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Constraints and exploratory windows in light-reduced marine habitats

F. UIBLEIN

Abstract: Adaptive responses to reduced light conditions in deep-sea organisms may be reflected by differentiation patterns accomplished in the evolutionary past or by ongoing processes of niche expansion. Recent studies on depth distribution and intraspecific morphological differentiation in secondary deep-sea fishes living in the Red Sea and adjacent areas of the Indian Ocean have provided novel insights into the possible mechanisms involved in the colonization of deeper, less illuminated zones. This paper briefly reviews these results and presents new comparative data of the trachichthyid fish *Hoplostethus mediterraneus*. This species shows a wide geographical distribution, with the Red Sea specimens being to some extent morphologically differentiated from those of other areas in the Atlantic, the Mediterranean, and the Indo-Pacific. In the Red Sea, *H. mediterraneus* occupies a depth range of between 365 and 1175 m and thus also occurs at levels beyond the estimated absolute depth-limit for perception of atmospheric light. In contrast to the bythitid *Oligopus robustus*, however, *H. mediterraneus* from below 1000 m depth do not show a reduced eye-size, and hence the possibility that these specimens still use light as an informational source cannot be excluded. On the other hand, the ophidiid *Neobythites stefanovi*, with an ocellus on the dorsal fin that may serve as an antipredator signal, is restricted to shallower depth zones above ca. 800 m. An upwards directed migration of this species during ontogeny indicates that this visual signalling structure may have functional significance only at more illuminated depths. Based on these results, it is concluded that each of the three fish species studied interact with the light level and other depth-related factors in a conservative, species-specific, as well as in a dynamic, highly exploratory manner.

Introduction

Animals living in deep-sea habitats or in deep marine caves reflect a great variety of adaptive responses to reduced light conditions. In this respect, patterns of differentiation accomplished in the evolutionary past, such as particularly large eyes, light organs, organs for sound production, or well-developed extra-optical sensory systems, can be distinguished from ongoing processes of niche expansion, such as migrations along illumination gradients, active colonization of dark zones, intraspecific morphological differentiation among populations from illuminated and adjacent dark areas, and accompanying behavioural shifts.

The deep Red Sea provides an environment of particular interest to study processes of niche expansion and intraspecific differentiation connected to depth-related variations in light level and associated factors. One important feature of the deep Red Sea is the exceptionally high temperature of about 21.5 °C from 200 m downwards to the bottom at more than 2000 m depth. This fact was revealed by measurements of water temperature performed during the two Austro-Hungarian expeditions with the sailing steamer S.M.S. "Pola" to the Red Sea (LUKSCH 1898, 1901). In major oceans such as the Atlantic or the Indian Ocean, temperature drops significantly to about 10 °C at 500 m and to less than 5 °C below 1500 m (EKMAN 1953).

Recent studies on deep-sea fishes of the Red Sea collected during the German MESEDA and "Meteor" 5 expeditions (KLAUSEWITZ 1986, KRUPP 1987, NIELSEN and UIBLEIN 1993, KLAUSEWITZ and UIBLEIN 1994) have confirmed the earlier conclusions of BALSS (1931) and others based on deep-sea material collected by the "Pola" expeditions. BALSS stated that due to the specific temperature conditions, an ancient, cold-water adapted deep-sea fauna is absent in the Red Sea and that species originating from shallow waters or their close relatives have colonized the deeper zones. Accordingly, fishes from nine different families that occur in the Indian Ocean at shallower levels have expanded their bathymetric distribution in the Red Sea (Tab. 1). Six of these typical secondary deep-sea fishes (cf. the definition given by ANDRIASHEV 1953) have been discovered in the Red Sea at depths greater than 1000 m, beyond the estimated absolute depth limit for vision in clear oceanic waters (CLARKE and DENTON 1961, DENTON 1990). The recently discovered ophidiid species *Neobythites stefanovi* NIELSEN and UIBLEIN 1993 (Fig.1) is restricted in its distribution to the more illuminated zones above 800 m, whereas the bythitid *Oligopus robustus* (SMITH and RADCLIFFE 1913) and the trachichthyid *Hoplostethus mediterraneus* CUVIER 1829 (Fig.1) have invaded depths greater than 1100 m.

Recent investigations on depth-related, intraspecific morphological variation in *N. stefanovi* and *O. robustus* from the Red Sea and the adjacent Gulf of Aden have provided novel insights into the possible mechanisms involved in processes of active niche expansion and morphological differentiation along illumination gradients (UIBLEIN et al. 1994a, KLAUSEWITZ and UIBLEIN 1994, UIBLEIN 1995). Here, these results shall be shortly reviewed and compared with new data on the depth distribution and intraspecific morphological differentiation of the trachichthyid fish *H. mediterraneus*. This species was first discovered in the Red Sea during the second "Pola" expedition in 1898 (POTT 1899, FUCHS 1901). Nearly 80 years later this species was collected again during the three MESEDA expeditions (KLAUSEWITZ 1986).

In 1987, the more recent "Meteor"-5 expedition also succeeded in catching several *H. mediterraneus* at eight different trawling stations in the central Red Sea. To gain information on the taxonomic status of the Red Sea specimens, this new material and specimens available from earlier collections were examined for possible geographical variations in morphometric and meristic characters.

Tab. 1: Depth distribution of nine fish species occurring in the Indian Ocean and the Red Sea. Data are from KLAUSEWITZ (1986), KRUPP (1987), NIELSEN and UIBLEIN (1993), KLAUSEWITZ and UIBLEIN (1994), and WOODS and SONODA (1973) *

Species	Indian Ocean	Red Sea
Iago omanensis (Carcharhinidae)	100 - 400 m	300 - 1650 m
Bembrops adenensis (Percophididae)	180 - 220 m	360 - 590 m
Harpadon erythraeus (Harpadontidae)	400 - 500 m	800 - 1150 m
Champsodon omanensis (Champsodontidae)	130 - 375 m	30 - 1100 m
Muraenesox cinereus (Muraenesocidae)	< 100 m	< 740 m
Cynoglossus acutirostris (Cynoglossidae)	220 m	740 - 1425 m
Neobythites stefanovi (Ophidiidae)	80 - 549 m	434 - 804 m
Oligopus robustus (Bythitidae)	50 - 549 m	363 - 1258 m
Hoplostethus mediterraneus (Trachichthyidae)	265 - 787 m *	365 - 1175 m

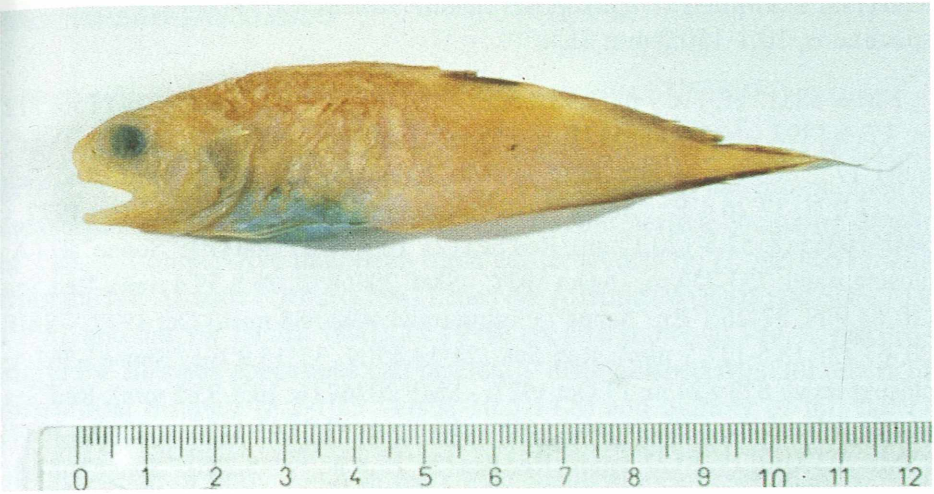
Materials and Methods

A total of 148 specimens of *Hoplostethus mediterraneus* from the Red Sea, with standard lengths between 10.1 and 150.2 mm, were available for examination at the fish collections of the Research Institute Senckenberg, Frankfurt, and the Natural History Museum Vienna. Material from the Mediterranean and from the NE Atlantic was also studied. A complete list of the material examined is given below. From a total of 40 specimens from the three different geographical areas, measurements of ten morphometric characters were obtained using an electronic caliper. In addition, counts of nine meristic characters were carried out.

During the three MESEDA expeditions with the research vessels "Sonne" and "Valdivia" and during the "Meteor"-5 expedition, trawl-hauls were taken at a total of 54 stations in the northern and the central Red Sea (UIBLEIN et al. 1994a). The MESEDA expeditions used a closing trawl, the "Meteor"-5 expedition a beam trawl. Both trawls were equipped with fine-meshed cod ends, the minimum mesh size being 8-10 mm. For analysis of depth distribution, the mid-depth of each trawling station was calculated from the depth ranges covered by the respective haul.

In a preliminary statistical examination of the Red Sea specimens of *H. mediterraneus*, in contrast to the earlier studies on *Neobythites stefanovi* and *Oligopus robustus* (cf. UIBLEIN et al. 1994a), no significant relationships between depth and any morphometric or meristic characters could be detected. To test the hypothesis that eye size in *H. mediterraneus* from zones beyond the estimated limit for vision of solar light is reduced (UIBLEIN et al. 1994a), orbit length measures of 10 specimens (20.6-127.3 mm SL) from below 1000 m and of 54 specimens (18.6-150.2 mm SL) from shallower zones were compared. To achieve proper size-adjustment, a log-log regression between the orbit length measures and SL was performed (REIST 1985). The regression was highly significant ($p<0.00001$) and strongly correlated ($r=0.99$). The residuals resulting from the regression function were then analysed for significant differences between the two bathymetric groups using one-way ANOVA. The residuals obtained from orbit length measures of 18 *Oligopus robustus* (ten from more than 1000 m and eight from lesser depths; cf. UIBLEIN et al. 1994a) were also examined.

Fig. 1: *Neobythites stefanovi*, family Ophidiidae (SMF 26785, 111 mm SL; on top), *Oligopus robustus*, family Bythitidae (below), and *Hoplostethus mediterraneus*, family Trachichthyidae (bottom), all from the Red Sea.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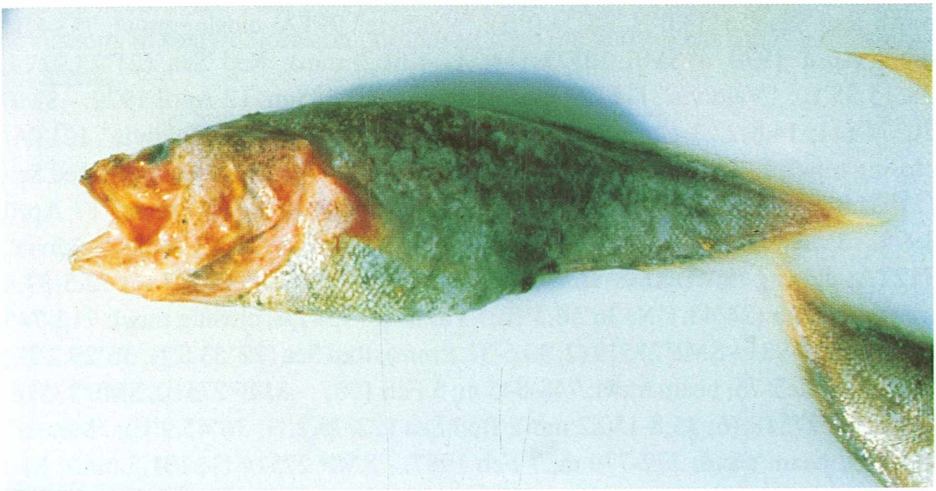

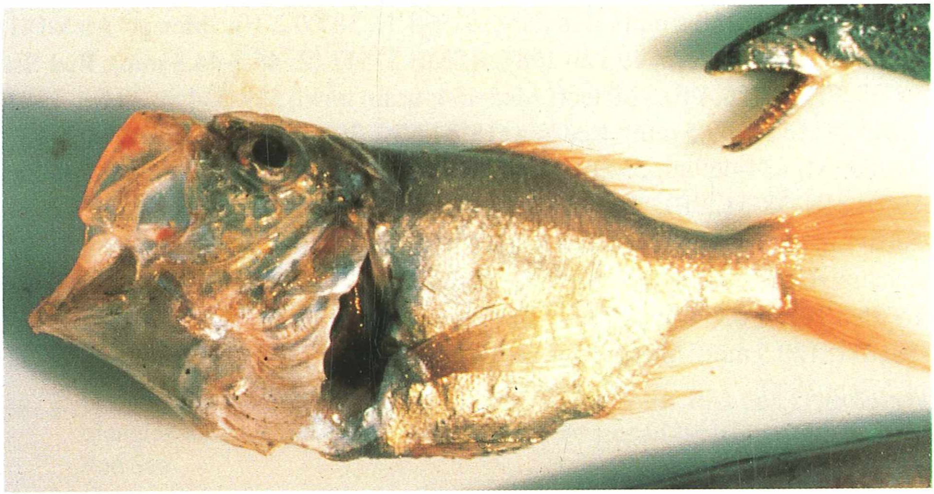

Material examined (*Hoplostethus mediterraneus* CUVIER 1829, total 153 specimens, 10.1-150.2 mm SL):

NMW 88812 (1; 116.7 mm); Red Sea (22°51'N, 38°2'E); "Pola"; trawl 156; 712 m; 4 Feb 1898. - NMW 88811 (1; 146.5 mm); Red Sea (26°75'N, 35°47'E); "Pola"; trawl 173; 868 m; 24 Feb 1898. SMF 20366 (4; 23.9-133.5 mm); Red Sea (21°12.0'N, 37°26.8'E); "Sonne" 25TA; closing trawl; 724-747 m; 15 Oct 1977. - SMF 20365 (8; 57.3-120.1 mm); Red Sea (21°10.8'N, 37°34.0'E); "Sonne" 27TA; closing trawl; 733-757 m; 16 Oct 1977. - SMF 20368 (5; 26.8-39.4 mm); Red Sea (20°54.9'N, 37°26.1'E); "Sonne"; closing trawl; 490-588 m; 17 Oct 1977. - SMF 20367 (3; 18.6-137.5 mm); Red Sea (21°14.45'N, 37°15.9'E); "Sonne" 36TA; closing trawl; 823-824 m; 17 Oct 1977. - SMF 20369 (6; 20.4-33.5 mm); Red Sea (21°25.2'N, 37°45.2'E); "Sonne" 66TA; closing trawl; 1043-1135 m; 23 Oct 1977. - SMF 20370 (7; 19.2-127.3 mm); Red Sea (21°25.8'N, 37°45.2'E); "Sonne" 68TA; closing trawl; 1051-1134 m; 24 Oct 1977. - SMF 20371, SMF 20372 (37; 13.7-108.3 mm); Red Sea (21°33.0'N, 38°21.0'E); "Valdivia" 99TA; closing trawl; 753-804 m; 9 April 1979. SMF 20373 (34; 11.4-61.3 mm); Red Sea (21°28.97'N, 38°15.55'E); "Valdivia" 111TA; closing trawl; 740-785 m; 12 April 1979. - SMF 20374 (11; 14.8-22.3 mm); Red Sea (21°26.5'N, 38°38.3'E); "Valdivia" 121TA; closing trawl; 779-801 m; 15 April 1979. - SMF 20375 (4; 12.7-16.6 mm); Red Sea (21°22.0'N, 39°04.0'E); "Valdivia" 122TA; closing trawl; 363-383 m; 17 April 1979. - SMF 20376 (6; 10.1-39.7 mm); Red Sea (21°17.2'N, 38°18.7'E); "Valdivia" 712TA; closing trawl; 1130-1175 m; 4 March 1981. - SMF 20377 (4; 12.5-87.8 mm); Red Sea (24°43.1'N, 36°56.2'E); "Valdivia" 734TA; closing trawl; 712-745 m; 7 March 1981.- SMF 27519 (2; 30.6-32.8 mm); Red Sea (22°53.8'N, 36°29.2'E); "Meteor" Me5-75; beam trawl; 748-845 m; 5 Feb 1987. - SMF 27510, SMF 27516, and SMF 27518 (6; 25.8-150.2 mm); Red Sea (22°35.2'N, 36°45.9'E); "Meteor" Me5-85; beam trawl; 772-779 m; 7 Feb 1987. - SMF 27514 (1; 101.5 mm); Red Sea (22°08.4'N, 37°28.9'E); "Meteor" Me5-99; beam trawl; 827-863 m; 9 Feb 1987. - SMF 27513 (1; 110.4 mm); Red Sea (19°56.1'N, 38°09.2'E); "Meteor" Me5-141; beam trawl; 807-863 m; 19 Feb 1987. - SMF 27517 (2; 44.3-44.8 mm); Red Sea (19°33.3'N, 37°16.4'E); "Meteor" Me5-154; beam trawl; 519-544 m; 20 Feb 1987. - SMF 27515 (1; 69.5 mm); Red Sea (18°34.5'N, 39°02.4'E); "Meteor" Me5-171; beam trawl; 434-469 m; 23 Feb 1987. - SMF 27512 (4; 47.7-116.2 mm); Red Sea (19°24.3'N, 38°31.2'E); "Meteor" Me5-193; beam trawl; 696-705 m; 28 Feb 1987. - SMF 27511 (1; 110.9 mm); Red Sea (19°18.2'N, 38°15.5'E); "Meteor" Me5-194; beam trawl; 681-537 m; 28 Feb 1987. - SMF 13316 (4; 70.4-135.4 mm); NE Atlantic (25°25.0'N, 16°0.9'W); "Meteor"-36; beam trawl; 337 m; March 1977. - NMW 55018 (1; 120.9 mm); Mediterranean (32°46.4'N, 19°58.3'E); "Pola", trawl 36; 600 m; 2 Sept 1890.

Results and Discussion

Geographical differentiation among *Hoplostethus* CUVIER

A photograph of *Hoplostethus mediterraneus* from the Red Sea is shown in Fig. 1, a distribution map in Fig. 2. The ranges of the morphometric measures expressed in % of SL and the ranges of the meristic counts are shown in Tab. 2. Comparative data from three earlier studies on *H. mediterraneus* from the NE Atlantic (QUERO 1982), the NW Atlantic (WOODS and SONODA 1973), and the SW Pacific (PAULIN 1979) are also shown in Tab. 2. Accordingly, the Red Sea specimens can be clearly distinguished from all others in interorbital distance (8.5-10.3 versus 10.5-14.8) and number of gill rakers (18-20 [11-14/1/5-7] versus 21-26 [14-17/1/5-8]). In all other characters, with the exception of body depth in the single Mediterranean specimen, a clear overlap occurs (see Tab. 2). The Red Sea specimens did not show any notable deviations in body coloration compared with those from the other geographical areas.

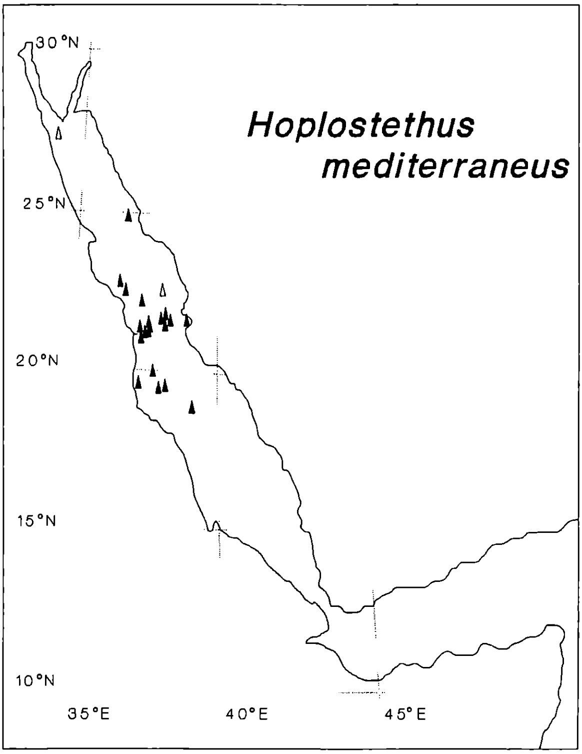

Fig. 2: Geographical distribution of *H. mediterraneus* in the Red Sea. The hollow triangles mark the two collecting stations of the second "Pola" expedition to the Red Sea.

Tab. 2: Comparison of 10 morphometric characters (in % SL) and of 9 meristic characters among *Hoplostethus mediterraneus* from the Red Sea (RS) and other areas (M...Mediterranean, NEA...NE Atlantic, NWA...NW Atlantic, SWP...SW Pacific). The comparative data shown are from QUERO (1982)[1], WOODS and SONODA (1973)[2], and PAULIN (1979)[3].

	RS	M	NEA	NEA [1]	NWA [2]	SWP [3]
Standard length	39.4-150.1	120.9	70.4-135.4	90.0-234.5	43.2-183.0	31.0-137.2
Morphometric characters						
Body depth	45.3-53.2	44.1	45.3-47.8	42.3-52.9	43.9-49.0	42.9-49.6
Caudal peduncle depth	10.0-13.4	10.6	11.2-11.7	11.0-13.1	10.7-13.2	11.1-13.4
Head length	37.9-44.7	38.9	38.4-40.8	36.7-40.8	37.0-43.0	36.7-40.5
Snout length	8.8-15.1	8.9	8.1-8.6	6.9-10.4	6.95-10.2	7.8-10.9
Orbit length	10.5-14.3	14.2	12.0-14.4	12.1-15.1	13.5-16.1	14.2-15.9
Interobital distance	8.5-10.3	11.8	10.5-11.0	10.4-14.8	11.2-14.6	11.3-13.2
Upper jaw length	24.0-31.4	26.7	25.2-28.2	24.3-28	23.1-28.7	
Caudal peduncle length	14.9-22.6	20.7	19.4-23.1		20.0-25.5	
Pectoral length	23.8-35.5	31.9	35.2-39.2	31-40	32.2-58.5	
Ventral length	16.8-28.4	21.2	21.1-27.5	21.9-27.4	19.0-25.2	
Meristic characters						
Dorsal spines	V-VII	VII	VI	V-VII	VI	VI
Dorsal rays	12-14	13	14	12-14	13	12-13
Pectoral rays	14-16	15	15	14-16	14-16	14-16
Ventral rays	I, 6	I, 6	I, 6	I, 6	I, 6	I, 6
Anal spines	II-III	III	III	III	III	III
Anal rays	9-11	11	10-11	10-11	10	9-10
Scutes	9-11	10	9-10	8-12	9-10	9-10
Gill rakers	18-20	22	22-23	21-25	23-26	22-24
Lateral line scales	27-29		27	26-29	28-29	28-30

These results indicate that *H. mediterraneus* from the Red Sea has undergone considerable differentiation and may represent a separate taxon, as also indicated in a recent systematic approach by KOTLYAR (1986), who described a new species, *H. marisrubri*, for the Red Sea. In order to arrive at a definitive conclusion on the taxonomic status of the Red Sea specimens examined in the present study, a thorough comparison with material from the Indian Ocean and the South Atlantic (see also SMITH and HEEMSTRA 1986) and with the specimens examined by KOTLYAR (1986) will be necessary. In this respect, it may be of particular importance to investigate the amount of overall morphological variability among specimens living in ecologically differing, adjacent areas such as the deep Red Sea and the deep sea of the Gulf of Aden (KLAUSEWITZ and UIBLEIN 1994, UIBLEIN 1995). QUERO (1982), for instance, reported pronounced differences in the number of gill rakers among *H. mediterraneus* populations from the NW and NE Atlantic.

In *Hoplostethus atlanticus* COLLETT 1889, a close relative of *H. mediterraneus*, significant variations in morphometric and meristic characters among populations from different geographical areas of the SW Pacific have been found (HADDON and WILLIS 1995). Whether these differences are genetically based is a question still under discusssion (ELLIOTT and WARD 1992, SMOLENSKI et al. 1993, ELLIOTT et al. 1995, HADDON and WILLIS 1995). In an electrophoretic comparison of *H. atlanticus* populations from the SW Pacific and the North Atlantic, no marked genetic differentiation could be detected and the possibility of ongoing gene flow or "gene hopping" over a distance as great as 21 000 km was ruled out (SMITH 1986). Studies on DNA variation also suggest some gene flow between these populations (ELLIOTT et al.1994).

Depth distribution and population structure in Red Sea *H. mediterraneus*

Twenty of the total fifty-four trawl-hauls carried out during the MESEDA and "Meteor"-5 expeditions to the Red Sea contained *H. mediterraneus* specimens (Fig. 3). This species occurred at particularly high frequencies between 600 and 900 m, with specimens captured at 12 of the 15 trawling stations in this depth zone. Two trawls from mid-depths of 762.5 and 778.5 m contained 34 and 37 individuals, respectively, which indicates a particularly high population density. At these depths, *H. mediterraneus* may be one of the dominant fishes. Below 1000 m, *H. mediterraneus* seems to be distributed more sparsely. While *Oligopus robustus* (Fig. 1) occurred at six of ten trawling stations in depths between 1000 and 1300 m (see UIBLEIN et al. 1994a), *H. mediterraneus* was captured only by three trawl-hauls, each containing between six and seven specimens.

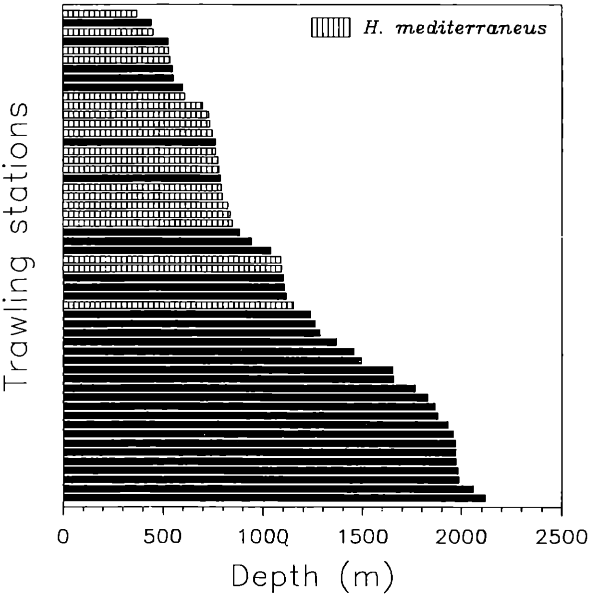

Fig. 3: Mid-depth distribution of the 54 trawl-hauls carried out by the three MESEDA and the "Meteor"-5 expeditions. Trawling stations containing *Hoplostethus mediterraneus* are indicated.

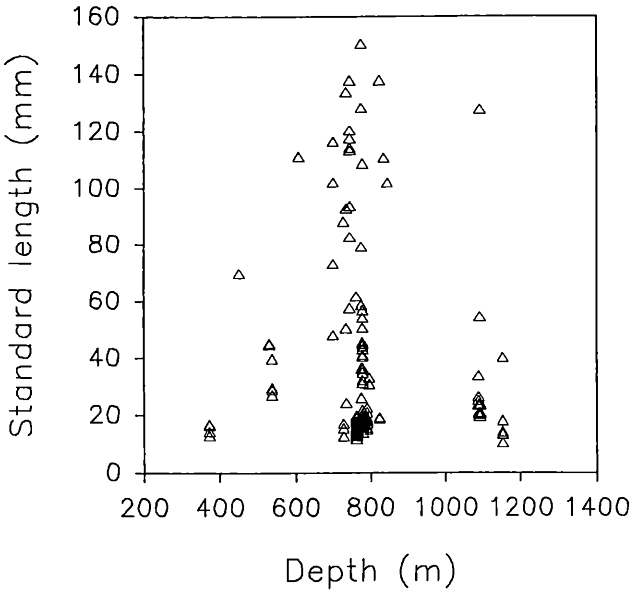

Fig. 4: Standard length against depth distribution in *Hoplostethus mediterraneus* of the Red Sea.

The proportion of small *H. mediterraneus* in the samples was exceptionally high. Of the 146 specimens collected during the MESEDA and "Meteor"-5 expeditions, 77 were smaller than 20 mm SL and only 15 were larger than 100 mm SL (Fig. 4). A similar size distribution pattern was reported by MERRETT and MARSHALL (1981) based on 430 *H. mediterraneus* from epibenthic samples collected in 279-981 m depth in the Atlantic off NW Africa. However, from these data alone it may be difficult to draw any definite conclusions on the population structure, because adults may not live so close to the bottom or may escape trawls more often than juveniles. As has been reported for *H. atlanticus*, the juvenile period in this particularly long-lived fish species is rather long, growth proceeds slowly, and maturity is not reached before about 30 years of age (MACE et al. 1990, FENTON et al. 1991). Adults may live to an age of 150 years (FENTON et al. 1991). No comparative data on the growth and age structure of *H. mediterraneus* are currently available.

Niche expansion along illumination gradients

In *H. mediterraneus*, as in *Oligopus robustus* (cf. UIBLEIN et al. 1994a), both juveniles and adults occur at depths of more than 1000 m (Fig. 4). Among *H. mediterraneus*, no significant variations in orbit length between bathymetric groups from zones beyond the estimated absolute depth limit of vision (1000 m, cf. DENTON 1990) and from more illuminated depths (<1000 m) could be discovered ($F(1,62)=2.2$, $p>0.1$; Fig. 5). In contrast, *O. robustus* specimens from depths below 1000 m show significantly smaller eyes ($F(1,16)=18.4$, $p<0.001$; Fig. 5). As has been shown earlier, the deeper living specimens also have smaller mouths and shorter pectoral fins (UIBLEIN et al. 1994a). Consequently, *O. robustus* may have undergone a shift in prey search mode from a visually guided, active pursuit of prey of a large size-spectrum at more illuminated, shallower depths to a non-visually oriented, less size-maximizing foraging style in deeper and darker zones (UIBLEIN et al. 1994a, KLAUSEWITZ and UIBLEIN 1994).

The absence of any significant differentiation in morphological characters among *H. mediterraneus* specimens from different depth zones indicates that this species has coped with the decreasing light intensity below 1000 m in a different way than *O. robustus*. All species belonging to the genus *Oligopus* have rather small eyes. They are equipped with a well-developed lateral line system and may show strong affinities to enter dark habitats (COHEN 1964). The closely related *Oligopus ater*, for instance, enters deep caves in the Mediterranean Sea (RIEDL 1965), lives there for longer periods, and most probably reproduces there successfully (BORI et al. 1985). All *Hoplostethus* species have large eyes (WOODS and SONODA 1973) that may allow light to be trapped even at weak illumination levels. In *H. atlanticus*, for instance, a retinal specialization for scotopic vision was found that may allow these fish to use photoperiod as a zeitgeber to time reproduction at depths below 1000 m (PANKHURST et al. 1987). The oligotrophic Red Sea should be particularly clear. Hence, the assumption that *H. mediterraneus* still uses light as an informational source at such depths may be justified. To examine this hypothesis, exact light measurements combined with experimental studies on light perception of this species will be necessary.

In the central Red Sea, *H. mediterraneus* and *O. robustus* were caught at different depths within a rather narrow geographical range (Fig. 6). Accordingly, specimens from depths of more than 1000 m live along the same slope and only a few km apart from shallower-dwelling conspecifics. The gene flow between these adjacent sites should be considerable, and hence the morphological variability among *O. robustus* specimens from different depths with different light levels indicates environmentally induced, phenotypic differentiation rather than a genetically manifested polymorphism.

As suggested by a recent study of the depth distribution and morphological differentiation of the ophidiid fish *Neobythites stefanovi* (Fig. 1), vertical migrations along illumination gradients are not uncommon in the Red Sea (UIBLEIN et al. 1994a). This species has an ocellus on the dorsal fin which consists of a dark spot surrounded by a white concentric ring. The ocellus undergoes several developmental stages during ontogeny (UIBLEIN et al. 1994a). Younger and smaller fish with a less developed ocellus are exclusively found at deeper zones of about 800 m (Fig.7). Subadults and adults - with an advanced developmental stage - occur at more illuminated depths above 600 m. The largest specimen, with a fully developed ocellus, was found at about 450 m. In shallower zones, food abundance should generally be higher and growth faster. At the same time, the visibility of the body shape and the number of visually hunting predators here should also increase. By presenting an eye-like structure on the dorsal fin, *N. stefanovi* may be able to cope with this increased predation pressure in the shallower zones. As shown in several other fish species, the ocellus may function as an antipredator signal that deflects predatory attacks to less vital parts of the body or deters predators from further pursuit. The signalling function of the ocellus has been emphasized in a comparative study between *N. stefanovi* populations from the Red Sea and the Gulf of Aden (UIBLEIN 1995). The generally deeper-living Red Sea population shows a vertically larger spot that should intensify the signalling and attention catching effect at these less illuminated depths.

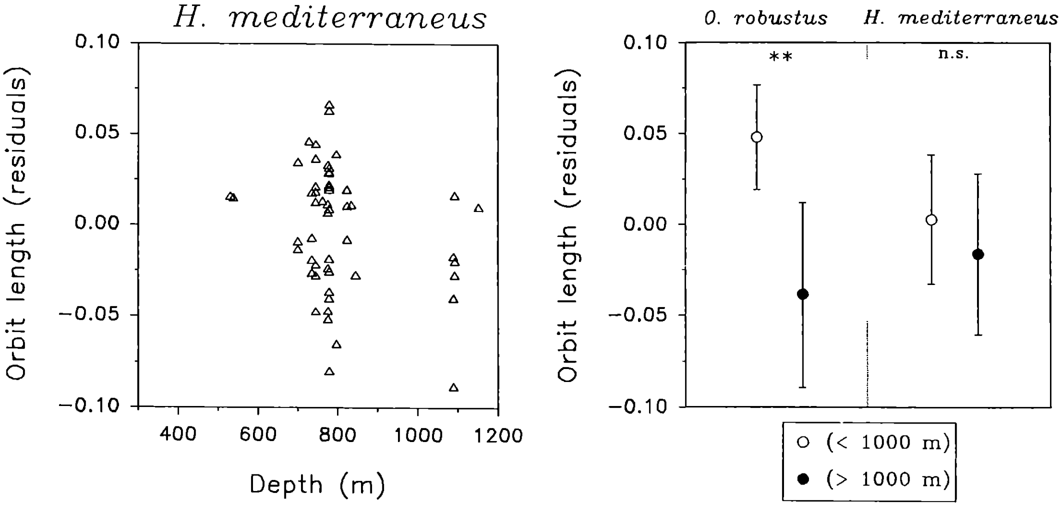

Fig. 5: Size-adjusted values of orbit length (residuals) against depth distribution in *Hoplostethus mediterraneus* and mean residuals of orbit length (with SD) for two bathymetric groups of *Oligopus robustus* and *Hoplostethus mediterraneus* (see text for further explanations).

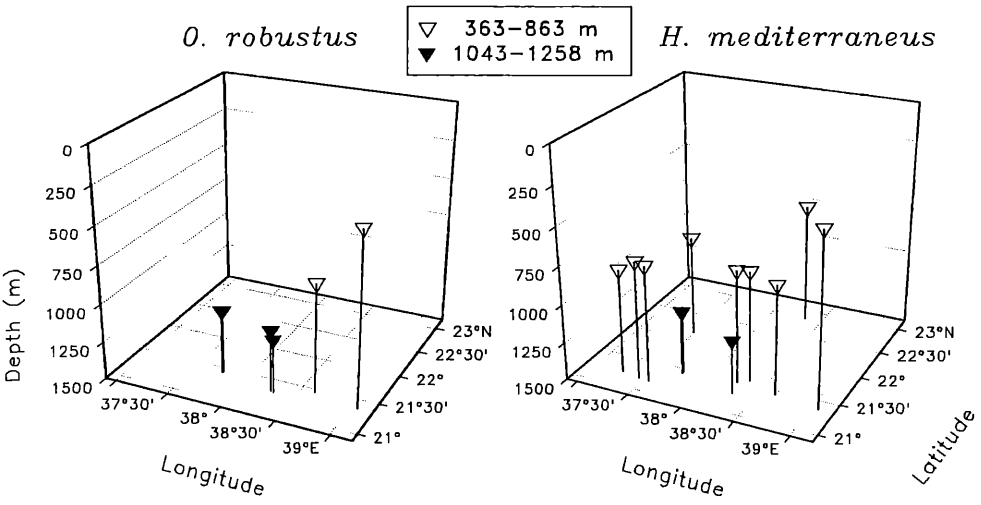

Fig. 6: Depth distribution in *Hoplostethus mediterraneus* and *Oligopus robustus* within a narrow geographical range in the central Red Sea. The distances between the longitudinal and between the latitudinal lines are about 50-60 km.

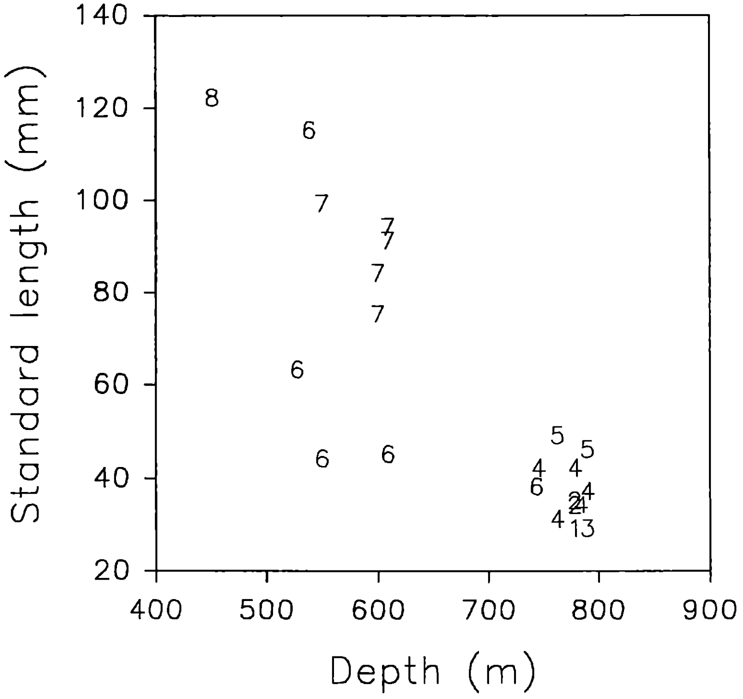

Fig. 7: The relationship between depth and SL in *Neobythites stefanovi* with the respective ocellus developmental stages (1-8) indicated (cf. UIBLEIN et al. 1994a).

Conclusions

The data on depth distribution and intraspecific morphological differentiation in fishes from the deep Red Sea presented here and in earlier papers (UIBLEIN et al. 1994a, KLAUSEWITZ and UIBLEIN 1994, UIBLEIN 1995) suggest that niche expansion along illumination gradients is a dynamic process that underlies certain environmental and organismic constraints. Each of the three species under investigation may interact with the factor light (and other depth-related variables) in a species-specific, conservative, as well as in a dynamic, highly exploratory manner.

Light no doubt plays a key role in inducing adaptive shifts in foraging, locomotion, or antipredator behaviour of deep-sea dwellers (see also CHILDRESS 1995). Organisms restricted to shallow waters, however, may also develop dynamic affiliations with illumination level. In a recent review of experimental and field studies of microhabitat choice in the freshwater ostracod *Cypridopsis vidua*, for example, the adaptive significance of the ongoing utilization of the interstitial as an "exploratory window" by this macrophyte-dwelling crustacean was emphasized (UIBLEIN et al. 1994a). Experimental studies of foraging behaviour in a facultative cave-dweller, the Pyrenean salamander *Euproctus asper*, demonstrated that this species shifts flexibly between alternative prey search modes in response to changing light level (UIBLEIN et al. 1992); it chooses among prey patches based both on visual detectability and nutrient content (UIBLEIN et al. 1995).

As we know today, the deep sea - similar to shallow waters - does not represent the stable and uniform environment it was theorized to be (see, for instance, GOLDSHMIDT et al. 1996, ROWE 1996, TYLER 1996). An important prerequisite for coping with ecological variability as well as for dynamic niche expansion along environmental gradients is a high phenotypic plasticity in behavioural, morphological, and physiological traits based on a wide reaction norm.

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References

ANDRIASHEV, A. P., 1953: Ancient deep-water and secondary deep-water fishes and their importance in a zoogeographical analysis.- In: Notes on special problems in ichthyology. - Moscow, Leningrad: Akad. Nauk SSSR, Ikhiol. Kom. (Translation from Ichthyol. Lab., Bureau of Comm. Fisheries, Washington DC).

BALSS, H., 1931: Expedition S.M. Schiff "Pola" in das Rote Meer, nördliche und südliche Hälfte 1895/96-1897/98. Zoologische Ergebnisse. XXXVI. Decapoden des Roten Meeres IV: Oxyrhyncha und Schlußbetrachtungen. - Denkschr. Österr. Akad. Wiss. Wien, math.-nat. Kl. **102**: 1-30.

BORI, C., GILI, J. M., GARCIA, A., 1985: Presencia de *Oligopus ater* Risso, 1810 (Pisces: Ophidiiformes) en cuevas submarinas del litoral NE de Mallorca. - Misc. Zool. **9**: 401-404.

CHILDRESS, J. J., 1995: Are there physiological and biochemical adaptations of metabolism in deep-sea animals? - TREE **10**: 30-36.

CLARKE, G. L., DENTON, E. J., 1961: Light and animal life.-In HILL, M. N., (Ed.): The sea. - New York: John Wiley & Sons.

COHEN, D. M., 1964: A review of the ophidiiform genus *Oligopus* with the description of a new species from West Africa. - Proc. U.S. Nat. Mus. **116**: 1-22.

DENTON, E. J., 1990: Light and vision at depths greater than 200 metres. - In HERRING, P. J., CAMPBELL, A. K., WHITFIELD, M., MADDOCK, L., (Eds): Light and life in the sea. - Cambridge: Cambridge Univ. Pr.

EKMAN, S., 1953: Zoogeography of the sea. - London: Sidgwick & Jackson.

ELLIOTT, N. G., WARD, R. D., 1992: Enzyme variation in orange roughy, *Hoplostethus mediterraneus* (Teleostei: Trachichthyidae), from Southern Australian and New Zealand waters. - Aust. J. Mar. Freshwater Res. **43**: 1561-1571.

ELLIOTT, N. G., SMOLENSKI, A. J., WARD, R. D., 1994: Allozyme and mitochondrial DNA variation in orange roughy, *Hoplostethus atlanticus* (Teleostei: Trachichthyidae): little differentiation between Australian and North Atlantic populations. - Mar. Biol. **119**: 621-627.

ELLIOTT, N. G., HASKARD, K, KOSLOW, J. A., 1995: Morphometric analysis of orange roughy (*Hoplostethus atlanticus*) off the continental slope of southern Australia. - J. Fish Biol. **46**: 202-220.

FENTON, G. E., SHORT, S. A., RITZ, D. A., 1991: Age determination of orange roughy, *Hoplostethus atlanticus* (Pisces: Trachichthyidae), using 210Pb 226Ra disequilibria. - Mar. Biol. **109**: 197-202.

FUCHS, T., 1901: Über den Character der Tiefseefauna des Roten Meeres aufgrund der von den österreichischen Tiefsee-Expeditionen gewonnenen Ausbeute. - Sitzungsber. Kaiserl. Akad. Wiss. Wien, math.-nat. Kl. **110**: 249-258.

GOLDSHMIDT, O., GALIL, B., GOLANI, D., LAZAR, B., EREZ, J., BARANES, A., 1996: Food as a factor for habitat selection in the deep-sea fishes of the northern Red Sea. - In UIBLEIN, F., OTT, J., STACHOWITSCH, M., (Eds): Deep-sea and extreme shallow-water habitats: affinities and adaptations. - Biosyst. Ecol. Ser. **11**: 271-298.

HADDON, M., WILLIS, T. J., 1995: Morphometric and meristic comparison of orange roughy (*Hoplostethus atlanticus*: Trachichthyidae) from the Puysegur Bank and Lord Howe Rise, New Zealand, and its implications for stock structure. - Mar. Biol. **123**: 19-27.

KLAUSEWITZ, W., 1986: Zoogeographic analysis of the vertical distribution of the deep Red Sea ichthyofauna, with a new record. - Senckenbergiana marit. **17**: 279-292.

KLAUSEWITZ, W., UIBLEIN, F., 1994: Tiefenwasser- und Tiefseefische aus dem Roten Meer. XVII. *Oligopus robustus*, a new record for the Red Sea, with comparative studies on specimens from the Gulf of Aden. - Senckenbergiana marit. **25**: 21-28.

KOTLYAR, A. ., 1986: Systematics and distribution of species of the genus *Hoplostethus* Cuvier (Beryciformes, Trachichthyidae). - Tr. Inst. Okeanol. Akad. Nauk SSSR **121**: 97-140 (in Russian).

KRUPP, F., 1987: Tiefenwasser- und Tiefseefische aus dem Roten Meer. XV. The occurrence of *Cynoglossus acutirostris* Norman 1939 in the Red Sea. Senckenbergiana marit. **19**: 249-259.

LUKSCH, J., 1898: Expedition S.M. Schiff "Pola" in das Rothe Meer, nördliche Hälfte (October 1895 - Mai 1896). Wissenschaftliche Ergebnisse. VI. Physikalische Untersuchungen. - Denkschr. Kaiserl. Akad. Wiss. Wien, math-nat. Kl. **65**: 351-422.

LUKSCH, J., 1901: Expedition S.M. Schiff "Pola" in das Rothe Meer, südliche Hälfte (September 1897 - April 1898). Wissenschaftliche Ergebnisse. XVIII. Physikalische Untersuchungen. - Denkschr. Kaiserl. Akad. Wiss. Wien., mat.-nat. Kl. **69**: 337-398.

MACE, P. M., FENAUGHTY, J. M., COBURN, R. P., DOONAN, I. J., 1990: Growth and productivity of orange roughy (*Hoplostethus atlanticus*) on the northern Chatham Rise. - N.Z. J. Mar. Freshwater Res. **24**: 105-119.

MERRETT, N. R., MARSHALL, N. B., 1981: Observations on the ecology of deep-sea bottom-living fishes collected off northwest Africa (08°-27°N). - Prog. Oceanogr. **9**: 185-244.

NIELSEN, J. G., UIBLEIN, F., 1993: Tiefenwasser- und Tiefseefische aus dem Roten Meer. XVI.A new species of *Neobythites* from the NW Indian Ocean and the Red Sea. - Senckenbergiana marit. **23**: 109-113.

PANKHURST, N. W., MCMILLAN, P. J., TRACEY, D. M., 1987: Seasonal reproductive cycles in three commercially exploited fishes from the slope waters off New Zealand. - J. Fish Biol. **30**: 193-211.

PAULIN, C. D., 1979: New Zealand roughis (Pisces: Berycomorphii, Trachichthyidae). - N.Z. J. Zool. **6**: 69-76.

POTT, P. von, 1899: Expedition S.M. Schiff "Pola" in das Rothe Meer. Südliche Hälfte (September 1897 März 1898). Beschreibender Theil. Vienna: Kaiserlich-Königliche Hof- und Staatsdruckerei.

QUERO, J.-C., 1982: Trachichthyidae.-In MAURIN, C., QUERO, J.-C. (Eds): Poissons des côtes nord-ouest Africaines (campagne de la 'Thalassa' 1962, 1968, 1970 and 1973). - Rev. Trav. Inst. Péches Marit. **45**: 29-43.

REIST, D., 1985: An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. - Can. J. Zool. **63**: 1429-1439.

RIEDL, R., 1966: Biologie der Meereshöhlen. - Hamburg und Berlin: Paul Parey.

ROWE, G. T., 1996: The cycling of organic matter in food-limited environments. - In: UIBLEIN, F., OTT, J., STACHOWITSCH, M. (Eds): Deep-sea and extreme shallow-water habitats: affinities and adaptations. - Biosyst. Ecol. Ser. 11: 233-260.

SMITH, M. M., HEEMSTRA, P. C., 1986: Smith's sea fishes. - Johannesburg: McMillan.

SMITH, P. J., 1986: Genetic similarity between samples of the orange roughy *Hoplostethus atlanticus* from the Tasman Sea, South-west Pacific Ocean and North-east Atlantic Ocean. - Mar. Biol. **91**: 173-180.

SMOLENSKI, A. J., OVENDEN, J. R., WHITE, R. W. G., 1993: Evidence of stock separation in southern hemisphere orange roughy (*Hoplostethus atlanticus*, Trachichthyidae) from restriction-enzyme analysis of mitochondrial DNA. - Mar. Biol. **116**: 219-230.

TYLER, P. A., 1996: Faunal responses to temporal disequilibrium in the deep sea. - In UIBLEIN, F., OTT, J., STACHOWITSCH, M. (Eds): Deep-sea and extreme shallow-water habitats: affinities and adaptations. - Biosyst. Ecol. Ser. **11**: 261-270.

UIBLEIN, F., 1995: Morphological variability between populations of *Neobythites stefanovi* (Pisces: Ophidiidae) from the deep Red Sea and the Gulf of Aden. - Mar. Ecol. Prog. Ser. **124**: 23-29.

UIBLEIN, F., DURAND, J. P., JUBERTHIE, C., PARZEFALL, J., 1992: Predation in caves: the effects of prey immobility and darkness on the foraging behaviour of two salamanders, *Euproctus asper* and *Proteus anguinus*. - Behav. Process. **28**: 33-40.

UIBLEIN, F., NIELSEN, J. G., KLAUSEWITZ, W., 1994a: Depth dependent morphological variation in two ophidiiform fishes from the deep Red Sea: evidence for species-specific structure in vertical distribution. - Cybium **18**: 15-23.

UIBLEIN, F., ROCA, J. R., DANIELOPOL, D. L., 1994b: Experimental observations on the behaviour of the ostracode *Cypridopsis vidua*. - Verh. Int. Ver. Limnol. **25**: 2418-2420.

UIBLEIN, F., ENGELKE, S., PARZEFALL, J., 1995: Trade-off between visual prey detectability and nutrient content in the patch choice of the Pyrenean salamander *Euproctus asper*. - Ethology **101**: 39-45.

WOODS, L. P., SONODA, P. M., 1973: Order Berycomorphi (Beryciformes). - In Cohen, D.M., (Ed.): Fishes of the western North Atlantic. - Mém. Sears Found. Mar. Res. **1**: 263-396.

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