an marine reserve and sites without industry or port (undisturbed), as well as in a seagrass-dominated bay. Planktivores were the most abundant feeding guild on coral reefs as well as at 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 of the fish community by reduction of total fish abundance by 50%, increased total abundance of herbivorous and detritivorous fishes, decreased total abundance of invertebrate & fish feeders, as well as increased relative abundance of planktivorous fishes.

KEYWORDS

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 and Ormond 1982, Abu-Hilal 1987, Abu-Hilal and Badran 1990, Abelson et al. 1999), shipping and port activities (Fishelson 1973, Loya 1975, Abu-Hilal 1985, Badran and Foster 1998) as well as tourism (Riegl and Velimirov 1991, Hawkins and 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 years 30-40% 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 has been 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 their relative abundance as long as dead corals still provide shelter. 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. Disturbed reefs are located in front of an industrial area and port, whereas undisturbed reefs are situated in a marine reserve and at sites without industry and port activity.

MATERIAL AND METHODS

Study sites

The investigation of the general trophic community structure of shore fishes in the Gulf of Aqaba is based on five coral reefs and the seagrass-dominated Al-Mamlah Bay

Fig. 1 Map of the Gulf of Aqaba with study sites at the Jordanian coast (*inset*): *1* Cement jetty (N 29°28.990‘; E 34°59.010‘), *2* Marine Science Station (N 29°27.250‘; E 34°58.359‘; distance from *1*: 3.4 km), *3* Tourist Camp (N 29°26.351‘; E 34°58.272‘; distance from *2*: 1.6 km), *4* Al-Mamlah Bay (N 29°24.345‘; E 34°58,549‘; distance from *3*: 3.7 km), *5* and *6* Jordan Fertiliser Industries and Jordan Fertiliser Industries jetty (N 29°22.134‘; E 34°57.667‘; distance from *4*: 4.1 km)

at the Jordanian coast (Fig. 1). The degree of human-induced disturbance is quite different 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 Fertilizer 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) (Table 1). In the past, parts of the reef flat were destroyed by land-filling for a parking place and the JFI jetty (Mahasneh and Meinesz 1984). A study on coral diseases revealed a ten-fold higher number of infected coral colonies at the JFI than in the marine reserve (Al-Moghrabi 2001). Values of phosphate concentrations (Badran and Foster 1998), heavy metals (Abu Hilal and Badran 1990), and algal cover (personal observation) 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 0.1-0.2 µM, which is proposed to consider reef waters as polluted (Bell 1992). The distance between disturbed and undisturbed sites is around 8 km.

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

Site		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

Visual census

The fish communities in shallow-water habitats along the Jordanian coast were surveyed by the visual census technique using SCUBA as described in English et al. (1994). Transects of 50 m length and 5 m width (250 m^2) were marked along lines at six sites parallel to the shore (Fig. 1, Table 1). At each site visual censuses were conducted along three transects at 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. The observer waited five to ten minutes after laying the transect line to allow fishes to resume their normal behaviour. Subsequently the diver swam 50 to 60 minutes 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 skill and technique of observers are a source of imprecision and/or bias (Thompson and Mapstone 1997). Therefore, the first author (M.A. Khalaf) 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 fish ecological studies on coral reefs (English et al. 1994). However, all our conclusions are restricted to day active and non-cryptic species (Brock 1982). At five sites (Cement jetty, Marine Science Station, Tourist Camp, Jordan Fertiliser Industries and Jordan Fertiliser Industries jetty) three censuses were conducted at each depth in November 1999 and March 2000. In 1997 and 1998 39 censuses were conducted at Al-Mamlah Bay in 6 m and 43 census in 12 m depth (Table 2). In this study a total of 212,349 fishes were counted, representing 198 species belonging to 121 genera and 43 families. Affiliation

of species to trophic groups is based on Khalaf and Disi (1997) and on field observations (Table 3).

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

Site	n	6 m	n	12 m
Cement jetty	3	November 1999	3	November 1999
Marine Science Station (MSS)	3	November 1999	3	November 1999
Tourist Camp	3	November 1999	3	November 1999
Al-Mamlah Bay	39	April 1997 – August 1999	43	April 1997 – August 1999
Jordan Fertiliser Industries (JFI)	3	April 2000	3	April 2000
Jordan Fertiliser Industries jetty (JFI jetty)	3	April 2000	3	March 2000

Statistical analysis

Community indices such as fish abundance, species richness (number of species), Pielou’s evenness (J’) and Shannon-Wiener diversity (H’; ln basis) were compared among sites and depths using one-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. F-test was performed with a spreadsheet analysis programme and one-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. Highly abundant species in contrast to species with very low abundance can disturb the analysis. Therefore, if necessary, data were standardised as indicated at the figures. MDS is a 3-dimensional ordination of samples brought down to a 2-dimensional plot. The quality of the MDS plot is indicated by the stress value. Values <0.2 give a potentially useful 2-dimensional picture, stress <0.1 corresponds to a good ordination and stress <0.05 gives an excellent representation.

Table 3 Affiliation of fishes from the Jordanian Red Sea coast to trophic groups is based on Khalaf and Disi (1997) and on field observations: *C* corallivore (feeds on corals), *D* detritivore (feeds on detritus), *H* herbivore (feeds on macroalgae; Scaridae: *H/C*), *IF* invertebrate feeder (feeds on benthic invertebrates, but not corals), *IFF* invertebrate & fish feeder (feeds on benthic invertevrates and fish, but not corals), *O* omnivore (no specialisation), *Pi* piscivore (feeds on fishes), *Pl* planktivore (feeds on plankton)

Torpedinidae		**Carangidae**		*P. trilineatus*		*Ecsenius aroni*	IF
Torpedo panthera	IFF	*Carangoides fulvoguttatus*	IFF	**Mugilidae**		*E. frontalis*	IF
Muraenidae		*Decapterus macrosoma*	Pl	*Crenimugil crenilabis*	D	*E. gravieri*	IF
Gymnothorax nudivomer	IFF	*Gnathanodon speciosus*	IFF	**Labridae**		*Exallias brevis*	C
Siderea sp.	Pi	**Caesionidae**		*Anampses caeruleopunctatus*	IF	*Meiacanthus nigrolineatus*	IF
S. grisea	Pi	*Caesio lunaris*	Pl	*A. lineatus*	IF	*Plagiotremus tapeinosoma*	Pi
Synodontidae		*C. suevicus*	Pl	*A. meleagrides*	IF	*Plagiotremus townsendi*	Pi
Saurida gracilis	Pi	*C. varilineata*	Pl	*A. twistii*	IF	**Gobiidae**	
Synodus sp.	Pi	**Nemipteridae**		*Bodianus anthioides*	IF	*Amblyeleotris steinitzi*	IF
S. variegatus	Pi	*Scolopsis ghanam*	IF	*B. axillaris*	IF	*A. sungami*	IF
Atherinidae		**Gerreidae**		*B. diana*	IF	*Amblygobius albimaculatus*	IF
Atherinomorus lacunosus	Pl	*Gerres oyena*	IF	*Cheilinus* sp.	O	*Bryaninops natans*	Pl
Holocentridae		**Haemulidae**		*C. lunulatus*	O	*Fusigobius longispinus*	IF
Myripristis murdjan	Pl	*Diagramma pictum*	IFF	*C. mentalis*	O	*Gnatholepis anjerensis*	IF
Neoniphon sammara	Pl	**Lethrinidae**		*C. trilobatus*	O	*Gobiodon citrinus*	
Sargocentron caudimaculatum	Pl	*Lethrinus* sp.	IF	*Cheilio inermis*	O	*Istigobius decoratus*	IF
S. diadema	Pl	*Monotaxis grandoculis*	IF	Cirrhilabrus rubriventralis	Pl	*Lotilia graciliosa*	IF
Fistulariidae		**Sparidae**		*Coris aygula*	IF	*Valenciennea puellaris*	IF
Fistularia commersonii	IFF	*Diplodus noct*	O	*C. caudimacula*	IF	**Acanthuridae**	
Centriscidae		**Mullidae**		*C. gaimard gaimard*	IF	*Acanthurus nigrofuscus*	H
Aeoliscus punctulatus	Pl	*Mulloidichthys flavolineatus*	IFF	*C. variegata*	IF	*A. sohal*	H
Syngnathidae		*Parupeneus cyclostomus*	IFF	*Gomphosus caeruleus klunzingeri*	IF	*Ctenochaetus striatus*	D
Corythoichthys flavofasciatus	IF	*P. forsskali*	IFF	*Halichoeres marginatus*	IF	*Naso unicornis*	H
C. nigripectus	IF	*P. macronema*	IFF	*Halichoeres scapularis*	IF	*Zebrasoma veliferum*	O
C. schultzi	IF	*P. rubescens*	IFF	*Hemigymnus fasciatus*	IF	*Z. xanthurum*	O
Trachyrhamphus bicoarctatus	Pl	**Pempheridae**		*Hologymnosus annulatus*	IFF	**Siganidae**	
Scorpaenidae		*Pempheris vanicolensis*	IFF	*Labroides dimidiatus*	IF	*Siganus argenteus*	H
Dendrochirus brachypterus	IF	**Chaetodontidae**		*Larabicus quadrilineatus*	C	*S. luridus*	H
Inimicus filamentosus		*Chaetodon auriga*	O	*Macropharyngodon bipartitus*	IF	*S. rivulatus*	H
Pterois miles	IFF	*C. austriacus*	C	*Novaculichthys macrolepidotus*	IF	**Scombridae**	
P. radiata	IF	*C. fasciatus*	O	*Oxycheilinus digrammus*	IF	*Euthynnus affinis*	IFF
Scorpaenidae		*C. melannotus*	C	*Paracheilinus octotaenia*	Pl	**Bothidae**	
Scorpaenopsis sp.	IFF	*C. paucifasciatus*	O	*Pseudocheilinus evanidus*	Pl	*Bothus pantherinus*	IF
S. barbata	IFF	*C. trifascialis*	C	*P. hexataenia*	Pl	**Samaridae**	
Synanceia verrucosa	Pi	*Heniochus diphreutes*	Pl	*Pteragogus cryptus*		*Samaris cristatus*	
Serranidae		*H. intermedius*	O	*P. pelycus*		**Soleidae**	
Anthias taeniatus	Pl	**Pomacanthidae**		*Stethojulis albovittata*	IF	*Pardachirus marmoratus*	IF
Cephalopholis hemistiktos	IFF	*Apolemichthys xanthotis*	O	*S. interrupta*	IF	**Balistidae**	
C. miniata	IFF	*Centropyge multispinis*	H	*Thalassoma lunare*	IFF	*Balistapus undulatus*	O
Epinephelus fasciatus	IFF	**Genicanthus caudovittatus**	Pl	*T. rueppellii*	IFF	*Pseudobalistes fuscus*	O
Grammistes sexlineatus	IFF	*Pomacanthus imperator*	IF	*Thalassothia cirrhosa*	IFF	*Sufflamen albicaudatus*	IF
Pseudanthias squamipinnis	Pl	*Pygoplites diacanthus*	IF	*Xyrichtys pavo*	IF	**Monacanthidae**	
Variola louti	IFF	**Pomacentridae**		**Scaridae**		*Aluterus scriptus*	O
Pseudochromidae		*Abudefduf vaigiensis*	O	*Calotomus viridescens*	H	*Amanses scopas*	O
Pseudochromis flavivertex	O	*Amblyglyphidodon flavilatus*	Pl	*Chlorurus gibbus*	H	*Cantherhines pardalis*	O
P. fridmani	O	*A. leucogaster*	Pl	*C. sordidus*	H	*Pervagor randalli*	O
P. olivaceus	O	*Amphiprion bicinctus*	Pl	*Hipposcarus harid*	C	*Pseudomonacanthus pusillus*	
P. springeri	O	*Chromis dimidiata*	Pl	*Leptoscarus vaigiensis*	H	**Ostraciidae**	
Priacanthidae		*C. pelloura*	Pl	*Scarus ferrugineus*	H	*Ostraccion cubicus*	O
Priacanthus hamrur	Pl	*C. pembae*	Pl	*S. fuscopurpureus*	H	*O. cyanurus*	O
Apogonidae		*C. ternatensis*	Pl	*S. ghobban*	H	*Tetrosomus gibbosus*	O
Apogon sp.	Pl	*C. viridis*	Pl	*S. niger*	H	**Tetraodontidae**	
A. aureus	Pl	*C. weberi*	Pl	*S. psittacus*	H	*Arothron diadematus*	O
A. cyanosoma	Pl	*Dascyllus aruanus*	O	**Pinguipedidae**		*A. hispidus*	O
A. exostigma	Pl	*D. marginatus*	O	*Parapercis hexophtalma*	IFF	*A. stellatus*	O
A. fraenatus	Pl	*D. trimaculatus*	Pl	**Uranoscopidae**		*Canthigaster coronata*	O
A. nigrofasciatus	Pl	*Neoglyphidodon melas*	C	*Uranoscopus sulphureus*	IFF	*C. margaritata*	O
Cheilodipterus lachneri	Pl	*Neopomacentrus miryae*	Pl	**Blenniidae**		*C. pygmaea*	O
C. macrodon	Pl	*Pomacentrus sulfureus*	O	*Aspidontus taeniatus taeniatus*	O	*Torquigener flavimaculosus*	O
C. novemstriatus	Pl	*P. trichourus*	IFF	*Cirripectes castaneus*	H	**Diodontidae**	
						Cyclichthys spilostylus	IF

ANOSIM significance test compares similarities of species compositions between the samples and can give evidence for 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 one-way layout of ANOSIM was performed with the original data, no transformation or standardisation was conducted.

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

RESULTS

Fish community parameters (Fig. 2)

Species richness did not show a 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.

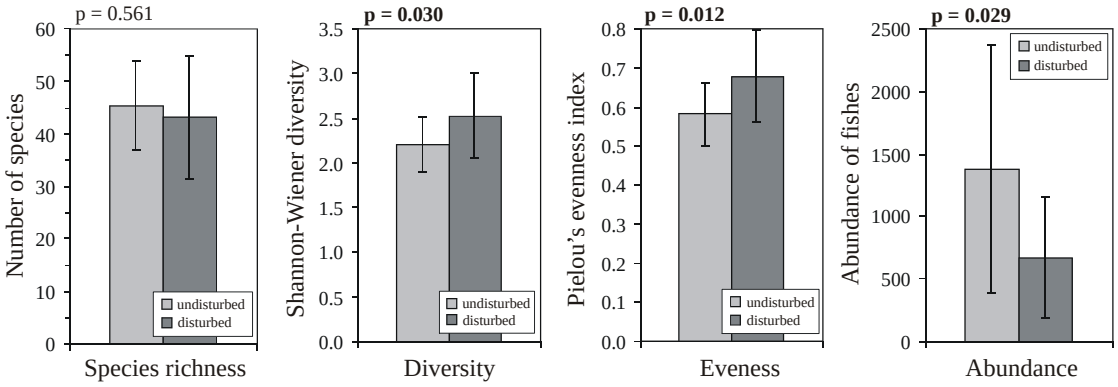


Fig. 2 Fish community parameters (species richness, diversity, eveness, abundance) of undisturbed and disturbed coral reefs at the Jordanian Red Sea coast, Gulf of Aqaba (significant one-way ANOVA p-values are bold)

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

In terms of number of species belonging to different feeding guilds, predators on invertebrates (25.3%) are the most common feeding guild, followed by planktivores (20.8%) and omnivores (19.2%).

In terms of relative abundance 58% of all fish specimen were planktivorous on coral reefs, while at the seagrass-dominated Al Mamlah Bay even 79%. Other important trophic groups on coral reefs were invertebrate & fish feeders (23.1%), omnivorous fishes (11.6%) and herbivores (3.4%). Those three groups showed a low relative abundance of 5% to 6.5% at Al Mamlah Bay.

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

Feeding guilds	Species richness		Relative abundance (%)	
	n (species)	% (species)	Coral reef	Seagrass-dominated habitat
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 & fish feeder	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

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

The total abundance of trophic groups at different sites revealed pattern connected to the benthic habitat or disturbance at the sites. Those patterns are all statistically highly significant.

Corallivores were less abundant at the seagrass-dominated site compared to coral reefs.

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

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

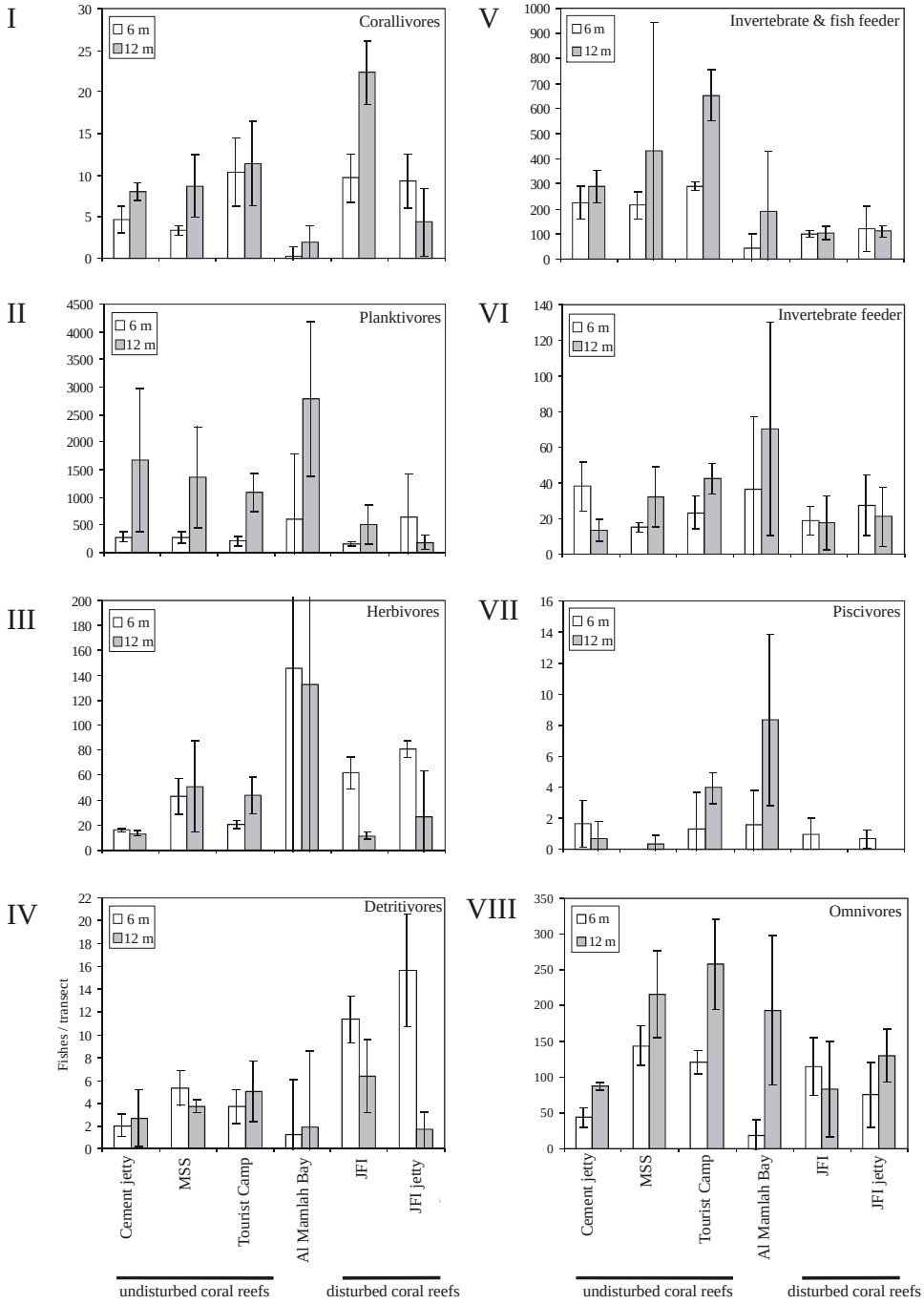


Fig. 3 Abundance of trophic fish groups (average and ±SD) at sites along the Jordanian Red Sea coast, Gulf of Aqaba. **I** Corallivores, **II** Planktivores, **III** Herbivores, **IV** Detritivores, **V** Invertebrate & fish feeder, **VI** Invertebrate feeder, **VII** Piscivores, and **VIII** Omnivores. Please note different scales

Table 5 One-way ANOVA for abundance of feeding guilds at sites along the Jordanian Red Sea coast, Gulf of Aqaba (significant p-values are bold; * indicates log(x+1) transformed data; *i.v.* inhomogenous variances; *S* seagrass-dominated habitat; *CR* coral reef; *uD* undisturbed coral reef; *D* disturbed coral reef; labels for feeding guilds see Table 3)

	Feeding guilds							
	C	Pl	H	D	IFF	IF	Pi	O
S *vs* CR	**<0.001*** S<CR	i.v.	i.v.	**<0.001** S<CR	**0.002** S<CR	**0.020*** S>CR	i.v.	i.v.
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*** 6m<12m	0.053*	0.885*	0.409	0.879	0.904	**0.035** 6m<12m
6 m vs 12 m (S)	i.v.	**<0.001** 6m<12m	**<0.001*** 6m>12m	0.616	i.v.	i.v.	**<0.001*** 6m<12m	i.v.
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** 6m>12m	**0.001*** 6m>12m	0.879	0.632	**0.022** 6m>12m	0.691
6 m (uD) *vs* 6 m (D)	0.090	i.v.	**<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)	i.v	**0.014** uD>D	0.230	0.878	i.v.	0.242	0.058	0.072

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

Invertebrate & fish feeder were more abundant on coral reefs and the number was higher on undisturbed than on disturbed coral reefs, especially on the shallow reef slope.

Invertebrate feeder had a larger population on the seagrass meadow.

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

Omnivores tended to be more abundant on the deep reef slope than on the shallow reef slope, but did not show a difference between sites.

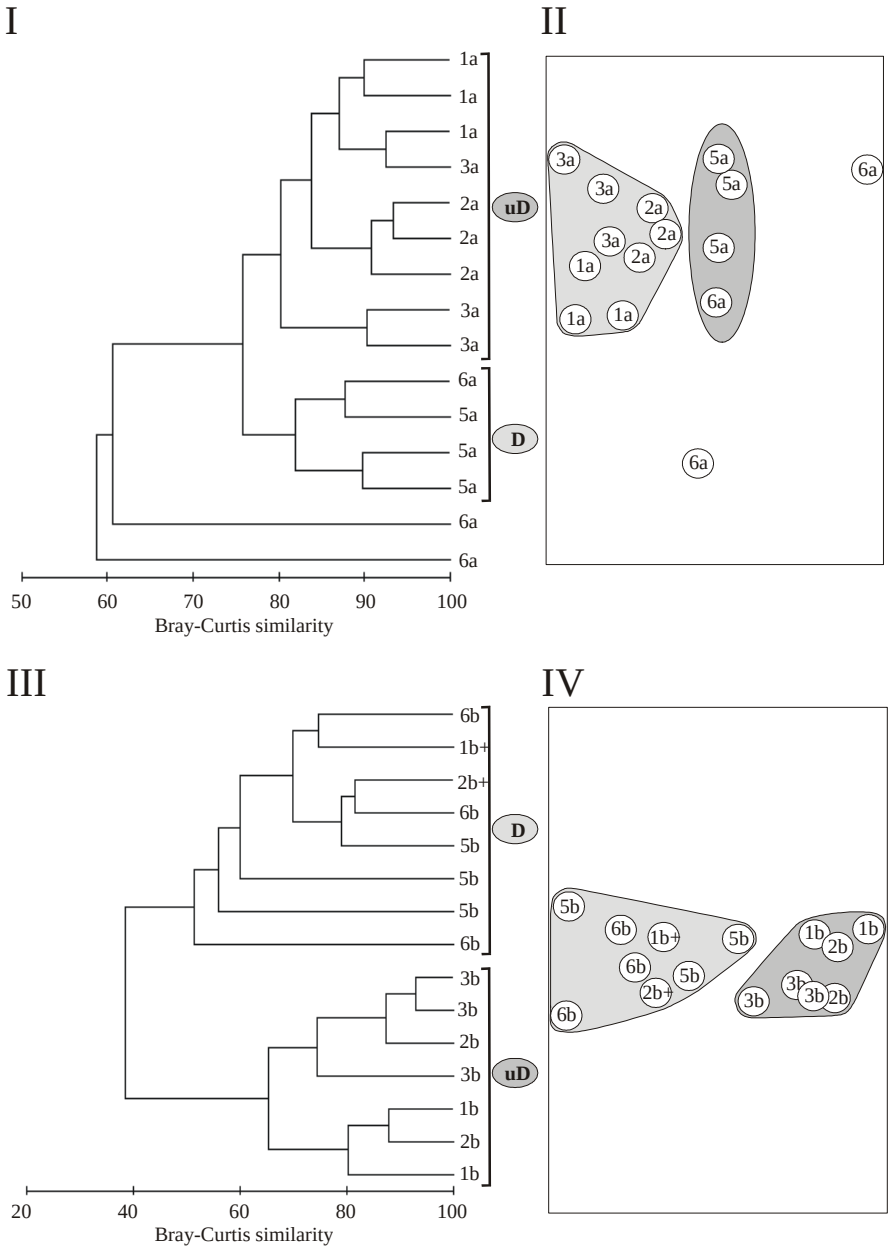


Fig. 4 Fish communities on disturbed and undisturbed coral reefs at the Jordanian Red Sea coast, Gulf of Aqaba (based on abundance of feeding guilds, no pelagic or semi-pelagic species). Dendrogram **I** and MDS plot **II** of the shallow reef slope (6 m, Bray-Curtis similarity, standardisation, group average; stress=0.05, ANOSIM: global R=0.0553, p<0.001) and dendrogram **III** and MDS plot **IV** of the deep reef slope (12 m, Bray-Curtis similarity, group average, stress=0.04, ANOSIM: global R =0.493, p=0.004). For site labels see Fig. 1 (*a* 6 m depth, *b* 12 m depth). *D* disturbed coral reefs, *uD* undisturbed coral reefs. + indicates mismatch)

Multivariate analysis

Cluster analysis and MDS plot based on abundance of feeding guilds on coral reefs at the shallow (6 m) and deep (12 m) reef slope revealed two cluster: (1) disturbed and (2) undisturbed coral reefs (Fig. 4). The analysis of the shallow reef slope showed two mismatches (samples 6a), but they did not change the general pattern. Dendrogram and MDS plot of the deep reef slope communities included two mismatches at disturbed reefs (1b and 2b) without affecting the division into the two groups. An ANOSIM test confirmed the pattern of both multivariate analyses (Fig. 4). The dendrogram and MDS plot for species abundance was more or less identical to the multivariate analysis of feeding guilds, and is therefore not presented here.

SIMPER analysis revealed that invertebrate & 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 (7.4%), herbivores (3.1%) and omnivores (1.7%) contributed a minor percentage to the dissimilarity between the two groups (Table 6). On deep reef slopes planktivores (64.2%) and invertebrate & fish feeders (23.5 %) contributed most of the dissimilarity between undisturbed and disturbed sites, whereas omnivores (7.4%), herbivores (2.1%) and invertebrate feeder (1.3%) played a minor role (Table 6).

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

Feeding guild	Contribution to dissimilarity (%) in 6 m depth	Contribution to dissimilarity (%) in 12 m depth
Invertebrate & fish feeder	48.41	23.45
Planktivores	41.27	64.19
Invertebrate feeder	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

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

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

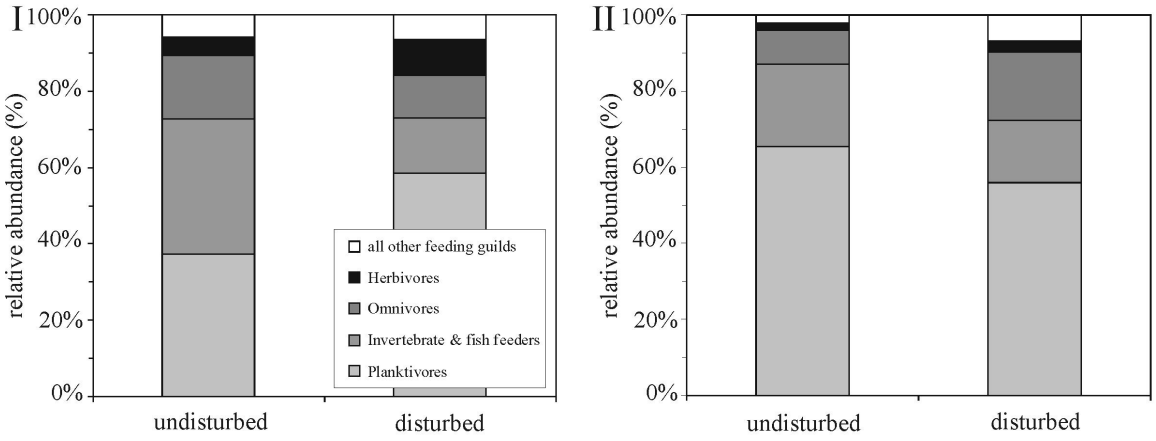


Fig. 5 Trophic composition of the fish fauna on disturbed and undisturbed coral reefs at the Jordanian Red Sea coast, Gulf of Aqaba. **I** shallow reef slope (6 m) and **II** deep reef slope (12 m)

DISCUSSION

Fish counts at the disturbed site took place in March and April 2000, whereas at undisturbed sites in November 1999. The question arises, if detected differences are due to seasonal changes within the fish community. Our study on the community structure of shore fishes at the Jordanian coast (Khalaf and Kochzius 2002) showed a strong spatial influence due to habitat composition, but did not show a temporal pattern. Studies on the colonisation of artificial reefs in Eilat (Rilov and Benayahu 1998, Golani and 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. If temporal changes would have been important, an opposite picture

would have been expected in our study. Therefore we can assume that temporal effects are not the reason for the observed differences.

Trophic structure of the fish 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 Gulf of Mexico (Williams and Hatcher 1983, Öhman et al. 1997, Pattengill et al. 1997, Rossier and Kulbicki 2000) (Table 7). Zooplankton as a source of food, at least for day active fishes, is rather independent from the benthic habitat composition. Similar pattern of transport of zooplankton result in a consistent dominance of planktivorous fishes on different coral reefs.

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

The relative abundance of piscivores is more than ten-fold higher on the coral reefs in the Sri Lanka, New Caledonia, Great Barrier Reef and Gulf of Mexico than at the Jordanian coast. These difference might be due to various factors such as prey availability, shelter and fishing, but might also due to methodological differences. Öhman et al. (1997) restricted their fish counts to 135 species and Williams and Hatcher (1983) used explosive charges.

Table 7 Relative abundance (%) of feeding guilds of fishes on coral reefs ([1]this study, [2]calculated from Öhman et al. 1997, [3]Williams and Hatcher 1983, [4]Rossier and Kulbicki 2000, [5]Pattengill et al. 1997)

	Aqaba[1]	Sri Lanka[2]	Great Barrier Reef[3]	New Caledonia[4]	Gulf of Mexico[5]
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

Table 8 Trophic composition of fish assemblages on coral reefs (percentage of species; [1]this study, [2]Rilov and Benayahu 2000, [3]Krupp et al. 1993, [4]Öhman et al. 1997, [5]Williams and Hatcher 1983, [6,7]Harmelin-Vivien 1989, [8,9,10]Letourneur et al. 1997, [11]Pattengill et al. 1997) and number of scleractinian coral species ([a]Antonius et al. 1990, [b]Rajasuriya et al. 1998, [c]Done 1982, [d]Adjeroud 1997, [e]Bouchon 1981, [f]UNEP/IUCN 1988)

	Aqaba[1]	Eilat[2]	Sanganeb atoll[3]	Sri Lanka[4]	Great Barrier Reef[5]	Tulear[6]	Moorea[7]	Moorea[8]	Reunion[9]	New Caledonia[10]	Gulf of Mexico[11]
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 & 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 feeders	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	[a]138		[a]146	[b]118	[c]212		[c]72		[e]120	[f]108	

*sessile invertebrate browsers

Beside the relative abundance, the trophic species composition reflects the trophic structure of the community as well (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. Detrivorous fishes play a minor role in terms of proportion to the ichthyofauna inventory on coral reefs. The number of herbivores varies considerable within the fish communities of the different regions and it seems that it is much lower on the oceanic islands of Moorea and Réunion, as well as in New Caledonia.

The proportion of species belonging to certain feeding guilds is very similar between the three considered sites in the Red Sea, but suggests some differences to sites in the Indian Ocean, Pacific and 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. The percentage of corallivorous species is only about half at the northern tip of the Gulf of Aqaba than in the central Red Sea and reefs in other parts of the Indo-Pacific. In comparison of the Gulf of Aqaba to the central Red Sea this might be due to lower scleractinian species richness in the gulf (Antonius et al. 1990). However, no general correlation between number of scleractinian corals and percentage of corallivorous species of a fish assamblage can be detected (Table 8).

Regarding the trophic structure of the ichthyofauna at the Jordanian coast in comparison to 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) invertebrate feeders represent the most fish species on coral reefs, (3) the relative abundance of feeding guilds other than planktivores seems to be strongly influenced by the benthic habitat, and (4) the trophic species structure of fish communities on Red Sea coral reefs seems to be different from reefs in other parts of the Indo-Pacific.

Comparison between coral reefs and the seagrass-dominated site

The reduced abundance of corallivores at the seagrass dominated site is not surprising, because these fishes are strongly connected to live stony corals (Bouchon-Navaro et al. 1985, Jennings et al. 1996, Öhman and Rajasuriya 1998, Khalaf and Kochzius 2002). Despite the low coral cover and reduced shelter, the abundance of

planktivorous fishes at 12 m depth is much higher at Al-Mamlah Bay. 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 Indo-Pacific (Weinstein and Heck 1979, Bell and Pollard 1989, Kochzius 1999). This higher prey availability correlates with a higher abundance of piscivores in the seagrass meadow than on 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 industry complex on the coral reef ichthyofauna. This phenomenon is not uncommon and was reported for a study on the effect of coral mining (Shepherd et al. 1992), as well as coral bleaching (Lindahl et al. 2001). Investigations on the impact of dredging revealed a significant reduction of species richness on some reefs, whereas other sites did not show a difference to undredged areas (Harmelin-Vivien 1992). However, experimental coral disturbance led to a significant decline in fish species richness (Lewis 1997). The higher diversity and evenness at the disturbed sites might be explained by the intermediate disturbance hypothesis (Connell 1978), i.e. the initial increase of diversity with increasing disturbance is followed by a decrease at high disturbance.

Abundance of fishes on disturbed reefs was half that of undisturbed reefs. In other areas significant declines in fish abundance have been caused by coral mining (Shepherd et al. 1992), turbidity and sedimentation due to dredging (Amesbury 1981), eutrophication (Chabanet et al. 1995) and experimental coral disturbance (Lewis 1997). However, disturbance of dredging in Moorea and Tahiti led to a decrease in fish abundance at some sites, but other reefs did not show a significant difference (Harmelin-Vivien 1992). Mass mortality of bleached corals in Tanzania even triggered an increase of 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 to reveal 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 &

fish feeders was higher on undisturbed reefs. The reduction of invertebrate & 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 can not support a higher number of invertebrate & fish feeders.

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

There is a shift towards planktivores on the shallow slope of disturbed reefs. The reason might be 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 health 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 disturbed reefs it can be observed that omnivorous fishes increased in their relative abundance. This guild of fishes consists of non-specialised feeders that can more easily cope with changes in the benthic habitat than invertebrate & fish feeders.

Besides negative effects on the source of food, recruitment to the degraded reef might be reduced, either by decrease of settlement due to habitat loss or by higher mortality due to loss of appropriate shelter sites (Shulman 1985, Schmitt and Holbrook 1999).

In summary, the human-induced disturbance led to changes of the fish community on coral reefs in front of the industrial complex: (1) reduction of fish abundance by 50%, (2) increased total abundance of herbivorous and detritivorous fishes, (3) decreased total abundance of invertebrate & fish feeders, and (4) as a result changes in the trophic composition, such as an increased relative abundance of planktivores.

These changes are most probably due to synergetic effects of coastal constructions, sedimentation, nutrient input, algal growth, coral destruction and heavy metal load. In course of future urbanisation and industrialisation of the Jordanian Red Sea coast an

increase of coastal construction and pollution is to be expected. Due to the short coastline of 27 km future industrial development should focus on already altered areas to keep the remaining coral reefs and seagrass meadows in a more or less natural state. 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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Chapter 4

[1]Kochzius M, [2*]Söller R, [3]Khalaf MA, [2]Blohm D

[1]Centre for Tropical Marine Ecology, Bremen, Germany

[2]Department of Biotechnology and Molecular Genetics, University of Bremen, Germany

[3]Marine Science Station, Aqaba, Jordan

*present address: ARTUS GmbH, Hamburg

Genetic population structure of the lionfish *Pterois miles* (Scorpaenidae, Pteroinae) in the Gulf of Aqaba and northern Red Sea

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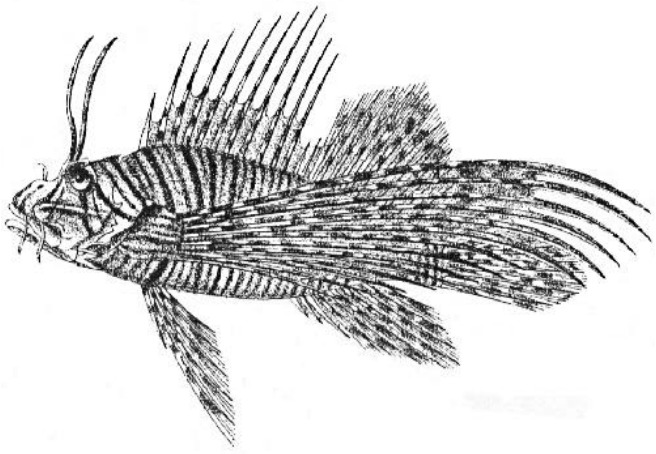

Pterois miles, taken from Klunzinger CB (1884) Die Fische des Rothen Meeres. 1. Theil. Schweizbart’sche Verlaghandlung, Stuttgart

ABSTRACT

Fishes on coral reefs, such as the lionfish *Pterois miles* (Plate 1), have a life history with two totally different phases: adults are relatively strongly side-attached, whereas larvae of virtually all species are planktonic. Therefore, large-scale dispersal and high gene flow could be expected. However, due to the fjord-like hydrography and topology of the Gulf of Aqaba isolation of populations might be possible. The gulf is a 180 km long and 6-25 km wide northern extension of the Red Sea and separated by a shallow sill. The aim of this study is to reveal genetic population structure, genetic diversity, and gene flow between populations of the lionfish *P. miles* in the Gulf of Aqaba and northern Red Sea. The applied molecular marker is a 166 bp sequence of the 5’ mitochondrial control region. It is the most variable mitochondrial gene in fishes and a suitable marker to investigate genetic population structure. Among 94 *P. miles* specimens 32 polymorphic sites were detected, yielding 38 haplotypes. Sequence divergence among haplotypes ranged from 0.6% to 9.9% and genetic diversity was high (h=0.85, π=1.9%). AMOVA indicates no restriction of gene flow between the Gulf of Aqaba and northern Red Sea (Φ_{ct} = 0.05258). Consideration of observed high genetic diversity, paleoceanography of the Red Sea, and life history of *P. miles* indicate that the revealed genetic population structure reflects high gene flow and panmixia. However, it is not possible to estimate on which time-scale gene flow operate. Therefore, coastal zone management in the Gulf of Aqaba has to follow the precautionary principle and should not rely upon fast replenishment or re-colonisation.

KEYWORDS

Genetic population structure, Gene flow, Molecular marker, *Pterois miles*, Coral Reefs, Red Sea

INTRODUCTION

Like many organisms on coral reefs, fishes have a life history with two totally different phases: adults are relatively strongly side-attached (Sale 1980), whereas larvae of virtually all species are planktonic (Leis 1991). *P. miles* is strongly site-attached and it seems that it returns to the same crevice in the reef to rest (Fishelson 1975, Fishelson 1997, personal observation). Therefore, gene flow by adult migration between distant populations is not expected. In contrast, eggs and larval stages of *P. miles* are planktonic (Fishelson 1975, Thresher 1984, Leis 1991) and have the potential to disperse over large areas. *P. miles* produces mucus-balls that embody the eggs and float below the surface. In the close relative *Dendrochirus brachypterus* the mucus-balls contain 2,000-15,000 eggs and hatching occurs after 36 hours under laboratory conditions (Fishelson 1975). Therefore, it is likely that the pelagic eggs of *P. miles* float as passive drifters a few days with the surface currents before the hatched larvae might start to control their dispersal by active swimming. Studies on late pelagic stages of coral reef fishes have demonstrated that they can swim against strong currents (Leis and Carson-Ewart 1997, Stobutzki and Bellwood 1997, Stobutzki 1998) and are able to detect coral reefs >1 km away (Leis et al. 1996). Hydrodynamic models of fish larval dispersal on the Great Barrier Reef have shown that only the inclusion of directional swimming of larvae at realistic speed reproduced the field observations of larval distribution (Wolanski et al. 1997). These studies have revealed that late pelagic stages of tropical shore fishes are not helplessly drifting with currents and can control where they are going. The larval duration time of *P. miles* is not known, but size at settlement to the reef is 10-12 mm (Tresher 1984). In members of the families Pomacentridae and Labridae the larval duration time ranges between 8 to 121 days (Victor 1986, Thresher et al. 1989).

Genetic homogenity over large areas is a common feature of tropical marine fishes and can reflect high dispersal capability resulting in high levels of gene flow (Shaklee 1984, Lacson 1992, Lacson and Morizot 1991, Planes et al. 1993, Doherty et al. 1995, Lacson and Clark 1995, Shulman and Bermingham 1995, Bernardi et al. 2001). Therefore, large-scale dispersal and high gene flow is expected for the lionfish *P. miles*. However, other studies on tropical marine fishes have shown significant genetic structuring on scales of 16-400 km (Bell et al. 1982, Planes 1993, Johnson et al. 1994, Planes et al. 1996, Planes et al. 1998). Studies of the population structure of

mesopelagic fishes in Norway have indicted restricted gene flow between populations in the fjord and offshore (Suneetha 2000).

The fjord-like Gulf of Aqaba is a deep, narrow northern extension of the Red Sea. It has a length of 180 km and is 6-25 km wide (Fig. 1). The depth can reach over 1,800 m, but averages 800 m. The Gulf of Aqaba is separated from the Red Sea by a shallow sill of 242-270 m depth at the Strais of Tiran. Desert and mountains, with a hot and dry climate flank the semi-enclosed basin. A high evaporation rate results in a high salinity of 41‰ and a thermohaline circulation that drives water exchange with the Red Sea proper (Reiss and Hottinger 1984). Calculations of the residence time of the upper 300 m vary from four month to one or two years. The inflow of Red Sea water reaching the northern tip of the gulf is estimated to 1% of that at the Straits of Tiran (Wolf-Vecht et al. 1992 and references therein). Simulation of wind-driven circulation by Berman et al. (2000) suggests a series of gyres distributed along the Gulf of Aqaba. Due to the curved shoreline at the northern tip of the gulf, more gyres develop in this part than in the south.

Gyres can cause retention of larvae of tropical shore fishes to their natal reef (Johannes 1978, Swearer et al. 1999) and therefore restriction in gene flow between populations in the northern Gulf of Aqaba and the Red Sea proper might be possible. Restriction of faunal exchange between the Gulf of Aqaba and northern Red Sea is indicated by analysis of species composition of shore fish communities from several sites in the Red Sea (Khalaf and Kochzius 2002), and Klausewitz (1989) suggested isolated development of the deep-sea fishes in the gulf.

Due to the special, fjord-like hydrographic and topographic situation in the Gulf of Aqaba, isolation of populations in the gulf might be possible. Investigations on the genetic population structure with molecular markers can give indications on connectivity of populations. The molecular marker applied in this study is a partial sequence of the 5’ mitochondrial control region. The control region is the most variable of all mitochondrial genes in fishes (Meyer 1993, Lee et al. 1995, McMillan and Palumbi 1997) and therefore a suitable marker for investigations on the genetic structure of populations (Avise et al. 1987, Moritz 1994, Parker et al. 1998, Féral 2002).

The aim of this study is to reveal (1) genetic population structure, (2) genetic diversity, and (3) gene flow between populations of the lionfish *P. miles* in a spatial

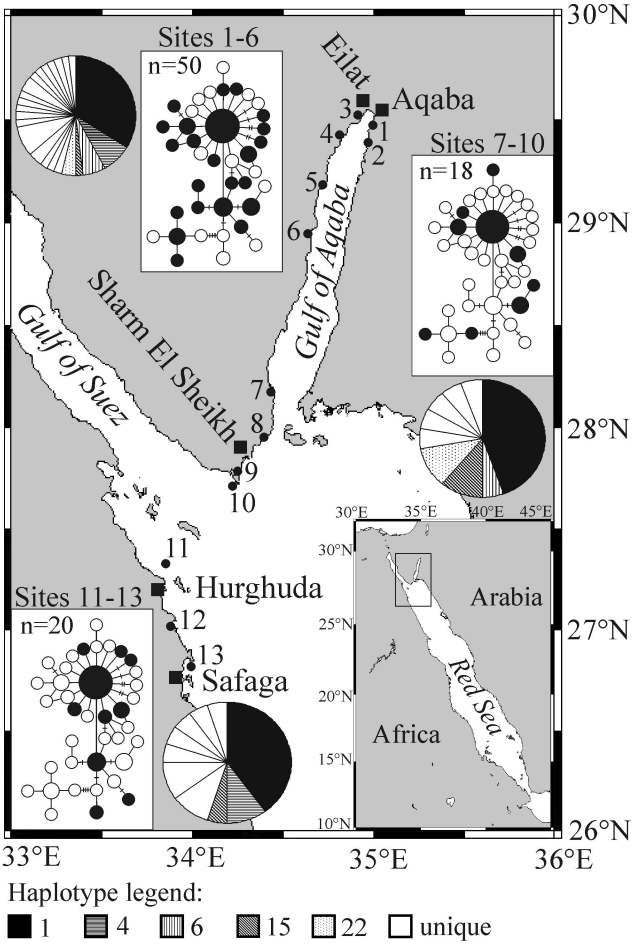

Fig. 1 Maps of the Red Sea and Gulf of Aqaba showing the sample sites (●, 1-13) of *Pterois miles*. Pie charts represent the frequency of shared haplotypes (numbers correspondent to Table 2) for each putative population. Solid circles in the minimum spanning network indicate the presence of a given haplotype in a putative population

scale of 10-350 km. These parameters can indicate if populations in the Gulf of Aqaba are isolated from the Red Sea proper.

MATERIAL AND METHODS

Sampling and DNA extraction

Fin clips of *Pterois miles* were collected in the field from August to October 1998 at 14 sites in the Gulf of Aqaba and northern Red Sea (Fig. 1, Table 1). *P. miles* is encountered frequently on coral reefs and in seagrass-dominated habitats (Khalaf and Kochzius 2002). Due to its venomous spines *P. miles* has virtually no predators and shows no escape behaviour. Therefore it was chosen for this study. While SCUBA diving, clips of 1 to 2 cm length from the feathery pectoral fin, depending on size of the fish, were cut off with a pair of scissors. In most cases this was possible without catching the fish. If necessary, lionfishes were caught with aquarium hand nets and released after fin clipping. Cutting off small fin clips is a non-destructive method to obtain DNA for PCR-based investigations on molecular markers (Wilson and Donaldson 1998). Due to venomous spines specimens have to be handled with caution. After the dive fin clips have been preserved in 70% ethanol.

P. miles specimens from Kenya, Sri Lanka, Indonesia and the sibling species *P. volitans* (Kochzius et al. submitted) from Taiwan were obtained from colleagues or purchased from an aquarium shop. Tissue (100-300 mg) was digested according to the

Chelex® method of Walsh *et al*. (1991) for 3 h at 54 °C in 1.5 ml reaction tube containing 50 µl 5% Chelex® (Bio-Rad Laboratories, Hercules), 2.5 µl 100 mM DTT (Dithiothreitol; Boehringer Ingelheim, Heidelberg), and 2.0 µl Proteinase K (20 mg/ml; Sigma, St. Louis). After centrifugation (3 min., 13,000 rpm) the supernatant was transferred to 500 µl reaction tube and stored at –20 °C.

Table 1 Sample sites of *Pterois miles* and *Pterois volitans*

# in map	Sampling site	Region	Sequenced samples
	Pterois miles		
1	Marine Science Station (MSS), Aqaba (Jordan)	Gulf of Aqaba	12
2	Saudi Arabian Border (Jordan)	Gulf of Aqaba	6
3	Interuniversity Institute (IUI), Eilat (Israel)	Gulf of Aqaba	8
4	Fjord, Taba (Egypt)	Gulf of Aqaba	9
5	Ras Burka (Egypt)	Gulf of Aqaba	10
6	Nuweiba (Egypt)	Gulf of Aqaba	5
7	Nahalet El Tel, Nabq (Egypt)	Gulf of Aqaba	4
8	Ras Nasrani, Sharm El Sheikh (Egypt)	Gulf of Aqaba	2
9	Marsa Bareika, Ras Mohammad (Egypt)	Northern Red Sea	4
10	Ras Mohammad (Egypt)	Northern Red Sea	8
11	Umm Gamar and Fanadir, Hurghada (Egypt)	Northern Red Sea	6
12	Makadi Bay (Egypt)	Northern Red Sea	6
13	Tobya Arba, Safaga (Egypt)	Northern Red Sea	8
	Kenya, Sri Lanka, Indonesia	Indian Ocean	6
			$\sum$ 94
	Pterois volitans		
	Taiwan	Western Pacific	5

Primers, polymerase chain reaction (PCR) and sequencing

Amplification of a 222 bp 5' mitochondrial control region fragment was conducted with the primers L-CR-01 (5'-TGTTTTATCACCATATCTAGGGTT-3') and H-CR-02 (5'-GAAATGGACTTGTTGGTCGG-3'). The primers have been designed on the basis of 8 Sebastes spp (Scorpaenidae) sequences (Rocha-Olivares et al. 1999). PCR reactions were set up in 50 µl reaction volume containing 10 mM Tris-HCL (pH 9.0), 50 mM KCL, 6 mM $MgCl_2$, 0.2 mM each dNTP (PeqLab, Erlangen), 0.2 µM each primer, 1 U Taq polymerase (Biomaster, Köln), 4 µl BSA (2 mg/µl; MBI Fermentas, St. Leon-

Rot), and 4 µl supernatant of the DNA extraction. Thermal cycling was started with 95 °C for 5 min and held at 85 °C until Taq polymerase was added (hot start) to inactivate Proteinase K, subsequently followed by 40 cycles of 94 °C (50 s), 50 °C (60 s), 72 °C (90 s), and a final step of 5 min at 72 °C for termination of the PCR.

PCR products were purified using the QIAquick PCR Purification Kit (QIAGEN, Hilden). Both strands were sequenced using the DyeDeoxy Terminator chemistry (PE Biosystems, Foster City) and an ABI Prism 310 automated sequencer (Applied Biosystems, Weiterstadt) according to the manufacturer’s recommendations.

Sequence, phylogenetic and population structure analysis

Sequences were controlled by aligning both strands with the programme Sequence Navigator (ver. 1.0.1; Applied Biosystems) and checking by eye. All sequences were checked for orthology to the EMBL sequence database.

Multiple alignment of sequences was done using Clustal implemented by Sequence Navigator (Applied Biosystems). Phylogenetic analysis for the description of evolutionary relationships among haplotypes was performed with PAUP* (ver. 4.0b8a; Swofford, 1998). Construction of neighbour-joining (NJ) trees (Saitou and Nei, 1987) was based on the sequence distance of Tamura and Nei (1993), which is regarded as the most appropriate substitution model (Kocher and Carleton, 1997). Maximum parsimony (MP) analysis was restricted to 10,000 trees obtained by heuristic search with the following search parameters: ignore uninformative characters, retain minimal trees, collapse zero length branches, steepest descent not enforced, branch swapping (TBR), accelerated transformation, save all minimal trees, and gaps treated as “fifth base”. Search for maximum likelihood (ML) trees followed the recommendations of Hershkovitz and Leipe (1998). Based on an MP tree and under the likelihood optimality criterion the tree was described and the following parameters were estimated: substitution rate matrix, gamma shape parameter, and invariant proportion. Based on the estimated values a ML tree-building search was conducted. Evaluation of statistical confidence in nodes was based on 100 non-parametric bootstrap replicates for ML and 1,000 non-parametric bootstrap replicates for NJ (Felsenstein, 1985). *Pterois volitans* (Plate 2) was used as outgroup for all trees, because morphological (Schultz 1986) and genetic studies (Kochzius et al. submitted) have shown that *P. miles* and *P. volitans* are

sibling species. Relationship of haplotypes was inferred by a minimum spanning network with the programme ARLEQUIN (ver. 2.000; Schneider et al. 2000).

Analysis of genetic population structure was also conducted with ARLEQUIN. Estimates of genetic variation were obtained in the form of haplotype diversity *h* (Nei 1987), nucleotide diversity π (Nei and Jin 1989), and mean number of nucleotide differences among all haplotypes in a putative population. Significance of population structure was tested by the analysis of molecular variance (AMOVA, Excoffier et al. 1992), which take into account Tamura-Nei distances between haplotypes, gamma shape parameter and geographic distribution. Φ-statistics of AMOVA quantify population structure at each level in a given hierarchy. For this hierarchical analysis, the samples were divided into four regions: northern Gulf of Aqaba (sites 1-6) southern Sinai (sites 7-10), Hurghada and Safaga (sites 11-13) and Indian Ocean (Fig. 1). The significance of Φ-statistics was tested by comparisons to null distributions constructed from 10,000 random permutations of the original data matrix. The hypothesis of neutral evolution was tested by Tajima’s *D*-test (Tajima 1989).

RESULTS

Polymorphic sites

The PCR products had a length of 222 bp and after removing of primers, areas of ambiguity as well as missing data, mtDNA control region sequences of 166 bp were obtained from 94 *Pterois miles* specimens (56 from the Gulf of Aqaba, 32 from the northern Red Sea, and 6 from the Indian Ocean) and 5 *P. volitans* specimens from Taiwan (Table 1). Among the 94 *P. miles* specimens, 32 polymorphic sites were detected yielding 38 haplotyps. These polymorphisms included 27 transitions and 8 transversions. The 166 bp sequence of haplotype 1 (Table 2) is available as a representative haplotype from EMBL database (accession number AJ431259). The control region sequence had a high A-T composition of about 69%, similar to other fishes (e.g. McMillan and Palumbi 1997). No heteroplasmy was detected in mtDNA control region of *P. miles*, i.e. non of the individuals contained several types of molecules differing in repeat copy numbers). Heteroplasmy was shown in the length of repeats in several fish species (Lee et al. 1995, Bentzen et al. 1998).

Table 2 Polymorphic sites of mtDNA control region haplotypes of *Pterois miles* (numbers) and *Pterois volitans* (Ptevol; outgroup). Haplotype one is the reference haplotype (EMBL database accession number AJ431259)

Haplotype	Base positions																																													
	003	011	013	016	017	018	019	021	025	027	037	038	041	045	047	049	056	057	058	062	064	079	080	089	098	105	108	115	117	118	119	120	121	124	125	126	127	128	138	141	145	149	151	162	163	165
1 (ref.)	C	T	A	A	T	T	C	T	T	A	T	A	G	A	A	G	G	A	C	G	A	A	C	C	G	G	T	C	G	A	A	C	T	T	C	A	G	T	T	T	T	T	C	A	A	A
2	.	.	.	.	.	C	G	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	.	.	.	.	.	.	.	.	.	.	.	.	A	.	G	.	A	.	.	.	.	.	T	.	.	.	.	T	A	.	.	.	.	.	.	.	.	.	.	C	.	.	.	G	.	G
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8	.	.	.	.	.	.	.	.	.	.	.	.	A	.	G	.	A	.	.	.	.	.	.	.	.	.	.	T	A	.	.	.	.	.	.	.	.	.	.	C	.	.	.	G	.	G
9	.	.	.	T	A	.	.	.	.	W	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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36	.	A	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
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Ptevol 01	.	.	.	W	.	.	.	.	.	R	C	.	.	.	G	A	A	C	T	A	.	T	-	G	A	.	C	.	A	.	.	T	.	C	.	G	.	C	C	.	C	C	T	C	.	.
Ptevol 02	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	.	A	C	T	A	.	T	-	G	A	.	C	.	A	.	.	T	.	C	T	G	A	C	C	.	C	C	T	T	.	.
Ptevol 03	S	.	.	.	.	.	.	C	.	.	.	.	.	.	G	A	A	C	T	A	.	T	-	G	A	.	C	.	A	.	.	T	.	C	T	G	.	C	C	.	C	C	T	C	.	G
Ptevol 04	.	.	.	N	.	.	.	.	.	.	C	.	.	.	G	A	A	C	T	A	.	T	-	G	A	.	C	.	A	.	.	T	.	C	T	G	.	C	C	.	C	C	T	C	.	G
Ptevol 05	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	A	A	C	T	A	.	T	-	G	A	.	C	.	A	.	.	T	.	C	T	G	.	C	C	.	C	C	T	C	.	.

Table 3 Measures (± SD) of genetic diversity in populations of *Pterois miles* and results of Tajima's (1989) neutrality test.

	Diversity index						
	n	No. of haplotypes	Haplotype *h*	Nucleotide π (%)	Mean pairwise difference (%)	No. of sites with substitutions *S*	Tajima's *D* statistic
Northern Gulf of Aqaba	50	23	0.874 ± 0.041	2.20 ± 1.26	3.65 ± 1.88	28	-1.4575 (p=0.05)
Southern Sinai	18	9	0.804 ± 0.091	2.04 ± 1.22	3.38 ± 1.82	16	-1.1680 (p=0.13)
Hurghada / Safaga	20	10	0.837 ± 0.076	1.25 ± 0.82	2.08 ± 1.21	12	-1.4336 (p=0.08)
Red Sea	88	35	0.848 ± 0.037	1.88 ± 1.10	3.12 ± 1.63	32	-1.5841 (p=0.05)
Indian Ocean	6	6	1.000 ± 0.096	1.90 ± 1.32	3.15 ± 1.89	8	-0.7353 (p=0.31)

Genetic diversity

Tamura-Nei sequence divergence among the mtDNA control region haplotypes of *P. miles* ranged from 0.6% to 9.9%. All putative regional populations showed high levels of haplotype diversity (*h*) ranging from 0.80 to 1.00 with an average of 0.86, and nucleotide diversities (p) ranging from 1.25% to 2.20% with an average of 1.95%. The average values for the Red Sea populations were *h*=0.85 and p=1.9%. Mean pairwise nucleotide difference between haplotypes within putative regional populations ranged from 2.08% to 3.65% with an average distance of 3.23% (Table 3). The null hypothesis of neutrality of the mtDNA control region mutations could not be rejected or was rejected on a very low significance level of *p*=0.05 (Table 3). This indicates that the applied mtDNA sequence was a neutral marker and not under selection.

Phylogeographic patterns and genetic population structure

The evolutionary relationships among the 38 *P. miles* haplotypes are shown in a ML tree rooted with 5 *P. volitans* haplotypes (Fig. 2). *P. miles* haplotypes can be assigned to "clade A" and "clade B". Haplotypes of "clade B" occur only in the northern Gulf of Aqaba and southern Sinai, whereas haplotypes of "calde A" are widely distributed (similar NJ tree not shown). However, only a few minor branches were supported by the bootstrap analysis of ML and NJ, but neither "clade A" nor "group B" were reliable (Fig. 2). The strict consensus MP tree (not shown) revealed mainly an unresolved polytomy, with a few clades that are also supported by the bootstrap analysis of the ML and NJ tree.

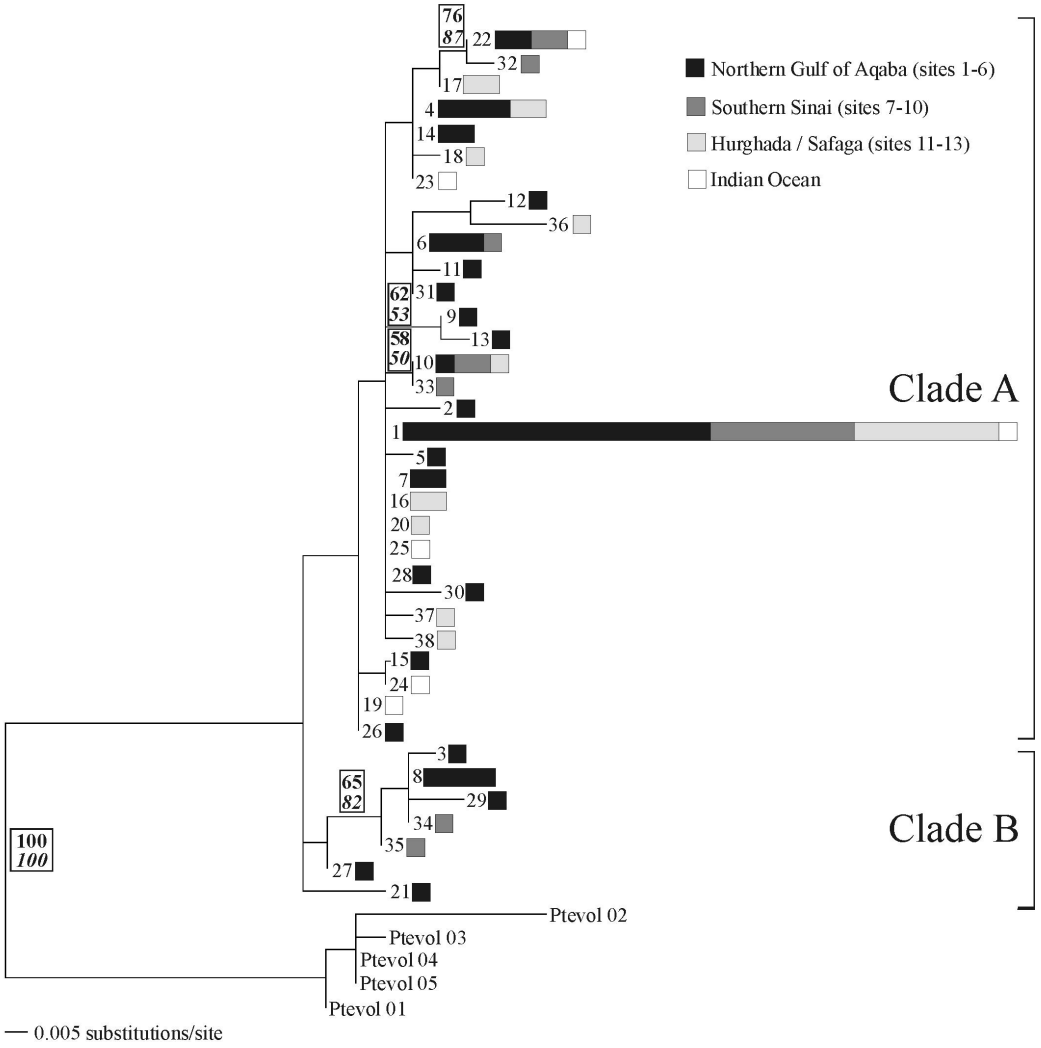

Fig. 2 Maximum-likelihood tree of mtDNA control region haplotypes (parameter for gamma distribution rate of 0.58). Values in boxes are the percentage bootstrap iterations that support the branch (ML 100 replicates; *NJ 1,000 replicates*). Haplotypes are labled with numbers corresponding to Table 2. Bars represent the frequency and geographical distribution of each haplotype

This unresolved polytomy is manifested in a star-like phylogeny of the minimum spanning network (Fig. 3). The most abundant haplotypes (1 and 4) are radiation origins to unique haplotypes. The dominant haplotype 1 accounted for 36 % of all *P. miles* specimens. The minimum spanning networks and haplotype frequency pie charts for each putative population shown on the map ascertain the wide distribution of haplotype 1 (Fig. 1) in the area under investigation. Specimens collected in Nabq (Gulf of Aqaba, sample site 7) have been included in the southern Sinai group due to the close vicinity of this site. Incorporation in the putative population of the northern Gulf of Aqaba did not change the results of the analysis and therefore samples from Nabq remained in the southern Sinai group for all further computations.

Table 4 Pairwise Φ_{ST} values among sample sites (*below the diagonal*) of *Pterois miles* determined from the AMOVA as implemented in the programme ARLEQUIN (Schneider et al. 1997). Significance of the pairwise Φ_{ST} values (*above diagonal*) was tested using 10,000 Monte-Carlo permutations of the data set. Comparisons showing significant differentiation are indicated with an asterisk.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 MSS, Aqaba n=12		0.88661	0.59629	0.76149	0.09677	0.29228	*0.04594	0.08700	0.30205	0.55132	0.24633	0.62854	0.15249	0.51906
2 Saudi border n=6	-0.28363		0.96481	0.99902	0.48583	0.41349	0.32356	0.31476	0.46530	0.63636	0.52297	0.84848	0.51711	0.64712
3 Eilat n=8	-0.10249	-0.50601		0.27370	0.38514	*0.04203	0.41447	0.28250	0.08993	0.35679	0.38905	0.67742	0.42424	0.24242
4 Taba n=9	-0.05659	-0.12100	0.04033		0.11339	0.34995	*0.02346	0.06452	0.35484	0.59140	0.27859	0.38123	0.13881	0.31183
5 Ras Burka n=10	0.05192	-0.01708	0.15341	0.06100		*0.00000	0.05670	0.15445	1.00000	0.11730	0.40176	0.16618	0.24927	0.32160
6 Nuweiba n=5	0.01871	0.00778	0.22059	0.05665	0.00292		0.01955*	*0.00880	0.50244	0.58749	0.11828	*0.01271	0.13783	0.18377
7 Nabq n=4	0.80806	-0.00182	0.22779	1.17328	1.61823	1.44567		0.20821	*0.00000	0.06158	0.20821	0.29521	0.73900	0.07625
8 Ras Nasrani n=2	0.28438	-0.01508	0.02920	0.33087	0.62554	0.61307	0.27571		0.12708	0.12708	0.30401	0.45161	0.17889	0.29912
9 Marsa Bareika n=4	0.03632	0.04431	0.26299	0.05448	0.00000	-0.00031	1.56489	0.60540		0.39101	0.44379	0.18377	0.13978	0.29717
10 Ras Mohammad n=8	-0.03562	-0.13576	0.05106	-0.06250	0.04050	-0.01116	1.01562	0.34237	0.02842		0.26393	0.54545	0.21603	0.31965
11 Hurghada n=6	0.09459	-0.03793	0.04289	0.17123	0.30550	0.29320	0.68417	0.10132	0.28462	0.20298		0.45650	0.19550	0.75953
12 Makadi Bay n=6	-0.05448	-0.23477	-0.10554	-0.00357	0.13439	0.12636	0.33042	-0.10301	0.11951	-0.05768	-0.10308		0.32356	0.80156
13 Safaga n=8	0.16614	-0.31060	-0.07627	0.41748	0.73711	0.60314	-0.60229	0.35724	0.69864	0.33899	0.48535	0.13143		0.11926
14 Indian Ocean n=6	-0.01323	-0.08691	0.08733	0.02866	0.14906	0.14011	0.98390	0.07559	0.13391	0.09629	-0.21659	-0.18954	0.55956	

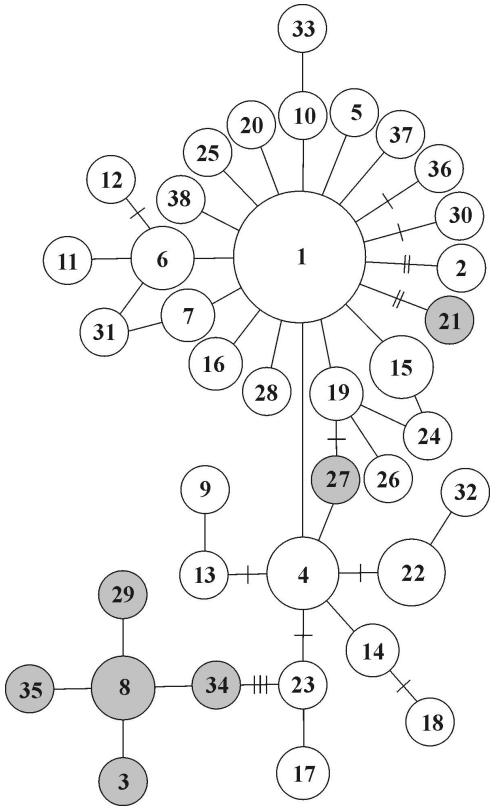

Fig. 3 Minimum spanning network of the 38 distinct haplotypes of *Pterois miles* in the Gulf of Aqaba and northern Red Sea. The diameter of circles represent the abundance of haplotypes, the numbers are as in Table 2. Connections between haplotypes indicate one mutational step, each transversal bars represents an additional mutational step. White haplotyps belong to "clade A" and grey haplotypes to "clade B" in the maximum-likelihood tree (Fig. 2)

Only 8.8% of the pairwise Φ_{ST} comparisons between all sample sites show significant differences, mainly between sites in the Gulf of Aqaba (Table 4). All molecular variance determined from the AMOVA was attributed to variance among populations within regions or within populations, and no significant population structure was detected (Table 5).

DISCUSSION AND CONCLUSIONS

None of the analytical tools, phylogenetic relationships, minimum-spanning net-work, haplotype frequencies, and AMOVA revealed a separation of *Pterois miles* populations in the Gulf of Aqaba and northern Red Sea. Haplotype frequencies showed a dominance of haplotype 1 in each putative population (Fig. 1) and the minimum spanning network of 38 haplotypes revealed a star-like phylogeny with no geographic pattern (Fig. 3). NJ, MP and ML trees showed clades, but weak or no support by bootstrap analysis. "Clade A" was not related to a geographic pattern, because the dominant hapotypes were present in all putative populations. Haplotypes of "clade B" occurred only in the northern Gulf of Aqaba and southern Sinai (Fig. 2), but AMOVA did not reveal restricted gene flow. The specimens from the Indian Ocean did not show a separation from the Red Sea samples, but this is most probably due to the low samples size (n=6) in the Indian Ocean. The most abundant haplotype 1 was present in the Indian Ocean, but large-scale distribution of dominant haplotypes in marine species is

common even in structured populations (e.g. Rocha-Olivares and Vetter 1999). A study on the genetic population structure of the crown-of thorns starfish has revealed a relative genetic isolation of Red Sea populations from the Indian Ocean (Benzie et al. 2000). For the study of this relationship in *P. miles* more samples from Indian Ocean populations are required.

The lack of genetic structure in populations of *P. miles* in the Gulf of Aqaba and northern Red Sea can reflect: (1) an unsuitable molecular marker, (2) the history of the population during the last glacial (population bottleneck or founder event), or (3) high recent gene flow and panmixia.

Table 5 Hierarchical analysis of molecular variance (AMOVA) of mtDNA control region haplotypes of *Pterois miles*. Analysis based on Tamura-Nei distance (1993) with a parameter for gamma distribution rate of 0.58

Source of variation	*df*	Sum of squares	Variance	% of variation	Φ statistic	p
Among regions	2	2.718	-0.03619	-2.28	Φ_{ct} = 0.05258	0.10
Among populations within regions	8	16.824	0.08523	5.38	Φ_{sc} = 0.03094	0.07
Within populations	64	98.290	1.53578	96.91	Φ_{st} = -0.02284	0.63

Suitability of the molecular marker

The control region is the most variable of all mitochondrial genes in fishes (Meyer 1993, Lee et al. 1995, McMillan and Palumbi 1997) and therefore a suitable marker for investigations on the genetic structure of populations (Avise et al. 1987, Moritz 1994, Parker et al. 1998, Féral 2002). Mitochondrial DNA is haploid and clonally inherited and therefore the signal from genetic drift is stronger than for nuclear loci (Waples 1998).

However, it seems unclear on what time scale processes revealed by molecular markers are operating (Bossart and Prowell 1998b). In many cases present-day pattern of genetic structure may reflect population response to climatic changes during Pleistocene glaciations and post-glacial expansions. Therefore, it seems uncertain that molecular markers detect processes on ecological time scales (Bossart and Prowell 1998a). This problem might be more connected to allozymes and some slow evolving mtDNA genes (e.g. cytochrome *b*), whereas highly variable mtDNA control region and

microsatellite markers are more likely to reveal ongoing evolution (Daemen et al. 2001). Comparisons of life history and genetic structure of marine fish and invertebrate populations have shown a correlation between dispersal capabilities and gene flow (Waples 1987, Doherty et al. 1995, Bohonak et al. 1998, Bohonak 1999).

Even though the sequence used in the present study was relatively short (166 bp), haplotype diversity (h=0.85) and nucleotide diversity (π=1.9%) were high in the Red Sea population, compared to other studies (Table 6). Mutation rates are certain to vary among different markers (mtDNA CR, mtDNA cyt *b*, mtDNA RFLP), but comparison of pattern in genetic diversity rather than absolute values should be justified. High genetic diversity was due to the relatively high number of 32 polymorphic sites in a relatively short sequence of 166 bp. Other studies have shown that sequences <190 bp can reveal genetic population structures (Quinn 1992, Burton 1998). Therefore, the variability of the applied molecular marker is sufficient for the investigation of genetic population structure.

History of the population during the last glacial

Haplotype diversity (h) and nucleotide diversity (π) can give an indication on the population history of the species. High values of h and π are indicators of a large stable population with long evolutionary history (Grant and Bowen 1998). This suggests that the observed homogeneity in genetic population structure be not due to a population bottleneck or founder event.

In the following we will present arguments for the persistence of a stable population in the Red Sea despite severe ecological changes in the Pleistocene. Paleoceanographic studies revealed that during the last glacial the sea level was dropped by 120 m (Rohling et al. 1998) and water exchange between the Red Sea and Indian Ocean at the shallow sill of Bab-el-Mandab was restricted or even interrupted (Braithwaite 1987). However, the extent of environmental change in the Red Sea is still controversial. Some authors assume hypersalinity that killed most marine life (Sheppard et al. 1992) or even conditions comparable with the present day Dead Sea (Braithwaite 1987), while others suggest survival of the fauna (Goren 1986, Klausewitz 1989, Rohling et al. 1998).

Table 6 Haplotype diversity (*h*), nucleotide diversity (π), number of specimen and haplotyps, sequence length (bp) and polymorphic sites, genetic merker (CR= control region; cyt *b*= cytochrome *b*), restricted gene flow, and geographic scale of studies on the genetic population structure of marine fishes (*=coral reef species)

Species	Family	h	π (%)	n (specimen)/ n (haplotypes)	bp sequence/ polymorphic sites	Marker	Restricted gene flow	Scale
Pterois miles[1]*	Scorpaenidae	0.85	1.9	94/38	166/32	mtDNA CR	no	10-350 km
Sebastolobus alascanus[2]	Scorpaenidae	0.99	1.5	93/83	463/-	mtDNA CR	no	>1000 km
Sebastolobus altivelis[2]	Scorpaenidae	0.96	1.2	55/43	463/-	mtDNA CR	no	>1000 km
Sebastes helvomaculatus[3]	Scorpaenidae	0.95	1.2	88/51	597/68	mtDNA CR	yes	>1000 km
Dascyllus trimaculatus[4]*	Pomacentridae	0.99	-	98/87	378/145	mtDNA CR	no/yes	10-750 km/>1000 km
Bothrocara hollandi[5]	Zoarcidae	0.66-0.85	0.3-0.6	296/32	240/17	mtDNA CR	no	>1000 km
Lates calcarifer[6]	Centropomida	0.76-0.93	2.4-5.0	270/63	270/-	mtDNA CR	yes	>1000 km
Gobiesox maeandricus[7]	Gobiesocidae	0.21-0.81	-	111/45	378/39	mtDNA CR	yes	200-400 km
Scomber scombrus[8]	Scombridae	0.99	2.9	205/124	272/106	mtDNA CR	yes	>1000 km
Amphiprion ocellaris[9]*	Pomacentridae	-	0.005	166/27	399/25	mtDNA cyt *b*	yes	>800 km
Anguilla anguilla[10]	Anguillidae	0.61-0.82	0.2-0.5	107/17	392/15	mtDNA cyt *b*	no	>1000 km
Stegastes leucostictus[11]*	Pomacentridae	0.41	0.3	61/7	-	mtDNA RFLP	yes	>1000 km
Abudefduf saxatilis[11]*	Pomacentridae	0.79	0.5	67/18	-	mtDNA RFLP	no	>1000 km
Ophioblennius atlanticus[11]*	Bleniidae	1	1.1	64/55	-	mtDNA RFLP	no	>1000 km
Gnatholepis thompsoni[11]*	Gobiidae	0.98	0.7	61/42	-	mtDNA RFLP	yes	>1000 km
Haemulon flavolineatum[11]*	Haemulidae	0.78	0.6	65/17	-	mtDNA RFLP	no	>1000 km
Halicoeres bivittatus[11]*	Labridae	0.74	0.7	57/23	-	mtDNA RFLP	yes	>1000 km
Thalassoma bifasciatum[11]*	Labridae	0.55	0.5	89/20	-	mtDNA RFLP	no	>1000 km
Holocentrus ascensionis[11]*	Holocentridae	0.94	0.6	61/34	-	mtDNA RFLP	no	>1000 km
Decapterus macarellus[12]	Carangidae	0.82	1.2-1.5	73/15	-	mtDNA RFLP	no	>1000 km
Decapterus macrosoma[12]	Carangidae	0-0.67	0-0.5	125/9	-	mtDNA RFLP	yes	>650 km
Seriola dumerili[13]*	Carangidae	0.91	0.55	444/49	-	mtDNA RFLP	no	100->1000 km
Lutjanus campechanus[13]*	Lutjanidae	0.74	0.22	707/92	-	mtDNA RFLP	no	100->1000 km
Epinephelus morio[13]*	Serranidae	0.39	0.06	100/16	-	mtDNA RFLP	no	100->1000 km
Sciaenops ocellatus[13]	Sciaenidae	0.95	0.57	869/118	-	mtDNA RFLP	yes	100->1000 km
Pogonias cromis[13]	Sciaenidae	0.78	0.48	300/37	-	mtDNA RFLP	no	100->1000 km
Cynoscion nebulosus[13]	Sciaenidae	0.86	0.45	470/81	-	mtDNA RFLP	yes	100->1000 km

[1]this study, [2]Stepien et al. 2000, [3]Rocha-Olivares and Vetter 1999, [4]Bernardi et al. 2001, [5]Kojima et al. 2001, [6]Chenoweth et al. 1998, [7]Hickerson and Ross 2001, [8]Nesbø et al. 2000, [9]Nelson et al. 2000, [10]Daemen et al. 2001, [11]Shulman and Birmingham 1995, [12]Arnaud et al. 1999, [13]Gold and Richardson 1998

Detailed paleoceanographic studies in the Gulf of Aqaba indicate the following oceanographic settings during the last glacial: (1) 51‰ salinity, (2) 17°C minimum winter temperature of the upper waters, and (3) connection of the Gulf of Aqaba and Red Sea with the Indian Ocean (Reiss and Hottinger 1984). Other studies suggest a glacial salinity of 50 ± 2‰ in the Red Sea proper (Rohling et al. 1998).

However, salinity of 45-50‰ may be expected to occur frequently in shallow inshore waters of the present day Red Sea. In the Arabian Gulf up to 60‰ salinity have been measured in waters of less than 10 m depth (Edwards 1987). Examples of corals, invertebrates, and plants from the Arabian Seas, as well as fishes from the Bitter Lake of the Suez Canal show that marine organisms can adapt to high salinity and low temperatures.

Studies in the Arabian Gulf have shown that three reef building coral species survive high salinity of up to 50‰ and can cope with temperatures of 17°C (Sheppard and Sheppard 1991). Submerged fossil terraces (>100m depth) in the Gulf of Aqaba and other parts of the Red Sea indicate that coral growth was possible even during periods of low sea level (Fricke 1996). Some echinoderms, seagrasses, brown and green algae can inhabit salinities >50‰ (Sheppard et al. 1992). Salinity in the Bitter Lake reached 48‰ (Morcos and Messieh 1973), but 13 Red Sea fish species have been found (Ben Tuvia 1975). High salinity seems not to reduce growth of *Mugil cephalus* (Botros 1971), and its fry tolerated 116-126‰ salinity (Hotos & Vlahos 1998). Many Red Sea species, such as *Pterois miles*, passed the high saline Bitter Lake waters and entered the Mediterranean (Golani and Sonin 1992). Additionally, low temperature is also not a limiting factor for all tropical shore fishes, e.g. *P. miles* occurs in warm-temperate waters along the South African east coast were winter temperatures drop to 15°C (Smith 1957).

The arguments summarised above indicate that many Red Sea organisms most likely survived the gradual increase of salinity as well as decrease of temperature over thousands of years and were able to adapt to the environmental change. Additionally, a complete extinction of the Red Sea fauna would make it difficult to explain the high number of endemics in the Red Sea (Klausewitz 1989). Therefore, a stable population in the Gulf of Aqaba and northern Red Sea is likely and fits to the high genetic diversity of the *P. miles* population in that area.

High gene flow and panmixia

As shown above, there are strong arguments for a large, stable *P. miles* population in the Gulf of Aqaba and northern Red Sea during the last glacial. Therefore, the revealed population structure indicates a high level of gene flow and panmixia. Studies on the ichthyoplankton in the northern Gulf of Aqaba have shown that highest abundance of larvae was reached in spring and summer (Cuschnir 1991, Froukh 2001). This coincides with a more efficient dispersal in the upper layer in summer and spring than in winter (Berman et al. 2000). Due to the oceanographic conditions and behaviour of fish larvae mentioned above, large-scale dispersal and high gene flow, resulting in panmixing of *P. miles* populations in the Gulf of Aqaba and northern Red Sea is likely.

CONCLUSIONS

Separating panmixia from founder events or bottlenecks in a genetic population structure can be problematic (Bossart and Prowell 1998a, 1998b), but knowledge about life history and oceanographic history of the environment of a species can give indications for interpretation (Bohonak et al. 1998, Grant and Bowen 1998, Waples 1998, Bohonak 1999). Consideration of observed high genetic diversity, paleoceanography of the Red Sea, and life history of *P. miles* indicate that the revealed genetic population structure reflects high gene flow and panmixia.

The Gulf of Aqaba is particularly vulnerable to human disturbances by urban and industrial pollution, shipping and port activities, as well as tourism (Hawkins and Roberts 1994, Badran and Foster 1998, Abelson et al. 1999). Studies on shore fish communities at the Jordanian coast have shown that fish abundance was 50% lower at an industrial site compared to undisturbed coral reefs, and that the trophic community structure was different (Khalaf and Kochzius in press).

In terms of marine conservation in the Gulf of Aqaba high levels of gene flow in *P. miles* implicate re-colonisation of restored habitats and replenishment of depleted stocks from the Red Sea proper. However, it is not possible to estimate on which time-scale gene flow between populations in the Gulf of Aqaba and Red Sea proper operate (Bossart and Prowell 1998b). Consequently, it is not clear how fast depleted populations will be replenished or restored habitats will be re-colonised. Therefore, coastal zone

management in the Gulf of Aqaba has to follow the precautionary principle and should not rely upon fast replenishment or re-colonisation.

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Chapter 5

[1]Kochzius M, [2*]Söller R, [3]Khalaf MA, [2]Blohm D

[1]Centre for Tropical Marine Ecology, Bremen, Germany

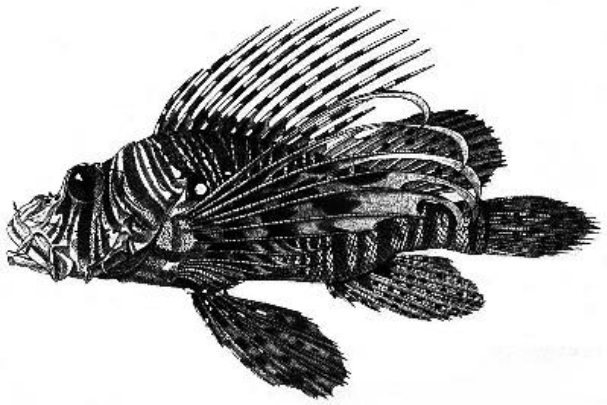
[2]Department of Biotechnology and Molecular Genetics, University of Bremen, Germany

[3]Marine Science Station, Aqaba, Jordan

*present address: ARTUS GmbH, Hamburg

Molecular Phylogeny and Biogeography of Lionfishes (Scorpaenidae, Pteroinae) Based on Mitochondrial DNA Sequences

Molecular Phylogenetics and Evolution (submitted)



Pterois volitans, taken from Cuvier G, Valenciennes A (1829) Histoire naturelle poissons. Vol. 4, Levrault, Paris

ABSTRACT

This study investigates the molecular phylogeny of 7 lionfishes of the genera Dendrochirus and Pterois, as well as the evolution of the sibling species *Pterois miles* and *P. volitans*. Phylogenetic analysis based on 964 bp of partial mitochondrial DNA sequences (cytochrome b and 16S rDNA) revealed two main clades: (1) “*Pterois*” clade (*Pterois miles* and *P. volitans*), and (2) “*Pteropterus-Dendrochirus*” clade (remainder of the species). Neither *Pterois* nor *Dendrochirus* were monophyletic. This result is not congruent to the current taxonomy and questions the recognition of separate genera. However, the molecular phylogeny corresponds with the morphological character of cycloid and ctenoid scales. Therefore we suggest merging the species of the “*Pteropterus-Dendrochirus*” clade into a single genus. Molecular clock estimates for *P. miles* and *P. volitans* suggest a divergence time of 2.4-8.3 my, which coincide with tectonic uplift and sea level changes during the ice ages that separated populations of the Indian and Pacific Ocean. The importance of Pleistocene environmental changes for speciation processes in the Indo-Malayan Archipelago is underlined by these findings.

KEYWORDS

Lionfish, Scorpaenidae, *Pterois*, *Dendrochirus*, Molecular phylogeny, Speciation, Biogeography

INTRODUCTION

Lionfishes (Pteroinae), also called firefishes or turkeyfishes, are a subfamily of the scorpionfishes (Scorpaenidae) and are native to the tropical Indo-Pacific. However, due to human activities *Pterois miles* entered the Mediterranean as a Lessepsian immigrant via the Suez Canal from the Red Sea (Golani and Sonin, 1992), and *Pterois volitans* was sighted in the Atlantic along the U.S. East Coast (NCCOS, 2001). The Pteroinae comprise 17 species within 5 genera: *Pterois* (8 species), *Dendrochirus* (5 species), *Ebosia* (2 species), *Brachypterois* (1 species), and *Parapterois* (1 species) (Eschmeyer and Rama-Rao, 1977; Nelson, 1994; FishBase, 1999). The genera *Pterois* Oken, 1817 and *Dendrochirus* Swainson, 1939 are mainly secretive coral or rocky reef dwelling fishes, that are nocturnally active and remain mostly stationary during daylight. They mostly feed on crustaceans, but some species also ambush fishes. All *Pterois* and *Dendrochirus* species have venomous spines at the dorsal, anal and pelvic fins. Poison is produced by glandular tissue in longitudinal grooves on each side of the spine and can be fatal to humans (Shiomi *et al.*, 1989; Randall *et al.*, 1997).

The two genera *Pterois* and *Dendrochirus* are closely related, but taxonomic relationships within this group of fishes are not clear and separate genera possibly may not be warranted (Eschmeyer and Randall, 1975). Taxonomic ambiguities are due to an unprecise description of the genus *Dendrochirus* by Swainson (1839), that was excoriated by several authors (Cantor, 1849; Swain, 1882; Jordan, 1917-1920). Several authors did not apply *Dendrochirus* and placed these species into the genus *Pterois* (e.g. Klunzinger, 1870; Günther, 1873; Beaufort and Briggs, 1962). Separation of the two genera is based on two morphological characters: (1) unbranched pectoral rays in *Pterois* and some upper branched pectoral rays in *Dendrochirus* (Swainson, 1839; Eschmeyer and Randall, 1975), and (2) upper pectoral rays free from membrane in *Pterois* and no rays free from membrane in *Dendrochirus* (Smith, 1957). Currently *Pterois* and *Dendrochirus* are recognised genera (Eschmeyer, 1998).

The sibling species *Pterois volitans* (Linnaeus, 1758) (Plate 2) and *P. miles* Bennett, 1828 (Plate 1) have been treated as synonym (Beaufort and Briggs, 1962; Randall, 1983), and Smith (1957) assumed that *P. miles* is the adult form of *P. volitans.* However, later Smith (1965) recognised two separate species. Meristic and morphometric analysis by Schultz (1986) supports the recognition of two sibling

species, but there is an overlap in characters. *P. miles* is distributed in the Red Sea, Persian Gulf and Indian Ocean (except Western Australia), whereas *P. volitans* occur in Western Australia, the Western and Central Pacific (Smith, 1986; Fig. 1).

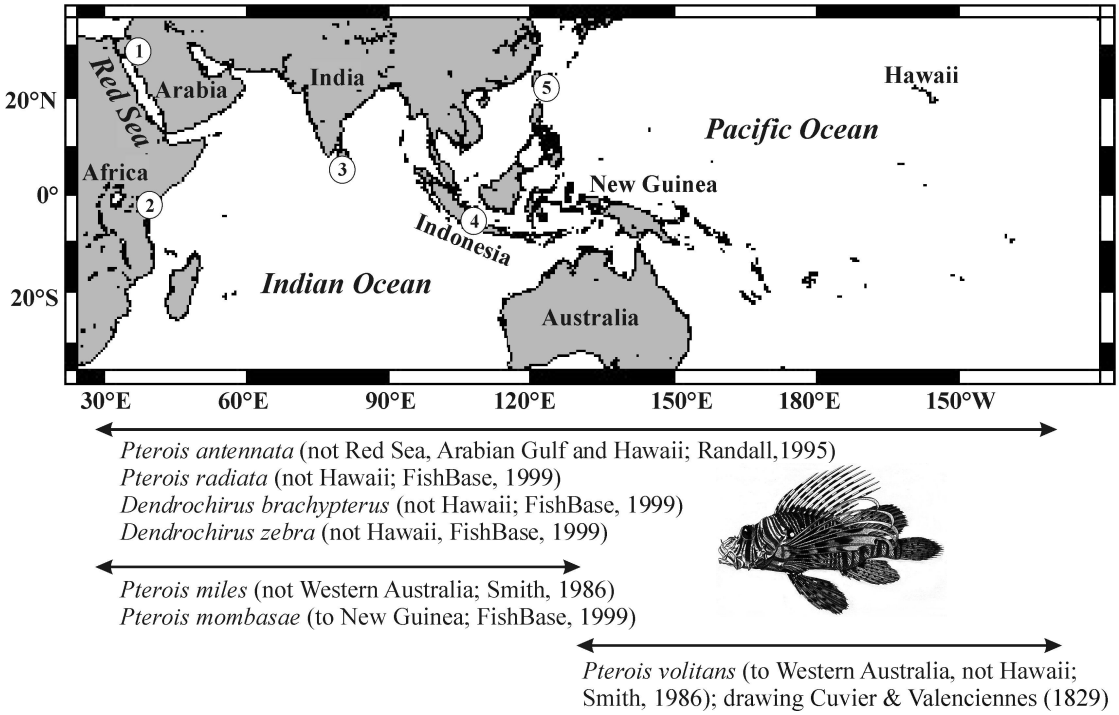


Fig. 1 Map of the Indo-Pacific with distribution of lionfish species considered in this study. Sampling locations: (1) Red Sea (Jordan), (2) Indian Ocean (Kenya), (3) Indian Ocean (Sri Lanka), (4) Java Sea (Indonesia), and (5) Western Pacific (Taiwan)

The two species presumably meet somewhere in the Indo-Malayan Archipelago, the centre of marine biodiversity (Briggs, 1999). Several theories are proposed to explain the high diversity of the Southeast Asian seas. They fall into three main categories: (1) centre-of-evolutionary-radiation from where new species disperse (Briggs 1999), (2) centre-of-overlap of the Indian Ocean and Pacific Ocean biota (Woodland 1983), and (3) centre-of-accumulation of species originated in peripheral areas (Jokiel and Martinelli, 1992). Several studies on molecular phylogenies (McMillan and Palumbi, 1995; Williams, 2000) and population genetics (Lacson and Clarke, 1995; Chenoweth *et al.*, 1998; Williams and Benzie, 1998; Barber *et al.*, 2000) of marine animals have shown a genetic discontinuity between the Indian Ocean and West Pacific, supporting the view of speciation in separated ocean basins (Benzie, 1998; 1999).

These study aims to investigate (1) the phylogenetic relationships between the two genera *Pterois* and *Dendrochirus*, and (2) the molecular biogeography as well as speciation of the sibling species *Pterois miles* and *P. volitans*. Sequences of different regions of the mitochondrial genome (cytochrome *b* and 16S rDNA) have been chosen for this analysis, because contiguous sites of the mitochondrial genome are less likely to result in a tree close to the whole genome tree (Cummings *et al*., 1995).

MATERIALS AND METHODS

Sampling and DNA Extraction

Fishes from several locations in the Indo-Pacific were collected in the field, obtained from colleagues or purchased from an aquarium shop. (Table 1) Identification to species level is based on Lieske and Myers (1994), Khalaf and Disi (1997), and Randall *et al*. (1997). Due to venomous spines specimens have to be handled with caution. Tissue samples (musculature and fin clips) or complete specimens have been preserved in 70% ethanol or frozen at –20 °C.

Table 1 List of Species, Localities, Database Accession Numbers, and Source of the Specimens Used in this Study

			Accession No	
Species	Abbreviations	Locality	cyt *b*	16S rDNA
Dendrochirus brachypterus (Plate 1)	Db	Red Sea, Jordan (FC); Indian Ocean, Kenya (AS)	AJ429412-14	AJ429434
Dendrochirus zebra (Plate 1)	Dz	Western Pacific, Taiwan (C)	AJ429415/16	AJ429399/400
Pterois antennata (Plate 1)	Pa	Indian Ocean, Kenya (AS)	AJ429417/18	AJ429401
Pterois miles (Plate 1)	Pm	Red Sea, Jordan (FC); Indian Ocean, Kenya (AS); Indian Ocean, Sri Lanka (AS); Java Sea, Indonesia (C)	AJ429419-26	AJ429402-04
Pterois mombasae (Plate 2)	Pmo	Indian Ocean, Kenya (AS)	AJ429427/28	AJ429405/06
Pterois radiata (Plate 2)	Pr	Red Sea, Jordan (FC)	AJ429429/30	AJ429407/08
Pterois volitans (Plate 2)	Pv	Western Pacific, Taiwan (C)	AJ429431-33	AJ429409-11

FC=field collection, AS=Aquarium shop, C=colleague (see acknowledgements)

Tissue (100-300 mg) was digested according to the Chelex® method of Walsh *et al*. (1991) for 3 h at 54 °C in 1.5 ml reaction tube containing 50 µl 5% Chelex® (Bio-Rad Laboratories, Hercules), 2.5 µl 100 mM DTT (Dithiothreitol; Boehringer Ingelheim,

Heidelberg), and 2.0 µl Proteinase K (20 mg/ml; Sigma, St. Louis). After centrifugation (3 min., 13,000 rpm) the supernatant was transferred to 500 µl reaction tube and stored at –20 °C.

Primers, Polymerase Chain Reaction (PCR) and Sequencing

Amplification of a partial sequence of the mitochondrial cytochrome *b* gene (cyt *b*) was conducted with the primers H15149 (5’-AAACTGCAGCCCCTCAGAATGATAT TTGTCC TCA-3’, Kocher *et al.*, 1989) and L14724 (5’-CGAAGCTTGATATGAAAA ACCATCG TTG-3’, Meyer *et al.*, 1990). PCR reactions were set up in 50 µl reaction volume containing 10 mM Tris-HCL (pH 9.0), 50 mM KCL, 1.5 mM $MgCl_2$, 0.2 mM each dNTP (PeqLab, Erlangen), 0.2 µM each primer, 1 U *Taq* polymerase (Biomaster, Köln), 4 µl BSA (2 mg/µl; MBI Fermentas, St. Leon-Rot), and 2-4 µl supernatant of the DNA extraction. Thermal cycling was started with 95 °C for 5 min and held at 85 °C until *Taq* polymerase was added (hot start) to inactivate Proteinase K, subsequently followed by 30-40 cycles of 93 °C (30 s), 50 °C (30 s), 72 °C (90 s), and a final step of 5 min at 72 °C for termination of the PCR.

A partial sequence of the mitochondrial 16S ribosomal gene was amplified with the primers 16sar-L (3’-CGCCTGTTTAACAAAAACAT-3’) and 16sbr-H (5’-CCGGTTT GAACTCAG ATCACGT-3’) (Palumbi *et al.*, 1991). PCR reactions were basically set up as described above, differing as follows: 2 mM $MgCl_2$, 2 µl DNA solution, and after hot start 30-35 cycles of 95 °C (30 s), 55 °C (45 s) and 72 °C (60 s).

PCR products were purified using the QIAquick PCR Purification Kit (QIAGEN, Hilden). Both strands were sequenced using the DyeDeoxy Terminator chemistry (PE Biosystems, Foster City) and an ABI Prism 310 automated sequencer (Applied Biosystems, Weiterstadt) according to the manufacturer’s recommendations.

Sequence and Phylogenetic Analysis

Sequences were controlled by aligning both strands with the programme Sequence Navigator (Applied Biosystems) and checking by eye. In addition, the cyt *b* sequence was translated to protein sequence using the vertebrate mitochondrial code available in the program EDIT-SEQ (Lasergene, DNASTAR; GATC GmbH, Konstanz) for cross-

checking. All sequences were checked for orthology to the sequence of the scorpionfish *Helicolenus hilgendorfii* (Miya *et al*., 2001; Accession No. AP002948).

Multiple alignment of sequences was done using Clustal implemented by Sequence Navigator (ver. 1.0.1; Applied Biosystems). The alignment is available from the EMBL server at ftp://ftp.ebi.ac.uk/pub/databases/embl/align/ALIGN_000286.dat.

All phylogenetic analysis were performed with PAUP* (ver. 4.0b8; Swofford, 1998). Skewness of tree length distributions (g_1) for the assessment of the phylogentic signal (Hillis, 1991; Hillis and Hulsenbeck, 1992) was calculated on the basis of 10^6 randomly sampled parsimony trees. Construction of neighbour-joining (NJ) trees (Saitou and Nei, 1987) was based on the sequence distance of Tamura and Nei (1993), which is regarded as the most appropriate substitution model (Kocher and Carleton, 1997). Maximum parsimony (MP) analysis was conducted by branch-and-bound search with the following search parameters: ignore uninformative characters, retain minimal trees, collapse zero length branches, steepest descent not enforced, branch swapping (TBR), accelerated transformation, save all minimal trees, and gaps treated as “fifth base”. Search for maximum likelihood (ML) trees followed the recommendations of Hershkovitz and Leipe (1998). Based on an MP tree and under the likelihood optimality criterion the tree was described and the following parameters were estimated: substitution rate matrix, gamma shape parameter, and invariant proportion. Based on the estimated values a ML tree-building search was conducted. Evaluation of statistical confidence in nodes was based on 1000 non-parametric bootstrap replicates (Felsenstein, 1985).

Several weighting schemes have been applied (transitions *vs* transversions: 1:3, 1:4, and 1:8), but the topologies of trees remained unchanged. Therefore, subsequent analysis was performed without weighting characters.

Timing of speciation in *Pterois miles* and *P. volitans* is based on rates established for other fishes, because no fossile record of a lionfish for a calibration of the molecular clock is available. The following sequence divergence rates were applied for the cyt *b* sequences in this study: (1) 0.8% per my for elasmobranchs (Cantatore *et al*., 1994), and (2) 2.8% per my for sticklebacks (Ortí *et al*., 1994). Molecular clock estimates for mtDNA (cyt *b* + 16S rDNA) are based on a sequence divergence rate of 0.5-0.9% per my in salmonids (Martin and Palumbi, 1993).

Choice of outgroup

The genera *Pterois* and *Dendrochirus* belong to the subfamily Pteroinae within the family Scorpaenidae. Therefore, *Helicolenus hilgendorfii* (Scorpaenidae: subfamily Sebastinae) was used as outgroup (Nelson, 1994).

RESULTS

Mitochondrial DNA Sequences (cytochrome b)

The PCR products had a length of 490 bp and after removing of primers, areas of ambiguity as well as missing data, cytochrome *b* sequences of 421 bp length were obtained from 34 specimens, representing 7 species and 2 genera of the scorpaenid subfamily Pteroinae (lionfishes). There were different haplotyps in each species and the DNA sequences have been submitted to the EMBL database (number of haplotyps in Table 4; accession numbers listed in Table 1). The sequences represent the first 140 amino acids of the cytochrome *b*: N-terminus, ab+, transmembrane A, bc-, transmembrane B, cd+, transmembrane C, partial de- (Kocher *et al.*, 1989, Irwin *et al.*, 1991, Whitmore *et al.*, 1994; Lydeard and Roe, 1997).

Phylogenetic analysis of 421 bp revealed 127 variable characters, of which 98 were phylogenetically informative applying parsimony criteria. The proportion of phylogenetically informative sites was 10 % at the first codon position, 0 % at the second codon position and 90 % at the third codon position (Table 2). The codon positions showed large differences in the base composition. No bias was observed at the first codon position, but second (G = 17%) and third positions (G = 13%) exhibited an anti-guanine bias. The mean base composition of all codon position was 25% adenine, 29% cytosine, 19% guanine, and 27% tymine. Base composition was homogenous between taxa at each and at all codon positions and is confirmed by a chi-square test (Table 2).

Mitochondrial DNA Sequences (16S rDNA)

The PCR product had a length of 610 bp. After removing of primers, areas of ambiguity as well as missing data, 16S rDNA sequences of 543 bp length were obtained of all specimens used for cyt *b* analysis but one specimen of *Pterois antennata*. The 16S rDNA sequence obtained from the other *P. antennata* specimen was combined with

both cyt *b* haplotyps in the phylogenetic analysis in order to prevent the exclusion of the second cyt *b* haplotyp in the analysis. The number of haplotyps was smaller than in cyt *b* (Table 4). The DNA sequences have been submitted to the EMBL database (accession numbers listed in Table 1). The secondary structure of the 16S rDNA, such as stems and loops, was determined on the basis of the model of Ortí *et al.* (1996).

Table 2 Parameters Obtained in the Analysis of cyt *b* Sequences

Parameters	1. position	2. position	3. position	all positions (codon)
Parsimony informative sites	10	0	94	98
Invariable sites	131	137	26	294
Average Ts/Tv ratio*	2.43	0.07	3.22	3.19
Proportion of Adenine	24 %	21 %	29 %	25 %
Proportion of Cytosine	24 %	23 %	39 %	29 %
Proportion of Guanine	26 %	17 %	13 %	19 %
Proportion of Tymine	26 %	39 %	19 %	27 %
Chi square test of base	$X^2 = 1.01$	$X^2 = 0.21$	$X^2 = 37.49$	$X^2 = 9.745567$
frequencies	df = 66	df = 66	df = 66	df = 66
	p = 1.00	p = 1.00	p = 0.99	p = 1

*only ratios between species

Table 3 Parameters Obtained in the Analysis of 16S rDNA Sequences

Parameters	stem	loop	remaining sequence	complete sequence
Parsimony informative sites	1	19	6	26
Proportion of invariable sites	98%	82%	93%	90%
Average Ts/Tv ratio*	-	3.65	1.89	3.85
Proportion of Adenine	14 %	37 %	32 %	28 %
Proportion of Cytosine	30 %	24 %	21 %	26 %
Proportion of Guanine	35 %	18 %	20 %	24 %
Proportion of Tymine	21 %	21 %	27 %	22 %
Chi square test of base	$X^2 = 0.14$	$X^2 = 2.17$	$X^2 = 1.06$	$X^2 = 1.01$
frequencies	df = 42	df = 42	df = 42	df = 42
	p = 1.00	p = 1.00	p = 1.00	p = 1.00

*only ratios between species

The number of 26 parsimony-informative characters out of 30 variable characters in a sequence of 543 bp was lower than in the cyt *b* sequence. The proportion of

phylogenetically informative sites was 4% in stems, 73% in loops, and 23% in the remaining parts of the sequence (Table 3). Stem and loop regions as well as the remaining sequence areas showed differences in the base composition (Table 3). An anti-adenine bias was observed in stems (A = 14%) and loops showed an anti-guanine and anti-tymine bias (G = 18%, T = 21%). However, only a minor anti-tymine bias was observed in the complete sequence (28% adenine, 26% cytosine, 24% guanine, and 22% tymine). Base composition was homogenous between taxa in each region and in the complete sequence, confirmed by a chi-square test (Table 3). An insertion of 2 bases was observed in one loop region of *Dendrochirus brachypterus*.

Pseudogenes

The amplification of nuclear pseudogenes can be excluded, because (1) PCR amplification did not produce more than one band, (2) no sequence ambiguities or background bands persisted, (3) no stop codons and indels have been observed in the sequence cyt *b* sequence, and (4) different haplotyps of a species were very closely related (Zhang and Hewitt, 1996). To date no pseudogenes have been detected in fishes (Benasasson *et al*., 2001).

Phylogenetic Signal

The phylogenetic signal was assessed for cyt *b* and 16S rDNA sequences separately by a plot of substitutions against Tamura-Nei sequence divergence, ratio of transition and transversions (ti/tv), and g_1 statistic. In both cases the plot of substitutions versus sequence divergence did not show saturation for transversions in general and transitions for ingroup comparisons, but saturation of transitions arise when comparing ingroup and outgroup (Fig. 2). The average ti/tv ratio of cyt *b* sequences was 3.00 and the range was 1.28 (ingroup/outgroup comparison) to 13.33 (ingroup comparison) (Table 2). 16S rDNA sequences showed an average ti/tv ratio of 3.85 and the range was 0.88 (ingroup/outgroup comparison) to 8.00 (ingroup comparison) (Table 3). The g_1 statistic revealed the same strong phylogenetic signal for cyt *b* and 16S rDNA (g_1=-0.5; $p<0.01$), as well as the combined data set (g_1=-0.48; $p<0.01$) (Hillis, 1991; Hillis and Huelsenbeck, 1992).

Table 4 Percent Tamura-Nei sequence Divergence (range) of Haplotyps for cyt *b* (above diagonal) and 16S rDNA (below diagonal) (abbreviations see Table 1)

	Within (# haplotyps)		Between							
	cyt *b*	16S rDNA	Db	Dz	Pa	Pm	Pmo	Pr	Pv	Hh*
Db	0.2-0.7 (3)	(1)		12.7-13.5	12.4-12.7	14.8-16.2	12.1-13.0	13.3-14.5	14.5-16.3	22.4-22.7
Dz	0.7 (2)	0.2 (2)	2.5-2.7		7.1-8.4	12.5-13.4	7.1-8.2	11.4-11.9	12.5-13.4	21.1-21.7
Pa	0.5 (2)	(1)	2.3	1.5-1.7		14.7-15.2	1.7-1.9	11.4-14.9	14.6-14.9	20.2
Pm	0.2-0.5 (8)	0.2-0.4 (3)	2.9-3.1	2.5-3.1	3.2-3.6		14.3-15.2	15.0-15.9	6.3-7.1	19.5-20.1
Pmo	0.7 (2)	0.2 (2)	2.1-2.3	1.3-1.7	0.2-1.3	3.0-3.6		10.5-11.1	14.3-14.9	19.6-20.2
Pr	0.2 (2)	(1)	1.5	1.3-1.5	2.8-3.2	2.7-3.0	1.1-1.3		15.5-16.8	22.1-22.4
Pv	0.2-1.5 (3)	0.2(3)	3.1-3.5	1.7-2.3	2.8-3.2	0.9-1.5	2.6-3.2	2.3-2.7		21.1
Hh*	(1)	(1)	6.2	7.4-7.7	7.5	7.5-7.7	7.2-7.5	7.0	7.4	

*outgroup: *Helicolenus hilgendorfii*

Phylogenetic analysis

Sequence divergence (Tamura and Nei, 1993) of cyt *b* and 16S rDNA sequences ranged from 0.2% for both sequences within a species to 22.7% and 7.7%, respectively in comparison to the outgroup. The average Tamura-Nei sequence divergence of cyt *b* and 16S rDNA between the sibling species *Pterois miles* and *P. volitans* was 6.7% and 3.5% respectively (Table 4). However, the species pair *Pterois antennata* and *P. mombasae* showed a much lower cyt *b* and 16S rDNA divergence of only 1.8% and 1.0% respectively (Tabel 4).

Applying the different cyt *b* sequence divergence rates, the speciation of *P. miles* and *P. volitans* dates back 2.4 to 8.3 million years. The combination of cyt *b* and 16S rDNA data suggests a divergence time of 3.9 to 7 million years (Table 5).

The majority of phylogenetically informative sites were in the third codon positions of the cyt *b* and loop regions of the 16S rDNA sequences. However, phylogenies based solely on these regions did not show differences to the complete data set. Therefore, the complete combined cyt *b* and 16S rDNA sequences of 964 bp were used for the analysis.

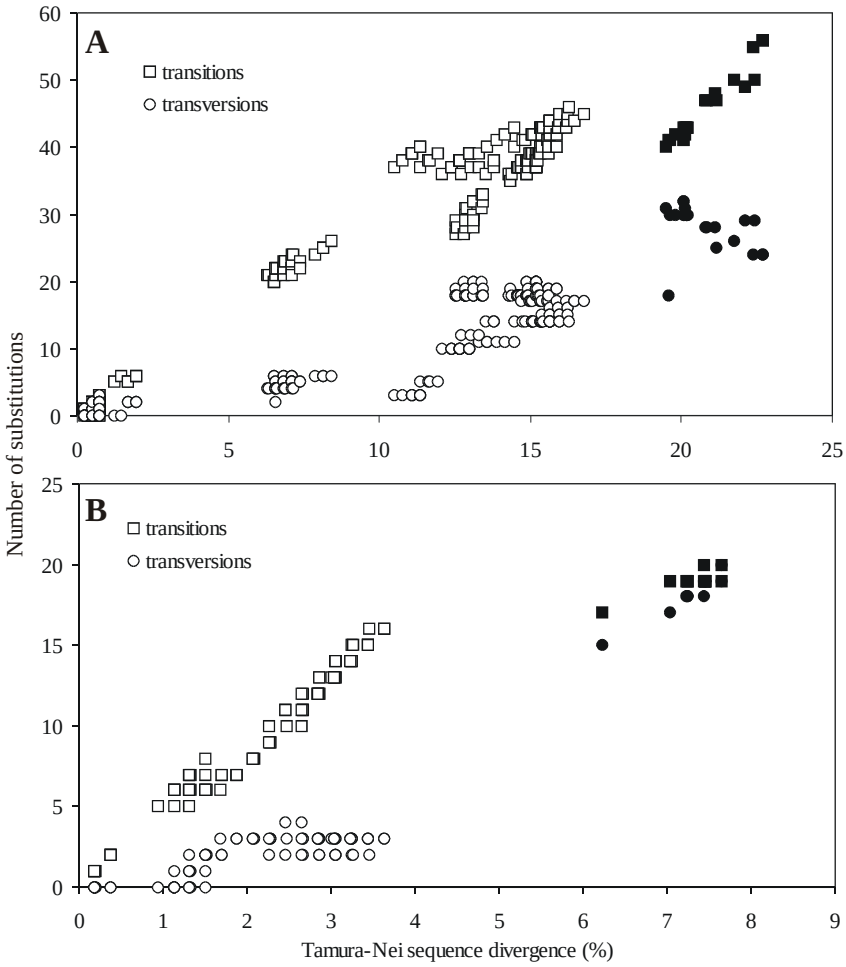


Fig 2 Substitution pattern for (A) cyt *b* and (B) 16S rDNA. The number of transitions and transversions is plotted against Tamura-Nei sequence divergence (Tamura and Nei, 1993) for all pairwise comparisons of taxa. Open symbols: ingroup comparisons; solid symbols: ingroup/outgroup comparisons

Table 5 Estimated Divergence Time for the Sibling Species *Pterois miles* and *Pterois volitans*

	cyt *b* average divergence	cyt *b* + 16S rDNA average divergence	cyt *b* (0.81-2.8%/my)	cyt *b* + 16S rDNA (0.5-0.9%/my)
P. miles – *P. volitans*	6.7%	3.5%	2.4-8.3 my	3.9-7.0 my

NJ and MP analysis of mtDNA sequences resulted in compatible trees, whereas ML analysis showed some difference. All main nodes were supported by the bootstrap test in all analyses. The MP analysis revealed 2 equally parsimonious trees with a length of 312 steps, consistency index of 0.7, homoplasy index of 0.3, and a retention index of 0.9 (excluding uninformative characters). NJ and MP trees revealed two main clades:

(1) the "*Pterois*" clade (*Pterois miles* and *P. volitans*), and (2) the "*Pteropterus-Dendrochirus*" clade with the remainder of the species (for naming of the clades see discussion) (Fig. 3 and 4). The ML tree showed a similar picture, but *Dendrochirus brachypterus* was basal to the main clades mentioned above (Fig. 5). A NJ tree based only on transversions revealed the same topology as the ML tree, but the basal node of the main clade had a very low bootstrap value (tree not shown). In all trees conspecifics formed monophyletic clades, but neither *Pterois* nor *Dendrochirus* were monophyletic. Within the "*Pteropterus-Dendrochirus*" clade, NJ, MP, and ML analysis obtained different relationships, but a distinct *Dendrochirus* clade was not present in any tree. All haplotyps of the sibling species *Pterois miles* and *P. volitans* were separated into distinct clades and all Red Sea and Indian Ocean specimen belong to *Pterois miles* (Fig. 3, 4, and 5).

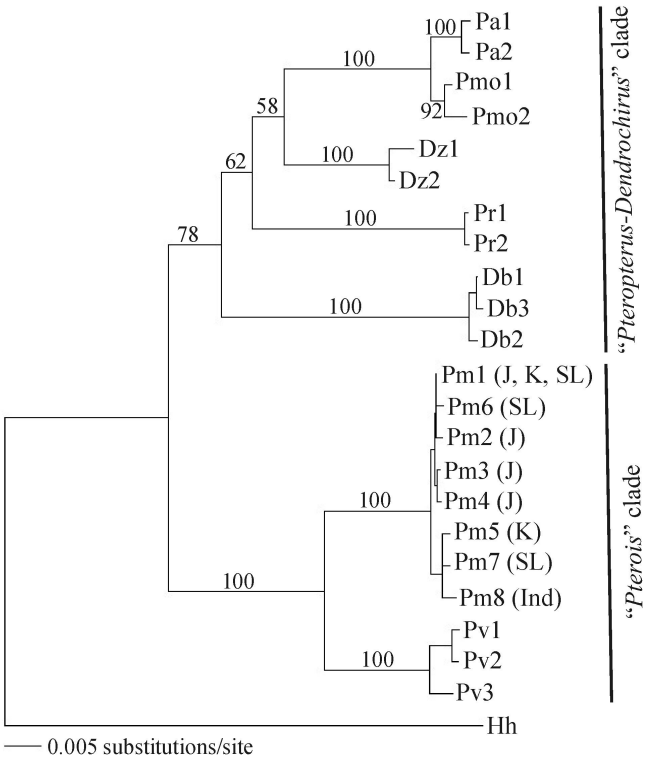


Fig. 3 Neighbor-joining tree from combined cyt *b* and 16S rDNA sequences based on Tamura-Nei sequence divergence (Tamura and Nei, 1993). Numbers at branches are bootstrap values based on 1000 replicates. Species and location abbreviations are given as in Table 1

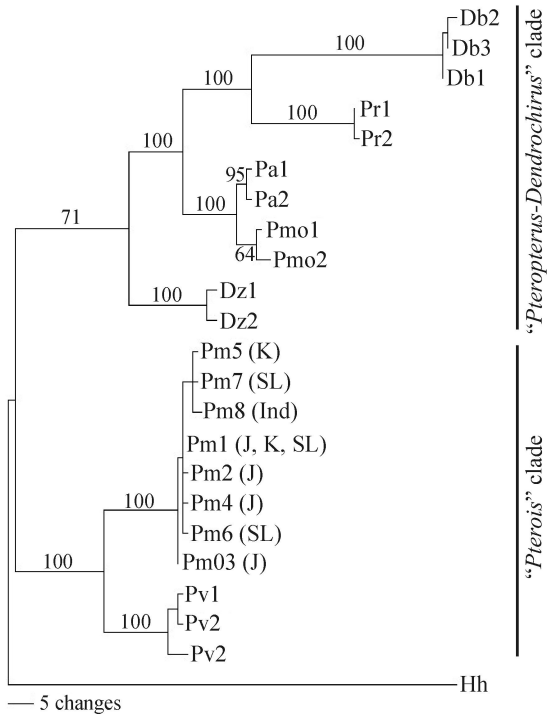


Fig. 4 Maximum parsimony tree from combined cyt *b* and 16S rDNA sequences. Numbers at branches are bootstrap values based on 1000 replicates. Species and location abbreviations are given as in Table 1

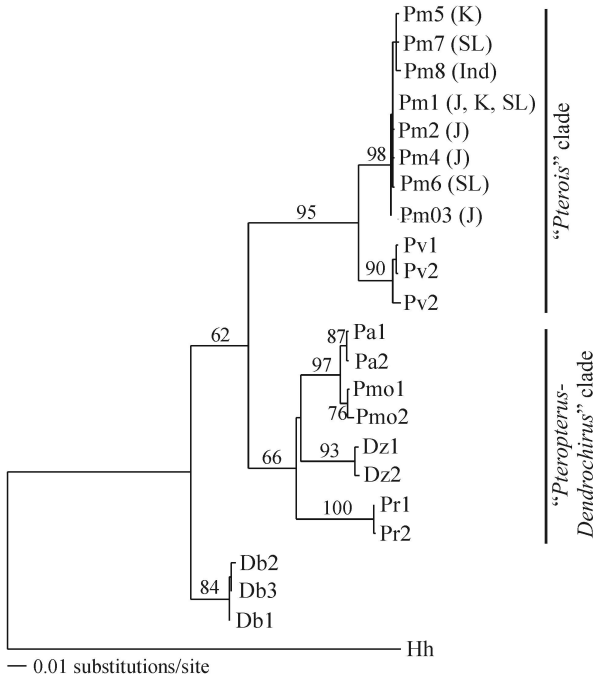


Fig. 5 Maximum likelihood tree from combined cyt *b* and 16S rDNA sequences. Numbers at branches are bootstrap values based on 1000 replicates. Species and location abbreviations are given as in Table 1

DISCUSSION

Mitochondrial DNA Sequences (Cytochrome b)

Phylogenetic signal of the cyt *b* sequence was nearly exclusively at the third codon position, as to be expected for closely related species (Meyer, 1993; Roe *et al*., 1997; Tinti *et al*., 2000; Farias *et al*., 2001). The cyt *b* sequences showed a base composition similar to other studies on fishes, with an anti-guanine bias at the second and more pronounced at the third codon position (Meyer, 1993; Whitmore *et al*., 1994; Lydeard and Roe, 1997; Roe *et al*., 1997; Johns and Avise, 1998; Rocha-Olivares *et al*., 1999a, 1999b; Tinti *et al*., 2000, Farias *et al*., 2001). However, the guanine content at the third codon position was higher in our study. The average ti/tv ratio of 3 was close to values of killifishes (Bernardi, 1997), surfperches (Bernardi and Bucciarelli, 1999), cichlid (Farias *et al*., 2001), and rainbow fishes (Zhu *et al*., 1994) (Table 2). The g_1 statistic indicates a strong phylogenetic signal in the cyt *b* sequences.

Mitochondrial DNA Sequences (16S rDNA)

Phylogenetically informative sites were mainly located in the loop regions, because these areas show a higher substitution rate than stems (Meyer, 1993; Ortí *et al*., 1996; Ortí, 1997). The observed anti-adenine bias in stems, and anti-guanine as well as anti-tymine bias in loops was similar to a study on piranhas (Ortí *et al*., 1996). The average ti/tv ratio of 3.85 was close to values of serranid fishes (Craig *et al*., 2001) as well as parrotfishes (Bernardi *et al*., 2000). Even tough the number of phylogenetically informative sites was lower than in the cyt *b* sequences, a strong phylogenetic signal in the 16S rDNA sequences was indicated by g_1 statistics.

Phylogeny of the Pteroinae

NJ, MP and ML trees revealed two major clades: (1) the “*Pterois*” clade and (2) the “*Pteropterus-Dendrochirus*” clade. Naming of the clades is according to Smith’s work on scorpaenids of the Western Indian Ocean (1957), who separated the species analysed in our study into three genera: (1) *Pterois* Oken 1817, (2) *Pteropterus* Swainson 1839, and (3) *Dendrochirus* Swainson 1839. The genus *Pterois* includes *P. miles*; the genus *Pteropterus* comprises *Pterois* (*Pteropterus*) *antennata*, *P.* (*Pteropterus*) *radiata*, and *P.* (*Pteropterus*) *mombasae*; and the genus *Dendrochirus* consist of *D. brachypterus* and *D. zebra*. The distinction between *Pterois* and *Pteropterus* is based on the existence of

ctenoid scales in *Pteropterus*, whereas *Dendrochirus* is defined on the basis of some branched upper pectoral rays and that none of these rays is free from membrane (Smith, 1957). However, the molecular phylogeny neither supports the classification by Smith (1957) nor the current separation into *Pterois* and *Dendrochirus* (Eschmeyer, 1998). Due to the unprecise description of the genus *Dendrochirus* by Swainson (1839), and the questioned separation of *Pterois* and *Dendrochirus* (Eschmeyer and Randall, 1975), it is likely that the applied meristic characters are not sufficient to reveal the phylogenetic relationships of these fishes. However, the type of scales is a feature that is congruent with the molecular phylogeny: species of the “*Pterois*” clade have only cycloid scales, whereas members of the “*Pteropterus-Dendrochirus*” clade have mainly ctenoid scales (Smith, 1957; Schultz, 1986). The two genera of the “*Pteropterus-Dendrochirus*” clade are not separated in the molecular phylogeny and therefore we suggest merging them into a single genus. Based on the correlation of scale type and molecular phylogeny, other species not covered in this study might be assigned to the two clades (genera) by scale type. Cycloid scales (“*Pterois*” clade): *Pterois lunnulata* and *P. russelli*; ctenoid scales (“*Pteropterus-Dendrochirus*” clade): *P. sphex*, *Dendrochirus barberi*, and *D. biocellatus* (Beaufort and Briggs, 1962; Eschmeyer and Randall, 1975). However, since the molecular phylogeny does not include this species, this classification has to be taken with caution.

The basal position of *Dendrochirus brachypterus* in the ML tree is partly inconsistent with the picture described above on the basis of the NJ and MP trees. However, since no morphological character is congruent to the ML phylogeny, it seems more likely that the NJ and MP trees reflect the evolution of lionfishes.

Speciation in the genus Pterois

The genetic distance between *Pterois antennata* and *P. mombasae* is very small and close to the intraspecific variation of *P. volitans*. However, morphological characters and high bootstrap values in the phylogenetic analysis of mtDNA sequences support the recognition of two species. Similar low levels of interspecific mtDNA divergence were observed in the scorpaenid subgenus *Sebastomus* (Rocha-Olivares *et al*., 1999a).

The sibling species *P. miles* and *P. volitans* are clearly separated on the basis of mtDNA sequences and can be regarded as distinct species. The genetic distance

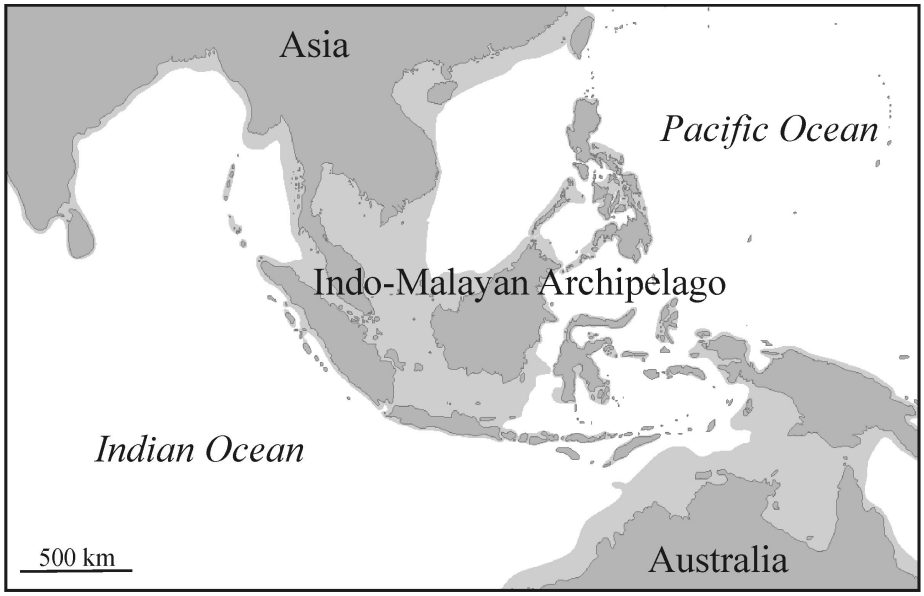


Fig. 6 Map of Southeast Asia with 120 m depth contours (light grey) and recent coastline (dark grey) (modified after Voris, 2000)

between these two species is around 2-fold higher than between *P. antennata* and *P. mombasae*. Even though more sampling *of P. miles* and *P. volitans* is necessary, our results support the view of allopatric (Schultz, 1986) or parapatric distributed species.

Molecular clock estimates of cyt *b* as well as combined cyt *b* and 16S rDNA data suggest a divergence time of 2.4-8.3 my. Even though the molecular clock hypothesis is questioned (Rodríguez-Trelles *et al*., 2001), this timing of speciation coincide with geological events that created vicariance between populations of the Indian and Pacific Ocean. These events started around 25 my ago with the collision of Australia with the arcs to the north, which started the formation of the Indo-Malayan Archipelago. Due to the rise of island chains between the Indian and the Pacific Ocean circulation pattern changed and at about 10 my the free exchange between the two ocean basins through the Indonesian seaway was reduced (Hall, 1998). Tectonic events and lowered sea level during Pleistocene glaciations of up to 120 m created several more or less isolated ocean basins and restricted the exchange between the Indian Ocean and the West Pacific (Fig. 6; McManus, 1985; Voris, 2000). These processes split up populations and allopatric speciation took place in the separated ocean basins (McManus, 1985; Pandolfi, 1992; Benzie, 1998; Randall 1998). A genetic break in the transition of the Indian and Pacific Ocean was observed between species of butterflyfishes (McMillan

and Palumbi, 1995) and starfishes (Williams, 2000), as well as in populations of fishes (Lacson and Clarke, 1995; Chenoweth *et al.,* 1998), a starfish (Williams and Benzie, 1998) and a stomatopod (Barber *et al*., 2000). The importance of Pleistocene environmental changes for speciation processes in the Indo-Malayan Archipelago is underlined by these and our findings.

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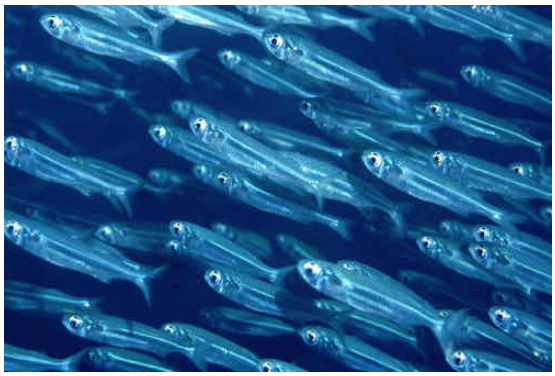
PLATES

(all photographs by Marc Kochzius)

Plate 1

Silversides (Atherinidae)

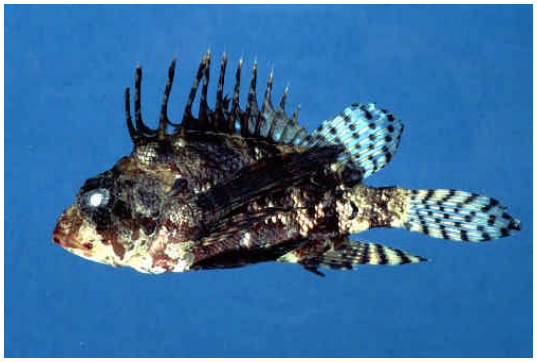


Robust silverside
Atherinomorus lacunosus (Bloch and Schneider, 1801); D IV to VII-I, 8 to 11; A I, 12 to 16; P 15 to 19; reaches 13 cm; Red Sea, Indo-Pacific

Squirrelfishes (Holocentridae)

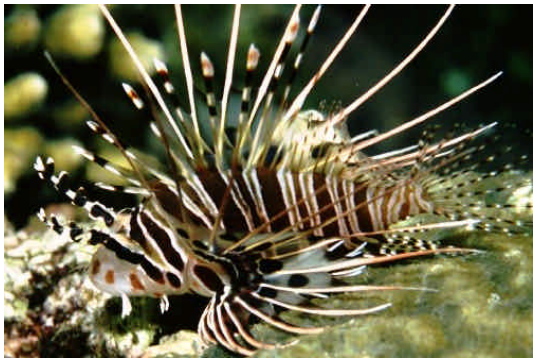
Crown squirrelfish
Sargocentron diadema (Lacepède, 1802);
D XI, 13 or 14; A IV, 9; P 14; attains 16 cm;
Red Sea, Indo Pacific

Scorpionfishes (Scorpaenidae)



Dwarf lionfish
Dendrochirus brachypterus (Cuvier, 1829)
D XIII, 9 or 10; A III, 5; P 17 or 18;
attains 15 cm; Red Sea and East Africa to Samoa and Tonga, north to Philippines

Zebra lionfish
Dendrochirus zebra (Quoy and Gaimard, 1825)
D XIII, 10 to 11; A III, 6 or 7; P 17;
reaches 18 cm; Red Sea and East Africa to Samoa

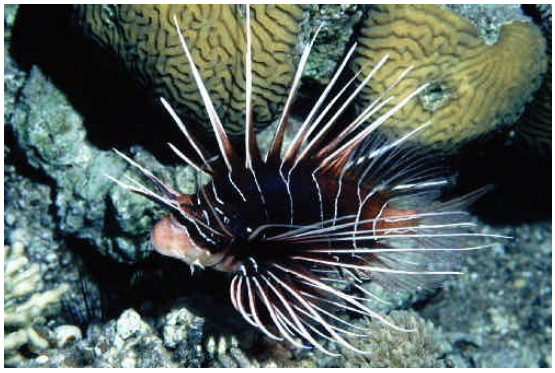


Ragged-finned firefish
Pterois antennata (Bloch, 1787)
D XII, 11 or 12; A III, 6; P 16 or 17;
reaches 20 cm; Red Sea and East Africa to southeastern Polynesia

Lionfish; turkeyfish
Pterois miles (Bennett, 1828)
D XIII, 10; A III, 6; P 14; attains 31 cm; Red Sea, Arabian Gulf, and Indian Ocean, not Western Australia

Plate 2

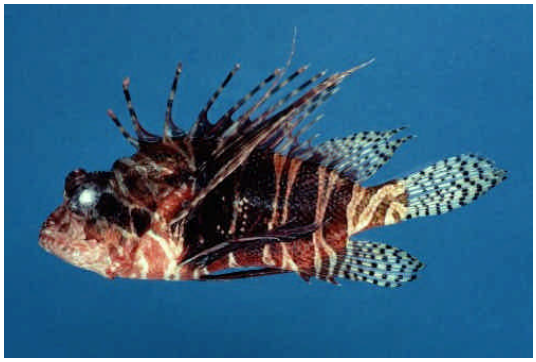
Scorpionfishes (Scorpaenidae)



Clearfin turkeyfish
Pterois radiata Cuvier and Valenciennes, 1829
D XII, 11; A III, 6; P 16; reaches 20 cm;
Red Sea, Indo-Pacific

Lionfish, red firefish
Pterois volitans (Linnaeus, 1758)
D XIII, 11; A III, 7; P 13 to 15; to 38 cm; Western Pacific and Western Australia

Cardinalfishes (Apogonidae)



Mombasa turkeyfish
Pterois mombasae (Smith, 1957)
D XIII, 10; A III, 6 to 7; P 18 to 20; attains 18 cm;
East Africa, Oman, Sri Lanka, southern Indonesia, northwestern Australia, and New Guinea

Golden cardinalfish
Apogon aureus (Lecepède, 1802)
D VII-I, 9; A II, 8; P 14; attains 14 cm
Red Sea and East Africa to Western Pacific

Cardinalfishes (Apogonidae)

Goldenstriped cardinalfish
Apogon cyanosoma Bleeker, 1853
D VII-I, 9; A II, 8; P 14; reaches 7 cm
Red Sea and East Africa to Western Pacific

Nineline cardinalfish
Cheilodipterus novemstriatus (Rüppell, 1838)
D VI-I, 9; A II, 8; P 12; reaches 12 cm
Red Sea, Gulf of Aden, and Arabian Gulf

Plate 3

Anthias (Serranidae, subfamily Anthiinae)

Striped anthias (male)
Anthias taeniatus Klunzinger, 1884
D X, 16 to 17; A III, 7; P 18 to 19; attains 13 cm
Red Sea

Scalefin anthias (male)
Pseudanthias squamipinnis (Peters, 1855)
D X, 16 to 18; A III, 7; P 17; reaches 15 cm;
Red Sea and East Africa and Western Pacific

Fusiliers (Caesionidae)

Lunar fusilier
Caesio lunaris Cuvier and Valenciennes, 1830
D X, 14; A III, 11; P 19 to 21; reaches 30 cm
Red Sea and East Africa to Western Pacific

Suez fusilier
Caesio suevicus Klunzinger, 1884
D X, 15; A III, 12; P 19 to 21; attains 25 cm
Red Sea

Goatfishes (Mullidae)

Yellowstriped fusilier
Caesio varilineata Carpenter, 1987
D X, 15; A III, 12; P 19 or 20; attains 28 cm
Red Sea and Indian Ocean

Forsskål's goatfish
Parupeneus forsskali (Fourmanoir and Guézé, 1976); D VIII, 9; A I, 7; P 16; reaches 28 cm
Red Sea and Gulf of Aden

Plate 4

Goatfishes (Mullidae)

Longbarbel goatfish
Parupeneus macronema (Lacepède, 1801)
D VII, 9; A I, 7; P 15 or 16; attains 29.5 cm; Red Sea and East Africa to Indonesia and Philippines

Butterflyfishes (Chaetodontidae)

Crown butterflyfish
Chaetodon paucifasciatus Ahl, 1923
D XIII, 20 to 23; A III, 16 to 18; P 14 to 16; reaches 14 cm; Red Sea

Angelfishes (Pomacanthidae)

Yellow-ear angelfish
Apolemichthys xanthotis (Fraser-Brunner, 1950)
D XIV, 17 to 19; A III, 17 or 18; P 16 or 17; attains 20 cm; Red Sea and Gulf of Aden

Zebra angelfish (male)
Genicanthus caudovittatus (Günther, 1860)
D XIV, 15 to 17; A III, 17 to 19; P 16; attains 25 cm; Red Sea and Western Indian Ocean

Damselfishes (Pomacentridae)

Yellowflank damselfish
Amblyglyphiodon flavilatus Allen and Randall, 1980; D XIII, 11 to 13; A II, 11 to 14; P 15 or 16; around 9.5 cm; Red Sea and Gulf of Aden

Whitebelly damselfish
Amblyglyphiodon leucogaster (Bleeker, 1847)
D XIII, 12 to 13; A II, 12 to 14; P 16 to 18; attains 14 cm; Red Sea and East Africa to Samoa and Micronesia

Plate 5

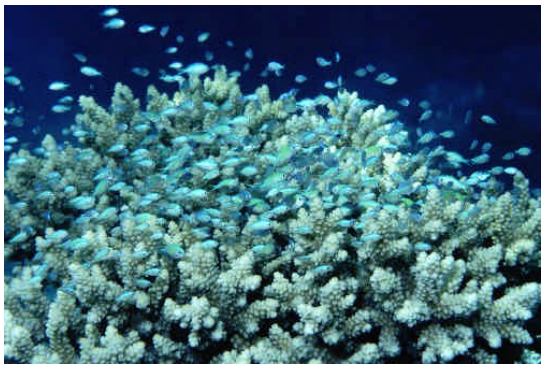
Damselfishes (Pomacentridae)

Twobar Anemonefish (small adult)
Amphiprion bicinctus Rüppell, 1830
D X, 15 to 17; A II, 13 or 14; P 17 to 21; around 12 cm; Red Sea, Gulf of Aden, and Socrota

Half-and-half chromis
Chromis dimidiata (Klunzinger, 1871)
D XII, 11 or 12; A II, 12; P 15 to 17; reaches 9 cm
Red Sea and Indian Ocean

Duskytail chromis
Chromis pelloura Randall and Allen, 1982
D XIV, 13 or 14; A II, 12 or 13; P 18 or 19; attains 13 cm; Gulf of Aqaba

Yellow-edge chromis
Chromis pembae Smith, 1960
D XIII, 11 or 12; A II, 11; P 17 to 19; reaches 13 cm; Red Sea and East Africa



Bluegree chromis
Chromis viridis (Cuvier and Valenciennes, 1830)
D XII, 9 or 10; A II, 10 or 11; P 17 to 19; attains 9.5 cm; Red Sea, Indo-Pacific

Banded dascyllus
Dascyllus aruanus (Linnaeus, 1758)
D XII, 11 to 13; A II, 11 to 13; P 17 to 19; reaches 7.5 cm; Red Sea, Indo-Pacific

Plate 6

Damselfishes (Pomacentridae)

Blackbordered dascyllus
Dascyllus marginatus (Rüppel, 1829)
D XII, 14 or 15; A II 13 or 14; P 17 to 19; reaches 9 cm; Red Sea, Gulf of Aden, and Gulf of Oman

Domino
Dascyllus trimaculatus (Rüppell, 1829)
D XII, 14 to 16; A II, 14 to 15; P 19 to 21; attains 14 cm; Red Sea, Indo-Pacific

Miry's damselfish
Neopomacentrus miryae Dor and Allen, 1977
D XIII, 11 to 13; A II, 11; P 18 or 19; reaches 11 cm; Red Sea

Reticulated damselfish
Pomacentrus trichourus Playfair and Günther, 1867; D XIV, 14 to 16; A II, 15 to 17; P 16 or 17; attains 11 cm; Red Sea to Mozambique

Wrasses (Labridae)

Social wrasse
Cirrhilabrus rubriventralis Springer and Randall, 1974; D XI, 10; A III, 10; P 14 or 15; attains 7.5 cm; Red Sea

Spottail coris
Coris caudimacula (Quoy and Gaimard, 1834)
D IX, 12; A III, 12; P 13; reaches 20 cm;
Red Sea and East Africa to Indonesia

Plate 7

Wrasses (Labridae)

Eightline wrasse
Paracheilinus octotaenia Fourmanoir, 1955
D IX, 11; A III, 9; P 14; reaches 9 cm; Red Sea

Rüppell's wrasse
Thalassoma rueppellii (Klunzinger, 1871)
D VIII, 13; A III, 11; P 15 to 16; attains 20 cm; Red Sea

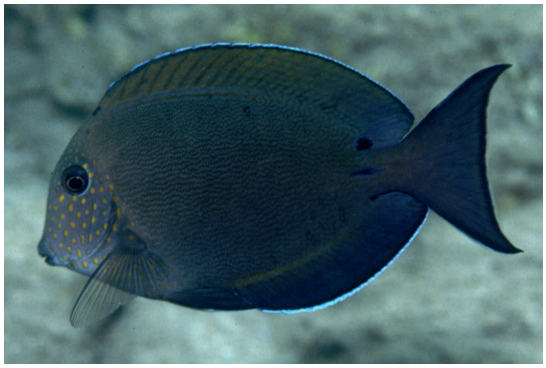
Parrotfishes (Scaridae)

Dotted parrotfish
Calotomus viridescens (Rüppell, 1835)
D IX, 10; A III, 9; P 13; reaches 27 cm; Red Sea

Blennies (Blenniidae)

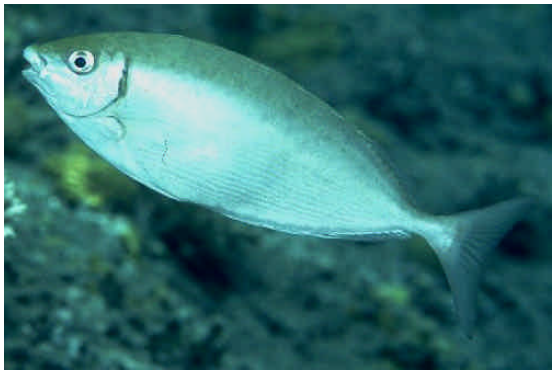
Blackline blenny
Meiacanthus nigrolineatus Smith-Vaniz, 1969
D IV or V, 23 to 26; A II, 14 to 16; P 26 to 28; reaches 9.5 cm; Red Sea and Gulf of Aden

Surgeonfishes (Acanthuridae)



Brown surgeonfish
Acanthurus nigrofuscus (Forsskål, 1775)
D IX, 24 to 27; A III, 22 to 24; P 16 or 17; reaches 21 cm; Red Sea, Indo-Pacific

Rabbitfishes (Siganidae)



Rivulated rabbitfish
Siganus rivulatus (Forsskål, 1775)
DXIII, 10; A VII, 9; P 17; reaches 30 cm; Red Sea, has entered the Mediterranean via the Suez Canal

Plate 8

Puffers (Tetraodontidae)

Crown toby
Canthigaster coronata (Vaillant and Sauvage, 1875);
D 9 or 10; A 9 or 10; P 16 or 17; attains 13 cm; Red Sea and East Africa to Micronesia and Hawaiian islands

Pearl toby
Canthigaster margaritata (Rüppell, 1829)
D 8 or 9; A 8 or 9; P 16-18; reaches 12 cm; Red Sea

Red Sea pufferfish
Torquigener flavimaculatus Hardy and Randall, 1983; D 8, A 8; P 17; attains 14 cm; Red Sea and East Africa