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Fish from the mesolithial of the Red Sea

Fische aus dem Mesolithial des Roten Meeres

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Summary: The structure and dynamics of fish communities from the mesolithial of the Red Sea was investigated. In Marsa Alam (middle Egypt) 27 fish species, in Dahab (Sinai, Egypt) 26 fish species with affinities to light reduced habitats were observed by relative low diversity. In Marsa Alam 81, in Dahab 75 individuals were counted within an observation time of one hour. The fish species were classified by two groups: speleophilous, day active ones, which use the cave-like habitats as hiding and/or spawning places, and heliophobous ones, which use such habitats as hiding place during day. The latter species possess special adaptations like enlarged eyes and often red coloration. The heliophobous *Myripristis murdjan* dominated in Marsa Alam by 31 %, in Dahab the speleophilous *Pseudochromis fridmani* by even 39 % abundance. Therefore the species identity was 80 %. Activity times coincided 66% due to the different structures of the respective habitats, which were more variable in Dahab favouring day active species. If the preferred prey is regarded, some differences between the localities were revealed (75 % coincidence). These were almost fully compensated, because identity values of the mode of foraging (95 %) and the position in the food chain (97 %) were high. Whereas herbivorous fish species were very rare, primary carnivores were present by 80 %, top predators by about 15 % in both localities. The relation of primary and secondary carnivores was 5 to 1 in Marsa Alam and 6 to 1 in Dahab. These results deviate from the general model (10 to 1) and means an advantage for the top predators. Further components were the parasitovores (cleaner fish) and parasites (sabletooth blennies). Finally, the functional definition of the sea caves of Riedl (1966) is improved and the term pseudocaves is introduced on the basis of the found results.

Key words: Mesolithial fish, Red Sea, abundance, prey and foraging, food chain

Zusammenfassung: Die Struktur und Dynamik von Fischgemeinschaften wurden im Mesolithial des Roten Meeres untersucht. In Marsa Alam (Mittelägypten) wurden 27 Fischarten, in Dahab (Sinai, Ägypten) 26 Fischarten mit Beziehungen zu höhlenartigen Habitaten beobachtet, bei denen aber die Diversität relativ niedrig war. In Marsa Alam waren 81 Individuen, in Dahab 75 Individuen pro Beobachtungseinheit von einer Stunde gezählt worden. Die Fischarten waren zwei Gruppen zuzuteilen: speleophile tagaktive Arten, die Höhlen als Verstecke oder Laichplatz benutzen und heliophobe, nachtaktive Arten, die Höhlen als Tagesversteck nutzen. Letztere haben spezielle Anpassungen wie vergrößerte Augen und oft rote Körperfärbung entwickelt. In Marsa Alam dominierten der heliophobe *Myripristis murdjan* mit 31 %, in Dahab der speleophile *Pseudochromis fridmani* mit 39 % Abundanz sehr deutlich. Daher war auch die Abundanz-Identität an den zwei Orten geringer als 50 %, während die Arten-Identität bei 80 % lag. Hinsichtlich der Aktivitätszeit gab es 66 % Übereinstimmung, die auf der unterschiedlichen Struktur der jeweiligen höhlenartigen Habitate beruhte, die in Dahab variabler war und tagaktive Arten begünstigte. Hinsichtlich der aufgenommenen Nahrung gab es zwar einige Unterschiede zwischen den Orten (75 % Übereinstimmung); sie wurden aber fast vollkommen kompensiert, wie der Vergleich des Nahrungserwerbs und der Stufen der Nahrungskette ergab (95 bzw. 97 % Übereinstimmung). Während herbivore Arten sehr selten auftraten, waren Karnivoren erster Stufe in beiden Orten um 80 % vertreten, während die Karnivoren zweiter Stufe zu ca. 15 % beobachtet wurden. Das Verhältnis Karnivore 1 zu Karnivore 2 war daher 5 zu 1 in Marsa Alam und 6 zu 1 in Dahab, ein Wert, der vom generellen Schema des Energieflusses (10 zu 1) abweicht und einen Vorteil für die Top-Prädatoren bedeutet. Weitere Komponenten waren mit geringer bzw. sehr geringer Abundanz noch die Parasitovoren (Putzerfische) und Parasiten (Säbelzahnschleimfische). Schließlich wurde die funktionelle

Definition der Meereshöhlen von Riedl (1966) auf Grund der gefundenen Erkenntnisse angepasst und der Begriff Pseudohöhle eingeführt.

Schlüsselwörter: Mesolithiale Fische, Rotes Meer, Abundanzen, Nahrung und Nahrungserwerb, Nahrungskette

1. Introduction

Whereas cave organisms from fresh and anchialine waters were frequently investigated in diverse habitats and continents (Iliffe & Kornicker 2009), in the Mediterranean studies on fish and other organisms from marine habitats with low light intensities are more frequent (Abel 1959; Arko-Pijevac et al. 2001; Bussotti et al. 2002; Bussotti et al. 2015; Riedl 1966; Zander & Jelinek 1975; Zander 1980, 1990). In tropic oceans some observations were done regarding cave crustaceans (Yager 1981; Wilkens et al. 2009), loriciferans (Heiner et al. 2009), but also on fish in Bermudas (Cullity 2012), in Australia (Hui et al. 2014) or in Vietnam (Ngai et al. 2015). But from tropic seas ecological studies from marine cavities, regarding structure (how many species in what abundance) or dynamics of inhabitants and their relationships (food chains, energy levels and their flow), are lacking.

According to Riedl (1966) marine caves may have different sizes and comprise small hollows as well as giant holes with many intermediate possibilities. Habitats with reduced light intensities as studied here are characterized as cavities and holes in the reef, voids between boulders or overhanging rocks or corals, where only reflecting or scattered light and also decreasing current prevail. Such habitats were summarized as mesolithion (Zander 1990, 2004), which is a definition without limits of sizes. Small-size animals can hide in small cave-like habitats, which are appropriate to their size and are called cryptobenthic species (Patzner 1999; Kovačiç et al. 2012). The special conditions during the course of evolution in the mesolithion improved in animals the development of large eyes for better seeing and of red coloration for better camouflage against potential enemies in dim light. These patterns clearly differ from the adaption in freshwater and anchialine caves, where the inhabitants have lost eyes and pigment (Wilkens 2004).

Ott (1988) constructed a model of energy flow in marine caves, but could not present real values of the single levels in the food chain. This lack of information should be improved by observations in the Red Sea. The fish were counted along the reefs during a distinct observation time. The aim of these studies was to find out the abundance of fish species and their modes of activity time, prey-category, way of prey foraging and level in the food chain. These parameters may help for a better understanding of the structure and, to a lower degree, of the dynamic of such special mesolithion habitats. Finally, it should be discussed whether the definition of marine caves of Riedl (1966) can be improved.

2. Material and methods

The studies were performed at the reefs of Marsa Alam (Red Sea, middle Egypt) in October 2015 and in Dahab (Red Sea, Golf of Aqaba, Sinai, Egypt) in October 2016 with help of SCUBA. Counting of fish was done by 12 (Marsa Alam) or 20 (Dahab) observation units of one hour, 6 or 10 each in the morning and in the afternoon, respectively. These dives and counts comprised a distance of about 100 m in 10 m depth and about 100 m back in a depth of 5 m along the reefs, which were sounded by a depth gauge. Thus, comparable results were attained. The numbers of counted fish were noticed on a writing table. In Marsa Alam results from dives were distinguished in different depths of 5 and 10 m; in both sites different times in the morning and four hours later in the afternoon were separately noticed. The investigated habitats comprised – according to the nomenclature of Riedl (1966; extended by Zander 1990)

– predominantly caves of minor size like small and micro caves, crevices, gaps between blocks and overhanging rocks (figs. 1-18).

As statistical parameters mean and standard deviation of all counts were calculated for every species. The modes of life of mesolithial fish were arranged in three categories: way of foraging, level of food chain and daily activity; these data were obtained from own observations, Eichler & Lieske (1994) and Froese & Pauly (2016). The structure of fish communities in both sites was compared with the calculation of diversity (H_s), evenness (J), Sörensen (species identity) and Renkonen (abundance identity) indices. According to Zaret & Rand (1972) values of more than 0.6 indicate low and values of more than 0.7 indicate high conformity.

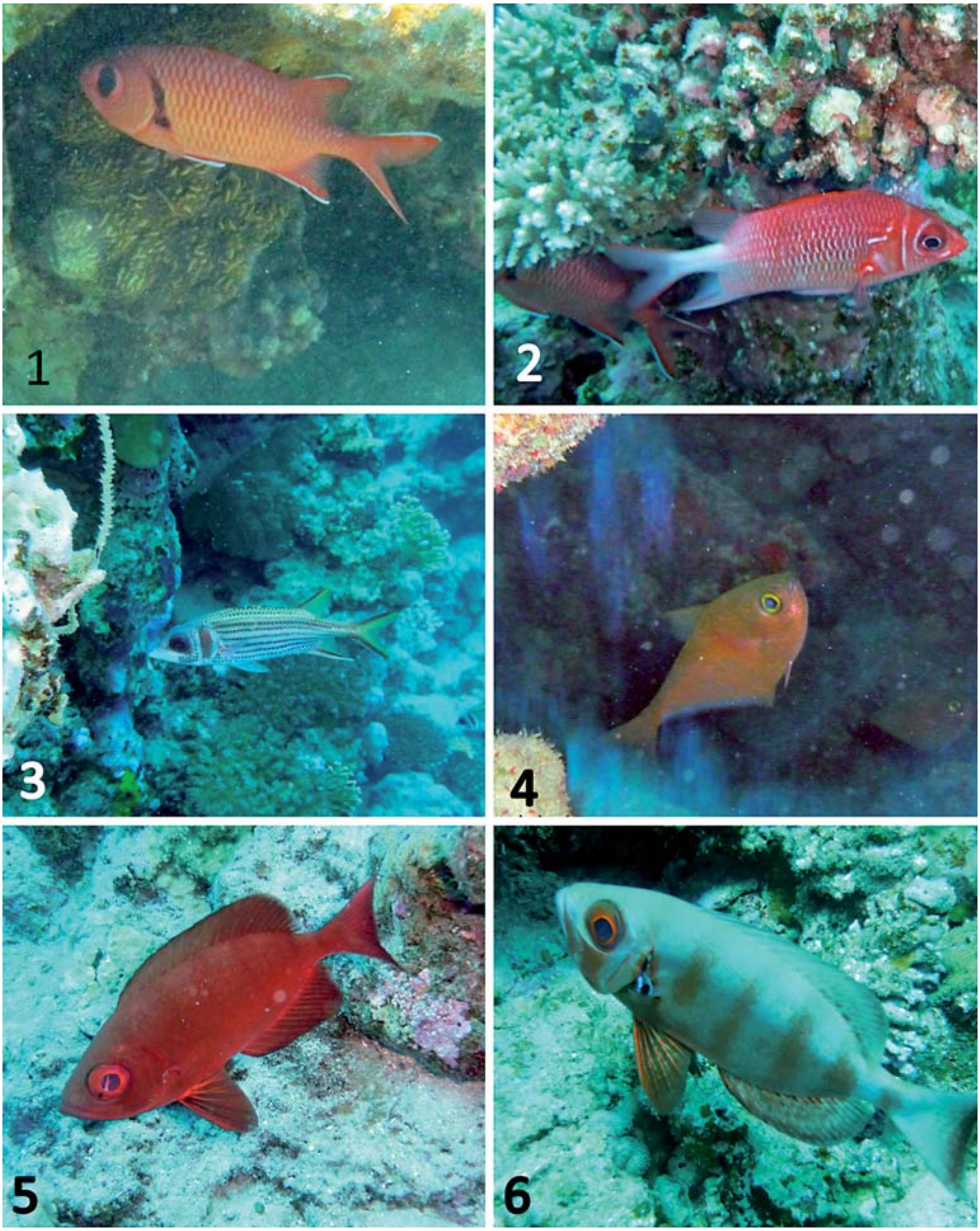
3. Results

In Marsa Alam 26, in Dahab 27 fish species with affinities to cavelike habitats were found (tabs 1, 2). The number of fish individuals per observation unit was with 79.5 (σ = 70.1, range 32-170) or 75.0 (σ = 41,7, range 31-165) almost identical, evenness was still homogeneous in Marsa Alam, but heterogeneous in Dahab (tab. 3). Almost 80 % species identy was found between the cave fish faunas of both localities. In contrast, abundance identity attained only less conformity (47 %, tab. 3). Figures 1-18 present an election of important fish species from this environment. The studies in Marsa Alam presented *Myriopristis murdjan* (fig. 1) by 31 observations per unit as the most abundant species, but the value of the standard deviation revealed a clumped dispersion (tab. 1). After this species *Pseudochromis fridmani* (fig. 13), *Neoniphon opercularis* (fig. 3), *Sargocentron caudomaculatus* (fig. 2) and *Priacanthus hamrur* (figs 5-6) followed in great distance. All other species attained less than 5 observations per unit. *N. opercularis, S. caudomaculatus, Cephalolophis argus* (fig. 8) show also a clumped dispersion. Frequency values were high (> 66 %) in *M. murdjan, P. fridmani, S. caudomaculatus, Cephalopholis miniata* (fig. 9) and

Tab. 1: Abundance, frequency and ecological characteristics of mesolithion fish from Marsa Alam (Red Sea, middle Egypt, 2015). Characteristic patterns regarding ways of life predominantly according to Eichler & Lieske (1994) and Froese & Pauli (2016).

Tab. 1: Abundanz, Frequenz und ökologische Merkmale von Fischen des Mesolithion aus Marsa Alam (Rotes Meer, Mittelägypten, 2015). Die Lebensformmerkmale folgen Eichler & Lieske (1994) und Froese & Pauli (2016).

	Mean abundance x	3 σ	Frequency of occurrence %	Figs 1-18	Prey category	Way of prey foraging	Level of food chain	Activity time
Myripristis murdjan	31.5	31	96	1	Plankton	Collector	3	Night
Pseudochromis fridmani	9.4	5.4	83	13	Plankton	Collector	3	Day
Neoniphon opercularis	7.6	6.2	58	3	Benthos	Collector	3	Night
Sargocentron caudomaculatus	5.8	4.4	75	2	Benthos	Collector	3	Night
Priacanthus hamrur	5.6	8	50	5-6	Plankton	Collector	3	Dawn
Cephalopholis miniata	4.2	2.2	81	9	Fish	Hunter	4	Day
Cephalopholis argus	4	3.8	62	8	Fish	Hunter	4	Day
Larabicus quadrilineatus	3.2	1.6	67	17	Parasites	Cleaner	5	Day
Aetholoperca rugoa	1.6	1.2	37	11	Fish	Hunter	4	Day
Pygoplites diacanthus	1.4	0.6	50		Benthos	Collector	3	Day
Pempheris vanicolensis	1.2	0.4	25	4	Plankton	Collector	3	Dawn
Cheilodipterus macrodon	1	0.6	25	7	Fish	Hunter	4	Night
Labroides dimidiatus	1	0.3	42	18	Parasites	Cleaner	5	Day
Variola louti	0.4	0.1	12	10	Fish	Hunter	4	Day
Heniochus intermedius	0.4	0.1	8	14	Plankton	Collector	3	Day
Pterois volitans	0.1	< 0.1	16	15	Fish	Net catcher	4	Dawn
Aspidontus taeniatus	< 0.1	< 0.1	8		Fish skin	Hunter	5	Day
Epinephelus aerolatus	< 0.1	< 0.1	8		Fish	Hunter	4	Dawn
Chaetodon semilarvatus	< 0.1	< 0,1	4		Benthos	Collector	3	Day
Chaetodon fasciatus	< 0.1	< 0.1	4		Benthos	Collector	3	Day
Chaetodon paucifasciatus	< 0.1	< 0.1	4		Algae	Collector	2	Day
Plectopomus laevis	< 0.1	< 0.1	4		Fish	Hunter	4	Dawn
Scorpaenopsis oxycephalus	< 0.1	< 0.1	4		Fish	Ambusher	4	Day
Pterois radiata	< 0.1	< 0.1	4	16	Fish	Net catcher	4	Dawn
Sidera griseus	< 0.1	< 0.1	4		Fish	Hunter	4	Dawn
Centropyge flavicaudata	< 0.1	< 0.1	3		Plankton	Collector	3	Day



Figs 1-6: Selection of mesolithion fish with notes on activity time and type of prey. **1** *Myripristis murdjan* (Holocentridae), night active, plankton feeder; **2** *Sargocentron caudimaculatus* (Holocentridae), night active, benthos feeder; **3** *Neoniphon opercularis* (Holocentridae), night active, benthos feeder; **4** *Pempheris vaniculensis* (Pempheridae), night active, plankton feeder; **5** *Priacanthus hamrur* (Priacanthidae), night active, plankton feeder, presenting cave coloration; **6** *P. hamrur* presenting daylight coloration.

Abb. 1-6: Auswahl von Mesolithion-Fischen mit Anmerkungen zur Aktivitätszeit und Art der Beute. **1** *Myripristis murdjan* (Holocentridae), nachtaktiv, Planktonfresser; **2** *Sargocentron caudimaculatus* (Holocentridae), nachtactiv, Benthosfresser; **3** *Neoniphon opercularis* (Holocentridae), nachtaktiv, Benthosfresser; **4** *Pempheris vaniculensis* (Pempheridae), nachtaktiv, Planktonfresser; **5** *Priacanthus hamrur* (Priacanthidae), nachtaktiv, Planktonfresser, in Dunkelfärbung; **6** *P. hamrur* in Tageslichtfärbung.

Tab. 2: Abundance, frequency and ecological characteristics of mesolithion fish from Dahab (Red Sea, Sinai, Egypt, 2016). Characteristic patterns regarding ways of life according to Eichler & Lieske (1994) and Froese & Pauli (2016).

Tab. 1: Abundanz, Frequenz un ökologische Merkmale von Fischen des Mesolithion aus Dahab (Rotes Meer, Sinai, Ägypten. Die Lebensformmerkmale folgen Eichler & Lieske (1994) und Froese & Pauli (2016).

	Mean abundance		Frequency		Prey	Way of prey	Level of	Activity
	x	3 σ	of occurence %	Figs 1-18	category	foraging	food chain	time
Pseudochromis fridmani	39.2	23.9	90	13	Plankton	Collector	3	Day
Priacanthus hamrur	7.9	12.6	65	5-6	Plankton	Collector	3	Dawn
Myripristis murdjan	5.7	7	75	1	Plankton	Collector	3	Night
Heniochus intermedius	3.6	2.5	90	14	Plankton	Collector	3	Day
Larabicus quadrilineatus	3.4	2.2	85	17	Parasites	Cleaner	5	Day
Cephalopholis argus	3.1	2.3	85	8	Fish	Hunter	4	Day
Pterois volitans	2.4	1	70	15	Fish	Net catcher	4	Dawn
Centropyge flavicauda	2.2	0.9	60		Plankton	Collector	3	Day
Labroides dimidiatus	1.7	1	70	18	Parasites	Cleaner	5	Day
Epinephelus fasciatus	1.4	1.5	30	12	Fish	Hunter	4	Day
Aetholoperca rugoa	1.4	1.5	60	11	Fish	Hunter	4	Day
Neoniphon opercularis	1.3	1.5	40	2	Benthos	Collector	3	Day
Cephalopholis miniata	1.2	1.1	60	9	Fish	Hunter	4	Day
Pygoplites diacanthus	1	0.7	60		Plankton	Collector	4	Day
Cheilodipterus quinquemaculatus	1	0.7	25		Fish	Hunter	4	Dawn
Variola louti	0.8	0.4	50	16	Fish	Hunter	4	Day
Grammistes sexfasciatus	0.5	0.3	45		Crayfish	Collector	3	Dawn
Apogon cyanosoma	0.5	0.3	15		Plankton	Collector	3	Night
Cheilodipterus macrodon	0.4	1.9	15	7	Fish	Hunter	4	Night
Meiocanthus nigrolineatus	0.3	0.1	20		Fish skin	Parasite	5	Day
Sargocentron caudomaculatus	0.2	< 0.1	20	2	Benthos	Collector	3	Night
Pterois radiata	0.2	< 0.1	5	16	Fish	Net catcher	4	Dawn
Scorpaenopsis oxycephalus	0.1	< 0.1	10		Fish	Ambusher	4	Day
Gymnothorax nudivomer	0.1	< 0.1	10		Fish	Hunter	4	Dawn
Pomacanthus imperator	< 0.1	< 0.1	5		Benthos	Collector	3	Day
Sidera griseus	< 0.1	< 0.1	5		Fish	Hunter	4	Dawn
Plectopomus aerolatus	< 0.1	< 0.1	5		Fish	Hunter	4	Dawn

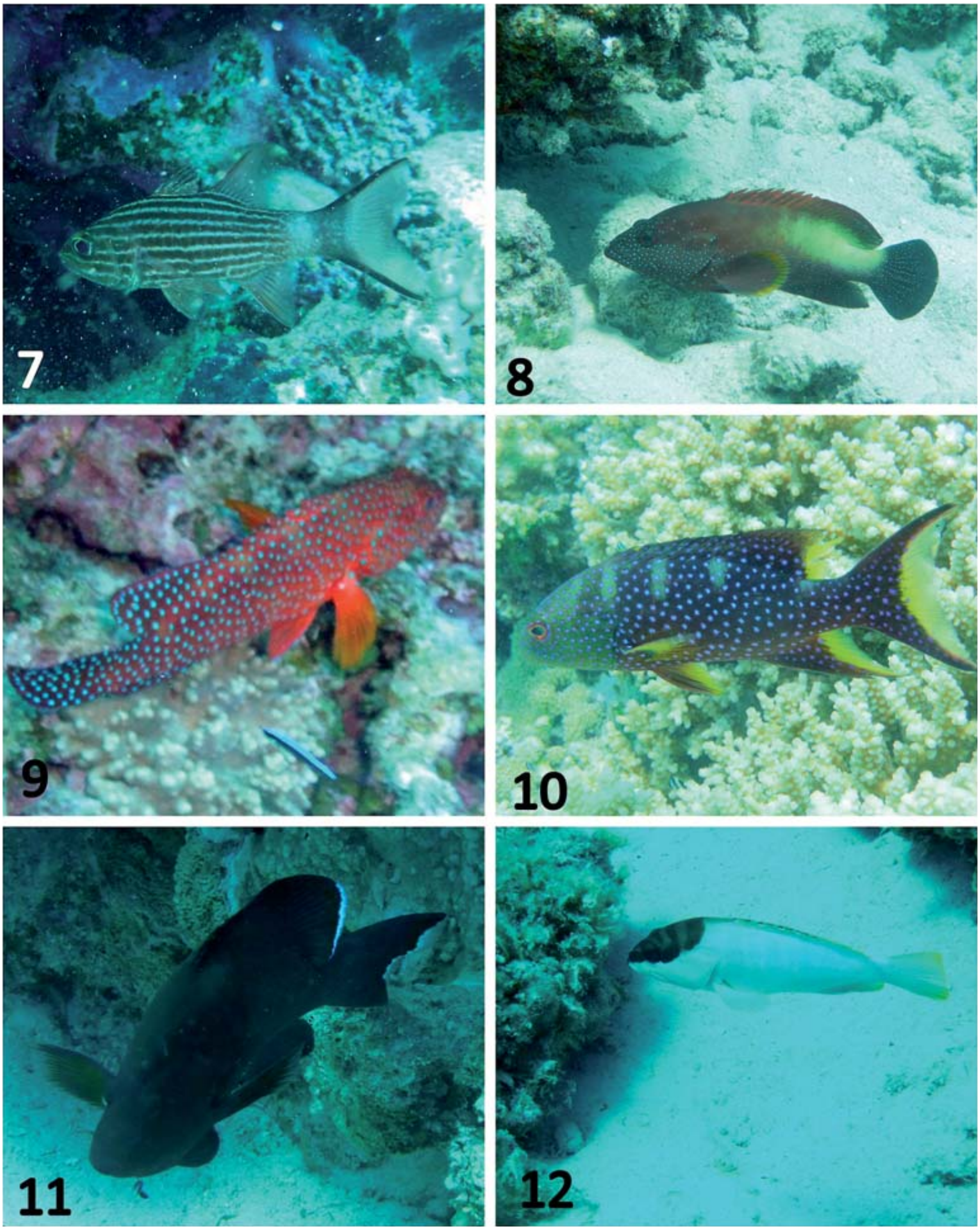
Tab. 3: Indirect and direct comparison of ecological characteristics of mesolithion fish from Marsa Alam (middle Egypt) and Dahab (Sinai, Egypt).

Tab. 3: Indirekter und direkter Vergleich ökologischer Merkmale von Fischen des Mesolithion aus Marsa Alam (Mittelägypten) und Dahab (Sinai, Ägypten).

	Marsa Alam		Dahab
Species richness	26		27
Diversity (Hs)	0.83		0.78
Evenness (J)	0.63		0.54
Individuals per observation unit	80.8		75.0
Species identity (Sörensen-Index)		0.79	
Abundance identity (Renkonen-Index)		0.47	
Activity time (Renkonen-I.)		0.66	
Food chain level (Renkonen-I.)		0.97	
Prey preference (Renkonen-I.)		0.74	
Mode of foraging Renkonen-I.)		0.95	

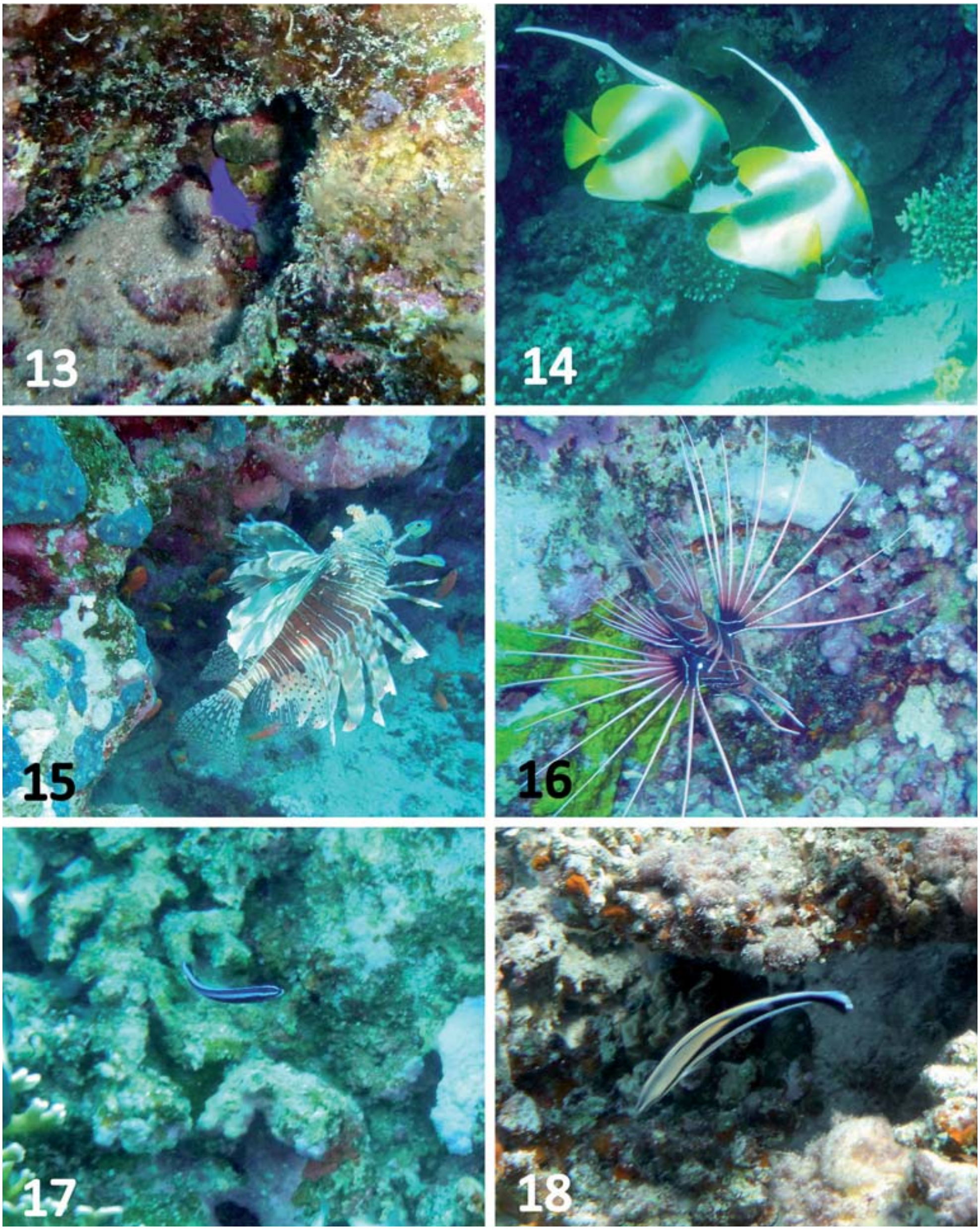
Larabicus quadrilineatus (fig. 17), which means regular presence during the observations (table 1). Differences of depths (5 or 10 m) were almost significant proved only in *C. argus*, which is in Marsa Alam more abundant in 10 m (3.3 per unit, σ = 1.4) than in 5 m (1.2 per unit, σ = 0.4). No significant difference was found between appearance in the morning or afternoon.

In Dahab a quite other situation was found. *Pseudochromis fridmani* was by 39 observations per unit in a great lead to the next abundant species *Priacanthus hamrur* and *Myripristis murdjan* (tab. 2). All other species attained an abundance of less than 4 %. Nevertheless, the cleaner species *Lararabicus quadrilineatus* (fig. 17) and *Labroides dimidiatus* (fig. 18) attained together 5 %. Con-



Figs 7-12: Selection of mesolithion fish with notes on activity time and type of prey. **7** *Cheilodipterus macrodon* (Apogonidae), night active, plankton feeder; **8** *Cephalopholis argus* (Serranidae), day active, fish predator; **9** *Cephalopholis miniata* (Serranidae), day active, fish predator; **10** *Variola louti* (Serranidae), day active, fish predator; **11** *Aetheloperca rugoa* (Serranidae), day active, fish predator; **12** *Epinephelus fasciatus* (Serranidae), day active, crayfish and fish predator.

Abb. 7-12: Auswahl von Mesolithion-Fischen mit Anmerkungen zur Aktivitätszeit und Art der Beute. **7** *Cheilodipterus macrodon* (Apogonidae), nachtaktiv, Planktonfresser; **8** *Cephalopholis argus* (Serranidae), tagaktiv, Fischräuber; **9** *Cephalopholis miniata* (Serranidae), tagaktiv, Fischräuber; **10** *Variola louti* (Serranidae), tagaktiv, Fischräuber; **11** *Aetheloperca rugoa* (Serranidae), tagaktiv, Fischräuber; **12** *Epinephelus fasciatus* (Serranidae), tagaktiv, Krebs- und Fischräuber.



Figs 13-18: Selection of mesolithion fish with notes on activity time and type of prey. **13** *Pseudochromis fridmani* (Pseudochromidae), day active, plankton feeder; **14** *Heniochus intermedius* (Chaetodontidae), day active, plankton feeder; **15** *Pterois volitans* (Scorpaenidae), night active, fish predator; **16**. *Pterois radiata* (Scorpaenidae), night active, fish predator; **17** *Larabicus quadrilineatus* (Labridae), day active, parasite predator (cleaner); **18** *Labroides dimidiatus* (Labridae), day active, parasite predator (cleaner).

Abb. 13-18: Auswahl von Mesolithion-Fischen mit Anmerkungen zur Aktivitätszeit und Art der Beute. **13** *Pseudochromis fridmani* (Pseudochromidae), tagaktiv, Planktonfresser; **14** *Heniochus intermedius* (Chaetodontidae), tagaktiv, Planktonfresser; **15** *Pterois volitans* (Scorpaenidae), nachtaktiv, Fischräuber predator; **16** *Pterois radiata* (Scorpaenidae), nachtaktiv, Fischräuber; **17** *Larabicus quadrilineatus* (Labridae), tagaktiv, Parasitenfresser (Putzer); **18** *Labroides dimidiatus* (Labridae), tagaktiv, Parasitenfresser (Putzer).

formity of species appearance was high in *P. fridmani*, *Heniochus intermedius* (fig. 14), *L. quadrilineatus*, *Cephalopholis argus*, *M. murdjan*, and *Pterois volitans* (fig. 15), which is confirmed by high frequency values (tab. 2). The question whether the abundances of morning and afternoon differ was only significant in *P. hamrur* with clear higher values in the morning ($m = 14.5 \pm 7.3$) in contrast in the afternoon ($m = 1.4 \pm 0.5$). Clear differences between observations in morning or afternoon present without to be significant the values of *P. fridmani* (43.4, $\sigma = 7.5$, and 25.3, $\sigma = 8.0$) and *C. argus* (4.1 and 2.1), where the higher values were also found in the morning.

The analysis of the ways of life revealed several differences between Marsa Alam and Dahab. The results of activity time proved that specimen of day active species dominated with more than 50 % in Dahab, but in Marsa Alam night active specimen dominated with more than 50 % before day active ones (fig. 19). The abundance identity

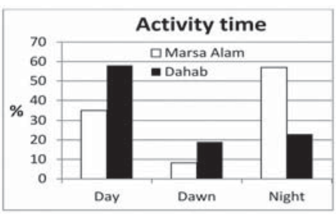


Fig. 19: Activity time (in %) of mesolithion fish from Marsa Alam and Dahab, Red Sea.
Abb. 19: Aktivitätszeiten (in %) von Mesolithion-Fischen aus Marsa Alam und Dahab, Rotes Meer.

was only 66 %, which is a relative low value (tab. 3). The results of the food chain levels revealed 80 % carnivores, whereas top predators surpassed in both localities the 10 % border, which was unexpectedly high in relation to the foregoing food chain level of primary carnivores (fig. 20). Top predator species were in Marsa Alam more abundant than in Dahab. Herbivorous are found to be unimportant. Obviously, the food chain levels of both localities are very similar (97 %, table 3). A special category is the cleaner fish species with more than 5 % in both localities (fig. 20).

The most preferred prey was plankton attaining 50 % in Marsa Alam and 70 % abundance

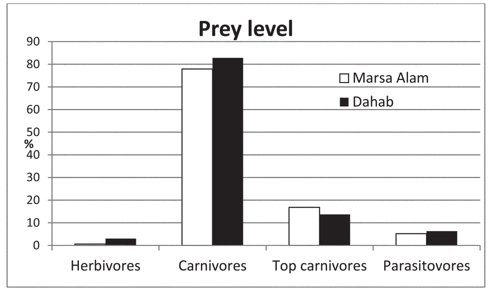


Fig. 20: Foodchain categories (in %) of mesolithion fish from Marsa Alam and Dahab, Red Sea.
Abb. 20: Kategorien der Nahrungskette (in %) von Mesolithion-Fischen aus Marsa Alam und Dahab (Rotes Meer).

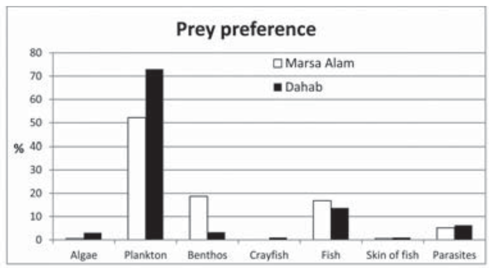


Fig. 21: Prey preference categories (in %) of mesolithion fish from Marsa Alam and Dahab, Red Sea.
Abb. 21: Kategorien bevorzugter Nahrung (in %) bei Mesolithion-Fischen aus Marsa Alam und Dahab (Rotes Meer).

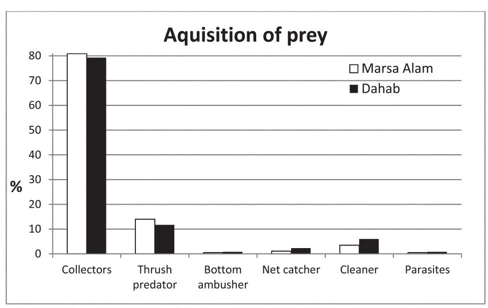


Fig. 22: Modes of foraging (in %) of mesolithion fish from Marsa Alam and Dahab, Red Sea.
Abb. 22: Art und Weise des Nahrungserwerbs bei Mesolithion-Fischen aus Marsa Alam und Dahab (Rotes Meer).

in Dahab (fig. 21). These values seem to be mutually compensated by benthos feeding species. The benthos values, therefore, surpass in Marsa Alam those from Dahab. The abundance of fish predators correspond to the food chain level analysis; its similarity attained a moderate value of conformity (74 %, tab. 3). The most abundant fish species of both localities prefer to collect their prey (80 %), mostly plankton or benthos (fig. 22). The most abundant top carnivores were thrush predators with about 10 % in both localities, followed by net catchers (*Pterois* spp.), which attained less than 3 % and the bottom ambusher (*Scorpaenopsis oxycephalus*) by less than 1 %. The cleaner wrasses as parasite feeders attained even values of ca. 5 %. Parasitic fish were only present by less than 0.2 %. The proportions of prey acquisition did not differ decisively between the two localities (fig. 22), matching the abundance identity of foraging mode was very high (95 %, tab. 3) .

4. Discussion

The following sentences are focused especially on two questions: what are the reasons for the differences between the localities of Marsa Alam and Dahab and, how food chain and energy flow do act in marine mesolithion. Depending on the former, the definition of dim lighted habitats will be discussed. The two deciding factors in marine caves as defined by Riedl (1966) or mesolithion as defined by Zander (1990) are decreasing light and decreasing currents. Decreasing currents cause for less plankton in the cave (Ott 1988). Decreasing light caused the evolution of large eyes with large lenses and few but enlarged rods and the reduction of melanophores (Zander 1980).

Similarities of the two investigated localities are present by numbers and composition of the mesolithial fish fauna, by the shares of components in food chain levels and mode of foraging. In contrast, no coincidence was found in the identity of abundance, which means a discrepancy in the respective quantitative composition of the fish. A moderate coincidence is still present in the category of food preference, whereas regarding the activity time the localities coincide by only 66 % (tab. 3). Reasons for differences may be the structure of habitats, which are mostly steep walls falling down from the reef flat in Marsa Alam, but which are variable in Dahab regarding the gradient of slopes and size of coral blocks. This result may be explained by the different structures and expressed by the dominance of the night active *Myripristis murdjan* in the steep walls of Marsa Alam and the day active *Pseudochromis fridmani* in the polymorphic coral reefs of Dahab. Both species are plankton feeders, but the amount of the food consumed is really higher in *M. murdjan* (size 15-20 cm) than in *P. fridmani* (size maximally 8 cm). Additionally, *P. fridmani* is day active, *P. murdjan* comes at dawn out of cavities. This observation is the reason for more night active specimens in Marsa Alam and more day active specimens in Dahab. Benthos feeders were more abundant in Marsa Alam and thus, probably due to lesser amounts of plankton, equalize the level of primary carnivores in both localities (tab. 3).

Herbivore fish species were very rare. Only *Chaetodon paucifasciatus* in Marsa Alam and *Centropyge flavicauda* in Dahab were algae grazers, but occurred in very low abundance. Zooplankton, which is the prey of the most collectors, arises at night from deeper to shallow water and supplies the demand of the night active suspension feeders. The benthos preying fish species have to come out of the cavelike habitats in order to get food, because benthos organisms are rare in the inner areas. This phenomenon is due to the decreasing current from the entrance to the rear of a cave (Riedl 1966) and may be also valid in the here investigated cavelike environments. The relation of plankton and benthos feeding species (carnivores 1) to fish preying species (carnivores 2) is in Marsa Alam about 5 to 1, in Dahab 6 to 1, which is divergent to the general value of 10 to 1 (Lindemann 1942). This relationship, therefore, means an advantage in favor of the top predators, which find here optimal conditions for their existence. The cleaner fish are collectors of parasites from other fish hosts and compete with sabletooth blennies, which parasitic peck fin and skin tissue from other fish (Wickler 1968).

The relation of cleaner fish, the abundance of which was low in both localities, to parasite fish is about 10 to 1; this relation may be balanced, because the latter imitate the coloration of cleaner fish in order to delude the potential hosts. If the parasite fish would become too abundant the cleaner symbiosis cannot operate profitably, because the hosts learn to become more cautious against possible attacks and, therefore, would compromise the cleaner symbiosis.

Riedl (1966) characterized in his comprehensive work the fauna of marine caves as part of the littoral system, in which the sedentary suspension feeder dominate. Better investigated is the structure of mesolithion ecosystems especially in the Mediterranean (Riedl 1966). Fish species from there had been objects of several studies (Abel 1959; Arko-Pijevac et al. 2001; Bussotti & Guidetti 2009; Bussotti et al. 2015; Zander 1980, 1990; Zander & Heymer 1976; Zander & Jelinek 1976; Patzner 1999; Kovačiç et al. 2012). These authors revealed that populations of France, Croatia and Turkey are differently adapted to the gradient of light decrease. Generally, in food chains the mean energy decreases from layer to layer of 10 % (Lindemann 1942; Odum & Odum 1955). Ott (1988) constructed a model of the energy flow in marine caves with only estimated quantities, but he was able to indicate the way for further studies. Also the present investigations could give only little insight in the dynamic of this biocoenosis, because they quantify only fish species by numbers. Naturally, regarding biomass *Pseudochromis fridmanni, Cheilodipterus* or *Apogon* spp. are not as heavy as *Myripristis murdjan* or *Priacanthus hamrur*. Herbivores find in contrast to full lighted habitats in less lighted ones little prey, therefore, the observed low values were expected. These had to be complemented by herbivore invertebrates, which would by far not attain the biomass of herbivore fish. In the next level, the carnivores, mesolithion fish may be also be completed by some invertebrates (e.g. crayfish), which also play no important role. The level of invertebrate top carnivores is simpler to be judged, because only *Octopus* spp. can come in question as a member of this category.

According to Riedl (1966) the function of marine caves is the same as an environment in the littoral with lowered light (less than 1 % of surface light) and current (less than 10 %) and with a minimal resting time of 2 months (this regards rocks and coral blocks). But caves in narrow sense are only a part of the extensive term mesolithion. It comprises also relative small habitats with the same quality of light and currents as described by Riedl (1966), e. g. crevices, gaps, overhanging rocks and corals, which can be called "pseudocaves", where the greatest part of fish are hyperbenthic. The "cryptobenthal" used by Patzner (1999) and Kovačić et al. (2012) is another part of the mesolithial, which is especially inhabited by small-size epibenthic fish.

Abel (1959) created also some categories by special regard of cave or mesolithial fish, respectively: speleoxenous, speleophilous and speleobiont species. The category speleoxenous comprises in the Red Sea species like *Pseudanthias squamipinnis*, which may be present before cavities, but are also found in free water. A part of speleophilous fish use the cave as resting or hiding place as do the most day active species found here, like *Pseudochromis fridmani*, serranids or chaetodontids. They may further be called speleophilous species. A certain difference presents the other part of fish, which are marked by large eyes and mostly red coloration like holocentrids, priacanthids and apogonids: heliophobous species. Speleobiont fish species with reduces eyes and pigment, which remain their whole life in caves, are missing in pseudocaves like those investigated here.

On the basis of Riedl's (1966) functional definition of marine caves here an improved version is presented. The "mesolithion" is part of the littoral system, which is influenced by dim light and decreasing currents, where sedentary suspension feeders dominate. The fish fauna is characterized by two groups: speleophilous species, which comprise day or dawn active fish, which use the mesolithion as hiding or spawning place, and, second, dark active heliophobous species, which present enlarged eyes and mostly red coloration as adaptation to low light intensity. Caves, pseudocaves (as was investigated in this study) and cryptobenthal are special structures of the mesolithion.

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