

Feeding habits and trophic level of sea bass (*Dicentrarchus labrax*) in the Messolonghi-Etoliko lagoons complex (Western Greece)

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The feeding habits and trophic level of sea bass (*Dicentrarchus labrax*) were investigated in the Messolonghi-Etoliko lagoons complex (Western Greece). The stomach content of 570 specimens was examined. Specimens with total length ranging from 17 to 748 mm were collected at monthly intervals during one-year period. Empty stomachs represented 34.5% of the total stomachs examined, showing high seasonal variation (maximum in November: 50%; minimum in May: 12%) as well as variation with size (class total length 17-31 mm: 9%; 141-200 mm: 58%). The most important prey items according to the Index of Relative Importance (IRI), were amphipods (*Gammarus* sp., IRI = 25.3%), shrimps (*Palaemon* sp., IRI = 22.5%), crabs (*Carcinus* sp., IRI = 20.8%), finfish (*Atherina boyeri*, IRI = 9.9%) and mugilids (Mugilidae) fry and juveniles (IRI = 8.9%) and copepods (IRI = 6.99%). Prey composition shifted progressively with increasing predator size: from small to medium size crustaceans as well as from small and medium size fish like *A. boyeri* and mugilids young individuals (fry and juveniles). The trophic level of sea bass in the area also increased with predator size ranging from 3 to 4.6. The role of the ecosystem as a nursery and feeding ground for sea bass, as well as the possible trophic competition with other lagoonal species, are also discussed.

Key words: sea bass, diet, food composition, trophic level, Messolonghi, lagoon.

INTRODUCTION

Information on the quality and quantity of consumed food by fish is important for the classic ecological theory, mainly in identifying omnivory, feeding competition, assessing predator-prey functional responses and structure as well as the stability of food webs (Gerking, 1994). Diet composition data are also used for the estimation of trophic levels. The trophic level expresses the relative position of an animal in the food webs that nourish them ranging, for marine animals, between 2 (herbivores/detritivores) and 5.5 (specialised predators such as marine mammals)

(Pauly *et al.*, 2000). The estimation of trophic level allows the development of new approaches to the analysis of marine food webs and thereby it is essential for the management of fisheries resources as well as for quantifying the effects of fishing on the ecosystem (Pauly *et al.*, 2000; Stergiou & Karpouzi, 2002).

Coastal lagoons and estuaries play an important role as nurseries, offering food and shelter for the larval, juvenile and adult stages of numerous fish species that spawn in the open sea (Costa *et al.*, 2002). The improvement of aquatic lagoon environments is among the aims of the EU Directive 2000/60/EC (Water Framework Directive, WFD), which defines qualitative, quantitative and ecological objectives aiming at the protection of these highly valuable ecosystems (Elliott & McLusky, 2002).

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The sea bass *Dicentrarchus labrax* (Linnaeus, 1758) is a demersal fish of high commercial interest which inhabits coastal waters up to about 100 m depth, although it is more common in shallow waters, on various substrates. It is a euryaline and eurythermal species, entering estuaries, lagoons and sometimes ascending rivers. Young fish form schools, but adults appear to be less gregarious. It is distributed in the North Atlantic from Norway and the British Isles, southward to Morocco, Canaries and the Senegal as well as in the Mediterranean and Black Seas (Pickett & Pawson, 1994).

Sea bass, along with gilthead sea bream (*Sparus aurata*) are the most important species of the Mediterranean aquaculture industry. Their total production in the Mediterranean reached 17×10^4 tn in 2004, with Greek aquaculture industry claiming almost half of the production and the relative contribution of the sea bass being about 40% (Dimitriou *et al.*, 2007). It is also very important for lagoon fisheries in the Mediterranean because of its euryhalinity and high commercial value (Ardizzone *et al.*, 1988); in Greek lagoons it represents about 5% of the annual yield (Anonymous, 2001).

An extensive amount of literature exists concerning sea bass feeding. Most of these studies were conducted in the estuarine systems of European Atlantic (Kennedy & Fitzmaurice, 1972; Aprahamian & Barr, 1985; Kelley, 1987; Pickett & Pawson, 1994; Cabral & Costa, 2001; Hampel *et al.*, 2005; Sa *et al.*, 2006; Martinho *et al.*, 2008) as well as in estuarine and lagoonal Mediterranean regions (Ktari *et al.*, 1978; Barnabe, 1980; Ferrari & Ghierregato, 1981; Roblin & Brusle, 1984; Kara & Derbal, 1996). These studies mainly focus on the young stages of the species, whereas few studies cover only adult (Kelley, 1987; Kara & Derbal, 1996) and/or adult specimens of the species (Kennedy & Fitzmaurice, 1972; Barnabe, 1980; Pickett & Pawson, 1994). However, the ontogenetic variation of the trophic level of sea bass has not yet been estimated.

Hence, the study of trophic ecology is fundamental and useful towards the understanding of the functional role of fish within their ecosystem. The need of quantifying the feeding behavior of fish in these ecosystems becomes more imperative if one considers the rapid expansion of aquaculture in the coastal zone and the increased awareness concerning its possible impact on the lagoonal fish populations (Dimitriou *et al.*, 2007). Also, a last aspect potentially related with the changes in the habits of the lagoonal species concerns the modification of environmental

parameters of the lagoons in the context of global climatic changes.

Under this scope, information concerning the feeding habits of sea bass in the area proved to be particularly useful not only for comparison with future studies but also for understanding the trophic role of the species in the ecosystem. The aim of the present study was to provide qualitative and quantitative information on food, feeding habits and trophic level of sea bass in the Messolonghi-Etoliko lagoon complex (Western Greece) with special emphasis on the ontogenetic and seasonal variation of its diet.

MATERIALS AND METHODS

Study area

The Messolonghi-Etoliko lagoon complex (Fig. 1) represents one of the most important coastal lagoon systems in the Mediterranean Sea and the largest one in Greece (150 km²), accounting for approximately 50% of the total Greek lagoon surface (Anonymous, 2001). It consists of six distinct lagoons (Fig. 1) that can be defined by their topographic, hydrological and biological characteristics. In the adjacent coastal area, a large number of fish farms (more than 25% of the total Greek fish farms) and hatcheries (20% of the total Greek hatcheries) operate which in 2004 produced more than 15% of the Mediterranean production and the relative contribution of the sea bass was about 40% (Dimitriou *et al.*, 2007). The total annual fish landings from the lagoonal complex decreased from 1500-2000 tn in the 1960's to 1300-1500 tn in recent years (1988-1998) and is provided by 200 fishermen working at the barrier traps and 700 individual fishermen fishing in the lagoon using several fishing gears (i.e. net, spear, long line, light) (Katselis *et al.*, 2003). The mean annual percentage contribution of the species of landings coming from the barrier traps during the period 1988-1998, was 51.9% Mugilidae species (*Liza saliens*, *Liza aurata*, *Liza ramada*, *Chelon labrosus* and *Mugil cephalus*), 18.1% eels (*Anguilla anguilla*), 13.7% gilthead sea bream and 1.4% sea bass (Katselis *et al.*, 2003). Sea bass in the lagoon is mainly being exploited by individual fishermen with various gears (nets, spear and long lines) but available data on its production do not exist. Hence, the sea bass landings were estimated at 4-5% of the lagoons total landings (Rogdakis, 2003). Water temperature in lagoons, is rapidly affected by air temperature due to the limited depth and a high correlation ($R^2 > 0.8$) has been found between these two param-

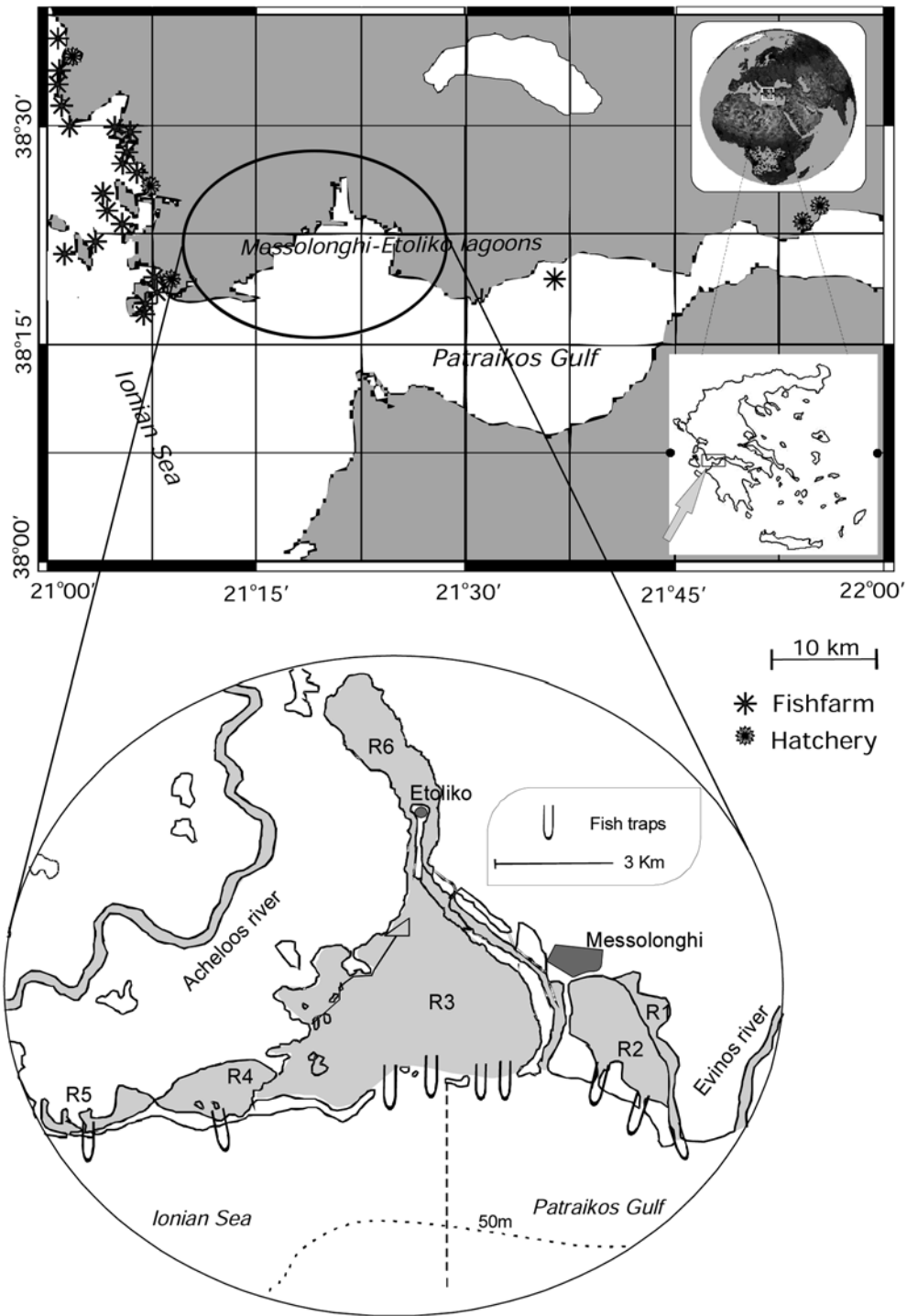


FIG. 1. Map of the study area.

ters in the study area (Ramfos *et al.*, 2007). Other biotic and abiotic features of the biotope as well as the fishing exploitation system and the seasonal analysis of the landings were presented in earlier papers (Katselis *et al.*, 2003, 2007).

Sampling

Samples of sea bass were collected on monthly basis, during the period from November 1993 to December 1994. Each month, one-daily sea bass landing was provided by a professional fisherman who was main-

ly operating at the central part of the lagoon (R3, Fig. 1) with trammel nets (mesh size of 22 to 24 mm). Individuals smaller than 60 mm were collected monthly by means of a fine-meshed beach seine net (mesh size 3 mm) at a station in Klisova lagoon (R2, Fig. 1). Immediately after collection the individuals were preserved in 10% formalin solution. Total length (TL) and wet weight (TW) of each specimen were measured to the nearest 0.1 mm and 0.01 g, respectively. Afterwards, the stomach was carefully removed and emptied. All prey items were identified and sorted to the lowest possible taxonomic level under a binocular stereoscope. Wet weight (PW) of each prey category in each stomach was obtained to the nearest 0.001 g after removal of all superficial water with filter paper. In total, the stomach content of 570 specimens was examined.

To estimate stomach fullness, the π index defined as: $\pi = 100 \times \frac{PW}{TW}$ was used. Four stomach fullness categories were defined; $\pi = 0\%$: empty, $0\% < \pi < 1\%$: semi-empty, $1\% < \pi < 2\%$: semi-full and $\pi > 2\%$: full stomach, according to Barnabe (1976).

The following indices were also used for the evaluation of the diet of the species (Hyslop, 1980):

Frequency of Occurrence (F_{pi}): $F_{pi} = (N_i/N_p)$, where N_i is the number of the stomachs in which the i^{th} food item was found and N_p is the number of non-empty stomachs.

Numerical Percentage (C_i): $C_i = \frac{n_i}{\sum_{i=1}^m n_i}$ where

n_i is the number of the i^{th} food item and m the number of food items encountered in the stomach.

Gravimetric Percentage (Wn_i): $Wn_i = \frac{PW_i}{\sum_{i=1}^m PW_i}$

where n_i is the number of the i^{th} food item and m the number of food items.

The relative importance of a food item in the diet of sea bass was assessed by the percent of modified Pinkas's Index of Relative Importance (IRI) (Pinkas et al., 1971):

$$IRI_i = \frac{F_{pi} \sqrt{C_i^2 + Wn_i^2}}{\sum_{i=1}^m F_{pi} \sqrt{C_i^2 + Wn_i^2}} \times 100$$

The Shannon-Wiener index (H') was used to estimate the trophic diversity in each stomach according to the formula $H' = -\sum_{i=1}^m p_i \times \ln p_i$ where p_i is the relative abundance of the i^{th} prey and m is the number of prey items in each stomach.

The trophic level (TrL) was estimated per season and per length class as follows (Pauly et al., 2000):

$TrL_j = 1 + \sum_{i=1}^m Wn_{ij} \times TrL_i$, where TrL_i is the fractional trophic level of prey i , Wn_{ij} is the gravimetric percentage of the i^{th} prey in the diet of j season or length class, and m is the total number of prey items. TrL values were calculated from each dataset using Troph Lab (Pauly et al., 2000), which is a stand-alone application for estimating TrL s and their standard errors (SE) (Stergiou & Karpouzi, 2002).

The relationship between TrL and the mid point of each length class considered here was quantified using the following modified logistic equation:

$$TrL(TL) = TrL_{min} + \frac{(TrL_{max} - TrL_{min})}{1 + e^{-a \cdot TL + b}}, \text{ where}$$

TrL_{min} and TrL_{max} are the low and upper asymptotic trophic level of species which represented the lower and maximum trophic level of the species, respectively. This equation describes two asymptotic trophic levels (upper and lower), a fact that is expected at feeding studies in relation to ontogenetic stages of fishes. Thus, this is more realistic than the one usually applied to the quantification of the relationship between the trophic level and length class size (Cortes, 1999), which describes only an upper asymptotic trophic level. Coefficients a and b of the above equation were estimated by non-linear regression analysis (Zar, 1999), using the SPSS 14.0 package (SPSS Inc, Chicago IL, USA).

Statistical differences in the diet composition with respect to length class and season were assessed by one-way analysis of variance by ranks (Kruskal-Wallis test) on the arcsine-root transformed numerical abundance of a given food item. The variation in fullness category was also tested by a chi-square test (χ^2) over a contingency table of number of stomachs (Zar, 1999).

In addition, in order to examine similarities on the IRI index among months, a simple clustering technique based on the Bray-Curtis similarity index was used (Bray & Curtis, 1957). To determine whether or not major shifts in species composition occurred between the groups defined by the cluster analysis we used a non-parametric analysis, permutation-based one-way analysis of similarities (One-Way ANOSIM test, R-statistic) (Clarke & Gorley, 2001). All prey categories with an overall value of IRI less than 0.03 were excluded from subsequent analyses (Field et al., 1982). The analyses were performed with the SPSS 14.0 (SPSS Inc, Chicago IL, USA) and PRIMER 5 (PRIMER-E Ltd, Ivydrige, UK) packages.

RESULTS

The total length of the captured individuals (n = 570) ranged from 17 to 748 mm (Fig. 2C). The mean total length showed significant differences among sampling months (Kruskal-Wallis test, H = 94.2, df = 11, p < 0.05) presenting higher values from March to July (Fig. 2B).

Feeding intensity

Of the 570 stomachs of sea bass examined, 197 (34.5%) were empty. The monthly proportion of empty stomachs varied significantly during the study period ($\chi^2 = 62.7$, df = 11, p < 0.05) showing maximum value in November (50%) and minimum in May (12.1%) (Fig. 3A). The proportion of empty stomachs among size classes also presented significant differences ($\chi^2 = 30$, df = 7, p < 0.05) ranging from 9% (class size: 17-31 mm) to 58% (class size: 141-200 mm). In general, specimens longer than 141 mm showed higher proportions of empty stomachs than smaller ones (TL < 140 mm) (Fig. 3B).

Diet composition

A total of 22 different prey items were identified in all stomachs, belonging to five major groups: crustaceans (copepods, isopods, amphipods, mysids, shrimp and crab larvae, shrimps – three genera – and crabs), finfish (six genera of finfish and finfish eggs), molluscs (bivalves, gastropods), polychaetes and aquatic plants. In terms of IRI index values, the most impor-

tant prey items were amphipods (*Gammarus* sp., IRI = 25.3%), shrimps (*Palaemon* sp., IRI = 22.5%), crabs (*Carcinus* sp., IRI = 20.8%), finfish (*Atherina boyeri*, IRI = 9.9%) and mugilids (Mugilidae) fry and juveniles (IRI = 8.9%) and copepods (IRI = 6.99%). The remaining prey items showed lower contribution in the diet of the species with IRI values ranging from 0.001 to 1.35% (Table 1).

Food in relation to fish size

The diet composition presented strong differences between fish size classes (Fig. 4). The contribution of the dominant prey items in the diet (copepods, amphipods, shrimps, crabs and fish) expressed either as gravimetric or as numerical percentage, differed significantly among the size classes (Kruskal-Wallis test, H > 33.7, df = 7, p < 0.05). The sea bass diet shifted from small size crustaceans (copepods and nauplii of decapods) at small individuals (TL: 17-31 mm), to medium size crustaceans (amphipods: *Gammarus* sp. and isopods: Sphaeromatidae and Idoteidae) at juveniles (TL: 32-200 mm) and to amphipods (*Gammarus* sp.), small shrimps (mainly *Palaemon* sp.) and crabs (*Carcinus* sp.) at the size class of 201-280 mm. At the larger size classes, the diet composition of sea bass shifted progressively to small and medium size fish like *A. boyeri* and young individuals of Mugilids (fry and juveniles) (Fig. 4A).

The Shannon-Wiener index (H') also differed significantly among fish size classes (H = 26.2, df = 7,

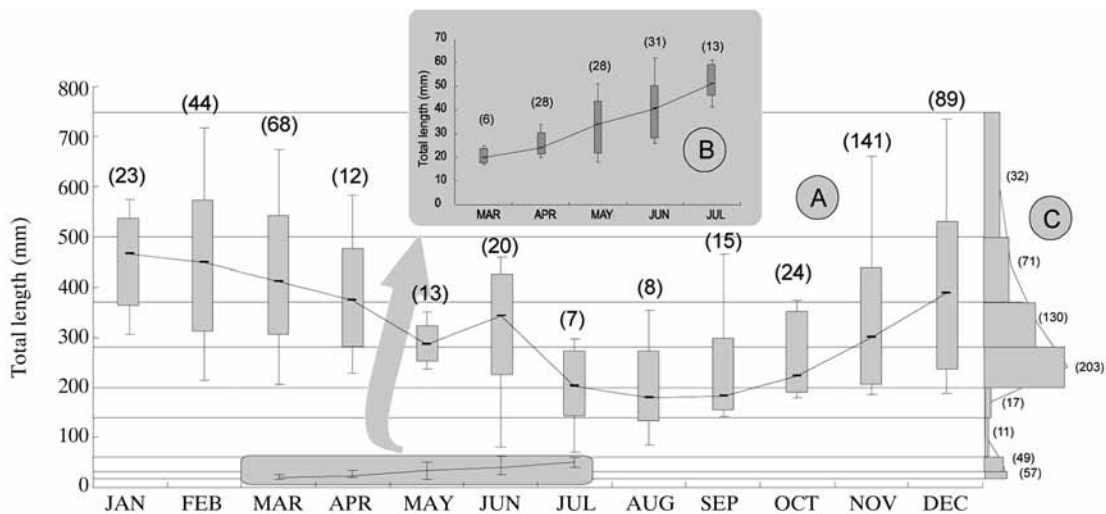


FIG. 2. Box-plots of adult (A), juvenile (B) sea bass total length and overall length distribution of the caught individuals (C) during the study period. The number of specimens is shown in parentheses.

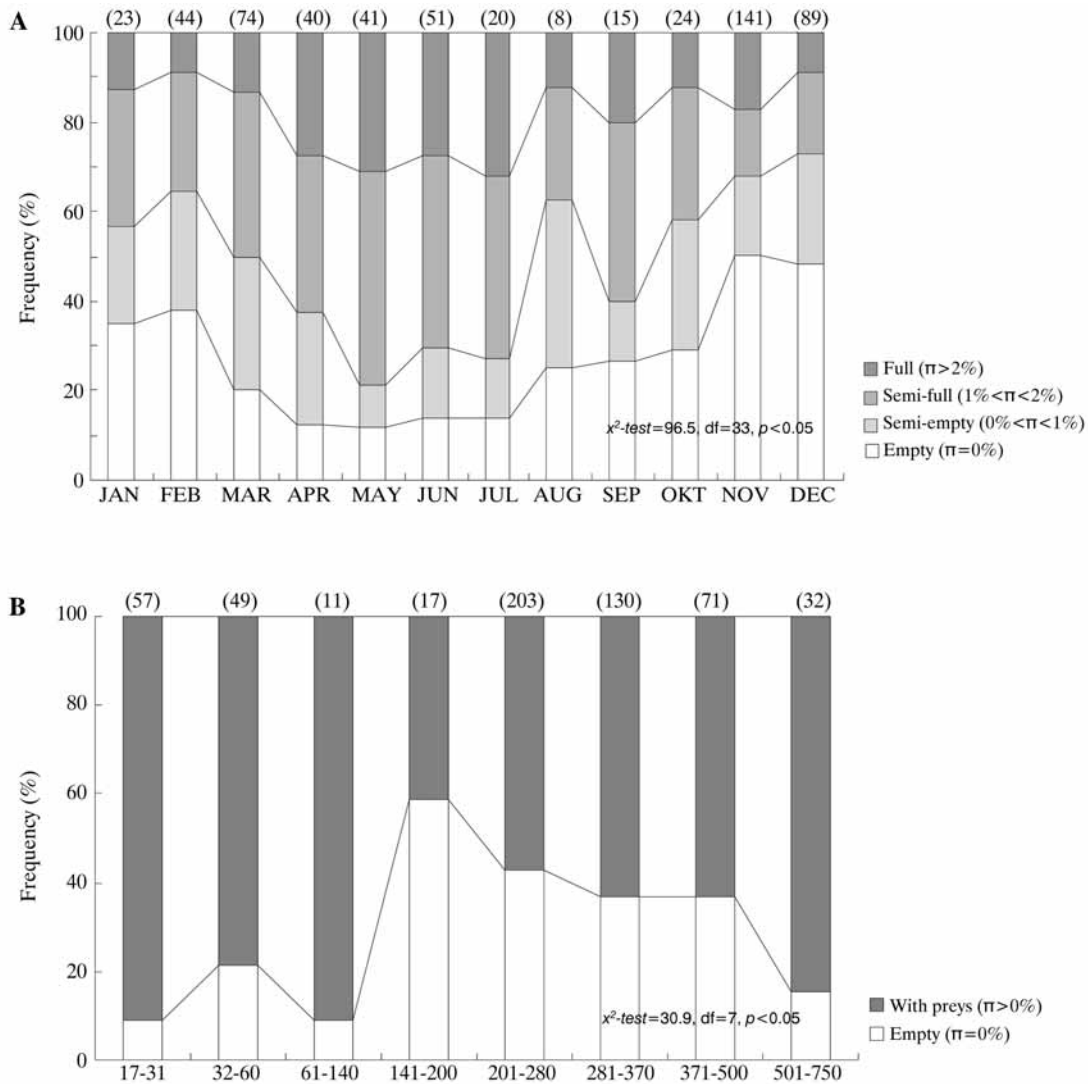


FIG. 3. Seasonal (A) and according to size classes (B) variation in the frequency of stomach fullness categories of sea bass in the Messolonghi-Etoliko lagoon complex. Number of specimens used in each size class is shown in parentheses.

$p < 0.05$). In general, smaller specimens (TL < 201 mm) showed mean values of H' less than 1 (except class 32-60 mm: $H' = 1.58$) whereas larger specimens (TL > 281 mm) had mean H' values higher than 1.90 (Fig. 4B).

Prey mean weight (PmW, g) showed an exponential increase in respect to predator total length (TL, mm): (PmW = $5.3 \times 10^{-6} TL^{2.01}$; $R^2 = 0.95$; $p < 0.05$).

The trophic level (TrL) of sea bass in the Messolonghi-Etoliko lagoons ranged from 3 to 4.6 showing increasing values with fish size ($H = 42.1$, $df = 7$, $p < 0.05$). The lower value of TrL was recorded at the size class of 17-30 mm. The TrL of small specimens (TL < 200 mm) was close to 3.3 whereas in the larger ones (TL > 400 mm) it was close to 4.2. An interme-

diante value of TrL (3.60) was recorded for specimens belonging to size class 201-280 mm. The relationship between TrL and total length (TL, mm) was:

$$TrL(TL) = 3.15 + \frac{(4.33 - 3.15)}{1 + e^{-0.02 \cdot TL + 4.6}}$$

[$R^2 = 0.91$; Standard error of estimate (SE_{est}) = 0.16] (Fig. 7).

Seasonal variation in diet composition

Bray-Curtis clustering based on monthly IRI values of prey items identified four groups of months at the 56% similarity level. Group I included autumn and winter months (from September to February), Group II summer months (June and July), Group III spring

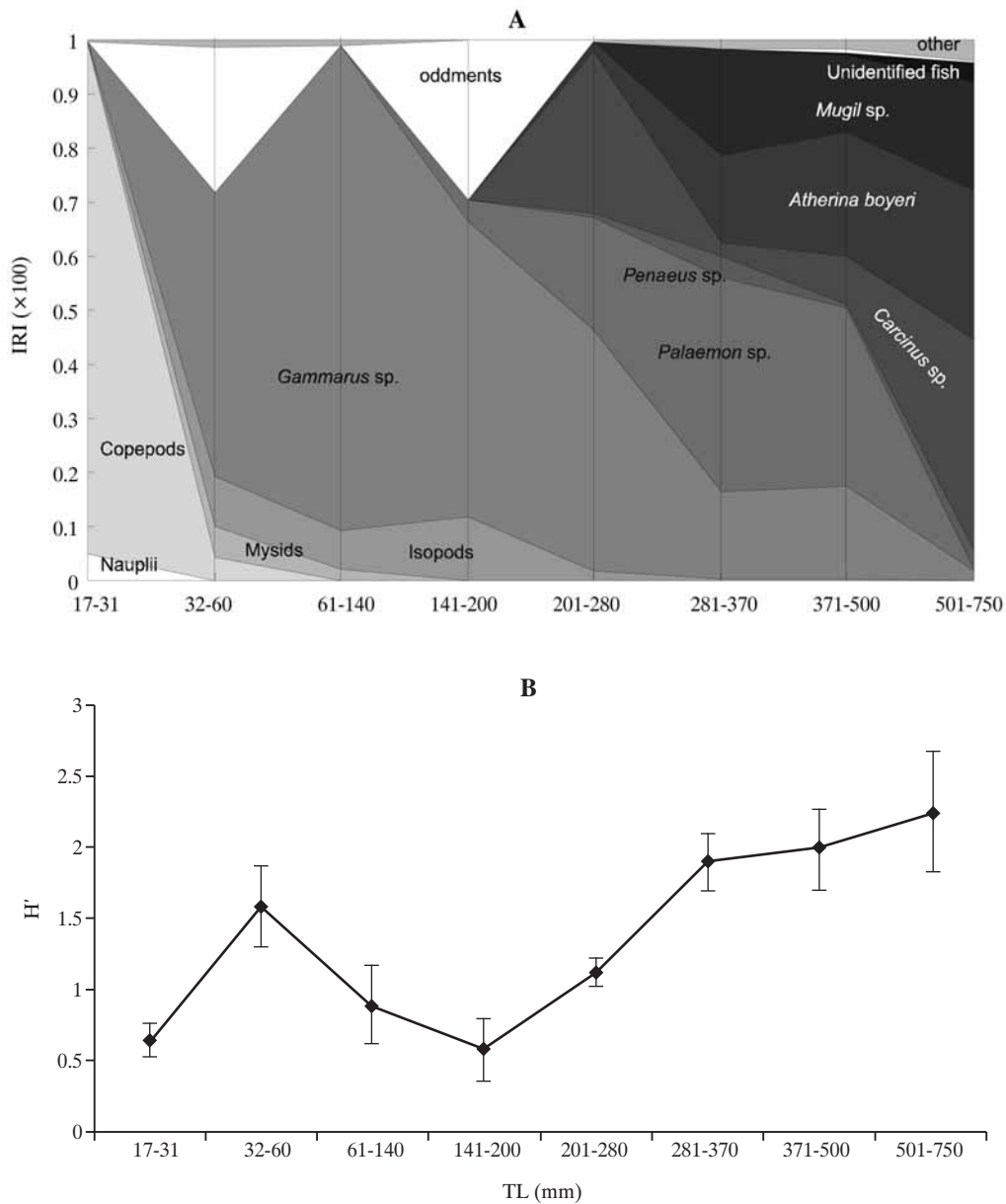


FIG. 4. Index of Relative Importance (IRI) (A) and mean values (vertical bars indicate the standard deviation) of Shannon-Wiener (H') diversity index (B) according to sea bass size classes in the Messo-longhi-Etoliko lagoon complex.

months (April and May) and finally Group IV included August and March (Fig. 5). These groups differed significantly in their species composition (R-statistic < 0.93 ; $p < 0.01$). Kruskal-Wallis test based on the individually arcsine-root transformed gravimetric as well as numerical percentage of a given food item, also, showed that the diet composition of sea bass was significantly different among the month-clusters ($H = 37.1$, $df = 11$, $p < 0.05$). The Shannon-Wiener diversity index of diet composition (H') also

differed significantly among the groups defined by the cluster analysis ($H = 12.1$, $df = 3$, $p < 0.05$).

Group I was characterized by the strong presence of *Carcinus* sp. (IRI = 28.2%), *Gammarus* sp. (IRI = 24.8%), *A. boyeri* (IRI = 18.3%) and Mugilids fry (IRI = 12.7%) as well as by the high diversity in diet composition ($H' = 1.84$). The diet composition in Group II was characterized by the dominance of *Gammarus* sp. (IRI = 63.2%), the low importance of *Palaemon* sp. (IRI = 14.3%) and *Carcinus* sp. (IRI = 9.6%) as

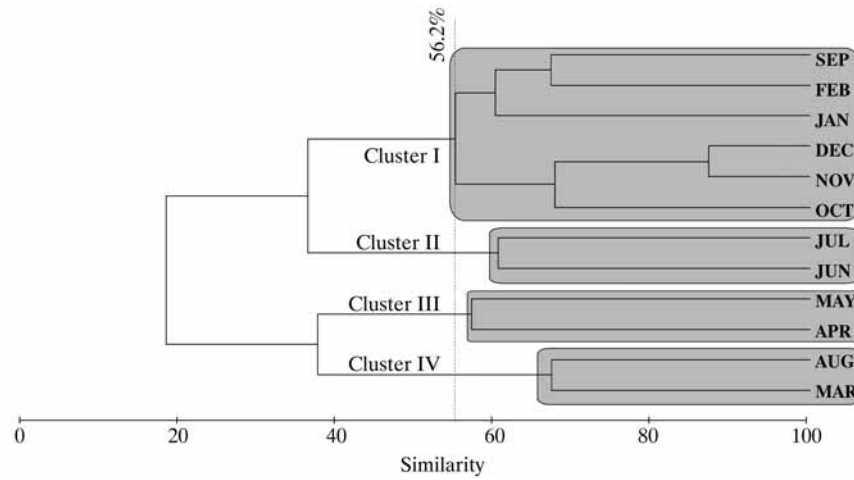


FIG. 5. Dendrogram of the cluster analysis comparing the diet of sea bass in the different sampling months, based on the monthly Index of Relative Importance (IRI).

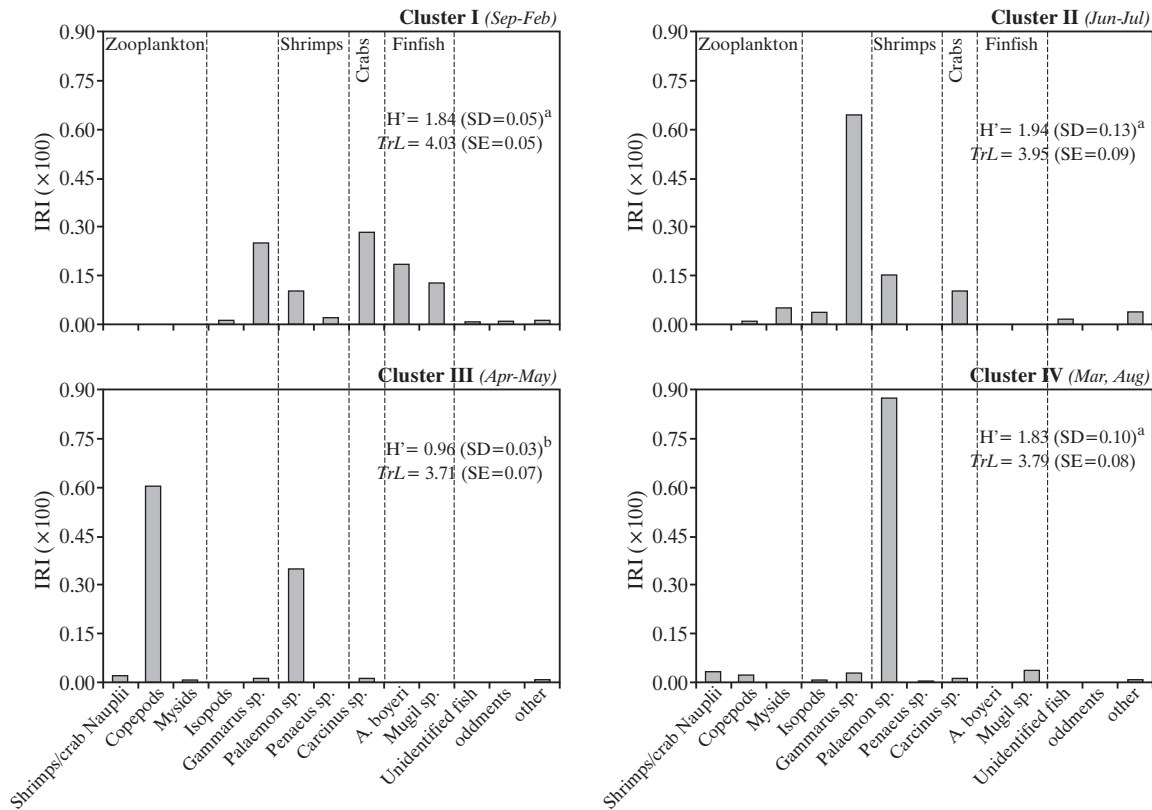


FIG. 6. IRI values of the different prey items in each Group of months as these were defined by the cluster analysis. Average values for the Shannon-Wiener diversity index (H') and estimated Trophic level are also shown for each Group. SD: standard deviation; SE: two times the standard error; a, b denote statistically homogenous values of H' among Groups.

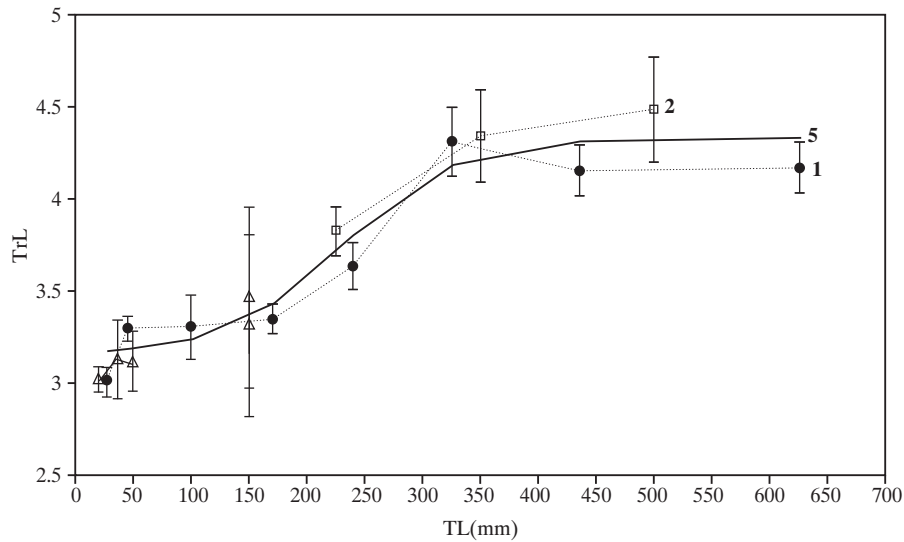


FIG. 7. Estimated sea bass trophic level of different size classes in various areas; (1) Messolonghi-Etoliko lagoons, Western Greece (present study); (2) Gulf Annaba, Algeria (Kara & Derbal, 1996); (3) Schelde estuary, Belgium and Netherlands (Hampel *et al.*, 2005); (4) Gulf of Lions, France (Roblin & Brusle, 1984); (5) model values estimated in the present study. Vertical bars indicate two times the standard error.

well as by the high diversity of diet composition ($H' = 1.94$) (Fig. 6). The diet composition in Group III was characterized by the lower diversity among Groups ($H' = 0.96$) whereas two prey items dominated (copepods: IRI = 60.3% and *Palaemon* sp.: IRI = 34.2%). The last group (IV) was characterized by the dominance of *Palaemon* sp. (IRI = 86.6%) (Fig. 6) as well as by high diversity ($H' = 1.83$).

Finally, no significant differences were found in the trophic level among the clusters ($H = 4.2$, $df = 3$, $p > 0.05$).

DISCUSSION

The stomach content analysis of sea bass in the Messolonghi-Etoliko lagoon complex revealed the significant ontogenetic and seasonal variation in the diet composition of the species. The feeding habits and strategies of sea bass have been studied in different areas using stomach content analysis (Kennedy & Fitzmaurice, 1972; Ktari *et al.*, 1978; Barnabe, 1980; Ferrari & Ghieregato, 1981; Roblin & Brusle, 1984; Arahamian & Barr, 1985; Kelley, 1987; Pickett & Pawson, 1994; Kara & Derbal, 1996; Cabral & Costa, 2001; Hampel *et al.*, 2005; Sa *et al.*, 2006; Martinho *et al.*, 2008) and have revealed marked preferences for small crustacean (zooplanktivores) in young ages. As predator size increases, a progressive shift in the diet occurs and the species feeds mainly on epibenthic

taxa (amphipods, isopods, shrimps and crabs) and afterwards on small fish, while showing an opportunistic feeding behavior at all sizes according to prey availability (Pickett & Pawson, 1994). As a general trend, this feeding behavior was also observed in the present study. However, significant discrepancies on lower taxonomic groups of prey items are more or less expected when comparing results from various geographical regions due to differences in prey composition and availability among the ecosystems (Martinho *et al.*, 2008).

The availability of prey with the appropriate size, along with water temperature, have been considered as the most important factors affecting the intensity of sea bass feeding (Pickett & Pawson, 1994). In the present study the maximum feeding intensity of sea bass (minimum percentage of empty stomachs: 12-15%) occurred during the period from April to July (Fig. 3A) and coincided with the first appearance of sea bass fry in the lagoon (Fig. 2B; Rogdakis, 2003). During this period of the year, copepod abundance usually presents an annual peak in Mediterranean lagoons (Lam Hai, 1985; Sei *et al.*, 1996; Ramfos *et al.*, 1999), thus increasing the possibility of consumption of this food by the majority of sea bass fries. Indeed, small-sized individuals of sea bass (17-31 mm) showed the maximum feeding intensity (percentage of empty stomachs < 10%, see Fig. 3B) as well as a strong preference for copepods as prey (Fig. 4A). These findings

support the important role of the Messolonghi-Etoliko lagoons as a nursery ground for the species, as has already been demonstrated for the 0⁺ age group in lagoonal, estuarine and salt-marsh environments (Ferrari & Ghiregato, 1981; Hampel *et al.*, 2005; Sa *et al.*, 2006; Martinho *et al.*, 2008). Moreover, the presence of both small (0⁺) as well as large (adult) individuals of sea bass in the Messolonghi-Etoliko lagoons (Rogdakis, 2003) reveals the twin role of the area on the ecology of species both as a nursery and feeding ground.

The progressive changes observed in the diet composition between small and large sea bass individuals were accompanied by an increase in prey diversity with predator size. This shift in diet reflects a combination of anatomical changes in the capture devices of the predator (mouth size and distance among the gill rakers) as well as the improved ability in capturing and handling larger prey (Gerking, 1994). Larger specimens consume larger prey and have a wide diet range as they can consume prey items that are not available to smaller fish. Given that prey size is correlated with its energetic value, it is possible that the larger fish try to maximize the energy intake by increasing the consumption of larger prey (Wooton, 1990). On the other hand, in general, diversity in diet composition was found low in sea bass individuals smaller than 200 mm, where copepods and amphipods constituted the main prey items. According to Eggers (1977), the diet diversity decreases with increasing prey density and populations of both copepods and amphipods are known to exhibit strong peaks in Mediterranean lagoons, especially during spring and summer months (Mistri *et al.*, 2001; Sei *et al.*, 1996). In all cases, differences in the diet pattern between individuals with different size decreased the intra-specific competition giving an advantage to the species to better exploit the available feeding resources.

The maximum percentage of empty stomachs (> 35%) in the study area occurred mainly during winter (i.e. November to February). The low temperatures of this period could partly explain the reduction in feeding intensity of sea bass. It has been noted that adult sea bass feed much less avidly in waters with temperatures below 10 °C (Pickett & Pawson, 1994) while in juveniles food intake decreases rapidly at temperatures below 10 °C and ceases at temperatures below 7 °C (Russell *et al.*, 1996). In the study area, the lower average minimum monthly air temperature estimated from a seven years time series (1991-1998) (Katselis *et al.*, 2007) was recorded in Fe-

bruary (4.9 ± 3.4 °C) while in November it was 9.24 ± 3.3 °C having a direct effect on water temperature (Ramfos *et al.*, 2007). On the other hand, the seasonality on the feeding activity of sea bass could be related with their spawning maturity (Wooton, 1990). Although the reproduction of the species occurs at the open sea during the period from December to March, at the same period the adults of lagoonal population were on the pre-maturity stages (Rogdakis, 2003). In our results, specimens at size classes between 141-280 mm showed higher percentages of empty stomachs (44-58%, Fig. 3B) when compared to larger specimens (TL > 281 mm), where the percentage of empty stomachs ranged from 15 to 32% (Fig. 3B). The observed high proportion of small individuals with empty stomachs in the present study could also be related to the onset of their seaward migration. Landings from the barrier traps, which reflect the rate of seaward migration, indicated that massive seaward migration of the species occurred mainly during November and the migrating population was composed mainly by young individuals (141-280 mm) (Katselis *et al.*, 2003). Young sea bass individuals are more sensitive than older ones to the drop of temperature (Pickett & Pawson, 1994) and their reduced feeding intensity could be a symptom of unfavourable ambient conditions which is followed by a seaward migration for refuge (Wooton, 1990). This migrating pattern of the species is also supported by the landings from nets deployed in the lagoon (no migrating specimens) during the period from November to February, which were mainly composed of older individuals (250-650 mm) (Katselis, unpublished data). Moreover, the diet of individuals belonging to the size class of 201-280 mm, which were mainly present in the samples from June to November (Fig. 2A), was characterised by changes in prey composition (decrease of amphipods and increase of shrimps and crabs) as well as by a progressive increase in the proportion of empty stomachs from summer towards winter months. This fact might indicate that the seaward migration of the species is also related to the reduced availability of the food sources in the lagoon in the context of a top-down control, as has been proposed by Wooton (1990). In this case, a possible reduction of the available food items with an appropriate size drives the fish to the sea-bed (Pickett & Pawson, 1994).

In the present study a seasonal variation of the diet composition, was also observed. However, given the strong seasonality of the new recruits (fry and 0⁺

age group) in the lagoon, the observed seasonal variation of the diet composition of sea bass, could be attributed mainly to the size class diet variation of the species and less to the species diet adaptation on the seasonal prey availability.

The estimated trophic level of sea bass in the study area ranged between 3 for younger and 4.6 for older individuals. The observed shift of the diet composition in relation to size was reflected in the corresponding increase of the species trophic level. The results of meta-analysis in sea bass diet data from other regions (Roblin & Brusle, 1984; Kara & Derbal, 1996; Hampel *et al.*, 2005) confirm both the range and the shift of the trophic level (Fig. 7). It is clear that the trophic level of 0⁺ age group is rather constant in relation to fish size (3 to 3.5). In this stage, a possible competition for the available food resources might exist with other lagoonal species such as gilthead sea bream, black goby (*Gobius niger*), red mullet (*Mullus barbatus*), sharpnose seabream (*Diplodus puntazzo*), and flatfish (*Solea* sp). These species occur in notable quantities in the landings of the study area (Katselis *et al.*, 2003) and their trophic level has been estimated between 3.2 and 3.6, whereas their diet composition covers a similar to the young sea bass prey spectrum, including copepods, amphipods, mysids and decapods (Stergiou & Karpouzi, 2002).

Finally, a study during the period 2000-2004 indicated that, the landings of gilthead sea bream in the Messolonghi-Etoliko lagoon complex have increased remarkably (~80%) and catches are dominated by small sized individuals. Although these changes in fish populations of the area have not yet been properly described and their exact causes still remain unclear, their connection to the adjacent fish farms seem to be a realistic scenario (Dimitriou *et al.*, 2007). Moreover, the general sense of researchers and fishermen is that the abundance of both species (sea bream and sea bass) has increased in the last years. During the present study, the annual Greek production of fish farms was about five folds lower than in 2004 (Dimitriou *et al.*, 2007) and thus, the expected impact of fish farms on the lagoonal population of sea bass may be considered as low. On the other hand, potential changes in the habits of lagoonal populations could be related to the modification of environmental parameters of lagoons in the context of global climatic changes. These facts reveal the importance of this study as a baseline for future studies.

In conclusion, this paper provides information on the feeding habits of sea bass in one important la-

goonal Mediterranean ecosystem where mid-term changes on biotic aspects have been recorded while this is also expected on abiotic aspects. Our results showed that two critical changes can be recognized in sea bass feeding behaviour. The first change took place at the length of 30 mm where the species shifted from plankton feeding to benthic feeding. The second change took place at the length of 201 to 280 mm where feeding shifted towards larger epifaunal prey such as shrimps and crabs, as well as small nektonic organisms (small finfish). The Messolonghi-Etoliko lagoon complex comprises a nursery and feeding ground for the species. The seasonal drop of water temperature and/or prey availability might be the common causes stimulating the massive seaward migration of the species in early winter.

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