FOOD AND FEEDING HABITS OF THE RED MULLET, MULLUS BARBATUS
(ACTINOPTERYGII: PERCIFORMES: MULLIDAE), OFF THE NORTHERN
TUNISIAN COAST (CENTRAL MEDITERRANEAN)

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Chérif M., Ben Amor M.M., Selmi S., Gharbi H., Missaoui H., Capapé C. 2011. Food and feeding habits of the red mullet, Mullus barbatus (Actinopterygii: Perciformes: Mullidae), off the northern Tunisian coast (central Mediterranean). Acta Ichthyol. Piscat. 41 (2): 109–116.

Background. The red mullet, Mullus barbatus L., is abundantly captured and targeted throughout the year in Tunisian waters but not all aspects of its biology have been studied well. One of them—the feeding behaviour of this fish may be important for stock assessment, ecosystem modelling, and understanding mechanism and processes which structure and influence the fish assemblages. The aim of this paper is to describe the diet of specimens from the northern coast of Tunisia, to analyse seasonal variations in its composition and to delineate feeding intensity in relation to sex and size.

Materials and methods. Red mullet were sampled from different landing sites along the northern Tunisian coast and the Gulf of Tunis. Random samples were taken from both commercial and demersal trawlers from January to December 2005. A total of 472 specimens were examined following the commonly accepted procedures. The following parameters were analysed: vacuity index, percentage frequency of occurrence, percentage numerical abundance, percentage gravimetric composition, and index of relative importance. The trophic level for any consumer species was calculated, for total sample, but also in relation to size, sex, and season.

Results. Mullus barbatus mainly fed on crustaceans and polychaetes. According to the classification of fishes in functional groups based on their TROPH red mullet is an omnivorous feeder, animal species being preferential preys. Basing on data assembled by Stergiou and Karpouzi for the Mediterranean ichthyofauna, the estimated trophic levels for the red mullet ranged between 2.79 and 3.57 units. Such within-species differences in trophic levels might reflect the combined effect of the following factors: area, year, length structure, and differential fishing pressure between years and/or areas, because fishing removes the largest individuals of a species, which generally have higher trophic levels.

Conclusion. The red mullet is not only omnivorous, but also opportunistic feeder with trophic level related to body size, season, geographic area and fishing pressure.

Keywords: Mullus barbatus, food composition, trophic level, Tunisia, central Mediterranean

INTRODUCTION
Of the three mulloid species recorded to date in Tunisian waters, two are commonly recorded the red mullet, Mullus barbatus L., and the surmullet (or striped red mullet), M. surmuletus L. (see Bradaï et al. 2004). Both species are abundantly captured throughout the year; the mean production reached 4434.7 t between 2004 and 2008 (Anonymous 2008). The third species is the Por’s goatfish, Upeneus pori Ben-Tuvia et Golani, 1989, one the Lessepsian migrant fish species, considered as successfully established in the eastern Mediterranean Sea (Golani et al. 2002). This latter species was firstly found in southern Tunisia by Ben Souissi et al. (2005), then, it migrated toward northern area, and was recorded in the brackish Lagoon of Bizerte by Azzouz et al. (2010). A second alien species was recorded only recently; it was identified as a specimen of the west African goatfish, Pseudupeneus prayensis (Cuvier, 1829), according to Azzouz et al. (2011).

Food and feeding habits of Mullus barbatus formed the object of several studies conducted from specimens

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caught off different Mediterranean areas (Wirszubski 1953, Jukic and Zupanovic 1967, Focardi et al. 1979, Caragitsou and Tsimenides 1982, Froggia 1988, Labropoulou et al. 1997, Badalamenti et al. 2000, Mahé et al. 2005, Layachi et al. 2007). With special regard to Tunisian marine waters, a single study was dealt three decades ago by Gharbi and Ktari (1979) for specimens caught in the Gulf of Tunis. The feeding behaviour of teleost species contributes to knowledge fish stock assessment and ecosystem modelling. Additionally, Kotrshall and Thomson (1986) noted that such study of feeding habits is necessary and useful to understand mechanism and processes which structure and influence fish assemblages. Thus, understanding of the food web structure of fishes may serve as a basis for the maintenance of trophic level balance, thereby preventing the fishing-induced trophic level decline (Stergiou and Karpouzi 2002) within an ecosystem context of fisheries management (see Browman et al. 2004). The aim of this paper is to describe the diet of Mullus barbatus northern coast of Tunisia, to analyse seasonal variations in its composition and to delineate feeding intensity in relation to sex and size, and also to try to assess regional differences between specimens from northern areas and the Gulf of Tunis.

MATERIALS AND METHODS

Red mullet, Mullus barbatus L., were sampled from different landing sites along northern Tunisian coast and the Gulf of Tunis (Fig. 1). This area is characterized by a small continental shelf with sandy and rocky bottoms, with depths not exceeding 200 m; the mean water temperature reached 13°C in winter and 24°C in summer (Azouz 1973). Monthly samples were collected from January to December 2005 from both commercial and demersal trawlers. After landing, commercially caught specimens were preserved on ice, and transported to the laboratory, where they immediately processed. A total of 472 specimens were examined. Total length (TL) was recorded to the nearest cm, and weighed for total mass to the nearest g. Males and females were separately considered. The stomach contents of fresh specimens were removed, examined, and weighed. The preys were removed, sorted, and identified to the lowest possible taxonomic level using keys and fields (Riedl 1963, Perrier 1964, 1975, Fischer et al. 1987). The preys were counted and weighed to the nearest decigram.

In order to assess changes in diet versus total length, the sample was divided into four size classes: the first (TL < 10 cm, n = 63), the second (10 < TL < 15 cm, n = 153), the third (15 < TL < 20 mm, n = 184) and the fourth (TL > 20 cm, n = 72). The four size classes were chosen as they approximate the age of the species, as determined from the Von Bertalanffy growth equation derived by Gharbi (unpublished*). Additionally, Gharbi (unpublished*) considered as adult all specimens larger than 13 mm TL.

To analyze the food and feeding habits of Mullus barbatus, we used some indices following Hureau (1970), Zander (1982), and Rosecchi and Nouaze (1987): vacuity index (VI = number of empty stomachs/total number of stomachs × 100), percentage frequency of occurrence (%F = number of stomachs containing prey i/total number of full stomachs × 100), percentage numerical abundance (%N = number of prey i/total number of prey × 100), and percentage gravimetric composition (%W = weight of prey i/total weight of all prey × 100). The index of relative importance (IRI) of Pinkas et al. (1971), as modified by Hacunda (1981): IRI = %F × (%N + %W). This index, that integrates the three previous percentages, allows an interpretation much more real for food by minimizing the skews caused by each one of these percentages.

In order to be able to determine the different categories of food, this food has been regrouped according to the classification proposed by Rosecchi and Nouaze (1987). The value of the index of every item is expressed in percentage of the sum of all indices (Σ IRI). Prey species were stored in decreasing order according to their percentage IRI contribution and then cumulative %IRI was calculated. In this order, the %IRI of first prey are gradually added until to obtain 50% or more, these items are main food; this calculation is pursued until has get 75% or more, these items are called secondary preys; the other items are accidentally accidental.

The diet composition data were also used for the estimation of the trophic level of the red mullet. The trophic level for any consumer species $i$ is (Pauly et al. 1998, Pauly and Christensen 2000, Pauly and Palomares 2000):

\[ \text{TROPH}_i = 1 + \sum_{j=1}^{C} DC_{ij} \times \text{TROPH}_j \]

\* Gharbi H. 1980. Contribution à l’étude biologique et dynamique des rougets (Mullus barbatus Linnaeus, 1758 et Mullus surmuletus Linnaeus, 1758) des côtes tunisiennes. PhD Thesis, Faculty of Sciences of Tunis, University of Tunis.
where TROPH\(_j\) is the fractional trophic level of prey \(j\), DC\(_i\) represents the fraction of \(i\) in the diet of \(i\) and \(G\) is the total number of prey species.

The TROPH and (SE) standard errors of red mullet in the study area were calculated using TrophLab (Pauly et al. 2000); a standalone Microsoft Access routine for estimating trophic levels, downloadable from www.fishbase.org. The relationship between TROPH and the mid point of each length class considered here was quantified using the following equation (Cortès 1999):

\[
\text{TROPH}_{Li} = \text{TROPH}_{L\infty} (1 - e^{-KL_i})
\]

where TROPH\(_{L\infty}\) is the asymptotic TROPH and \(K\) is the rate at which TROPH\(_{L\infty}\) is approached (abbreviations as in Cortès (1999)). Statistical differences (\(P < 0.05\)) in basic diet composition as a function of size and season were established by applying a c2 test (Sokal and Rohlf 1987).

**RESULTS**

**Overall analysis of the diet.** A total of 472 stomachs of red mullet were examined, the TL of specimens ranged between 8 and 21 cm for males, and between 8 and 24 cm for females. In all, 286 stomachs contained food or remains of food, with VI = 60.6% (\(\chi^2 = 22.63, P < 0.05\)). Seven major systematic groups occurred in guts: polychaetes, crustaceans, molluscs, echinoderms, nematodes, teleosts, and algae (Table 1). It should be taken into consideration that, as a result of the degree of digestion of the prey, the determination to the level of species was often not possible.

The food composition of red mullet caught off northern Tunisian constituted mainly of crustaceans; polychaetes were secondary preys while molluscs, echinoderms, nematodes, teleosts, and algae were less frequent items in stomach contents.

The three diet indexes (Table 1) showed that crustaceans were preferentially consumed, and identified in higher abundance (51.71%), weight (47.46%), and occurrence (131.1%). The crustaceans were mainly decapods (Pagurus sp.; F = 29.74%), amphipods (Gammarus gammarus; F = 25.13%), and euphausiids (Nyctiphanes sp.; F = 22.09%). Less abundant crustaceans included mysids (Paramysis sp.; F = 18.23%), isopods (F = 21.34%), and cumaceans (F = 14.57%). Polychaetes (Nereis caudata) are also consumed in fairly large proportions (F = 59.31%).

* Mullus barbatus fed occasionally on molluscs species identified in relative abundance 11.96% and weight 13.68%. Among them, mesogastropoda (Turitella sp.; F = 11.05%) and bullomopha (Philine sp.; F = 7.73%) were the most recorded. Additionally, echinoderms were present in fairly large proportions by mass and number (%W = 7.18; %N = 7.31 respectively). Other taxa found in the stomach contents, but of lesser importance, were nematodes, teleosts, and algal remains (Table 1).

### Table 1

| Prey item taxonomic identity | %F | %N | %W | %IRI |
|-----------------------------|----|----|----|------|
| Polychaeta                  |    |    |    |      |
| Phyllocodida                |    |    |    |      |
| Nereidae                    |    |    |    |      |
| *Nereis caudata*            | 59.31 | 18.28 | 23.52 | 14.72 |
| Crustacea                   |    |    |    |      |
| Decapoda                    |    |    |    |      |
| Paguridae                   |    |    |    |      |
| *Pagurus* sp.               | 29.74 | 10.42 | 14.65 | 23.41 |
| Amphipoda                   |    |    |    |      |
| Gammaridae                  |    |    |    |      |
| *Gammarus gammarus*         | 25.13 | 9.31 | 12.74 | 17.17 |
| Euphausiacea                |    |    |    |      |
| Euphausiidae                |    |    |    |      |
| *Nyctiphanes* sp.           | 22.09 | 8.21 | 8.27 | 14.34 |
| Mysidacea                   |    |    |    |      |
| Mysidae                     |    |    |    |      |
| *Paramysis* sp.             | 18.23 | 7.12 | 4.12 | 7.76 |
| Isopoda                     |    |    |    |      |
| Unidentified remains        | 21.34 | 9.06 | 5.52 | 9.25 |
| Cumacea                     |    |    |    |      |
| Unidentified remains        | 14.57 | 7.59 | 2.16 | 5.54 |
| Total Crustacea             | 131.1 | 51.71 | 47.46 | 77.47 |
| Mollusca                    |    |    |    |      |
| Mesogastropoda              |    |    |    |      |
| Turritellidae               |    |    |    |      |
| *Turitella* sp.             | 11.05 | 5.11 | 3.17 | 2.44 |
| Bullomopha                  |    |    |    |      |
| Philinidae                  |    |    |    |      |
| *Philine* sp.               | 7.73 | 3.32 | 2.35 | 1.38 |
| Pectinoidea                 |    |    |    |      |
| Pectinidae                  |    |    |    |      |
| Unidentified remains        | 5.35 | 1.31 | 2.52 | 0.66 |
| Nuculoidea                  |    |    |    |      |
| Nuculanidae                 |    |    |    |      |
| *Nucula pella*              | 6.98 | 2.22 | 5.64 | 0.27 |
| Total Mollusca              | 31.11 | 11.96 | 13.68 | 4.75 |
| Echinodermata               |    |    |    |      |
| Ophiuroidae                 |    |    |    |      |
| Amphiuridae                 |    |    |    |      |
| Unidentified remains        | 7.48 | 2.22 | 3.49 | 0.65 |
| Echinoida                   |    |    |    |      |
| Regularia                   |    |    |    |      |
| Unidentified remains        | 8.91 | 2.97 | 2.42 | 0.92 |
| Asteroidea                  |    |    |    |      |
| Unidentified remains        | 6.13 | 2.12 | 1.27 | 0.37 |
| Total Echinodermata         | 22.52 | 7.31 | 7.12 | 1.94 |
| Teleostei                   |    |    |    |      |
| Unidentified remains        | 9.45 | 3.28 | 2.35 | 0.32 |
| Nematoda                    |    |    |    |      |
| Unidentified remains        | 6.72 | 2.43 | 1.71 | 0.18 |
| Algae                       |    |    |    |      |
| Unidentified remains        | 4.71 | 1.01 | 1.23 | 0.15 |
| Total unidentified remains  | 12.54 | 4.02 | 2.87 | 0.47 |

%N = percentage by number; %W = percentage by weight; %F = percentage by occurrence; %IRI = index of relative importance.
Analysis based on the feeding index (%IRI) showed that crustaceans were mostly ingested by *Mullus barbatus*, decapods (%IRI = 23.41), amphipods (%IRI = 17.17), and euphausiasids (%IRI = 14.34), (see Table 1). The TROPH of *M. barbatus* from northern Tunisian coast was 3.39 (SE = 0.45) indicating that the species could be considered an omnivore, however animal prey were mainly found in stomach contents (2.9 < TROPH > 3.7).

**Diet related to sex.** Of the 168 male stomach contents examined (TL ranged between 8 and 21 cm), 98 were empty (VI = 20.76%), whilst of the 304 female stomach contents examined (TL ranged between 8 and 24 cm), 188 were empty (VI = 39.83%): VI significantly differed between males and females ($c^2 = 11.02$, $P < 0.05$). The %IRI index indicates that the main prey group was crustaceans for both males and females, %IRI = 78.53 and %IRI=81.47, respectively (Table 2). The trophic level did not change with sex, it was 3.35 (SE = 0.41) for males and 3.38 (SE = 0.43) for females ($c^2 =0.67$, $P >0.05;$ df= 1).

**Diet related to size.** The diet of *Mullus barbatus* showed changes related to size (Table 3). Teleosts were found only in the smallest size class of specimens (TL < 10 cm) and algae only in the larger classes. Additionally, %IRI index analysis applied to all size-classes showed that crustaceans and polychaetes constituted the main prey category. Molluscs were the secondary prey; remaining prey such as echinoderms and nematodes were of minor importance and maybe accidental food. The percentage of the index of relative importance (%IRI) of polychaetes, crustaceans, and molluscs varied significantly between size categories ($c^2 = 85.42; P < 0.05; df=3$).

The importance of crustaceans and polychaetes increased with size, concomitantly the importance of molluscs and echinoderms decreased (Table 4). However, remains of preys such as nematodes and algae were not significantly different among the size classes. The trophic level of *Mullus barbatus* increased with size (Fig. 2). The relation between TROPH and size (TL, cm) was asymptotic:

$$TROPH_L = 3.44(1 - e^{-0.43L})$$

**Seasonal variation in the diet composition.** The analysis of stomach contents showed that VI was affected by seasonal changes, higher in spring and summer, reaching 61.5% and 67.3%, respectively, and decreased from 46.9% to 40.4% during autumn and winter, respectively. These percentages were significantly different within the year ($c^2 = 17.51$, $P >0.05;$ df= 3).

### Table 2

| Prey item | Male | Female |
|-----------|------|--------|
| %IRI      | %IRI |
| Polycheta | 13.09| 12.64  |
| Crustacea | 78.53| 81.47  |
| Mollusca  | 4.86 | 3.15   |
| Echinodermata | 1.42 | 0.94   |
| Nematoda | 0.13 | 0.18   |
| Osteichthyes | 0.08 | 0.12   |
| Algae | 0.11 | 0.27   |
| Unidentified items | 1.78 | 1.23   |

%IRI = index of relative importance.

### Table 3

| Prey item | Fish length class (%IRI) [cm] |
|-----------|------------------------------|
|           | <10  | 10–15 | 15–20 | >20 |
|           | (n = 63) | (n = 153) | (n = 184) | (n = 72) |
| Polycheta | 12.97 | 12.7  | 14.02 | 14.24 |
| Crustacea | 77.68 | 78.22 | 80.14 | 80.34 |
| Mollusca | 3.43 | 2.71 | 2.35 | 2.03 |
| Echinodermata | 2.72 | 2.43 | 1.16 | 1.17 |
| Nematoda | 1.35 | 1.33 | 0.67 | 0.32 |
| Osteichthyes | 0.11 | 0.6  |  |  |
| Algae | 0.64 | 0.47 | 0.78 |
| Unidentified items | 1.74 | 1.37 | 1.19 | 1.12 |

%IRI = index of relative importance.

### Table 4

| Prey item | Winter (n = 115) | Spring (n = 109) | Summer (n = 107) | Autumn (n = 131) |
|-----------|------------------|------------------|------------------|------------------|
| %IRI      | %IRI             | %IRI             | %IRI             | %IRI             |
| Polycheta | 14.23            | 13.4             | 13.46            | 14.67            |
| Crustacea | 78.56            | 78.9             | 79.37            | 77.82            |
| Mollusca | 3.11             | 3.41             | 3.64             | 4.02             |
| Echinodermata | 1.1             | 0.67             | 0.91             | 0.73             |
| Nematoda | 0.1              | 0.1              | 0.13             | 0.21             |
| Osteichthyes | 0.12            | 0.1              | 0.12             | 0.1              |
| Algae | 0.19             | 0.1              | 0.08             | 0.08             |
| Unidentified items | 1.12          | 1.2              | 1.45             | 1.31             |

**Fig. 2.** Relation between trophic level (TROPH) and total length (TL) of *Mullus barbatus* off the northern Tunisian coast
Crustaceans and polychaetes were the dominant prey groups throughout the year, especially in autumn and winter. Crustaceans occurred in stomach contents throughout the year, the maximum %IRI (=79.37) was recorded in summer. Polychaetes were also present in guts during all seasons, while teleosts were only found in summer and autumn (Table 4).

Seasonal significant differences weren’t found for remaining prey group (c² = 1.17, P > 0.05). The TROPH of red mullet did show significant changes with season; 3.41 in spring, 3.40 in summer, 3.36 in autumn, and 3.38 in winter (c² = 7.67; P < 0.05; df = 3).

**DISCUSSION**

The food composition of red mullet, *Mullus barbatus* L., caught off northern Tunisian was mainly constituted by crustaceans species, polychaetes were secondary preys while mollusces, echinoderms, nematodes*, osteichthians, and algae were of minor importance in stomach contents. This diet composition was partially in agreement with previous studies carried out in other marine areas. In the Tunisian coast, Gharbi and Ktari (1979) noted that red mullet caught in the Gulf of Tunis fed on crustaceans (amphipods, decapods, and isopods) and less intensively on polychaetes and molluscs. Layachi et al. (2007) reported that specimens from the Mediterranean coast of Morocco consumed crustaceans amphipods, polychaetes, and bivalves while decapods, isopods and nematodes were secondary preys. Studies conducted in western Greek Sea showed that the diet of *Mullus barbatus* consisted in crustaceans, polychaetes, and bivalves (Caragitsou and Tsimenidis 1982, Papaconstantinou and Caragitsou 1987). By contrast, other studies conducted in the same area pointed out that the species mainly fed mainly on polychaetes, mollusces, echinoderms, and a bit less on teleosts (Vassilopoulou and Papaconstantinou 1993, Labropoulou and Eleftheriou 1997, Machias and Labropoulou 2002), while similar pattern was reported in specimens from the eastern Mediterranean by Wirszubski (1953). These changes in diet are not very important; they could be the results of sampling and/or biological environment. The large spectrum of both prey groups and of prey items species recorded in guts indicated that red mullet could be considered specialist an opportunistic feeders. The morphological characteristics and the foraging behaviour of *Mullus barbatus* account for both prey type selection and the feeding patterns observed (Labropoulou et al 1997, Machias and Labropoulou 2002).

The high levels of vacuity index recorded in spring and summer suggest that red mullet from the Tunisian coast eat less during these seasons. Such phenomenon is probably due to the fact that breeding period occurred in spring and early summer, and during this period gonads increased in size and mass and completely filled the visceral cavity (Cherif et al. 2007). Similar patterns were observed in other Mediterranean regions for *Mullus barbatus* from Morocco (Layachi et al. 2007).

Changes in food composition with fish size are well established***) noted that mullet present a relatively small seasonal changes. The main diet components of male and female red mullet were crustaceans and polychaetes throughout the year in agreement with observations carried out on red mullet from the Gulf of Lions (northwestern Mediterranean) by Bautista-Vega et al. (2008). Diet changed are linked to prey availability in relation with the dynamics of the water masses in the region, similar patterns were reported for Moroccan coast (Layachi et al. 2007), the Gulf of Lions (Gharbi and Ktari 1979), Spanish waters (Aguirre and Sánchez 2005), and western Greece Sea (Vassilopoulou and Papaconstantinou 1993). The diet of *Mullus barbatus* from the northern Tunisian coast showed the importance of decapods (*Pagurus sp.*) and amphipods (*Gammarus gammarus*) throughout the year, in agreement with previous feeding studies that pointed out the occurrence of same preys in stomachs of other demersal teleost species, such as *Mullus surmuletus* and *Labrus merula*, indicating the abundance of such preys off the northern Tunisian coast (Gharbi and Ktari 1979, Ben Slama et al. 2007).

Our results indicate that *Mullus barbatus* mainly fed on small crustaceans and polychaetes. Conversely, large crustaceans, such as shrimps were not found in guts probably because *M. barbatus* feeds on small benthic invertebrates, inhabiting sandy and/or muddy bottoms, and detected by chemoreceptor barbels on the chin (Hureau 1986). N’Da (unpublished***)) reported that mullet collected from the Bay of Biscay fed on small preys such as cumaceans, amphipods, copepods, the largest items were gobidiids having between 10 and 15 mm total length. N’Da (unpublished***)) noted that mullet present a relatively small

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* Editor’s comment: some nematodes found in the alimentary tract of fishes may be parasites and not food items.

** See footnote on page 110.

*** N’Da K. 1992. Biologie du rouget de roche Mullus surmuletus (Poisson Mullidae) dans le nord du golfe de Gascogne: reproduction, larves et juveniles. PhD Thesis, Université de Bretagne Occidentale, France.
mouthing and small teeth, it is rather specialized for suction captures of small preys which live in or on the substrate.

According to the classification of fishes in functional groups based on their TROPH (Stergiou and Karpouzi 2002), red mullet is an omnivorous feeder, however animal species were more consumed than algae, for instance. Similar feeding habits were reported for red mullet elsewhere such as in Mediterranean area. Basing on data assembled by Stergiou and Karpouzi (2002) for the Mediterranean ichthyofauna, the estimated trophic levels for the red mullet ranged between 2.79 and 3.57 units. The changes of trophic levels recorded in *M. barbatus* might reflect the combined effect of the following factors: area, year, length structure, and differential fishing pressure between years and/or areas, because fishing removes the largest individuals of a species, which generally have higher trophic levels (Stergiou and Karpouzi 2002, Negzaou-Garali et al. 2008). The differences could also reflect the impact of other factors such as different methodology during investigations.

In conclusion, the results of the presently reported study and data from other areas show that red mullet is not only omnivorous, but also opportunistic feeder with trophic level related to body size, season, geographic area and fishing pressure which cannot be also excluded. Since 1980, the general use of shrimp boats with non selective nets, almost involved the destruction of benthic resources throughout the Tunisian marine waters, playing a negative role on local biodiversity, and considerably reducing prey species availability (Gharbi et al. 2004). The study of natural diets of fish species is very useful approach for understanding aspect of the species biology and ecology, towards a more sustainable management of their stocks and the development of conservation measures (La Mesa et al. 2007, Kitsos et al. 2008). A competition pressure for food cannot be totally excluded in the future between these closely related species, as it is the case for other Mediterranean areas, where *M. barbatus* and *M. surmuletus* were progressively replaced by other invasive species (Golani 1994). So a recent paper on diet composition of *M. barbatus* is needed to explain a probable interspecific competition between mullid species in the area. Food seems to be sufficiently available, at present, for two mullids species, this explained why we have cited both sympatric species. To date, it seems impossible to state if the biological environment will be qualitatively and quantitatively sufficient for other related which feed on same preys species.

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Received: 18 November 2010
Accepted: 16 April 2011
Published electronically: 30 June 2011