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Food selection and habitat preferences in deep-sea fishes of the northern Red Sea

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Abstract: Due to the water circulation in the Red Sea, the values of abiotic parameters such as temperature and oxygen concentration are close both in the photic and aphotic zone. The food web of eight common fish species inhabiting the deep waters of the Red Sea and the Gulf of Aqaba, from a total of 42 collected species, has been investigated. Two methods for studying the feeding habits of these fishes were used: the qualitative analyses of the stomach contents and the stable carbon isotopic composition (the $\delta^{13}C$) in the tissue of organisms.These fishes are not morphologically adapted to life in the dark deep sea, where light intensity is less than 1 % of the sea surface irradiation. It is assumed the abundance of food is the main factor for the selection of this new ecological niche.

Introduction

The Red Sea is a long, narrow basin approximately 2000 km in length and averaging 280 km in width. The average depth is 491 m, but the deep axial troughs reach 3000 m. The shallow (100 m) Bab el Mandeb Straits in the south are 26 km wide, sharply limiting the exchange of water with the Indian Ocean. In the north, the Red Sea ends in the Gulf of Aqaba, a narrow, deep (1800 m) trench, and the much shallower Gulf of Suez.

The thermohaline circulation of waters from the Indian Ocean into the Red Sea and its appendices, the Gulf of Aqaba and the Gulf of Suez, strongly affects the bathymetric distribution of the Red Sea ichthyofauna, especially the deep-sea inhabitants. Warm surface water (28-30 °C) flows to the Red Sea through the Straits of Bab el Mandeb. These surface waters, following the wind and current regime, are transported to the northern Red Sea and then enter the Gulf of Aqaba; on their way north they cool and become saltier. This gulf is separated from the Red Sea by the sill of Tiran at a depth of approximately 220 m. The high surface temperatures (20.5-27.3 °C) are then transported north towards Eilat and Aqaba, where they become cooler and denser. The thermohaline circulation causes the bottom waters to eventually exit the Red Sea system back to the Indian Ocean (Fig. 1).

These hydrographic and climatologic conditions induces a very weak stratification, an almost constant temperature throughout the water column, and the presence of "warm water" (20.5-21.5 °C) close to the bottom.

The high temperature, together with the physical barrier of the sill of Bab el Mandeb, cause the deep waters of the Red Sea and its appendages to be almost inaccessible to the typical deep-sea ichthyofauna. KLAUSEWITZ (1989) and BARANES and GOLANI (1993) showed that the fishes of the aphotic zone in the Red Sea are not "primary" but "secondary" deep-sea fishes. Most of them are coral reef or shallow habitat fishes that invaded deeper zones.

The Red Sea, being an oligotrophic sea with poor primary production, is unlikely to enable sustainable populations of ichthyofauna in the aphotic zone. Nonetheless BARANES and GOLANI (1993) recorded 69 species in the aphotic zone of the Gulf of Aqaba. They pointed out that the deep waters of the gulf seem to be well provided with sustenance at all trophic levels. This raised questions about the origin of the food for the benthic inhabitants, its supply rate, and the possibility that the search for food enabled their migration from the rich photic zone to the aphotic zone characterized by "unfriendly" abiotic parameters.

In order to answer these questions, we conducted a study from January 1992 to June 1995 to define the diet of the common fish species inhabiting the aphotic zone, and to determine their relative trophic position in the food web. The research area included the Gulf of Aqaba, the northern Red Sea, and the Dahlak Archipelago (southern Red Sea).

To produce a model of the food web in the aphotic zone, two separate analyses were conducted; the first was a conventional stomach content analysis (quantitative and qualitative) and the second one an analysis of the stable carbon isotopes. This isotopic analysis has been used in the past to determine trophic levels on land (including lakes) and in the marine environment (MCCONNAUGHEY and MCROY 1979a, b, FRY and SHERR 1984, ZOHARY et al. 1994). Unlike traditional stomach content analyses, this method provides information on the **digested** food which is integrated in the tissue of the animal within the residence time of carbon in this tissue.

Carbon atoms in nature have two stable isotopes with a different frequency; the more common isotope in the biosphere is the lighter one (^{12}C: 98.89 %; ^{13}C: 1.11 %) (NIER 1950). Relatively recent studies have demonstrated that ^{13}C: ^{12}C isotope ratios can be used as tracers in determining the likely pathways of carbon flow within a food web (e.g., FRY and SHERR 1984). The analysis of the carbonic gas (CO_2), measuring the isotopic composition, shows the deviation from standard δ^{13}C values. The carbon isotope composition

Figure 1.

General Pattern of Water Circulation in the Red Sea

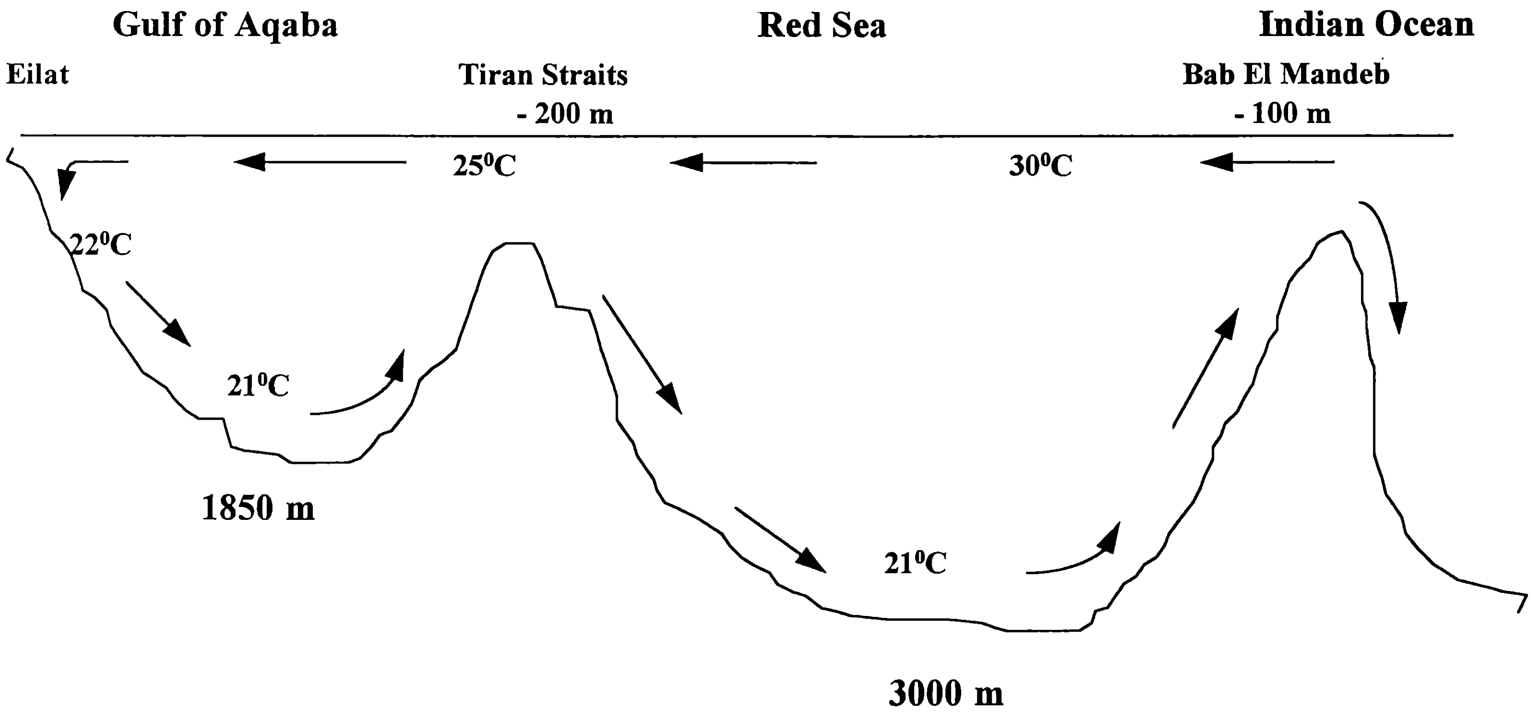


Fig. 1: General pattern of water circulation in the Red Sea.

($\delta^{13}C$) of a consumer is a slightly enriched average of the composition of food items consumed and converted into body tissue (DE NIRO and EPSTEIN 1978). When the carbon sources have distinctly different $\delta^{13}C$ values, their consumers can be traced.

The ratio between ^{13}C and ^{12}C rises with the pathway of the C in the food web because ^{12}C is lost faster than ^{13}C. Accordingly, organisms higher up the food chain are richer in the heavy isotope than those at the base of the chain (MCCONNAUGHEY and MCROY 1979). From research conducted at the Interuniversity Institute Eilat (IUI) (LORIAN 1991, EREZ unpubl. data,) we may summarize the flow of the $\delta^{13}C$ values in the coral reefs of the Gulf of Aqaba as follows:

$\delta^{13}C$ (‰)			
(-16)	-	(-21)	Plankton
	↓		↓
(-10)		(-19)	Fish
(-23)		(-19)	Sediment

Materials and Methods

Fishes were collected at least once a month from January 1992 to November 1993. Most of the sampling was conducted in the aphotic zone of the Gulf of Aqaba, although the main effort concentrated on the northern part of the gulf between depths of 150-900 m. Six additional samplings were conducted at 800-1500 m at the southern part of the gulf, between Ras Abu Galum and the Straits of Tiran. Five samples were taken in the northern part of the Red Sea proper, south of the Tiran Straits, and two samples were taken around the Dahlàk Archipelago.

Most of the material was obtained by using a monofilament trammel net, usually baited and set overnight. Traps of various shapes and sizes, as well as bottom longlines with hooks of Kirby type no. 4 and 5 were also used as fishing gear. The fishing gear was set with a small boat (7 m) provided with a mechanical winch. The exact depth at the working site was determined by echo-sounder. An experimental beam trawl was used several times, although this equipment was difficult to handle in coral areas.

The stomach content analysis was restricted to fishes. The collected fishes were dissected after recording their length and weight, and the whole stomach was preserved in 10 % buffered formaldehyde. The lowest possible taxon of each of the different items in the stomach was determined. Pieces of certain organisms in the stomachs were taken as sufficient evidence of predation on that particular species. The relative frequency of each food item in all stomachs analysed was calculated. In addition, the total number of identifiable prey per stomach was calculated for the most common fish species.

The ratio of stable carbon isotopes was analyzed by examining the CO_2 and comparing the $^{13}C\ ^{16}O\ ^{16}O$ and $^{12}C\ ^{16}O\ ^{16}O$ in the sample. Results are reported as deviations (in ‰) from the ^{13}C: ^{12}C ratio of the PDB carbonate standard (in which the ^{13}C is 0 ‰) using:

$$\delta^{13}C\ (‰) = \{[^{13}C:\ ^{12}C_{\text{sample}}/^{13}C:\ ^{12}C_{\text{standard}}] - 1\} \times 1000$$

A value larger than or close to 0 means that the sample is rich in the heavy isotope (^{13}C) compared to the standard. When the sample shows negative values it is poorer (lighter) in ^{13}C.

For $\delta^{13}C$ analyses, tissue from animals (about 10 g) and samples from fresh animals were washed in distilled water and dry frozen (-20 °C) for several days. The tissue samples from fishes were: muscles from the predorsal region (without skin), the liver, and fins (caudal, pectoral, and dorsal). For invertebrates they were: tissue from the leg muscle (without carapace), arms in sea stars, and muscles of sea urchins. In cephalopods and nudibranchs, the whole animal or pieces of muscle, if found as a stomach content, were sampled.

Samples were combusted at 550 °C for 14-20 h in vacuum-sealed 6 mm Pyrex ampoules with 100 mg of copper oxide (physically mixed with the organic matter and with a silver wire) (SOFER 1980). Comparisons carried out at our laboratory have shown that $\delta^{13}C$ values obtained from subsamples treated this way agreed within 0.4 ‰ with subsamples prepared by combustion at 900 °C in quartz tubes, with no specific trend. The combusted ampoules were broken into a high vacuum line; the CO_2 that evolved was purified from water passing through a propanol-liquid nitrogen cold trap at -90 °C and then collected into 6 mm pyrex ampoules which were sealed immediately. The isotopic composition of the CO_2 gas was determined by a VG602 ratio mass spectrometer. The precision of the analytical method, determined on several dozen replicate samples, was roughly ± 0.2 ‰.

Temperature profiles were measured with an STD; light profiles were measured using two LICOR sensors PAR spectrum, one measuring on-board-incident-light and the other measuring the underwater light intensity; oxygen was measured by Winkler titration. All these measurments were conducted on board the IUI research vessel, the "University I".

Results

Bathymetric distribution of the collected deep-sea fishes

A total of 1564 fish specimens were collected. These specimens belong to 42 species from 30 families; 4 species are elasmobranchs and 38 are bony fishes (Tab. 1). The frequency (by depth) of each fish species collected is shown in Tab. 2. The frequency of the deep-sea fishes collected in the northern Red Sea is shown in Tab. 3.

Plotting the size of the *Iago omanensis* specimens against depth reveals two distinct groups within the population (Fig. 2). When plotting the males and females separately, it appears that most of the males inhabit the deeper waters, while the larger females prefer shallower areas. (Fig. 3).

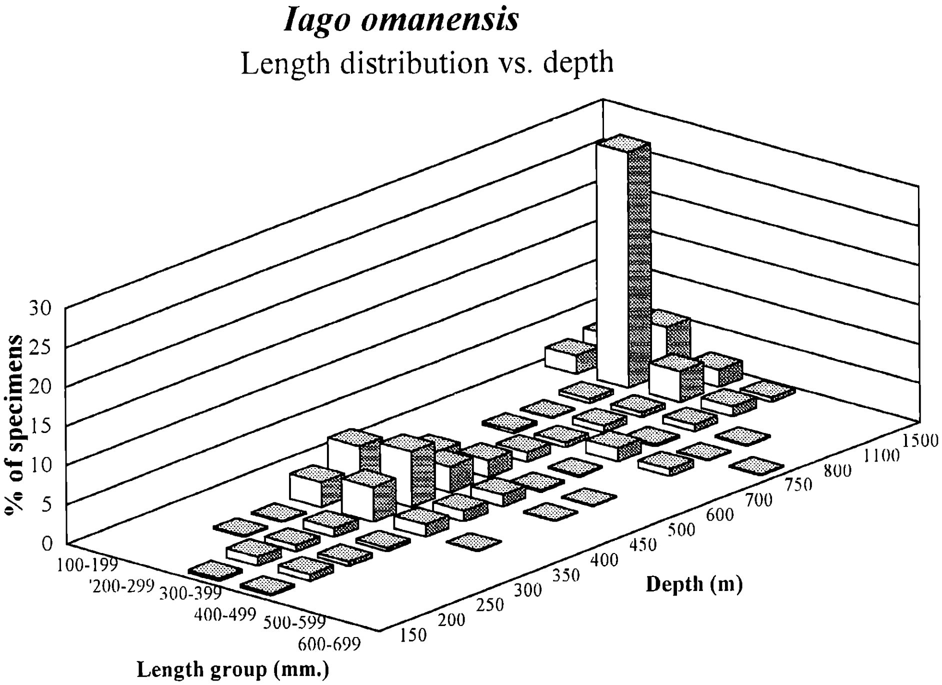


Fig. 2: Bathymetric distribution of *I. omanensis*

In a collection of 87 *I. omanensis* specimens in the northeast of the Dahlak Archipelago, we found 57 (250-451 mm) males and 30 (267-459 mm) females at a depth of 1570 m.

Tab. 1: List of fish species collected in the aphotic zone of the Gulf of Aqaba

Family	Species	Number of Specimens
CARCHARHINIDAE	*Carcharhinus plumbeus*	3
TRIAKIDAE	*Iago omanensis*	1171
	Mustelus mosis	8
RHINOBATIDAE	*Rhinobatos punctifer*	1
MURAENIDAE	*Gymnothorax johnsoni*	10
CONGRIDAE	*Rhynchoconger trewavasae*	20
MURAENESOCIDAE	*Muraenesox cinereus*	8
SYNODONTIDAE	*Saurida tumbil*	30
	Synodus doaki	1
MORIDAE	*Physiculus marisrubri*	14
TRACHICHTHYIDAE	*Hoplostethus mediterraneus*	1
HOLOCENTRIDAE	*Ostichthys hypsipterygion sufensis*	3
	Ostichthys acanthorhinus	2
MONOCENTRIDAE	*Monocentris japonicus*	2
TRIGLIDAE	*Pterygotrigla hemisticta*	16
PLATYCEPHALIDAE	*Cociella crocodila*	1
DACTYLOPTERIDAE	*Dactyloptena peterseni*	2
SCORPAENIDAE	*Scorpaenopsis oxycephala*	1
CHAMPSODONTIDAE	*Champsodon omanensis*	1
URANOSCOPIDAE	*Uranoscopus marisrubri*	1
SERRANIDAE	*Epinephelus areolatus*	1
	Epinephelus epistictus	5
	Epinephelus radiatus	1
PRIACANTHIDAE	*Priacanthus sagittarius*	2
	Pristigenys niphonia	1
ACROPOMIDAE	*Acropoma japonicus*	8
CARANGIDAE	*Trachurus indicus*	1
	Carangoides equula	1
SPARIDAE	*Argyrops spinifer*	93
	Polysteganus coeruleopunctatus	59
NEMIPTERIDAE	*Parascolopsis eriomma*	14
	Parascolopsis sp.	6
	Parascolopsis baranesi	3
	Nemipterus randalli	1
SCIAENIDAE	*Atrobucca geniae*	25
PINGUIPEDIDAE	*Parapercis somaliensis*	3
MULLIDAE	*Parupeneus rubescens*	2
	Upeneus subvittatus	25
LUTJANIDAE	*Paracaesio sordidus*	4
ARIOMMATIDAE	*Ariomma brevimanus*	2
BOTHIDAE	*Bothus pantherinus*	1
MONACANTHIDAE	*Thamnaconus modestoides erythraeensis*	13
30	**42**	**1564**

Tab. 2: Relative frequency of each fish species collected at different depth zones between 150-1500 m; + = Less than 3 specimens collected

	Depth in m.													
Species	150	200	250	300	350	400	450	500	600	700	750	800	1100	1500
Rhinobatos punctifer	+													
Synodus doaki	+													
Paracaesio sordidus	100													
Bothus pantherinus	+													
Parascolopsis eriomma	71	29												
Parupeneus rubescens	+	+												
Thamnaconus modestoides erythraeensis	62	30			8									
Mustelus mosis	38			25		37								
Gymnothorax johnsoni	20	10				70								
Argyrops spinifer	22	13	5		4	2	54							
Upeneus subvittatus	4	8	4		12	60	12							
Polysteganus coeruleopunctatus	2	8			7	34	19	27		3				
Muraenesox cinereus	13						25		12	13	25	12		
Iago omanensis	0.6	2	1.5	1.7	9.2	14.3	7.5	3.8	1.5	3.5	1.5	2.1	39.3	11.4
Epinephelus areolatus		+												
Epinephelus radiatus		+												
Carangoides equula		+												
Ostichthys hypsipterygion sufensis		67				33								
Atrobucca geniae		24	4		20	32	20							
Pristigenys niphonia			+											
Priacanthus sagittarius			+		+									
Monocentris japonicus			+			+								
Dactyloptena peterseni			+			+								
Carcharinus plumbeus			33					67						
Cociella crocodila				+										
Pterygotrigla hemisticta				19	44	37								
Acropoma japonicus				12	37	25	13	13						
Saurida tumbil				23	33	10	20		7	7				
Parapersis somaliensis					100									
Ariomma brevimanus					+									
Scorpaenopsis oxycephala						+								
Champsodon omanensis						+								
Trachurus indicus						+								
Parascolopsis sp						67	33							
Rhynchconger trewavasae						50		30			10	5		5
Uranoscopus marisrubri							+							
Nemipterus randalli							+							
Physiculus marisrubri								7						93
Ostichthys acanthorhinus								+	+					
Hoplostethus mediterraneus										+				
Epinephelus epistictus											60	40		

Tab. 3: Relative frequency of the fish species collected

Species	Frequency (%)	Species	Frequency (%)
Uranoscopus marisrubri	0.06	*Carcharhinus plumbeus*	0.19
Epinephalus areolatus	0.06	*Ostichthys h. suffensis*	0.19
Champsodon omanensis	0.06	*Parapersis somaliensis*	0.19
Cociella crocodila	0.06	*Paracaesio sordidus*	0.26
Scorpaenopsis oxycephala	0.06	*Epinephalus epistictus*	0.32
Epinephalus radiatus	0.06	*Parascolopsis nsp1*	0.38
Nemipterus randalli	0.06	*Mustelus mosis*	0.51
Bothus pantherinus	0.06	*Muraenesox cinereus*	0.51
Trachurus indicus	0.06	*Acropoma japonicus*	0.51
Pristigenys niphonia	0.06	*Gymnothorax johnsoni*	0.64
Carangoides equula	0.06	*T. modestoides erythraeensis*	0.83
Hoplostethus mediterraneus	0.06	*Physiculus marisrubri*	0.90
Synodus doaki	0.06	*Parascolopsis eriomma*	0.90
Rhinobatos punctifer	0.06	*Pterygotrigla hemisticta*	1.02
Ostichthys acanthorhinus	0.13	*Rhynchoconger trewavasae*	1.28
Parupeneus rubescens	0.13	*Upeneus subvittatus*	1.60
Priacanthus sagittarius	0.13	*Atrobucca geniae*	1.60
Ariomma brevimanus	0.13	*Saurida tumbil*	1.92
Monocentris japonicus	0.13	*Polysteganus coeruleopunctatus*	3.77
Dactyloptena peterseni	0.13	*Argyrops spinifer*	5.95
		Iago omanensis	74.87

Fig. 4 shows that there is a segregation by size in *Rhynchoconger trewavasae* as well as in *Mustelus mosis* and *Gymnothorax johnsoni*; in the latter, most of the population is in deep water, the largest being also found close to the limit of the photic zone (150-200 m).

Argyrops spinifer, Polysteganus coeruleopunctatus, Upeneus subvittatus, Atrobucca geniae, Thamnaconus modestoides erythraeensis, Pterygotrigla sp., Saurida tumbil, and *Muraenesox cinereus* showed no correlation between the fish size and sampling depth.

In those species present in both the photic and aphotic zone, the specimens were generally much larger in the aphotic zone. *E. epistitus* specimens do not exceed 259 mm in the coral reef, while specimens of 640-910 mm were collected in the deep sea (BARANES and GOLANI 1993).

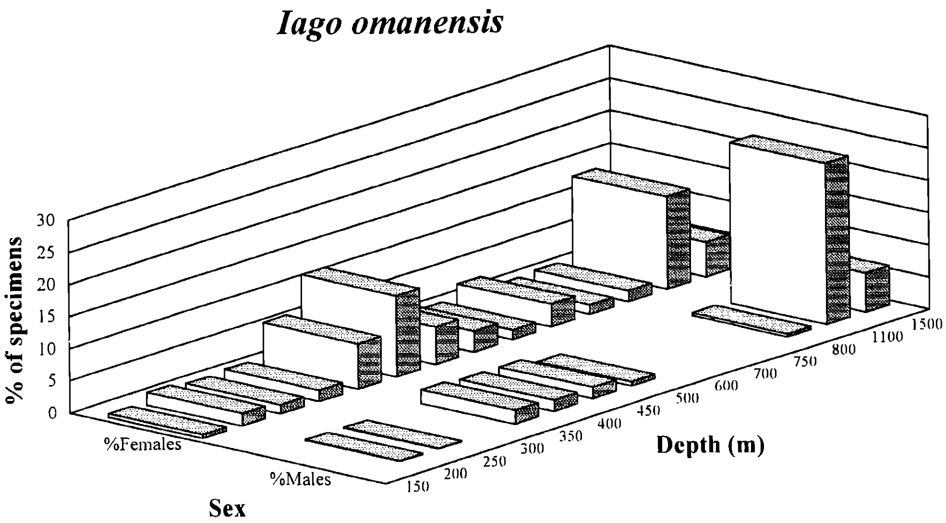


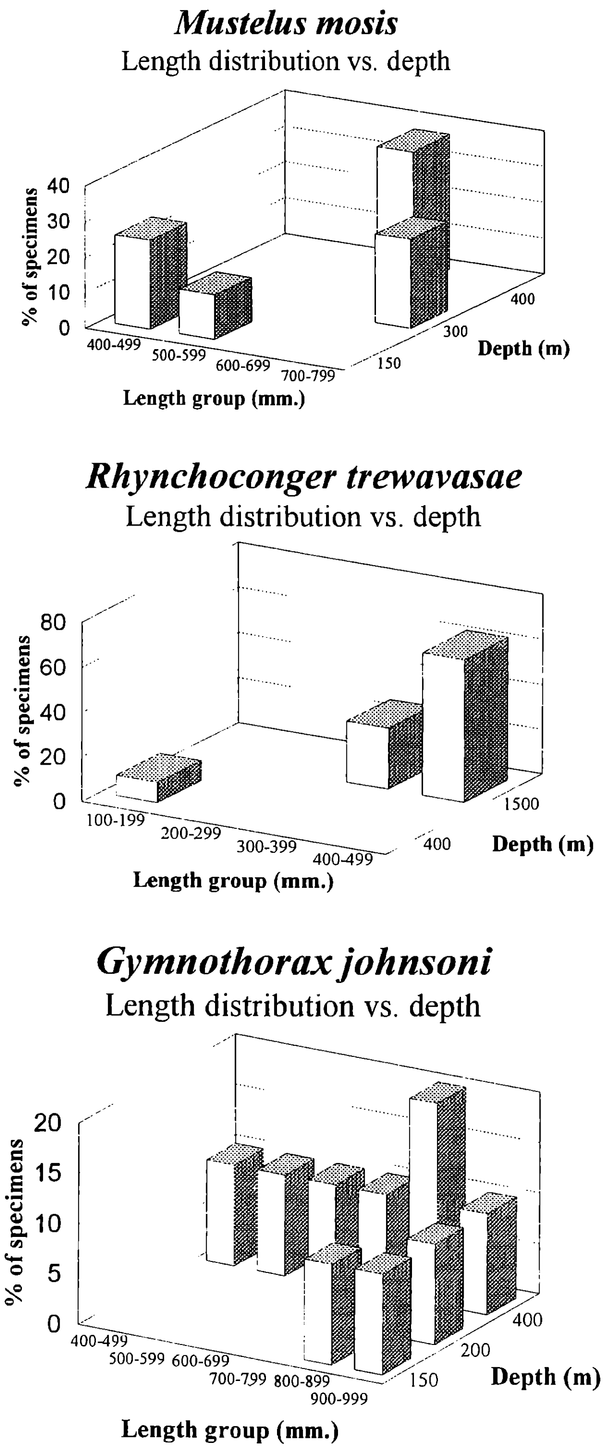
Fig. 3: Distribution of sexes vs. depth in *Iago omanensis*

Stomach contents of the most common fish species collected

The stomach contents of 417 fishes belonging to the eight most common species were examined: *Iago omanensis, Mustelus mosis, Argyrops spinifer, Polysteganus coeruleopunctatus, Upeneus subvittatus, Saurida tumbil, Atrobucca geniae*, and *Muraenesox cinereus.*

The main food of *Iago omanensis* (more than in 50 % of the stomachs examined) are the cephalopods *Enigmoteuthis dubia* and *Abraliopsis* sp. In 40 % of the stomachs, remains of fishes (*Champsodon* sp. and myctophids) were found. The common decapod *Parapandalus narval*, unidentified matter, and terrestrial food items were also found in 20 % of the stomachs (Fig. 5A).

There was no evidence of sexual differences in the feeding habit of *Iago omanensis* (Tab. 4, Fig. 6A). As previously shown by WALLER and BARANES (1994), no seasonality occurs in the feeding habits of *I. omanensis* in the northern Red Sea.



Mustelus mosis
Length distribution vs. depth

Rhynchoconger trewavasae
Length distribution vs. depth

Gymnothorax johnsoni
Length distribution vs. depth

Fig. 4: Bathymetric distribution by size in *M. mosis*, *R. trewavasae* and *G. johnsoni*

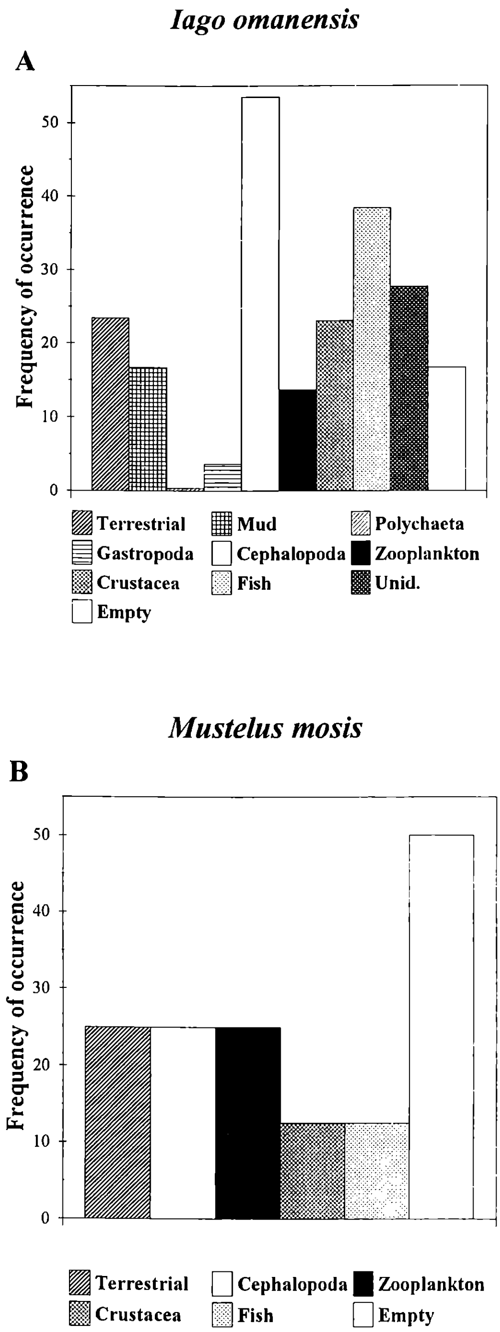


Fig. 5: Stomach content of *I. omanensis* and *M. mosis*

Tab. 4: Frequency of occurrence of food items in *Iago omanensis*

Stomach content	Females	Males	Total
Terrestrial	29.96	0.93	23.41
Mud	12.24	21.30	16.72
Polychaeta	0.42	0.00	0.33
Gastropoda	0.84	8.33	3.68
Cephalopoda	51.90	67.59	53.51
Zooplankton	11.81	13.89	13.71
Other Crustacea	27.43	11.11	23.08
Fish	31.22	45.37	38.46
Unid.	15.61	44.44	27.76
Empty	17.30	16.67	16.72
Total # of stomachs	237	108	345

Mustelus mosis feed equally on cephalopods, decapods, and terrestrial food items (25 %). 10 % of the stomachs contained remains of *Penaeus sp.* (Fig. 5B).

The diet of the two sparids, *Argyrops spinifer* and *Polysteganus coeruleopunctatus*, is similar. In both species, 40 % decapods and 20 % fishes were found in the stomach contents. Pieces of shell of *Murex sp.* and remains of the cephalopod *Enigmoteuthis dubia* were also found in *Argyrops spinifer*. Only in *Argyrops spinifer* there was evidence of terrestrial food. (Fig. 6B).

Upeneus subvittatus was found to feed mainly on decapods (20 %); nudibranchs and cephalopods represented only 10 % of the diet. *Saurida tumbil* is a fish predator (15 %), but also feeds on decapods (5 %). Both *Atrobucca geniae* and *Muraenesox cinereus* feed mainly on fishes (40 %), although it should be pointed out that most of the stomachs (60 %) were empty and that the fish remains found could not be more closely identified.

The composition of stable carbon isotopes in fishes and invertebrates from the aphotic zone

Analyses of $\delta^{13}C$ values from samples of tissue (muscle) were conducted on 11 common fish species, on 9 invertebrates, and on sediments samples. The results are expressed in Tab. 5 and Tab. 6 in ascending order from the lightest (poor in ^{13}C) to the heaviest value (rich in ^{13}C).

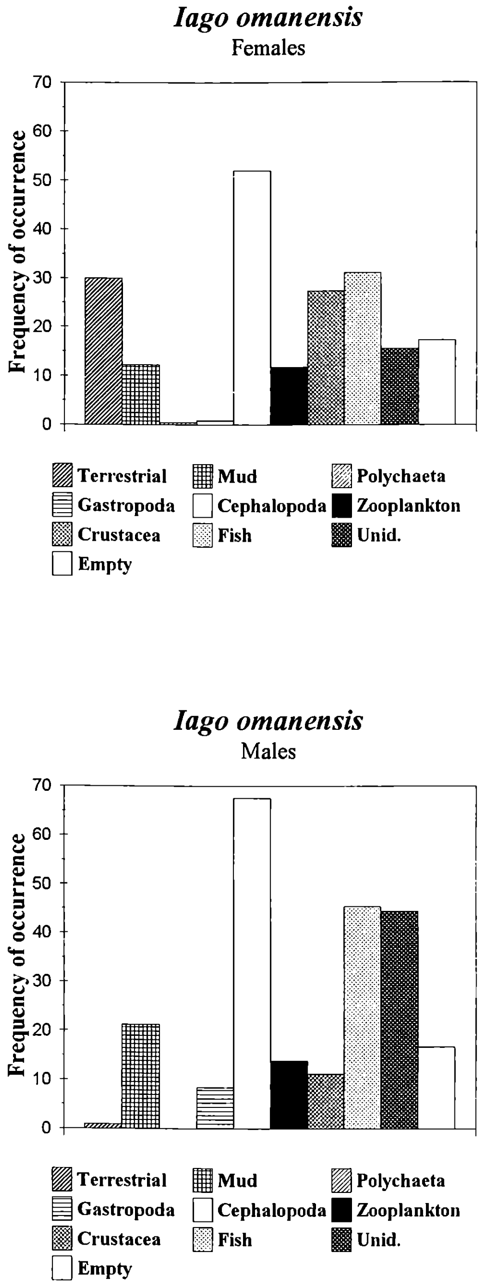
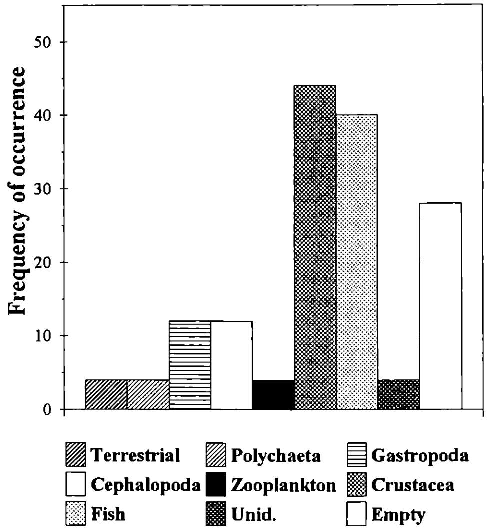


Fig. 6A: Stomach content of females and males in *I. omanensis*

Argyrops spinifer



Polysteganus coeruleopunctatus

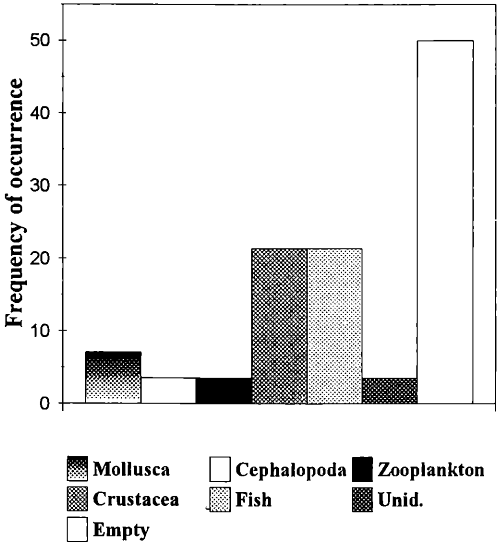


Fig. 6B: Stomach content of *A. spinifer* and *P. coeruleopunctatus*

Tab. 5: $\delta^{13}C$ Values of 11 common fish species collected between 150-1500 m.

Species	Family	$\delta\,^{13}C$ ‰ average
Upeneus subvittatus	MULLIDAE	-17 74
T. modestoides erythraeensis	MONACANTHIDAE	-17.38
Paracaesio sordidus	LUTJANIDAE	-17.23
Argyrops spinifer	SPARIDAE	-16.93
Mustelus mosis	TRIAKIDAE (שריר)	-16.75
Polysteganus coeruleopunctatus	SPARIDAE	-16.56
Iago omanensis	TRIAKIDAE	-16.47
Saurida tumbil	SYNODONTIDAE	-15.95
Epinephelus epistictus	SERRANIDAE	-15.69
Carcharinus plumbeus	CARCHARHINIDAE	-15.09
Muraenesox cinereus	MURAENESOCIDAE	-15.09

Tab. 6: $\delta^{13}C$ Values of invertebrates and organic matter collected.

Species	Sample	$\delta\,^{13}C$ ‰ average
mud	in fish stomach	-23.30
Terrestrial food	in fish stomach	-20.85
Sediment	at 250 and 550m. depth	-20.60
mud	in fish stomach	-19.50
Enigmoteuthis dubia	MOLLUSCA, Cephalopoda	-18.61
Gorgonia sp.	COELENTERATA, Gorgonacea	-17.69
Parapandalus narval	CRUSTACEA, Pandalidae	-17.42
Zooplankton	in fish stomach	-17.20
Parapandalus serratifrons	CRUSTACEA, Pandalidae	-17.03
Astropecten sp.	ECHINODERMATA Asteroidea	-16.85
Leucosia signata	CRUSTACEA, Leucosiidae	-16.76
Charybdis acutidens	CRUSTACEA, Portunidae	-16.20
Octopus	CEPHALOPODA, Octopoda	-15.84

The $\delta^{13}C$ values for fishes ranged from -15.09 ‰ to -17.74 ‰. The heaviest value, -15.09 ‰ was found in *Muraenesox cinereus* and *Carcharhinus plumbeus*; the lightest value, -17.74 ‰ was found in *Upeneus subvittatus*.

The $\delta^{13}C$ values obtained at different depths for tissue from *P. coeruleopunctatus, Iago omanensis*, and *Argyrops spinifer* is presented in Tab. 7.

Analyses of $\delta^{13}C$ from invertebrates tissue and organic matter is shown in Tab. 6. These values range from -15.84 ‰ to -23.3 ‰. The heaviest value, -15.84 ‰, was found in an as yet unidentified octopus; the lightest, from -19.50 ‰ to -23.3 ‰ were noted in sediment, in mud, and in other unidentified organic matter found in the fish stomach contents.

Abiotic parameters

Fig. 7 shows the temperature profiles in the northern Red Sea, where the water column mixes almost every year; deep waters, however, have almost constant temperatures in the aphotic zone year around.

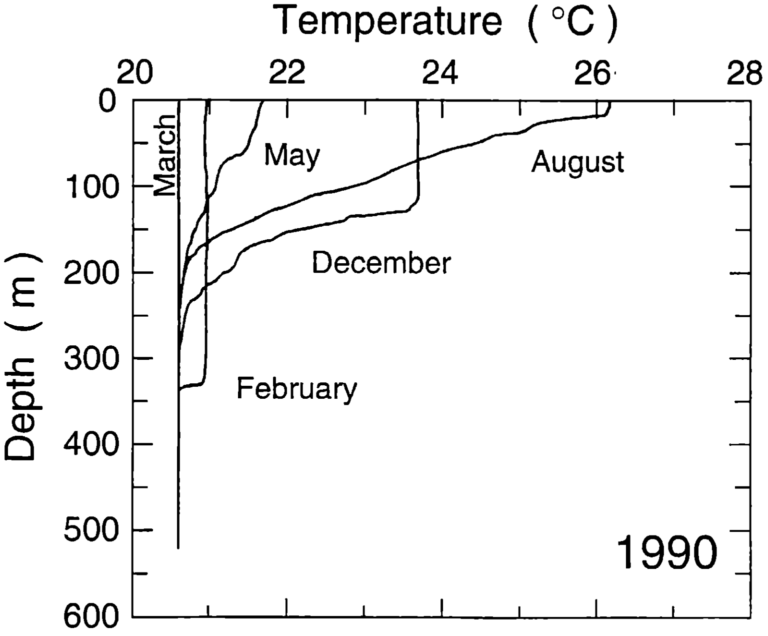


Fig. 7: Temperature profiles measured in different months of the year 1990 at station A1 in front of IUI, northern Gulf of Aqaba, Red Sea.

Fig. 8 shows that the limit of the photic zone (1 % light from the surface, -2.0 in log scale) is around 90 m; in years where massive phytoplankton blooms occur, it can be as shallow as 30 m.

Tab. 7: $\delta^{13}C$ values of three common fishes collected at different depths.

Species	$\delta^{13}C$	Depth	Average	S.D
Iago omanensis	-16.09	250	-16.09	-
	-16.26	350	-16.46	0.15
	-16.53			
	-16.60			
(embryo)	-15.34	450	-16.28	0.55
	-15.59			
(embryo)	-16.01			
	-16.37			
	-16.43			
	-16.75			
	-16.76			
	-17.00			
	-16.17	750	-16.73	0.33
(fin)	-16.84			
	-16.91			
	-16.99			
Polysteganus coeruleopunctatus	-16.72	150	-17.11	0.38
	-17.49			
	-15.52	400	-16.13	0.61
	-16.74			
	-16.34	750	-16.34	-
Argyrops spinifer	-16.51	150	-16.82	0.27
	-16.75			
	-16.75			
	-17.25			
	-17.13	350	-17.13	-
	-17.02	450	-17.08	0.06
	-17.13			

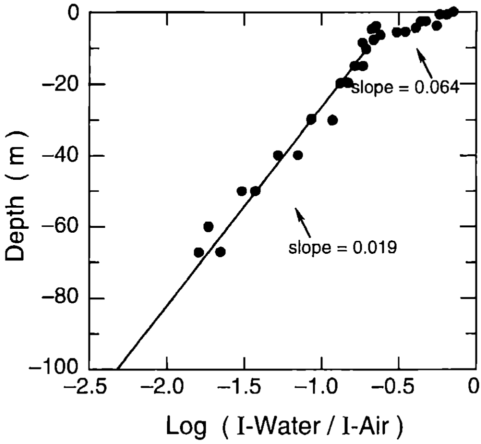


Fig. 8: Depth profile of the log of the fraction of the light intensity which reaches a certain depth as measured on 6 Oct. 1991 in front of IUI, northern Gulf of Aqaba, Red Sea.

The oxygen concentration (Fig. 9) during most of the year is almost constant in the aphotic zone and is not much lower than in surface waters.

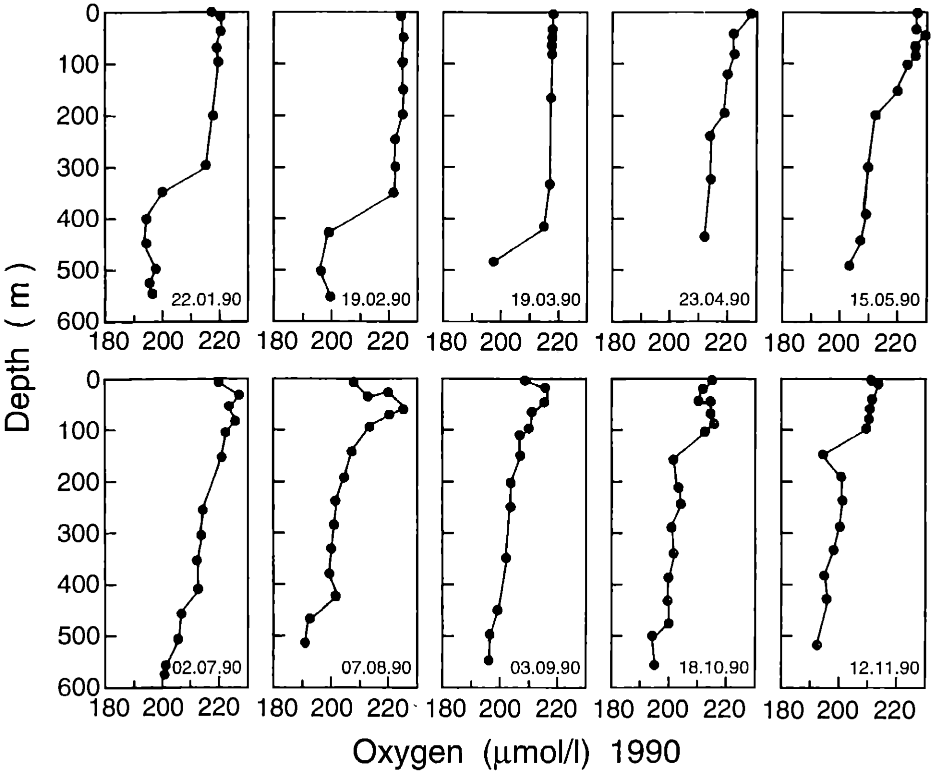


Fig. 9: Oxygen profiles measured in different months of the year 1990 at station A1 in front of IUI, northern Gulf of Aqaba, Red Sea.

Discussion

Almost all the fish species collected are of shallow-water origin, and their distribution in the Gulf of Aqaba is much deeper than was previously recorded from other localities.

GOREN (1993) pointed out that only 1.67 % of the Red Sea fauna are deep-sea fishes, compared with 11.75 % off South Africa and 10.6 % in the Mediterranean . The fish species usually inhabiting the deep sea show morphological adaptations to the biotope (SUMICH 1988, NYBAKKEN 1988) such as color pattern, photophores, large eyes, and peculiar development of the sensitive cells of the lateral line. GAGE and TYLER (1992) showed that species of the family Moridae have numerous, small, pointed teeth and a large number of gill rakers which allow them to feed on a large variety of prey. None of these adaptations have been found in the deep-sea ichthyofauna of the Red Sea.

Most of the mature *Iago omanensis* males were found in the deeper waters of the Red Sea (1100-1500 m), and most of the pregnant females between 350 and 500 m. It should be pointed out that the deeper waters of the Red Sea are in the southern part of the Gulf of Aqaba and the middle trench of the Red Sea proper. We may assume bathymetric and horizontal segregation in sexes in *Iago omanensis.*

A bathymetric segregation by size was found in *Rhynchoconger trewavasae, Mustelus mosis, Gymnothorax johnsoni*, and *Upeneus subvittatus.* Such segregation reduces intraspecific competition for food. The bathymetric distribution of the other species collected (*Polysteganus coeruleopunctatus, Atrobucca geniae, Thamnaconus modestoides erythraeenesis, Pterygotrigla sp., Saurida tumbil*, and *Muraenesox cinereus*) is apparently size-independent.

Bathymetric separation between species showing similar feeding habits reduces interspecific competition. Such separations have been found in *Iago omanensis* (range 150-1500 m) and *Mustelus mosis* (100-200 m); in the two sparids, *Argyrops spinifer* and *Polysteganus caeruleopunctatus*, there is an overlap in the range of the habitat, although *Argyrops* is much more common at 150-450 m and *Polysteganus* prefers deeper water.

The major, immediately available food source in the Gulf of Aqaba's aphotic zone is composed of organisms which migrate between the aphotic and the photic zone, either in the course of their growth or in the form of daily or seasonal migration. Plankton and micronekton show high biomasses near the deep-sea bottom and are consumed by the benthic mega- and macrofauna

(ZENKEVICH and BIRSTEIN 1956, MERRETT 1987). Another source of food is the dead organisms that sink from the photic zone.

A second category of food is those items which are not immediately available. These include the remains of animals and plants which - before becoming accessible - are recycled by bacteria and other benthic microorganisms. Such items are chitin (from crustacean shells), cellulose (of terrestrial origin or from phytoplankton blooms and algae), and organic matter which slides down the slope. THIEL (1979) observed "mudfloats" comprised of mud, blue-green algae, insects, as well as parts of shellfish and other molluscs. These structures measure approximately 40 cm^2. THIEL assumed that these floating "bodies" will ultimately sink and that the incorporated organic matter will become food for organisms in the deep sea.

The stomach content analyses of the common fish species show that fishes, crustaceans (crabs), and cephalopods are the main food. Fish remains were found in the stomachs of 7 species (88 %), crustaceans in 6 species (75 %), and cephalopods in 5 species (63 %). The presence of fishes and pelagic cephalopods, along with benthic crustaceans, points to benthopelagic feeding habits. We also determined an absence of "dominant" food in the diet of *Polysteganus caeruleopunctatus*, *Argyrops spinifer*, *Mustelus mosis*, *Iago omanensis*, *Upeneus subvittatus*, and *Saurida tumbil*, in which we found both pelagic and benthic food (crustaceans, nudibranchs, worms) as well as terrestrial food.

The stomachs of *Atrobucca geniae* and *Muraenesox cinereus* contained only pelagic fishes. GOLANI and BEN TUVIA (1982) stated that *M. cinereus* feed mainly on decapods in the Mediterranean Sea.

Although invertebrates were not intentionally collected, their frequent occurrence in the stomach contents shows that they are certainly an important component in the diet of most of the deep-sea fishes. Observations from a submarine dive at 400 m depth support this assumption (BARANES and GOLANI 1993, BARANES unpubl. data).

DAYTON and HESSLER (1972) noted that the best feeding strategy for deep-sea fishes (where food is rare) is the generalist approach, i.e., all available food is taken. Some species also feed on terrestrial food and dead organisms from the photic zone, in addition to their predatory habits, and therefore may be considered as omnivores (e.g., *Iago omanensis*).

Based on our results, we generated a model of the food web of the aphotic zone in which *Iago omanensis* is the top predator at the peak of the pyramid (Fig.10). At the base of the food chain are decomposers which feed on organic matter in the sediment, on terrestrial food, and on bodies of dead organisms or algae from the photic zone. The intermediate levels are represented by benthic and pelagic organisms. The level in which fishes are placed depends on their occurrence in the stomach contents and on their respective size. The "small fishes" such as the Astronesthidae, Gonostomatidae, and Myctophidae are found at this level. *Vinciguerria lucetia* and *Astronesthes martensii* were common in the stomachs of *Iago omanensis* and *Saurida tumbil.* The position of Echinodermata and Decapoda in the food chain is based on their occurrence in the stomach contents. There were no remains identified as *Iago omanensis* in the stomachs of other sharks (e.g., *Carcharhinus plumbeus, Galeocerdo cuvier*) or in *Muraenesox cinereus.*

The $\delta^{13}C$ values in the most common fishes of the aphotic zone range between -17.74 and -15.09 ‰. These values are within ± 1 ‰ of those measured in the invertebrates of the aphotic zone (-15.84 to -18.61 ‰); we may thus assume that the fishes feed on invertebrates.

For fishes, the ranges of $\delta^{13}C$ may be separated into three levels: 1) heavy values (-15.95 to -15.09 ‰); 2) intermediate values (-16.93 to -16.47 ‰); and 3) light values (-17.74 to -17.23 ‰). LORIAN (1991) showed that the first level characterizes the composition of the carbon in omnivores, open-water predators, and predators from the deep sea. Accordingly, three groups can be distinguished: (1) the predators *Epinephelus epistictus* and *Saurida tumbil;* (2) the omnivores such as *Iago omanensis;* (3) *Upeneus subvittatus, Argyrops spinifer*, and *T. modestoides erythraeensis.*

With respect to the diet selection of invertebrates we assume that the "heavy" consumers feed on remains of dead organisms in the benthos and on organic matter sinking down from the upper water layer. "Light" consumers feed on remains of plankton and fecal pellets from the photic zone, which reach the benthos as marine snow. The cephalopod *Enigmoteuthis dubia* ($\delta^{13}C$: -18.61 ‰) feed mainly on plankton and small fishes (plankton feeders) which migrate vertically between the photic and aphotic zone.

The intraspecific comparison of δ^{13} C values from specimens collected at different depths shows no change in diet dependent on the bathymetric distribution.

In *Iago omanensis*, the results of the stomach content analysis deviate from those of the $\delta^{13}C$ analysis. The stomachs contained approximately 30 % terrestrial food, an amount that could indicate a "food value" (WALLER and BARANES 1994). However, the $\delta^{13}C$ analysis revealed a clear dominance of fishes and invertebrates in the diet. Based on these findings we assume that the stomachs of *Iago omanensis* contain items that are not digested and do not enter the tissue as C values. This assumption agrees with earlier data (WALLER and BARANES 1994) suggesting that the mud found in the *Iago omanensis* stomachs plays the role of a "buffer" and has no dietary value.

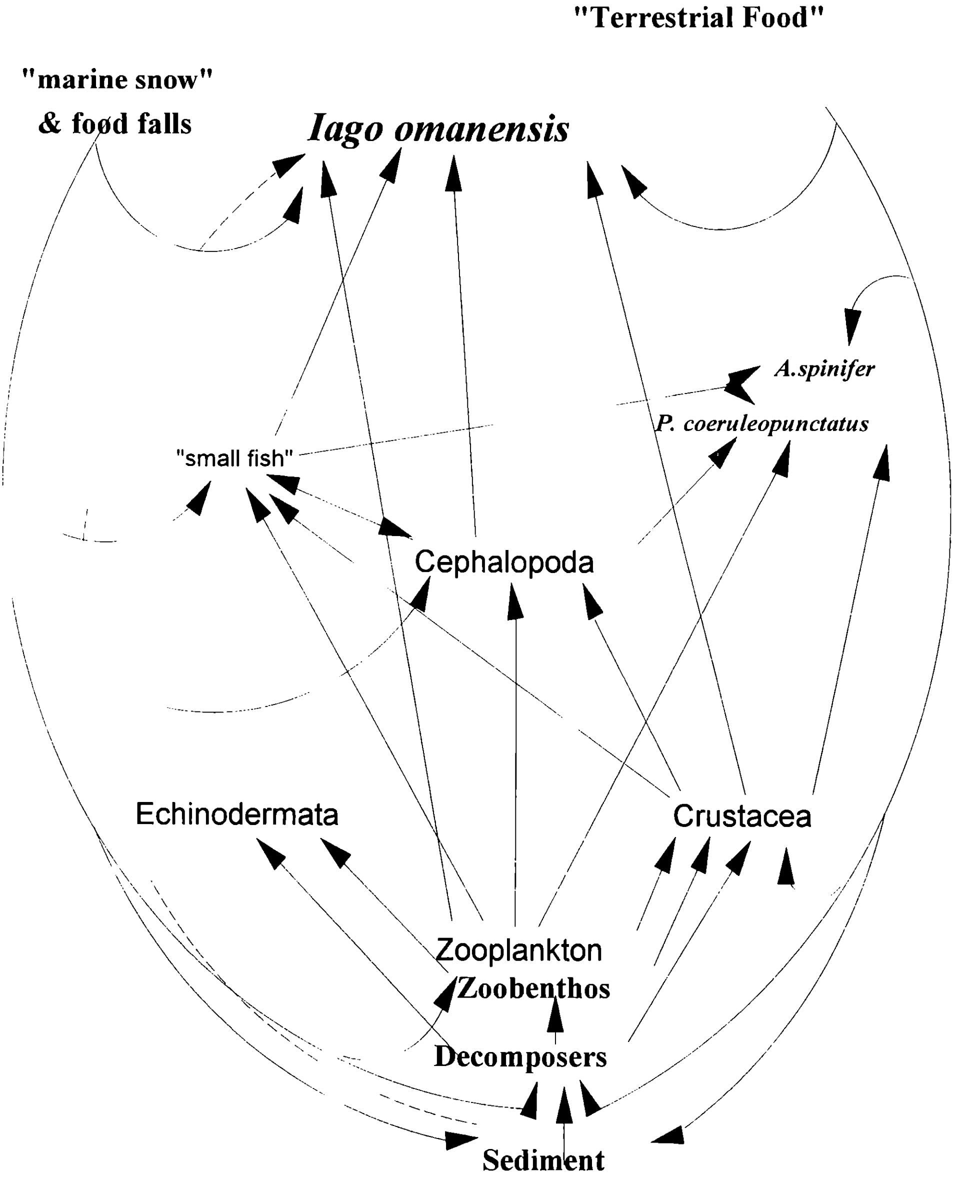


Fig. 10: A food web model based on stomach content analysis

The $\delta^{13}C$ analyses were used to model the food web in the aphotic zone (Fig. 11). Fishes feeding on fish and invertebrate prey show the heaviest $\delta^{13}C$ values (-15.95 to 15.09 ‰) and are on the highest trophic level ("6" in Fig. 11). The omnivores, with intermediate $\delta^{13}C$ values (-16.93 to -16.47 ‰), are on the intermediate trophic level ("5" in Fig. 11). The benthivorous fish are set in level 3, the invertebrate decomposers in level 2, and the benthivorous invertebrates with light $\delta^{13}C$ values (-18.61 to -17.23 ‰) in the lowest trophic level ("1" in Fig. 11). The deep-sea octopus ($\delta^{13}C$: -15.84 ‰) is set in trophic level 4 in Fig. 11.

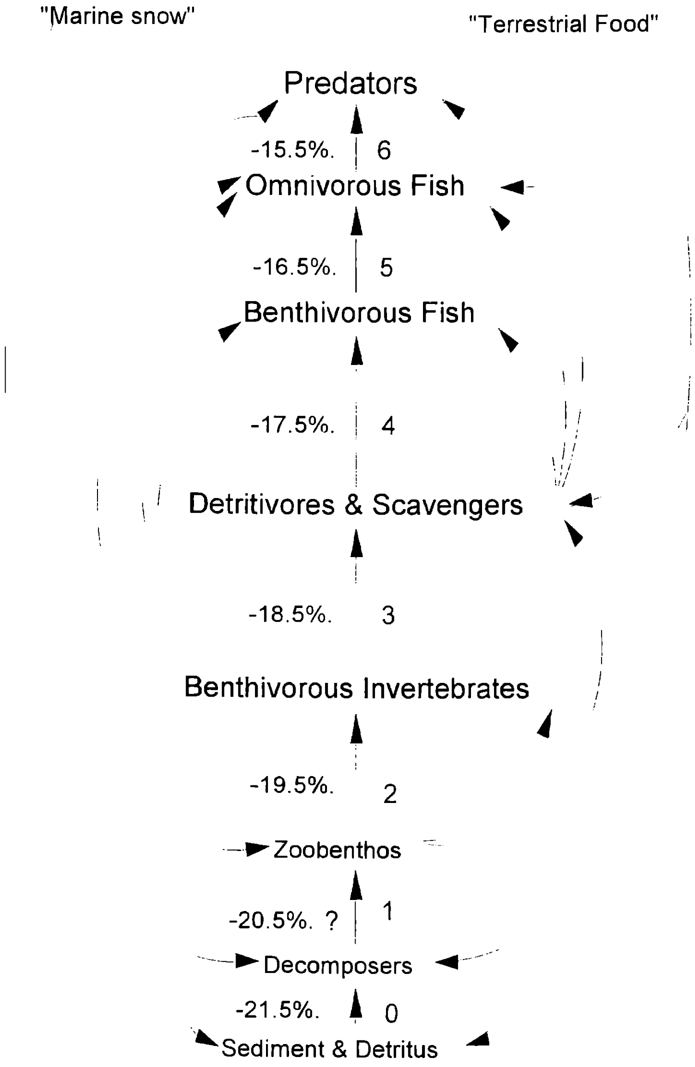


Fig. 11: Model of the food web in the aphotic zone of the Gulf of Aqaba. For further explanations see text.

The large arrows show the direction of carbon flow from the "donor" to the "receiver", and the difference in $\delta^{13}C$ values between donor and receiver are approximately 1-2 ‰.

The lowest trophic level ($\delta^{13}C$ values of -21.5 ‰) is found in the sediment. We assume that the origin of the organic matter in the sediment is from the upper water layers (open sea and the coral reef). This organic matter is used as food by the decomposers in the sediment and by the organisms feeding on the decomposers near the sediment. This group is considered to be the link between the organic matter and the benthivorous invertebrates.

The highest trophic level, comprising *Muraenesox cinereus* and *Carcharhinus plumbeus,* is above that of *Iago omanensis,* indicating that the former two species feed on the *Iago* population.

Conclusions

The combination of two methods to investigate fish food selection has allowed us to better understand the trophic relationships among organisms in the aphotic zone of the Gulf of Aqaba. The method more commonly used, i.e., the analysis of stomach contents, has led to the taxonomic identification of food items consumed. However, this method did not allow an accurate picture of quantitative food selection, nor did it give way to the assumption that all items found in the stomach are of "food value". In contrast, the $\delta^{13}C$ analysis clearly established the chain between donors and receivers of carbon. We believe that both methods compliment each other and that research on the food web should utilize both concurrently.

The circulation pattern of the water in the Red Sea, together with an almost hermetic seal (Bab el Mandeb), prohibits the penetration of primary deep-sea fishes into the Red Sea. Those fishes from the crowded coral reef habitat that are also found in the deep waters of the Red Sea have similar conditions as in the surface layers: high temperature and similar oxygen concentrations. Despite lacking the morphological adaptations of typical deep-sea fishes (BARANES and GOLANI 1993) and often retaining color patterns (lure and camouflage) typical for reef fishes, these species seem to have found a suitable habitat in the aphotic zone of the Red Sea.

Although foraging success has been shown to primarily depend on light intensity and then on depth of feeding (MCMAHON and HOLANOV 1995), food availability is certainly an important precondition of vertical habitat selection in the deep sea.

In the areas under investigation, food reaches the benthic zone fast enough and in sufficient quantity to sustain a well-developed ichthyofauna. Furthermore, as shown by the *Epinephelus epistictus* specimens caught in deep water, the fishes are much larger than those collected in the reef habitat (BARANES and GOLANI 1993). We may also assume that intra- and interspecific competition is less important in the aphotic zone, and that the amount of food there is sufficient to allow the growth and reproduction of these "new" deep-sea inhabitants.

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