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Feeding behaviour and feeding ecology of two substrate burrowing teleosts, *Mullus surmuletus* (Mullidae) and *Lithognathus mormyrus* (Sparidae), in the Mediterranean Sea

Verhalten bei der Nahrungsaufnahme und Nahrungsökologie von zwei substratgrabenden Teleostiern, *Mullus surmuletus* (Mullidae) und *Lithognathus mormyrus* (Sparidae), im Mittelmeer

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Summary: The fish assemblages which follow the sediment burrowing Striped Red Mullet (*Mullus surmuletus*, Mullidae) and the Striped Sea Bream (*Lithognathus mormyrus*, Sparidae) has been investigated in 2003-4 by SCUBA diving at the Italian Island of Elba (Toscany). The study focussed on the preference for specific food organisms and on adaptations in the feeding behaviour in order to reveal the trophic niche of both syntopic species. *M. surmuletus* takes up endobenthic organisms by ploughing through the sand or whirling up the sediment; digging pits is another method for reaching the endofauna. In contrast, *L. mormyrus*, approaching from the suprabenthal, indiscriminately engulfs some sediment, filters it in the mouth cavity and selects preferably molluscs. Thus, its feeding actions are more frequent than in *M. surmuletus* which searches for food with its pair of barbels and preys mainly on decapod and isopod crustaceans. The variety of prey organisms is wider in *M. surmuletus* than in the more food-specialized *L. mormyrus* which results in a rather limited trophic niche overlap. Also the structure of the gill arches differs in both species: In. *L. mormyrus* the rakers are both longer and wider. The number of branchial spinules studding the rakers, although quite variable, is in *L. mormyrus* clearly higher and the interspinular clefts wider than in *M. surmuletus*. Differences emerge also from scanning electron microscopical inspection of the branchial spinules: in *L. mormyrus* they are hooked while in *M. surmuletus* they are smooth. The local guilds of fishes usually following the two host species while feeding was somewhat larger (eight species) in *M. surmuletus* than in *L. mormyrus* (six species). But in both hosts prevailed *Diplodus sargus* while *Coris julis*, in other publications the most frequent follower, was rarer in this study. The host species themselves could even become followers in the mutually other species.

Key words: *Mullus surmuletus, Lithognathus mormyrus*, nutrition, feeding behaviour, following species, gill rakers, gill fine structure

Zusammenfassung: Auf Sedimentböden der Insel Elba (Toscana, Italien) wurden 2003-4 die Fressgemeinschaften der bodenwühlenden Fische *Mullus surmuletus* und *Lithognathus mormyrus* vergleichend untersucht. Die Frage war dabei zu klären, welche Nahrungsorganismen jeweils bevorzugt werden und welche Anpassungen an das Fressverhalten existieren, damit die Nischen beider Arten erkannt werden können. *M. surmuletus* frisst vom Substrat ausgehend und verwendet dabei verschiedene Techniken wie Durchpflügen und Aufwirbeln des Substrats oder Ausheben von Sandgruben mit anschließendem Aufpicken oder Aufsaugen, um an die Endofauna zu gelangen. Dagegen stößt *L. mormyrus* aus dem Suprabenthal scheinbar ziellos auf den Boden und nimmt dabei Sediment auf, das im Mundraum filtriert wird. Daher sind dessen Fressaktivitäten häufiger als die von *M. surmuletus*, der mit Hilfe seiner Barteln die Beute gezielt sucht. Die Hauptnahrung von *M. surmuletus* besteht aus Crustacea, besonders Decapoda und Isopoda, während *L. mormyrus* Mollusca bevorzugt. Die Nischenbreite der Nahrung ist bei *M. surmuletus* größer als bei *L. mormyrus*, der somit spezialisierter erscheint. Die Nischenüberlappung der jeweiligen Nahrungskomponenten stellte sich als gering heraus. Die Kiemenreusen sind bei *L. mormyrus* deutlich länger und breiter als bei *M. surmuletus*, auch die Lücken zwischen den Dornen sind bei ersterem weiter. Die Zahl der Kiemendornen ist bei beiden Arten auf den verschiedenen Kiemenbögen variabel, bei *L. mormyrus* aber deutlich höher. Unterschiede ergaben sich auch in der rasterelektronenmikroskopischen Analyse der Kiemendornen, die nur bei *L. mormyrus* Haken tragen. Zudem weisen beide Arten ein System von Rinnen mit Drüsen ähnelnden Erhebungen auf. Das Spektrum der Folgerarten ist bei *M. surmuletus* größer (acht Arten) als bei *L. mormyrus* (sechs Arten), wobei *Diplodus sargus* bei beiden Arten dominierte, während *Coris julis*, der in anderen Untersuchungen am häufigsten folgte, hier seltener auftrat. Auch die beiden Wirte konnten Folger bei der jeweilig anderen Art sein.

Schlüsselwörter: *Mullus surmuletus, Lithognathus mormyrus*, Nahrungserwerb, Nahrung, Kiemenreusen, Folgerarten

1. Introduction

Among partnerships of fish species those of substrate burrowers and their followers are well known (Abel 1962, Fricke 1970, Moosleitner 1982, 2008). The followers take advantage from the feeding activity of the burrowers picking small endofauna from the agitated sediment. It has been proposed that the eroded sediment clouds are the trigger for the followers (Fricke 1970, 1975, Moosleitner 1982). This commensal partnership (Cheng 1967) favours one partner, the follower, without adversely affecting the burrower as their "host".

All mullet species (family Mullidae—Goatfishes) are sediment burrowers. They detect their food organisms with two barbels arising from their lower jaw. In the wake of the two Mediterranean mullid species, *Mullus surmuletus* (fig. 1) and *Mullus barbatus* (Lombarte et al. 2000), occur mostly members of Labridae and Sparidae. However, there are other fish species in the Mediterranean with a similar feeding ecology. In contrast to its suprabenthic relatives,

Fig. 1: *Mullus surmuletus* probing with its barbels (only one is visible) the wall of a sand pit for prey.
Abb. 1: *Mullus surmuletus* tastet mit den Barteln (nur eine ist sichtbar) die Wand einer Sandgrube nach Nahrung ab.

Fig. 2: *Lithognathus mormyrus* pushing into the sand bottom in order to find prey.
Abb. 2: *Lithognathus mormyrus* beim Zustoßen in den Sandboden beim Aufspüren von Beute.

the Striped Sea Bream, *Lithognathus mormyrus* (fig. 2), (Sparidae—Sea Breams) is feeding epibenthically at the bottom. On sandy bottoms of the Mediterranean, *M. surmuletus* and *L. mormyrus* are often found associated. The bream may follow the burrowing mullet, but sand burrowing behaviour of the bream could also be observed with other fish species as followers. Thus, the resulting facultative feeding local guilds have a changing composition and species number.

Therefore, it was interesting to comparatively analyse the ecological niche (sensu PIANKA 1994; additional interpretations by ZANDER 2004, 2006) of these two unrelated, but trophically similar species of sand burrowers. Beside adaptations in general body morphology, such as different shape and coloration (FRICKE 1970), a more effective exploitation of this niche could have evolved from detailed structural, physiological and ethological specializations of the fish. Since activity time and habitat seem identical in the two species, these aspects of the niche can be neglected and the third main dimension of the niche (HUTCHINSON 1957), the trophic dimension, gets in the focus of interest. Therefore, the present study analyses and compares the feeding behaviour, the composition of food and morphological details of the feeding apparatus in these two common Mediterranean fish species.

2. Material and Methods

The study on *Mullus surmuletus* and *Lithognathus mormyrus* was performed by SCUBA diving in the bights of Fetovaia and Seccheto, Island of Elba, Toscany Archipelago, Mediterranean Sea (fig. 3). Because Fetovaia was sheltered against the prevailing west winds, the diving was done mostly at the western shore. Main observation time was between 9 and 11 h and 17 and 19 h. Feeding behaviour was recorded by an underwater video camera (Sony DRC-PC 120E) mounted with a halogen lamp. Each recorded observations lasted at least one min. Parameters

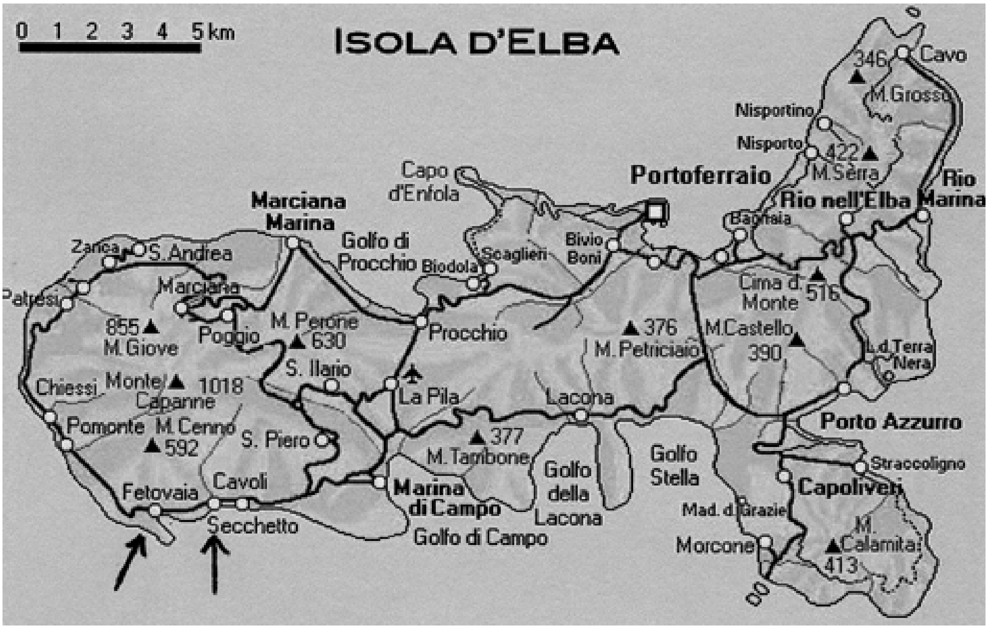

Fig. 3: Map of Elba (Tuscany) with the study localities of Fetovia and Secchetto (arrows).
Abb. 3: Karte der Insel Elba (Toscana) mit den Untersuchungsstellen Fetovaia und Secchetto (Pfeile).

such as date, time, type of substrate, temperature, water depth, fish size (five classes), and group size of schools were noted. After each dive the recordings were computer-evaluated, the feeding activity of both fish species per minute counted, frequency and species composition of following fishes identified. Each feeding procedure has been defined as starting with a vertical body position (in relation to the substrate), the subsequent uptake of organisms or substrate, and ending when the fish resumed its normal horizontal swimming position.

For laboratory studies 41 specimens were caught by a local fisherman in the wider investigation area: 27 *M. surmuletus* were caught 2003 in Secceto, four in Fetovaia; ten *L. Mormyrus* were caught 2004 in Marina de Campo. The fish were subjected to the measurement of standard length (SL), total length (TL) to the lower cm, and wet weight (g). After excision of the stomach, the gut content of the fishes was fixed in buffered 5% seawater-formalin. The prey organisms were identified under the stereomicroscope (20x magnification) to the lowest possible taxonomic level and measured to the lowest mm. If based on fragments, prey organisms were counted when two shells (bivalves), an apex (gastropods), or two eyes (crustaceans) were found.

All data were statistically evaluated using the computer programmes Excel, Access and SPSS. Beside mean value (x) und standard deviation (s) relative abundances (percentage of items in a population) and frequencies (percentage of the population with a distinct pattern) were assessed. The normal distribution was examined by the Kolmogorov-Smirnov test. If the latter was negative, the Man-Whitney-U test and the Spearman correlation were calculated. The limit of significance was ≤ 0.05, in cases exceeding this value, results were considered as a "trend" only. The relation of prey size to the standard length of the preying fish was examined by regression analysis. For calculation of the species diversity the Shannon-Wiener index was used. Niche width (according to Levins 1968) resulted from the equation $B=1/\Sigma P_i^2$, niche overlap (Schoener 1970) from $T=1\text{-}0.5\Sigma_i(Px_i\text{-}Py_i)$ with T-values beyond 0.6 being significantly different (Keast 1968).

The investigations of the gill rakers were based on two heads of adult *M. surmuletus* and three heads of adult *L. mormyrus*. After assessment of the total head length from the tip of the mouth to the posteriormost margin of the operculum, the operculum was removed, the gill apparatus excised and fixed in 5% formalin. The measurements (in mm) on the first left gill arch comprised total length of arch, number, length and width of rakers, width of clefts, number of branchial spinules per raker. For SEM-studies (tool: Leo 1525) a piece of the median gill arch of 10 mm length was excised, freeze-dried and gold sputtered before inspection.

3. Results

3.1. Feeding behaviour

Both fish species search for epifauna and endofauna mainly in the shallow sublittoral, but they have different feeding techniques. *Mullus surmuletus* uses its pair of independently movable barbels as effective tools for digging (see fig. 1). They are equipped with numerous chemoreceptors which enable to detect the prey. Once a prey organisms is located, the mullet pushes its head by vigorous beats of the pectoral fins and the strong anal fin into the sand before it grasps the prey. While scanning the bottom another technique is used: the beating pectoralia and a directed jet of water whirl up the sand and the prey organisms become suspended in the water column, where they can be easier picked or pipetted. A third method of *M. surmuletus* is bulldozing with the head through the sand and the digging of sand pits, the flanks of which are then searched by the barbels. The same scanning behaviour was also observed at the slopes of ripple marks (fig. 1).

In contrast, *Lithognathus mormyrus* shows just one technique while searching for food, a rather unspecific filtration of sand: Swimming about 50 cm above the sand surface it swoops down pushing its head seemingly unsystematically into the sediment (see fig. 2). Emerging again from the bottom the sand grains are ejected through the opercular clefts. By this mode of feeding the striped sea bream leaves crater-like pits in the sand. Also in this species scanning of the slopes of sand ripples was observed.

The feeding activity of both species differs significantly ($p \leq 0.001$). *L. mormyrus* is feeding about twice as frequent per time unit as does *M. surmuletus* (x = 12,2 and. 6,0/s = 6,79 and 5,87, fig. 4). That means, the sea bream takes less time for detecting food and rather indiscriminately filtrates much sand while the mullets take more time for a directed search for prey.

Especially the juveniles of both species tend to aggregate in schools. School size is negatively correlated with body size, though in *L. mormyrus* less clearly ($p > 0.05$) than in *M. surmuletus* ($p \leq 0.001$). In red mullets, school size negatively correlates also with feeding activity and individual body size, although this relation was not significant. That means, the bigger the mullets and their schools the less frequent they feed. This negative relation is clearer and significantly ($p \leq 0.05$) found in the sea bream.

Both species were observed searching for food together, with the mullets following the striped sea bream more often than vice versa. Already from a few meters sight mullets join a feeding sea bream, but at that distance they are still looking for food on their own. Spotting another digging fish species, the butt, *Bothus podas*, causes both *M. surmuletus* and *L. mormyrus* to join and search for food together.

Both sand digging species are followed by other fish species when the sand cloud whirled up by the feeding activity acts as trigger, regardless whether *M. surmuletus* and *L. mormyrus* feed in groups or as single individuals. The size of the group does not significantly influence the number of commensalic followers, although a slightly negative trend could be observed. When agitating the sand the mullets expose the prey organisms which are then picked up by the commensals. In contrast, the sea bream takes up the sediment and expels it through the gill clefts. The following fish search in the ejected sand for their prey. The commensal fish never have a significant impact on the feeding activity of the two sand digging species (fig. 5). On the other hand, it could be observed that juvenile

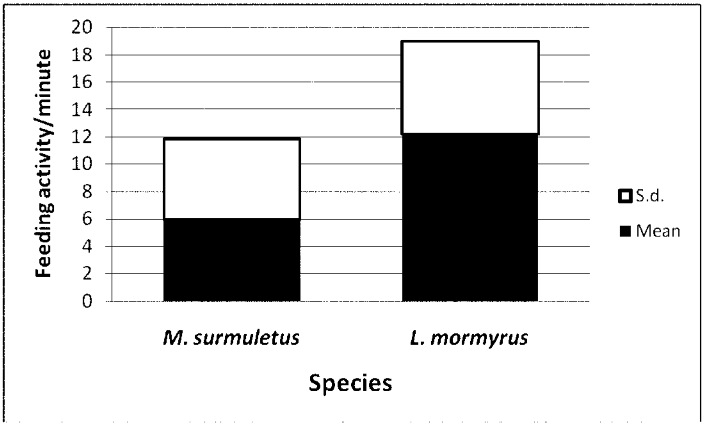

Fig. 4: Feeding activity of *Mullus surmuletus* and *Lithognathus mormyrus*. Mean = mean value, S. d. = standard deviation.

Abb. 4: Fressaktivität von *Mullus surmuletus* und *Lithognathus mormyrus*. Mean = Mittelwert, S.d. = Standardabweichung.

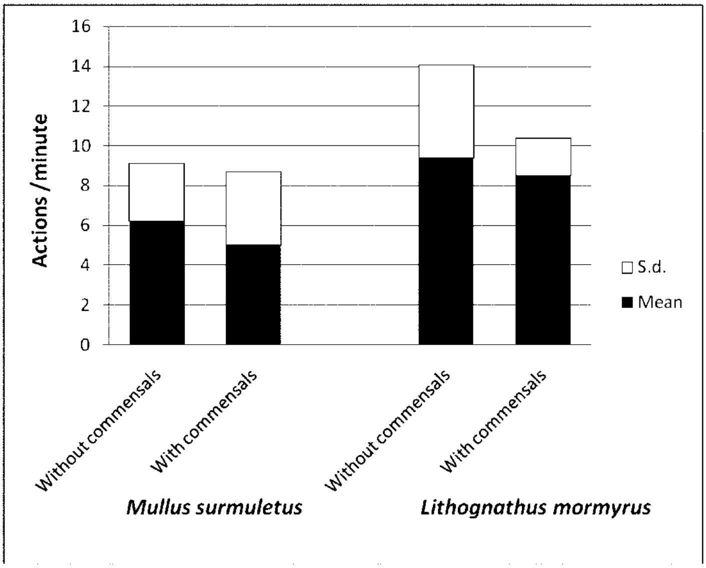

Fig. 5: Feeding activity of *Mullus surmuletus* and *Lithognathus mormyrus* in relation to the absence or presence of commensals. Mean = mean value, S. d. = standard deviation.

Abb. 5: Fressaktivität von *Mullus surmuletus* and *Lithognathus mormyrus* in Abhängigkeit vom Fehlen oder von der Präsenz von Kommensalen. Mean = Mittelwert, S.d. = Standardabweichung.

mullets are followed by juvenile commensals only, e.g. *Diplodus vulgaris*.

Digging in the sand, *M. surmuletus* was in most observations (78 %, n = 60) pursued by nine commensal fish species, the most common being the sparids *Diplodus sargus* (36 %) and *D. vulgaris* (28%). Clearly rarer as follower was the labrid *Coris julis* (10 %) (fig. 6). The frequency of followers within these three species were 40, 47 and 19 %, respectively. Their behaviour was different: In groups up to four specimens *D. sargus* followed the mullets behind the tail or along the flanks of their body without any direct contact. In contrast, *D. vulgaris* mostly swam near the head of the mullet exhibiting a somewhat jerkily swimming that allowed for an optimal manoeuvring and rapid grasping of the agitated prey items. Along rocky shores with aufwuchs and in *Posidonia* meadows, *Coris julis* was a frequent follower, but occurred less numerous over sand bottom. This species had direct body contact and picked for prey both in the agitated sand cloud and in the surrounding sand bottom. This behaviour applied also to *Symphodus mediterraneus* and *Symphodus cinereus*, while *Spondylosoma cantharus* only fed in the sand cloud. *L. mormyrus* and *Bothus podas*, being sand digging species themselves, were also observed as commensals of mullets.

Among the food association with *L. mormyrus* we found six different commensal species (fig. 6) found in 46 % of all observed digging events

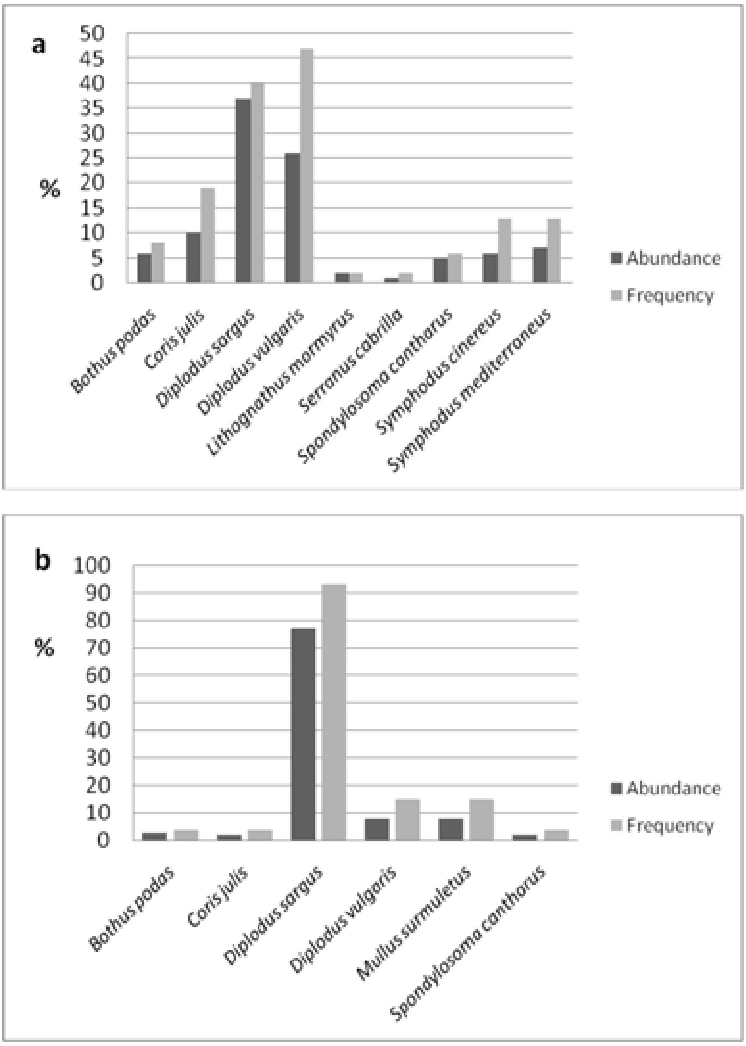

Fig. 6 a and b: Abundance (percent of followers in the host populations) and frequency (percent of hosts which were followed) in *Mullus surmuletus* (**a**) or *Lithognathus mormyrus* (**b**).
Abb. 6 a und b: Abundance (Anteil der Kommensalen in der Wirtspopulation) und Frequency (Anteil der Wirte mit den jeweiligen Kommensalen) bei *Mullus surmuletus* (**a**) oder *Lithognathus mormyrus* (**b**) begleiten.

(n=59). By far the most abundant was *D. sargus* (77%) observed in 90% of all digging activities, In contrast, *M. surmuletus* and *D. vulgaris* had an abundance of 8% each and a frequency of 15% only. Corresponding to the high proportion of sand ejected through the gills of the sea bream, the regularly pursuing species picked their food objects also in the ejected sand and not only from the sand bottom or the sand pits eroded by *L. mormyrus*. In this digging species *B. podas*, *C. julis* and *S. cantharus* were not often observed as followers. Feeding mainly in the sand cloud, they showed the same feeding behaviour as described for the burrowing of *M. surmuletus*.

3.2. Food composition and overlap

Mullus surmuletus: Main food items were Crustacea (abundance 70%; frequency 76 %), especially decapods (33% abundance) and isopods (23%) (fig.7a). Compared to this dominance of crustaceans, the abundance of polychaetes (14%), echinoderms (7%) and molluscs (only 3%) was subordinate only. While polychaetes occurred fairly regularly (52% frequency), the presence of molluscs and echinoderms as food items was scarcer (23% and 14% respectively).

Lithognathus mormyrus: Contrasting to the striped red mullets, this species fed almost

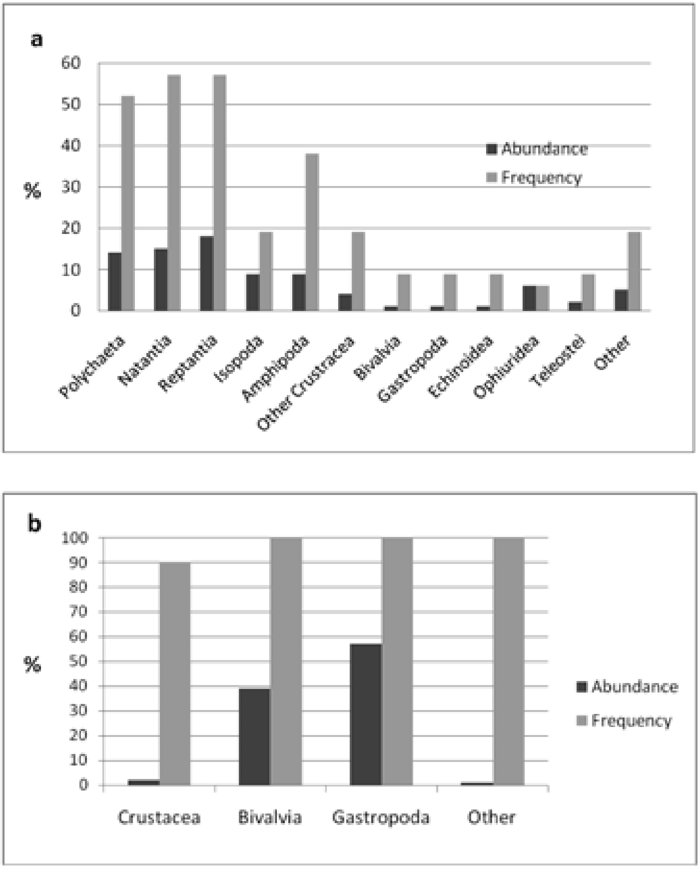

Fig. 7a and b: Main prey components found in the guts of *Mullus surmuletus* (a) and *Lithognathus mormyrus* (b). Abundance = percent of food items in the predator population, frequency = percent of predators with the respective food items.

Abb. 7a und b: Hauptnahrungskomponenten, die in den Verdauungstrakten von *Mullus surmuletus* (a) oder *Lithognathus mormyrus* (b) gefunden wurden. Abundance = Anteil der Komponenten in der Prädator-Population, Frequency = Anteil der Prädatoren mit der jeweiligen Komponente.

selectively on molluscs which prevailed in the food spectrum with 96 % abundance and 100 % frequency (fig. 7b). Although crustaceans ranked second, their abundance with only 2% was as negligible as that of all other food components (frequency in crustaceans 90%).

The average size of the food objects ingested was 6.29 mm (±4.78) in *M. surmuletus*, while *L. mormyrus* preferred considerably smaller food (2.19 mm, ±0.93), although with a larger statistical spread (df=698; p≤0.001, F=309.81). The minimal size of prey was 0.28 mm in *M. surmuletus* and 0.58 mm in *L. mormyrus*. The niche breadth of *M. surmuletus* was calculated as NB=1.94 and, therefore, clearly wider than in L. mormyrus (NB=1.02). Evident already from the lower number of food components, *L. mormyrus* is apparently the more specialized species in the (food) resource utilization. Hence, the niche overlap (NO<0.6) is low and both species do not seem to compete much.

3.3. Morphology of the gillrakers

In both species studied here, the length of the gillrakers increases steadily from the external towards the median gill arch (fig. 8). However, in Mullus surmuletus (2.3 ±0.04 mm) the rakers are considerably shorter than in *Lithognathus mormyrus* (5.3 ±1.4 mm). Also the width of the rakers is in *L. mormyrus* about 4 x wider than in *M. surmuletus* (1.2±0.7 mm vs. 0.3 mm).

In *L. mormyrus*, the cleft between the gillrakers increases regularly posteriad, while in *M. surmuletus* the narrowest clefts are between the median rakers. The median cleft width in *L. mormyrus* is 0.9±0.6 mm, in *M. surmuletus* only 0.4±0.1 mm. Also the number of branchial spinules (branchiospinulae) differs in both species, moreover,

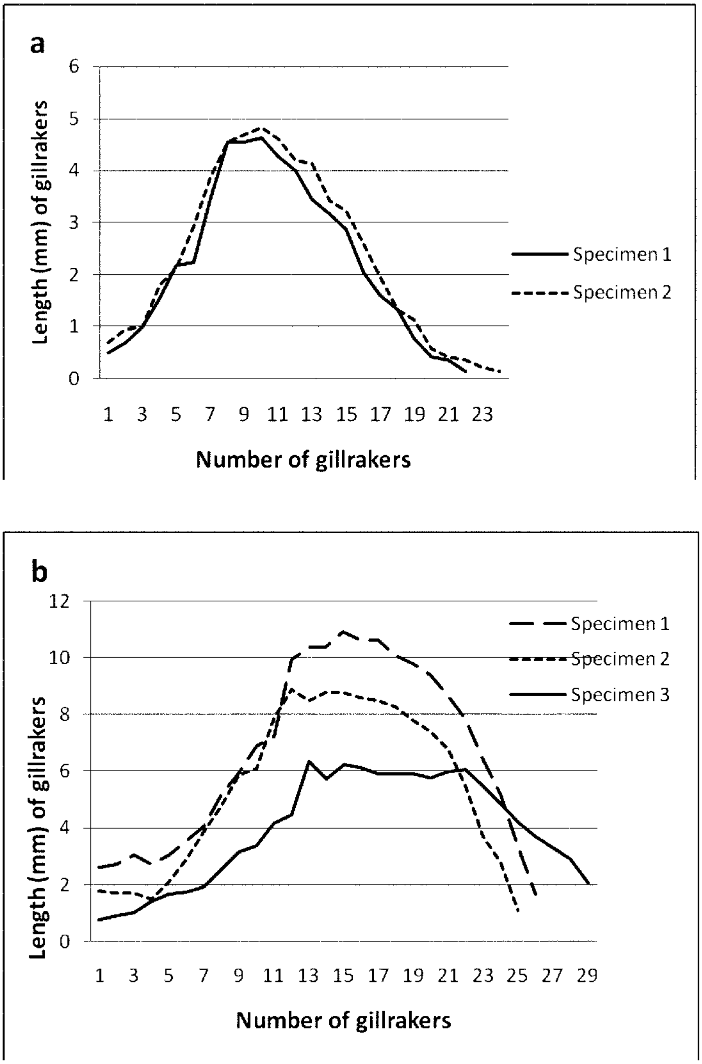

Fig. 8 a and b: Length of gillrakers on the left first arch of adult *Mullus surmuletus* (**a**) and *Lithognathus mormyrus* (**b**).
Abb. 8 a und b: Länge der Kiemenreusen auf dem linken ersten Kiemenbogen von adulten *Mullus surmuletus* (**a**) und *Lithognathus mormyrus* (**b**).

it also varies within the various gill arches of the same specimen. In both species, the longest and widest branchial spinules are present in the middle of the gill arches, in the area of the widest gillrakers. In *L. mormyrus*, most spines are concentrated basally, while in *M. surmuletus* they are regularly distributed along the entire length of the gillraker. Therefore, the median number of spines per raker (N=143) is in L. mormyrus much higher than in *M. surmuletus* (N=27).

The SEM analysis revealed further differences: Both species differ in the structure of the branchial spinules: Positioned only at the inner side of the rakers, in *M. surmuletus* they are smooth and unhooked at their tips (fig. 9 a) while in *L. mormyrus* their distal ends have marked hooks (fig. 9 b). Between two parallel rows of gillrakers, there is a trough. In *M. surmuletus*, this trough has numerous cylindrical bulges (fig. 9 c). Similar bulges occur also in a fold at the basis of the branchial spinules. Underneath this fold, there are additional spinules originating from humps and directing towards the bases of the gillrakers. The spinules in *L. mormyrus* are also positioned in several rows with their tips converging to each others. The trough between these rows is studded by lobate extensions.

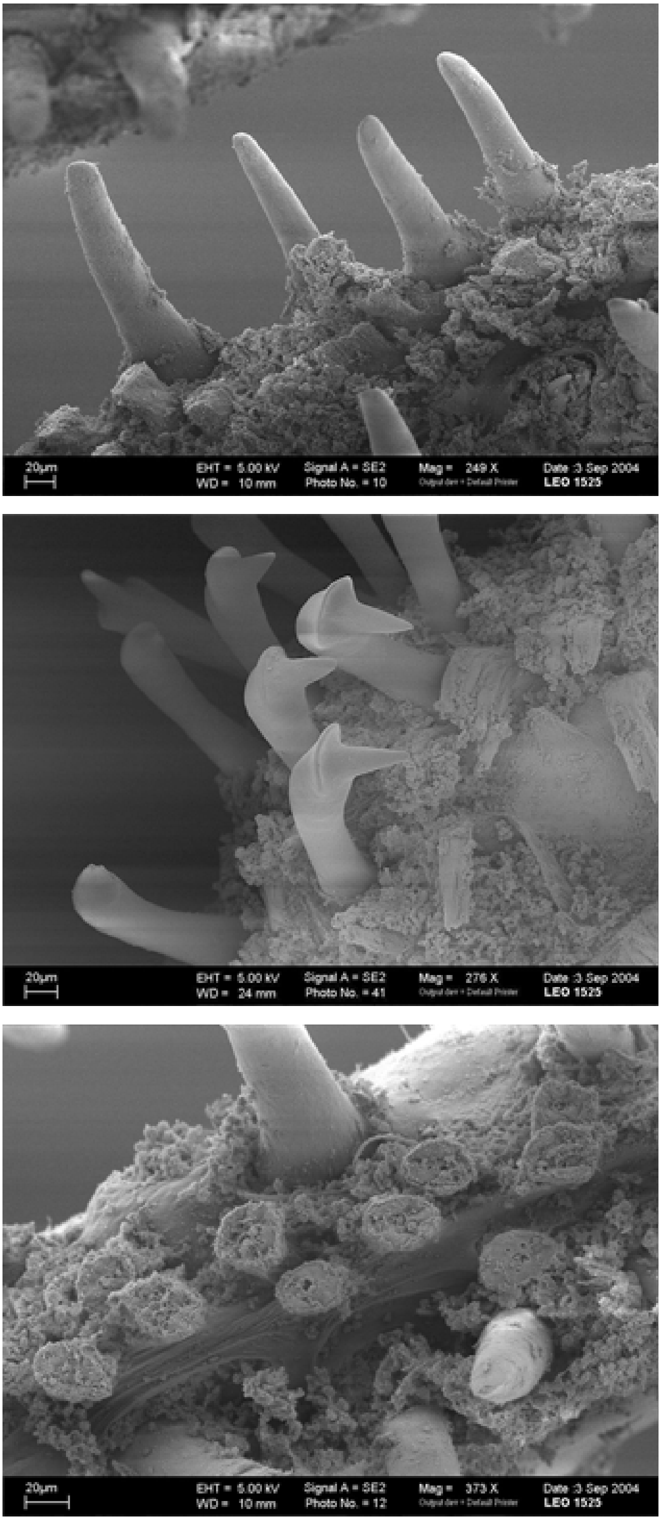

Fig. 9 a-c: SEM-photos of branchial spinules. (**a**) *Mullus surmuletus*, (**b**) *Lithognathus mormyrus*, (**c**) free trough formed by branchial spinules, which are surrounded by cylindrical bulges in *Mullus surmuletus*.

Abb. 9a-c: REM-Fotos von Branchiospinulae bei (**a**) *Mullus surmuletus*, (**b**) *Lithognathus mormyrus*, (**c**) freie Rinne zwischen den Branchiospinulae, umgeben von zylindrischen Erhebungen bei *Mullus surmuletus*.

4. Discussion

When resources are limited, syntopic species acquire different ethological, physiological and morphological adaptations realizing different niches and avoiding negative competiton (Odum 1959). This results in low values of niche overlap. It is investigated here, to what extent the often co-occurring sand burrowing fish species Mullus surmuletus and Lithognathus mormyrus compete for food and hold different ecological niches. Hence, food spectra and morpho-ethological adaptations for food uptake are discussed.

The striped red mullet, *Mullus surmuletus*, has a relatively wide food spectrum with decapod crustaceans predominating, but also with a regular diet of polychaete worms (compare Arculeo et al. 1989a, Badalamenti & Riggio 1989, Golani 1994, Labrapoulou & Eleftheriou 1997, Mazzola et al. 1999, de Pirro et al. 1999). A recent study showed a rather area-dependent food composition variably dominated by copepods, decapods or polychaetes (Klimpel et al. 2008). In contrast, the sea bream, *Lithognathus mormyrus*, with a narrower food spectrum feeds mainly on small bivalves and gastropods (Penades & Acuna 1980). The lower nutritive value of these smaller and shelled specimens might explain the considerably higher weight of the average stomach content and the higher feeding activity in the sea bream. Thus, the trophic dimension of both substrate burrowing species is well separated.

Trophic differences may already be indicated by the diverging digging behaviour: short, intermittent feeding phases in the sea bream vs. longer and more intense digging phases in the mullet. This can also relate to differences in the relative species composition of the flocks of "follower" fishes which typically accompany as commensals sediment-digging fish (Moosleitner 1982).

Differences in the nutritive specialization between sea bream and mullet are markedly expressed in morphological and ethological features. The compressed body shape and the coloration betray *Lithognatus mormyrus* as an inhabitant of the open water. This species encounters food organisms at the bottom by chance only. In contrast, *Mullus surmuletus* is better adapted to a benthic life. Its spindle-shaped to depress body and flattened head enable a body position horizontally to the substratum (Abel 1962). Larger areas can be continuously and effectively scanned and escape reactions are easily possible (Gosline 1984). Equipped with independently moving barbels studded with taste buds, mullets effectively sense prey organisms (Gosline 1984, McCormick 1993, Lombarte & Aguirre 1997). The absence of teeth in the upper jaw is considered another adaptation enabling "pipetting" of food items by a water jet technique (Gosline 1984, Aguirre 1997).

With increasing size of food particles fish species tend to have coarser and shorter gill-rakers, particularly evident comparing benthivorous predators to planktivorous filter feeders (Rauther 1937, Lindsay 1981, Hessen et al. 1988). The effectivity of this heterogeneous filter system (Hoogenboezem et al. 1990) is proven by the fact that the stomach never contained prey organisms considerably below the size of the clefts between the gill rakers. Moreover, the strong gillrakers of benthivores protect the delicate gills from abrasion by sand particles (Zander 1906, Wright et al. 1983). Both functions would explain the presence of robust and relatively short gillrakers in *M. surmuletus* as compared to the longer and denser gill rakers in *L. mormyrus*. As documented by stomach analyses, this heterogeneous filter system warrants a diverging prey size and an effective separation of food from sediment particles. The filtration of sand through the gill clefts, as described by Abel (1962), Fricke (1970) and Moosleitner (1982) for mullets, could not be observed in this study.

The two species differ also in the shape of branchial spinules on the gill rakers, in the presence of cylindrical bulges and in the occurrence of lobate extensions. However, since the function of these structures is unknown, a possibly diverging functional interpretation remains speculative.

As was already found in other investigations (Abel 1962, Fricke 1970, Moosleitner 1982, Zander 2003, Velte 2006) red mullets and sea breams do not profit from their followers. While in this study their associations consisted mainly of sparids, in other habitats and Mediterranean regions labrids, especially *Coris julis*, were the most common followers.

5. Conclusions

The red mullets and sea breams, *Mullus surmuletus* and *Lithognathus mormyrus*, studied in the Mediterranean were found to clearly differ in their ecological niche. The most profound difference is betrayed by the trophic dimension: different food composition and prey size are reflected by morphological differences in the feeding apparatus. Regarding habitat choice, the syntopic occurrence is limited: In contrast to *L. mormyrus*, *M. surmuletus* extends its feeding area beyond sandy bottoms also to sea grass meadows and rocky shores. Although they have a fairly similar time dimension, feeding activity in *L. mormyrus* is clearly higher. These ecological and behavioural differences between both species warrant a niche separation effective enough to preclude a massive and negative competition.

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