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Diet, growth and reproduction of four flatfishes on the Portuguese coast

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SUMMARY: Four flatfish species were collected between January 2003 and June 2005 from commercial fishing vessels operating with gill nets and bottom trawls along the Portuguese coast in order to examine feeding habits, age and growth and reproduction. *Citharus linguatula* (Linnaeus, 1758), *Lepidorhombus boscii* (Risso, 1810) and *Microchirus azevia* (de Brito Capello, 1867) fed mainly on crustaceans, whereas *Platichthys flesus* (Linnaeus, 1758) fed mainly on echinoderms and crustaceans. Feeding activity was highest in spring and summer; females and small individuals showed the lowest vacuity index values. For all the species, significant differences were found in the proportion of prey items according to season, sex and size class. *M. azevia* had the largest diet spectrum. Ages were determined from sagittal otoliths. The von Bertalanffy growth equation coefficients differed between sexes. The asymptotic length L_{∞} of females was higher than that of males, except in *C. linguatula*. The lowest growth coefficient was obtained for *P. flesus* ($k=0.11$ for males and $k=0.10$ for females) and *M. azevia* showed the highest growth coefficient estimates ($k=0.40$ for females and $k=0.30$ for males). The highest proportion of individuals at spawning stage was recorded in winter for *L. boscii*, *P. flesus* and *M. azevia*, and in autumn for *C. linguatula*.

Keywords: flatfish, diet, growth, otoliths, reproduction, Portuguese coast.

RESUMEN: DIETA, CRECIMIENTO Y REPRODUCCIÓN DE CUATRO ESPECIES DE PECES PLANOS EN LA COSTA PORTUGUESA. — Cuatro especies de peces planos fueron capturadas desde enero de 2003 hasta junio de 2005 por embarcaciones comerciales operando con redes de enmalle y arrastre de fondo, a lo largo de la costa portuguesa, con objeto de examinar los hábitos alimenticios, la edad, el crecimiento y el ciclo sexual. *Citharus linguatula* (Linnaeus, 1758), *Lepidorhombus boscii* (Risso, 1810) y *Microchirus azevia* (de Brito Capello, 1867), se alimentaron sobre todo de crustáceos. La dieta de *Platichthys flesus* (Linnaeus, 1758) estuvo compuesta principalmente por equinodermos y crustáceos. La mayor actividad alimenticia se observó en la primavera y el verano. Las hembras y los individuos más pequeños presentaron valores de índices de vacuidad más bajos. Para todas las especies se encontraron diferencias significativas en la proporción de ítems alimenticios según la estación, el sexo y la talla. *M. azevia* presentó el espectro más amplio de dieta. Las edades fueron determinadas a partir de los otolitos *sagittae*. Los coeficientes de la ecuación de crecimiento de von Bertalanffy fueron diferentes para los dos sexos. La talla asíntótica L_{∞} de las hembras fue mayor que la de los machos, excepto para *C. linguatula*. El coeficiente de crecimiento más bajo se observó para *P. flesus* ($k=0.11$ para los machos y $k=0.10$ para las hembras), *M. azevia* presentó el mayor coeficiente de crecimiento ($k=0.40$ para hembras y $k=0.30$ para machos). La mayor proporción de individuos maduros en *L. boscii*, *P. flesus* y *M. azevia* se observó en invierno y en *C. linguatula* en otoño.

Palabras clave: peces planos, dieta, crecimiento, otolitos, reproducción, costa portuguesa.

INTRODUCTION

A large number of flatfish species occur on the Portuguese coast (e.g. Nielsen, 1986a,b,c,d; Quéro *et al.*, 1986a,b; Cabral, 2000a). This species richness is usually higher than that found in Northern Europe

and similar to that found in the Mediterranean, since many flatfish species are at their southern or northern distribution limits along the Portuguese coast (e.g. Quéro *et al.*, 1986a; Desoutter, 1997). The zoogeographic importance of this latitudinal area, representing the transition between northeastern Atlantic

warm-temperate and cold-temperate regions, has long been recognised (Ekman, 1953; Briggs, 1974).

The majority of flatfish occurring on the Portuguese coast have a high commercial value and are caught by fisheries as target or by-catch species. Flatfish catches represent 4% of all the fish biomass landed on the Portuguese coast. However, the importance of flatfish fisheries is considerably higher due to the high commercial value of flatfish species, which account for nearly 11% of the economical value of all landings. According to official data, flatfish landings increased from 1998 to 2005 (source: Direcção Geral das Pescas e Aquicultura [DGPA]).

Knowledge on the ecology of some flatfish species—especially those that are considered fisheries by-catches—is scarce. Spotted flounder *Citharus linguatula* (Linnaeus, 1758), four-spotted megrim *Lepidorhombus boscii* (Risso, 1810), flounder *Platichthys flesus* (Linnaeus, 1758) and bastard sole *Microchirus azevia* (de Brito Capello, 1867) are very different flatfish species with distinct distribution areas. The spotted flounder is distributed in the eastern Atlantic and Mediterranean, inhabiting soft bottoms from the coastline to a depth of about 200 m (Nielsen, 1986a). Four-spotted megrim occurs in the northeast Atlantic from the British Isles south to Cape Bojador, and is also found in the Mediterranean. It is common on soft bottoms at depths down to 700-800 m (Nielsen, 1986b). Flounder is common around the coasts of northern Europe and the Mediterranean. This species occurs on soft bottoms from shallow water down to 50 m, and can tolerate brackish or fresh water (Nielsen, 1986d). Bastard sole occurs from the southern range of the Iberian Peninsula to the western part of the Mediterranean Sea and off the African coast, southward to Senegal. It is common on mud and sand of the continental shelf, from the shore down to 250 m (Quéro *et al.*, 1986a).

Diet, age and growth and reproduction of *Citharus linguatula* have been studied in the Mediterranean and on the Atlantic coast of Morocco (e.g. Belghyti *et al.*, 1993; Redon *et al.*, 1994; Vassilopoulou and Papaconstantinou, 1994; García-Rodríguez and Esteban, 2000). Studies on four-spotted megrim diet, age and growth and reproduction have been conducted in the western Europe and Mediterranean (e.g. Santos, 1994; Vassilopoulou and Ondrias, 1999; Landa *et al.*, 2002; Vassilopoulou, 2006). Several authors have studied the diet, age and growth and reproduction of *Platichthys flesus* in northwestern Europe and in

the Black Sea (e.g. Summers, 1979; Beaumont and Mann, 1984; Andersen *et al.*, 2005; Çiloğlu, 2005). Age and growth and reproduction of *Microchirus azevia* have been studied on the south coast of Portugal, in the Mediterranean and in southern Morocco (e.g. Belaid and Marinaro, 1983; Marfin and Hajji, 1988; Andrade, 1998; Afonso-Dias *et al.*, 2005).

Studies conducted on the Portuguese coast have shown that *P. flesus* feed mainly on crustaceans, polychaetes and molluscs (Vinagre *et al.*, 2005). Santos (1994) determined for *Lepidorhombus boscii* a maximum total length of 398 mm. Longevity of *M. azevia* was 8 years and a maximum total length of 327 mm (Andrade, 1998). *L. boscii* and *M. azevia* spawns from winter to spring (Santos, 1994; Afonso-Dias *et al.*, 2005).

Despite these studies, knowledge on these species is scarce and integrative and comparative studies are lacking. As the Portuguese coast is a transition between temperate and subtropical waters of the north-eastern Atlantic coasts, studies conducted in this area may provide important information for determining these trends. Therefore, the aim of the present work was to study the diet, age and growth and reproduction of four-spotted megrim, bastard sole, spotted flounder and flounder off the Portuguese coast.

MATERIALS AND METHODS

Sampling surveys and samples processing

Samples were collected bimonthly between January 2003 and June 2005 from commercial fishing vessels operating with gill nets and bottom trawls along the Portuguese coast. The whole Portuguese coast was sampled regularly throughout the year (a minimum of 40 individuals were obtained per sampling time and area).

Fish were identified, measured (total length to nearest 1 mm) and weighed (total and eviscerated wet weight with 0.01 g precision). Stomachs and gonads were removed and frozen (-20°C) for further analysis. Sagittal otoliths were removed, cleaned and kept dry for later age determination.

Diet

The stomach contents of 344 individuals of *C. linguatula* (149-293 mm), 317 individuals of *L. boscii* (149-346 mm), 325 individuals of *P. flesus* (150-

430 mm) and 314 individuals of *M. azevia* (149-313 mm) were analysed. Each prey item was identified to the lowest taxonomic level possible, counted and weighed (wet weight to 0.001 g). The relative importance of each prey item in the diet was expressed as a percent of numerical abundance (NI – numerical index), occurrence of food items in stomachs (OI – occurrence index) and weight (GI – gravimetric index) (Hyslop, 1980). Feeding activity was evaluated by the vacuity index (VI) defined as the percent of empty stomachs (Hyslop, 1980).

Correspondence analyses (CA) were run to evaluate diet variation with season, sex and fish length according to each of the three index values. Prey items were grouped in a broader taxonomic level and four seasons, and two size classes (size class 1: <250 mm and size class 2: ≥250 mm total length) were created. These analyses were performed using CANOCO version 4.5 (ter Braak and Smilauer, 2002).

Diet differences between seasons, sexes and fish size were evaluated using χ^2 tests (Zar, 1984) and with a 0.05 significance level.

Prey diversity was determined for each season, sex and size class using the Shannon-Wiener diversity index H' (Shannon and Weaver, 1949), expressed as

$$H' = -\sum_{i=1}^s P_i \ln P_i,$$

where P_i is the numerical proportion of the i th prey category in the diet and S is the total number of different prey categories consumed by the predator. This index corresponds to the dietary breadth (Marshall and Elliott, 1997).

Age and growth

Age was evaluated based on otolith readings. For each specimen, two counts of otolith annuli were made under a dissecting microscope. Whenever the two readings of the same otolith resulted in different age estimates, the data were not considered for further analysis. A total of 321 individuals (216 females and 105 males) of spotted flounder, 302 individuals (199 females and 103 males) of four-spotted megrim, 314 individuals (209 females and 105 males) of flounder and 292 individuals (147 females and 145 males) of bastard sole were used for age determination.

Estimates of theoretical growth in length were obtained by fitting length-at-age data to the von Bertalanffy growth equation:

$$L_t = L_\infty (1 - e^{-k(t-t_0)}),$$

where L_t is the total length, L_∞ is the asymptotic length, k is the growth coefficient and t_0 is the theoretical age at zero length. The growth parameters of this model were estimated iteratively using the least squares method in *Statistica* software. This analysis was performed separately for males and females.

Reproduction

Gonads were observed macroscopically and a maturation stage was assigned to each individual, according to the scale: I, immature; II, development; III, spawning; and IV, post-spawning (Cabral, 1998). For each season, the percentage of fish in stages I, II, III and IV was determined.

The gonadosomatic index (GSI) was also determined for each sex and season. The GSI was expressed as the percentage of the weight of gonads in relation to eviscerated weight of fish. Age and length at first maturity were determined.

RESULTS

Diet

C. linguatula fed mainly on mysids and fishes, *L. boschii* mainly on decapods and fishes, *M. azevia* mainly on polychaetes and decapods, and *P. flesus* mainly on echinoderms (particularly Holothuroidea), bivalves and crustaceans (amphipods and decapods) (Table 1).

Vacuity index was higher for spotted flounder (34%) than for four-spotted flounder (19%), flounder (26%) and bastard sole (29%). The lowest values of vacuity occurred in summer, particularly for females and for the smallest fishes (Table 2).

The correspondence analysis (CA) based on the three indices considered as averaged per season, sex and size class explained ca. 30% of the variance in the first two axes (29.8%, 37.8% and 31.5%, respectively for NI, OI and GI). The three ordination diagrams (NI, OI and GI) were similar and the four species were well discriminated, so we presented only the best diagram: the numerical index diagram (Fig. 1).

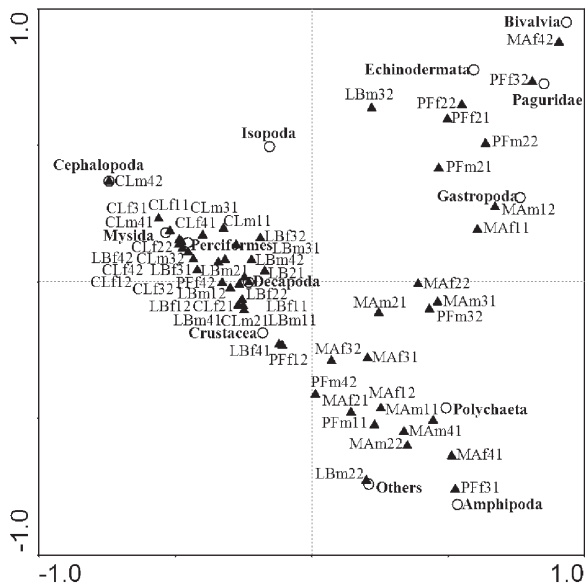
In the ordination diagram obtained for numerical data it can be seen that *C. linguatula* was mostly associated with Mysida and fishes. The females' diet

TABLE 1. – Numerical (NI), occurrence (OI) and gravimetric (GI) index values of prey items identified in stomachs of *C. linguatula*, *L. boscii*, *P. flesus* and *M. azevia* off the Portuguese coast.

Species Index	<i>C. linguatula</i>			<i>L. boscii</i>			<i>P. flesus</i>			<i>M. azevia</i>		
	NI	OI	GI	NI	OI	GI	NI	OI	GI	NI	OI	GI
Foraminifera				63.7	0.8	<0.1				2.6	1.1	<0.1
Bivalvia	<0.1	0.2	<0.1				17.8	23.0	26.3	9.0	4.3	3.6
<i>Pecten</i> spp.										2.1	1.1	1.1
<i>Ensis</i> spp.							2.6	2.7	4.0			
Bivalvia n.i.	<0.1	0.2	<0.1				15.2	20.3	22.3	6.9	3.2	2.5
<i>Antalis entalis</i>										1.3	1.1	0.5
Gastropoda	<0.1	0.2	<0.1	0.1	0.7	<0.1				7.3	3.2	2.4
<i>Hydrobia ulvae</i>										1.3	0.5	<0.1
<i>Scaphander</i> spp.										4.3	1.1	1.2
Gastropoda n.i.	<0.1	0.2	<0.1							1.7	1.6	1.1
Cephalopoda	4.2	11.2	32.9	0.1	0.7	10.0						
<i>Sepia officinalis</i>	<0.1	0.2	0.2									
Loliginidae	1.5	4.2	27.4									
<i>Alloteuthis</i> spp.	0.7	2.1	20.7									
<i>Loligo vulgaris</i>	<0.1	0.2	0.6									
Loliginidae n.i.	0.7	1.9	6.1									
Octopodidae	0.1	0.3	0.6									
Cephalopoda n.i.	2.5	6.5	4.7									
Polychaeta				0.7	4.3	1.9	8.1	25.1	36.5	30.9	33.4	52.6
<i>Aphrodita aculeata</i>										5.6	6.9	5.9
Polychaeta n.i.							8.1	25.1	36.5	25.3	26.5	46.7
Crustacea	80.9	52.0	20.2	33.1	82.7	64.7	18.2	25.7	6.3	36.5	42.8	31.2
<i>Balanus</i> spp.							0.2	0.5	<0.1			
<i>Squilla mantis</i>				0.2	1.4	2.1						
Decapoda	5.7	14.3	9.2	22.8	34.5	42.8	5.5	15.0	5.3	11.6	12.1	11.5
Paguridae										4.3	4.2	6.0
Brachyura	<0.1	0.1	<0.1	1.8	7.9	9.8	5.4	14.4	5.0	6.0	6.3	3.9
Caridea	3.9	9.5	6.6	21.0	26.6	33.0	0.2	0.5	0.3	0.9	1.1	1.5
Crangonidae	0.9	2.2	0.8	0.4	2.2	0.8						
<i>Crangon crangon</i>	0.1	0.3	0.2	0.4	2.2	0.8						
<i>Philocheras</i> spp.	0.6	0.8	0.5									
<i>Philocheras sculptus</i>	<0.1	0.4	<0.1									
Crangonidae n.i.	0.1	0.7	0.1									
<i>Alpheus glaber</i>	0.7	2.1	3.7									
Palaemonidae	0.8	3.3	1.2									
<i>Palaemon longirostris</i>	<0.1	0.3	0.3									
<i>Palaemonetes varians</i>	<0.1	0.3	0.2									
<i>Processa</i> spp.	0.5	1.5	0.4									
Palaemonidae n.i.	<0.1	1.2	0.3									
Caridea n.i.	1.4	4.2	2.1	20.7	24.5	32.2						
Decapoda n.i.	1.8	4.5	2.6							0.4	0.5	<0.1
Euphausiacea	1.0	0.3	0.2									
Mysida	63.6	22.5	4.8	2.2	13.7	5.3	0.7	2.1	<0.1			
<i>Leptomysis</i> spp.	26.4	6.9	1.6									
Mysida n.i.	37.2	15.6	3.2				0.7	2.1	<0.1			
Isopoda	0.3	0.8	<0.1	3.8	9.4	9.6	0.5	1.6	0.1			
<i>Eurydice</i> spp.	0.1	0.2	<0.1									
<i>Limnoria</i> spp.	<0.1	0.2	<0.1									
Isopoda n.i.	0.2	0.5	<0.1				0.5	1.6	0.1			
Amphipoda	<0.1	0.2	<0.1	0.1	0.7	<0.1	9.9	2.1	0.1	9.9	12.2	6.4
Crustacea n.i.	10.4	13.8	4.8	3.9	23.0	4.8	1.4	4.3	0.8	15.0	18.5	13.3
Echinodermata	<0.1	0.2	<0.1	0.2	1.4	<0.1	51.9	15.0	20.7	9.4	10.6	2.2
Crinoidea							0.3	1.1	<0.1			
Ophiuroidea				0.1	0.7	<0.1				3.0	3.7	1.0
Holothuroidea							51.4	13.4	20.7			
Echinoidea	<0.1	0.2	<0.1									
Echinodermata n.i.				0.1	0.7	<0.1	0.2	0.5	<0.1	6.4	6.9	1.2
Actinopterygii	12.5	29.8	44.5	2.1	9.4	23.3	1.0	2.1	3.7			
Pleuronectiformes	0.3	0.5	2.9									
<i>Arnoglossus</i> spp.	<0.1	0.2	0.6									
Pleuronectiformes n.i.	0.3	0.3	2.3									
Ammoditidae							0.3	0.5	2.4			
<i>Callionymus</i> spp.	<0.1	0.2	0.1									
<i>Callionymus reticulatus</i>	<0.1	0.2	1.8									
Trachinidae	<0.1	0.2	0.2									
Gobiidae	0.2	0.4	1.8									
<i>Gobius niger</i>	0.1	0.2	1.0									
<i>Pomatoschistus microps</i>	<0.1	0.1	0.1									
Gobiidae n.i.	<0.1	0.1	0.7									
<i>Trachurus trachurus</i>	0.1	0.2	5.5									
<i>Lepidotrigla cavillone</i>	<0.1	0.2	0.5									
<i>Merluccius merluccius</i>	<0.1	0.2	0.3									
Actinopterygii n.i.	11.6	27.7	31.4				0.7	1.6	1.3			
Unidentified	2.1	6.4	2.1				2.9	9.1	6.5	3.0	3.7	7.8

TABLE 2. – Vacuity index (VI) for each season (W, winter; Sp, spring; S, summer; A, autumn), sex (F, females; M, males) and size class (I, size class I; II, size class II) for *C. linguatula*, *L. boscii*, *P. flesus* and *M. azevia*.

	Season				Sexes		Size class		
	W	Sp	S	A	F	M	I	II	
<i>C. linguatula</i>	46.84	32.12	24.43	33.93	31.01	38.46	33.87	35.38	34.01
<i>L. boscii</i>	31.03	15.56	14.29	25.00	14.29	26.42	17.65	22.22	19.23
<i>P. flesus</i>	30.77	21.98	25.00	43.75	19.77	33.33	20.00	27.35	25.66
<i>M. azevia</i>	32.26	36.84	23.44	25.00	27.63	30.77	25.77	36.36	29.08

FIG. 1. – Ordination diagrams of the correspondence analyses performed on numerical index values of prey found in guts of *C. linguatula* (CL), *L. boscii* (LB), *P. flesus* (PF) and *M. azevia* (MA) (f, females; m, males; 1, winter; 2, spring; 3, summer; 4, autumn; 1, size class I; 2, size class II).

in spring, summer and winter was composed of decapods. Small males were associated with crustaceans in spring, and the largest males were associated with cephalopods in autumn. The diet of *L. boscii* was composed mainly of decapods and fishes. Crustaceans were associated with small females in autumn. *P. flesus* was chiefly associated with echinoderms in the spring. Amphipods were associated with small females in summer. The largest females' diet was associated with pagurids in summer. The diet of *M. azevia* was composed mainly of polychaetes and in winter it was associated with gastropods. Bivalves were associated with females. In autumn the diet of small females was composed of amphipods.

C. linguatula, *L. boscii*, *P. flesus* and *M. azevia* showed significant differences in their diets between seasons ($\chi^2=414.0$, d.f.=33, $P<0.05$; $\chi^2=384.8$, d.f.=33, $P<0.05$; $\chi^2=523.6$, d.f.=33, $P<0.05$ and $\chi^2=60.0$, d.f.=11, $P<0.05$, respectively).

Significant differences in the diet were observed between sexes in *C. linguatula*, *L. boscii* and *P. flesus* ($\chi^2=31.7$, d.f.=11, $P<0.05$; $\chi^2=461.6$, d.f.=11, $P<0.05$ and $\chi^2=115.9$, d.f.=11, $P<0.05$, respectively).

The diet of individuals of the two size classes also differed significantly in spotted flounder, four-spotted megrim and flounder ($\chi^2=294.5$, d.f.=11, $P<0.05$; $\chi^2=558.4$, d.f.=11, $P<0.05$ and $\chi^2=133.7$, d.f.=11, $P<0.05$, respectively).

M. azevia and *C. linguatula* showed the highest values of dietary diversity, obtained for the winter ($H'=2.24$) and spring ($H'=2.26$), respectively. For the majority of the species, males (*C. linguatula*: $H'=1.93$; *P. flesus*: $H'=2.01$; *M. azevia*: $H'=2.40$) showed a higher dietary breath than females (*C. linguatula*: $H'=1.81$; *P. flesus*: $H'=1.43$; *M. azevia*: $H'=2.39$). However, *L. boscii* showed an opposite trend, the females' diet ($H'=1.70$) being more diverse than that of males ($H'=0.66$). For *C. linguatula* and *M. azevia* the dietary diversity increased with size (size class I: $H'=1.81$; size class II: $H'=2.12$ and size class I: $H'=2.30$; size class II: $H'=2.49$, respectively). On the other hand, *L. boscii* and *P. flesus* showed the opposite trend: dietary diversity was higher for smaller-size individuals (size class I: $H'=1.43$; size class II: $H'=0.61$ and size class I: $H'=1.52$; size class II: $H'=1.51$, respectively).

Age and growth

The total length of fishes analysed varied between 149 and 275 mm for spotted-flounder, between 149 and 346 mm for four-spotted megrim, between 200 and 430 mm for flounder, and between 149 and 275 mm for bastard sole. The age ranged from 1 to 7 years in spotted flounder, from 2 to 9 years in four-spotted megrim, from 2 and 14 years in flounder, and from 2 and 7 years in bastard sole.

All species showed a differential growth according to sex. For the majority of the species (*L. boscii*, *P. flesus* and *M. azevia*) females attained higher lengths than males, except for *C. linguatula* (Figs. 2

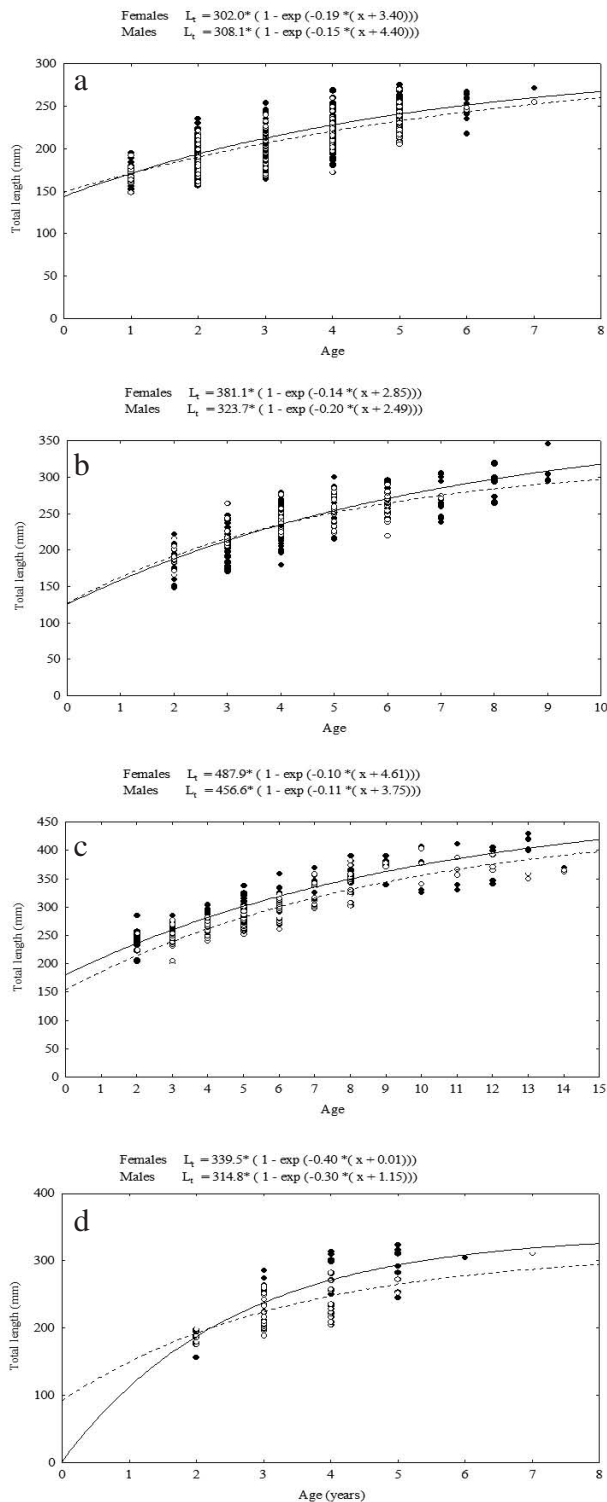


FIG. 2. – von Bertalanffy growth curves fitted to length-at-age data of *C. linguatula* (a), *L. boscii* (b), *P. flesus* (c), and *M. azevia* (d) (females, black circles and solid lines; males, empty circles and dashed lines).

a,b,c,d). The estimated asymptotic lengths for spotted flounder were higher for males than for females (L_{∞} =308.1 mm and L_{∞} =302.0 mm, respectively).

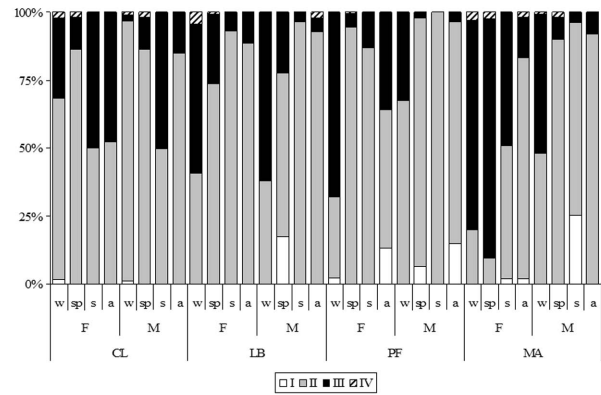


FIG. 3. – Percentage of individual of *C. linguatula* (CL), *L. boscii* (LB), *P. flesus* (PF) and *M. azevia* (MA) in each maturation stage (I, Immature; II, Development; III, Spawning; IV, Post-spawning), according to season (w, winter; sp, spring; s, summer; a, autumn) and to sex (F, females; M, males).

For the other species, an opposite trend was noticed: four-spotted megrim females, L_{∞} =381.1 mm and males, L_{∞} =323.7 mm; flounder females, L_{∞} =487.9 mm and males, L_{∞} =456.6 mm; and bastard sole females, L_{∞} =339.5 mm and males, L_{∞} =314.8 mm. The growth coefficient of spotted flounder (females, k =0.19; males, k = 0.15) and bastard sole (females, k = 0.40 and males, k =0.30) were higher for females than males, while for four-spotted megrim estimated k for males was higher than that of females (females, k =0.14 and males, k = 0.20). For flounder, growth coefficient estimates were similar for both sexes (females, k =0.10 and males, k =0.11). The t_0 estimates for spotted flounder were -3.40 for females and -4.40 for males; those for four-spotted megrim were -2.85 for females, and -2.49 for males; those for flounder were -4.61 for females and -3.75 for males; and those for bastard sole were -0.01 for females and -1.15 for males.

Reproduction

For all the species studied, the percentage of individuals in each maturation stage per season was in agreement with results relative to GSI values (Figs. 3 and 4).

The highest GSI values were obtained in winter for *L. boscii*, *P. flesus* and *M. azevia*, corresponding to the period with the highest percentage of individuals in stage III (spawning). The GSI values obtained for *C. linguatula* were high in autumn.

L. boscii and *C. linguatula* were the species for which the sexual maturation occurred in individuals with the lowest age and size (2 years for both, and 182 mm and 190 mm, respectively). Except for *P.*

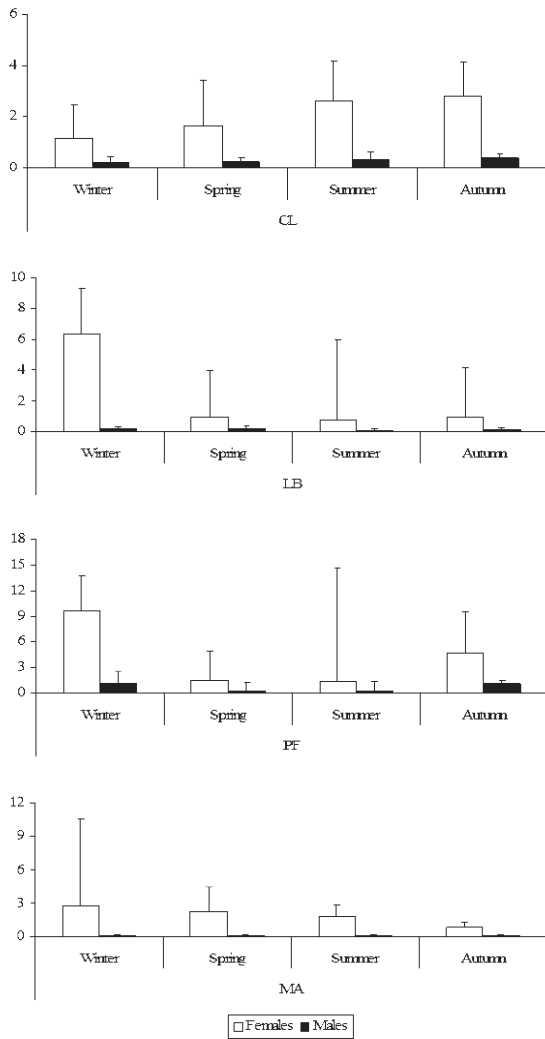


FIG. 4. – Gonadosomatic index mean values per season determined for each sex (standard deviation is represented above bars).

flesus (females, 3 years and males, 2 years), all the other species had the same age at first maturity for both sexes. *M. azevia* attained the first sexual maturity at 3 years of age.

DISCUSSION

Diet

The present study showed that *Citharus linguatula* fed mainly on mysids and fishes, *Lepidorhombus boscii* mainly on decapods and fishes, *Microchirus azevia* mainly on polychaetes and decapods, and *Platichthys flesus* mainly on echinoderms, bivalves and crustaceans. Studies conducted in western Europe (e.g. de Groot, 1971; Serrano *et al.*, 2003;

Vinagre *et al.*, 2005), in the Mediterranean (e.g. Morte *et al.*, 1999; de Juan *et al.*, 2007) and on the Atlantic coast of Morocco (Belghyti *et al.*, 1993) have reported similar results to those obtained herein (Table 3). The present study was the first approach to the feeding ecology of *M. azevia*, and our results revealed that the diet of this species was similar to that of other Soleidae, the main prey being crustaceans, polychaetes and molluscs (e.g. Cabral, 2000b; Darnaude *et al.*, 2001).

The relative importance of each prey differed greatly according to species. Several authors have reported differences in the feeding behaviour between Pleuronectiformes families (de Groot, 1971; Braber and de Groot, 1973; Holmes and Gibson, 1983). Diet composition depends mainly on prey detection mode and gut morphology. Citharidae, Scopthalmidae and Pleuronectidae are visual predators, responding primarily to moving prey, while Soleidae are mainly night feeders consuming less mobile or sedentary prey (de Groot, 1971; Braber and de Groot, 1973). The present study showed that feeding activity was higher in summer, the females showed lower vacuity values than males and the largest individuals had lower feeding activity than the smallest ones. This feeding behaviour is consistent with the findings of several authors (Belghyti *et al.*, 1993; Vassilopoulou, 2006; de Juan *et al.*, 2007). However, some authors (Redon *et al.*, 1994; Morte *et al.*, 1999; de Juan *et al.*, 2007) have reported that the vacuity index was highest in spring-summer. The variations in feeding activity result from the interactions of many factors, such as prey availability and reproductive process. In temperate areas, the highest productivity is recorded in spring and summer, which may increase the prey availability. Also, females have higher energetic needs for growth and reproduction, which could explain the lower vacuity values (Pitt, 1973; Lozán, 1992). Smaller fish have higher growth rates during the first years of life, which is usually related to a more intense feeding activity during this period to maximise growth (Vassilopoulou and Ondrias, 1999).

The diet of the four flatfish species analysed in this study showed seasonal, ontogenic and sexual variations, which were concordant with previous studies (e.g. Redon *et al.*, 1994; Andersen *et al.*, 2005; Vassilopoulou, 2006). These variations could be related to changes in space and time of benthic prey (e.g. Matallanas, 1982; Wootton, 1998). Several authors (e.g. Braber and de Groot, 1973; Gerking,

TABLE 3. – Summary of main prey items, growth parameters and reproduction season for *Citharus linguatula*, *Lepidorhombus boscii*, *Platichthys flesus* and *Microchirus azevia* in different areas.

Species	Main prey items	Growth parameters	Reproduction season	Area	Author
<i>C. linguatula</i>	Mysids and fishes	Females: $L_{\infty} = 302.0$ mm; $k = 0.19$; $t = -3.40$ Males: $L_{\infty} = 308.1$ mm; $k = 0.15$; $t = -4.40$	autumn	Portugal	Present study
	Mysids, euphausiids, prawns, cephalopods and fishes	No data	No data	Morocco (Atlantic coast)	Belghyti <i>et al.</i> , 1993
	Mysids, decapods and fishes	No data	No data	Spain (Mediterranean coast)	Redon <i>et al.</i> , 1994
	No data	$L_{\infty} = 253.4$ mm; $k = 0.25$; $t = 1.68$	No data	Turkey (Aegean Sea)	Türker Çakir <i>et al.</i> , 2005
	Crustaceans and fishes	No data	No data	Spain (Mediterranean coast)	de Juan <i>et al.</i> , 2007
	No data	Females: $L_{\infty} = 258.8$ mm; $k = 0.26$; $t = -0.417$ Males: $L_{\infty} = 229.4$ mm; $k = 0.29$; $t = -0.457$	No data	Aegean Sea	Vassilopoulou and Papaconstantinou, 1994
<i>L. boscii</i>	Decapods and fishes	Females: $L_{\infty} = 381.1$ mm; $k = 0.14$; $t = -2.85$ Males: $L_{\infty} = 323.7$ mm; $k = 0.20$; $t = -2.49$	winter	Portugal	Present study
	No data	Females: $L_{\infty} = 398.0$ mm; $k = 0.16$; $t = -1.86$ Males: $L_{\infty} = 348.0$ mm; $k = 0.20$; $t = -1.44$	winter and spring	Portugal	Santos, 1994
	Decapods, mysids, amphipods and fishes	No data	No data	Spain (Mediterranean coast)	Morte <i>et al.</i> , 1999
	No data	Females: $L_{\infty} = 305.0$ mm; $k = 0.18$; $t = -1.11$ Males: $L_{\infty} = 255.3$ mm; $k = 0.22$; $t = -1.08$	No data	Mediterranean waters	Vassilopoulou and Ondrias, 1999
	No data	$L_{\infty} = 343.9$ mm; $k = 0.27$; $t = -1.99$	No data	Ireland	Robson <i>et al.</i> , 2000
	No data	Females: $L_{\infty} = 456.0$ mm; $k = 0.17$; $t = 0.07$ Males: $L_{\infty} = 399.0$ mm; $k = 0.17$; $t = -0.37$	No data	Northeast Atlantic	Landa <i>et al.</i> , 2002
	Decapods, mysids, isopods, amphipods and fishes	No data	No data	Mediterranean waters	Vassilopoulou, 2006
	<i>P. flesus</i>	Echinoderms, bivalves, amphipods and decapods.	Females: $L_{\infty} = 487.9$ mm; $k = 0.10$; $t = -4.61$ Males: $L_{\infty} = 456.6$ mm; $k = 0.11$; $t = -3.75$	winter	Portugal
No data		No data	spring	Poland	Cieglewicz, 1962
No data		No data	spring	Scotland	Rae, 1971
Crustaceans, polychaetes, bivalves and gastropods		No data	No data	Scotland	Summers, 1979
No data		Females: $L_{\infty} = 485.0$ mm; $k = 0.53$; $t = 0.67$ Males: $L_{\infty} = 351.8$ mm; $k = 0.67$; $t = 0.31$	No data	France (Atlantic coast)	Deniel, 1981
Insects, molluscs and crustaceans		No data	No data	England	Beaumont and Mann, 1984
			winter	Portugal	Sobral, 2007
			winter	France (Atlantic coast)	Masson, 1988
		Females: $L_{\infty} = 386.9$ mm; $k = 0.70$; $t = -0.02$ Males: $L_{\infty} = 304.5$ mm; $k = 0.99$; $t = -0.04$			Vianet <i>et al.</i> , 1989
Copepods, polychaetes, oligochaetes, amphipods, isopods and fishes		No data	No data	Denmark	Andersen <i>et al.</i> , 2005
No data	Females: $L_{\infty} = 412.4$ mm; $k = 0.16$; $t = -3.24$ Males: $L_{\infty} = 335.7$ mm; $k = 0.18$; $t = -3.53$	winter and spring	Turkey (Black Sea)	Çiloğlu, 2005	
Crustaceans and polychaetes	No data	No data	Portugal	Vinagre <i>et al.</i> , 2005	

TABLE 3 (cont.). – Summary of main prey items, growth parameters and reproduction season for *Citharus linguatula*, *Lepidorhombus boscii*, *Platichthys flesus* and *Microchirus azevia* in different areas.

Species	Main prey items	Growth parameters	Reproduction season	Area	Author
<i>M. azevia</i>	Polychaetes and decapods	Females: $L_{\infty} = 339.5$ mm; $k = 0.40$; $t = -0.01$ Males: $L_{\infty} = 314.8$ mm; $k = 0.30$; $t = -1.15$	winter	Portugal	Present study
	No data	No data	spring	Algeria	Belaid and Marinaro, 1983
	No data	$L_{\infty} = 479.9$ mm; $k = 0.16$; $t = -0.56$	No data	Morocco	Marfi and Hajji, 1988
	No data	Females: $L_{\infty} = 347.1$ mm; $k = 0.28$; $t = -1.08$ Males: $L_{\infty} = 336.7$ mm; $k = 0.30$; $t = -1.07$	No data	Portugal	Andrade, 1998
	No data	No data	winter and spring	Portugal	Afonso-Dias <i>et al.</i> , 2005

1994; Platell and Potter, 1998) have shown that an increase in size of fish is associated with an increase in the consumption of larger prey, reflecting in some species a combination between increase in mouth size and improved ability to handle prey and to swim faster. This is in agreement with the optimum foraging theory (Gerking, 1994), according to which larger predators consume larger prey to maximise the energy gain relative to capture effort.

M. azevia showed a broader diet spectrum than the other three flatfish species, according to season, sex and size class. The diet breadth of *M. azevia* was higher in seasons when the feeding activity was lowest, which could correspond to a balance to compensate the decrease in prey availability during these seasons (Vassilopoulou, 2006).

Age and growth

The present study showed that the asymptotic length (L_{∞}) obtained for *C. linguatula* was higher than that obtained in studies conducted in the eastern Mediterranean (Vassilopoulou and Papaconstantinou, 1994; Türker Çakir *et al.*, 2005). The opposite situation was observed for the growth coefficient (k). The estimate of von Bertalanffy parameters obtained for *L. boscii* is in agreement with those estimated by several authors in different geographical locations (e.g. Santos, 1994; Vassilopoulou and Ondrias, 1999; Robson *et al.*, 2000). The growth coefficient (k) was similar to those obtained in previous studies, except for Robson *et al.* (2000), who reported a higher growth coefficient. The values of asymptotic length for *P. flesus* obtained in this work were higher than those of earlier studies. This fact could be related to the smaller length of the fish in the studies

conducted in the North Atlantic and the Mediterranean (Deniel, 1981; Vianet *et al.*, 1989). The growth coefficient obtained in this study was smaller than those obtained in previous studies. Growth studies for *M. azevia* were scarce and all were conducted on the Portuguese coast. The estimate of von Bertalanffy parameters obtained in this work was similar to that of Andrade (1990, 1998) for the southern coast of Portugal (Table 3).

Growth can be influenced by many factors. Latitudinal variations in temperature induce variations in maintenance metabolism (Pauly, 1994a). The different growth patterns between sexes could be explained by the differences in metabolism between females and males, such as differences in oxygen consumption (Pauly, 1994b), differences in the level of surplus energy between reproduction and somatic growth (Rijnsdorp and Ibelings, 1989), and differential food ingestion (Lozán, 1992).

Reproduction

The analysis of seasonal variation of gonadal development and the GSI values suggests that the spawning period of *L. boscii*, *P. flesus* and *M. azevia* occurs in the winter, and that of *C. linguatula* occurs in the autumn. Studies on the reproduction of spotted flounder are scarce and report only length and age at first maturity. Vassilopoulou and Papaconstantinou (1994) and García-Rodríguez and Esteban (2000) suggested that age at first maturity was between the first and the third year of life, being earlier in males. The results obtained in the present study were consistent with those of previous studies, except for the length at first maturity, which was higher than that of earlier studies. The pattern of sexual devel-

opment pointed out for *M. azevia* is consistent with the existing literature (Andrade, 1990; Afonso-Dias *et al.*, 2005). The age at first maturity obtained in the present study was similar to that of earlier studies (Belaid and Marinaro, 1983; Andrade, 1990; Afonso-Dias *et al.*, 2005). The results concerning the seasonal variation of gonadal development in the present work for *L. boschii* were similar to those of previous studies (Santos, 1994). The spawning season of *P. flesus* proposed by several authors outlines a latitudinal gradient, with later spawning at higher latitudes. Studies carried out in Northern Europe have shown that flounder spawns at the end of spring (e.g. Ciegiewicz, 1962; Solemdal, 1967; Rae, 1971), while in northern French and Spanish coasts the spawning occurs mainly in the winter (e.g. Deniel, 1981; Masson, 1988). Similar results were shown in the previous studies conducted, whereas on the Portuguese coast the spawning occurs mainly in winter (Sobral, 2007). Our results were in agreement with earlier work (Table 3). The length at first maturity obtained in the present study was higher than those reported in previous studies (e.g. Masson, 1988; Kosior *et al.*, 1996), which could be explained by the higher growth rates at lower latitudes.

Further studies on the bioecology of these species are needed in order to bring new insights into the population dynamics of these commercially important flatfish species.

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