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Feeding ecology, growth and sexual cycle of the sand sole, *Solea lascaris*, along the Portuguese coast

CÉLIA M. TEIXEIRA, ANA PINHEIRO AND HENRIQUE N. CABRAL
Universidade de Lisboa, Faculdade de Ciências, Centro de Oceanografia, Campo Grande, 1749-016 Lisboa, Portugal

Sand sole, Solea lascaris*, were collected along the Portuguese coast, between October 2002 and July 2003, to examine feeding habits, age and growth and sexual cycle. The most important prey items were Mysidacea, Amphipoda and Polychaeta. Differences in diet according to season and length size were found: Amphipoda were very important in diet during winter, while Echinodermata were consumed mostly in summer; smaller individuals feed on Amphipoda while larger feed on Decapoda. Age of* S. lascaris *was determined from sagittae otoliths. The length of fish analysed ranged from 61 mm to 340 mm. The von Bertalanffy growth equation parameters differed significantly between sexes ($L_\infty = 342.3$ mm, $k = 0.50$, $t_o = -0.87$ and $L_\infty = 264.5$ mm, $k = 0.82$, $t_o = 0.13$, females and males, respectively). The highest values of the gonadosomatic index were obtained in winter and spring, when the highest proportion of individuals at spawning stage was recorded.*

Keywords: feeding ecology, growth, reproduction, flatfish, *Solea lascaris*, Portuguese coast

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INTRODUCTION

A large number of flatfish species have been reported for the Portuguese coast (e.g. Nielsen, 1986a, b, c, d; Quéro *et al.*, 1986a, b; Cabral, 2000a) and though many of them have a high commercial interest, few studies have been conducted on Pleuronectiformes biology in Portuguese waters (e.g. Dinis, 1986; Andrade, 1990; Cabral, 1998, 2000a, b; Cabral & Costa, 1999; Cabral *et al.*, 2002).

The sand sole, *Solea lascaris* (Risso, 1810) is a Soleidae with a wide geographical distribution, from the southern North Sea to the Gulf of Guinea and the Mediterranean, inhabiting sandy and muddy bottoms at depths of 5 to 350 m (Quéro *et al.*, 1986a).

Despite its broad distribution, most studies on *S. lascaris* biology were conducted along the west coast of Brittany (France) and the Portuguese coast and have considered essentially its growth and reproduction (e.g. Deniel, 1981; Dinis, 1986; Deniel *et al.*, 1989; Andrade, 1990). The diet of *S. lascaris* was previously studied along the west Brittany (France) and Algerian coasts (Marinaro Bouabid, 1983; Rodriguez, 1996).

The studies conducted along the Portuguese coast, reported that *S. lascaris* spawns from January to June, southerly populations having an earlier spawning season (Dinis, 1986; Andrade, 1990; Gomes, 2002). A similar latitudinal gradient has been reported for growth parameters with specimens of the central coastal area showing a lower growth coefficient than those collected in Algarve (Andrade, 1990). Dinis (1986) determined longevity of 11 years and a maximum total length of 355 mm. Cabral *et al.* (2002) mention that juvenile sand sole fed on small Crustacea and Bivalvia.

Corresponding author:
C.M. Teixeira
Email: cmteixeira@fc.ul.pt

Solea lascaris is a species with a growing commercial interest. In Portugal, its landings have quadrupled in the last decade (from about 28 tonnes in 1990 to 116 tonnes landed in 2000), coming to represent 6.4% of the landed flatfish. Still less common than other commercially important sole species such as *Solea solea* (Linnaeus, 1758) and *Solea senegalensis* Kaup, 1858, with which *S. lascaris* are fished, it reaches high values in auction giving it a great economic importance (DGPA, unpublished data).

As a commercially important species, increasingly exploited and poorly known, the study of *S. lascaris* ecology has become of particular importance for fisheries management purposes. Thus, the aim of the present work was to study the feeding ecology, growth and sexual cycle of *S. lascaris* along the Portuguese coast.

MATERIALS AND METHODS

Sampling surveys and samples processing

A total of 665 individuals were collected seasonally (autumn, winter, spring and summer), between October 2002 and July 2003, from commercial fishing vessels operating with gill nets and bottom trawls along the Portuguese coast (Figure 1).

All fish were 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. Then, the stomach contents were removed for identification and gonads were weighed. Each prey item was identified to the lowest taxonomic level possible, counted and weighed (wet weight to 0.001 g). Sagittae otoliths were removed, cleaned and kept dry for later age determination.

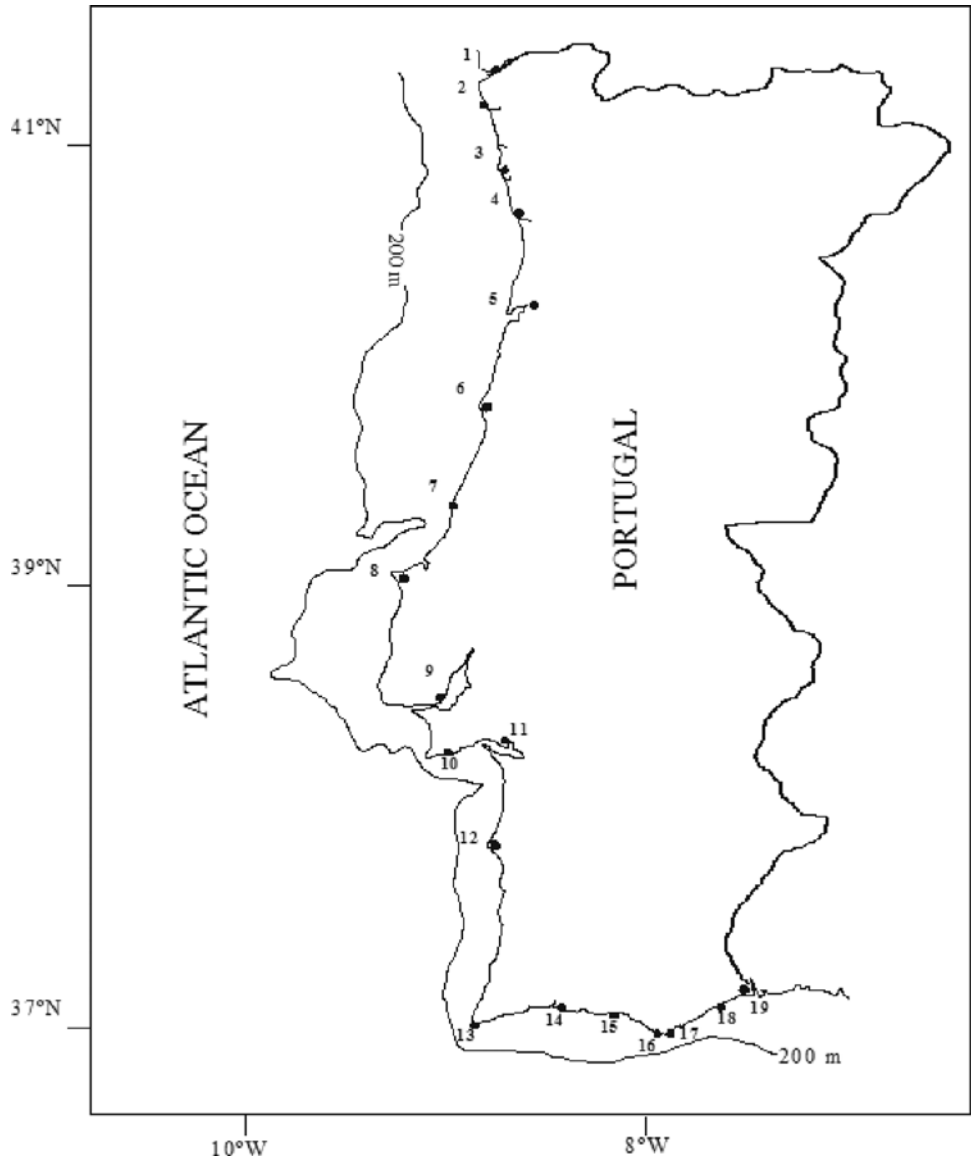

Fig. 1. Map of mainland Portugal landing ports (1, Caminha; 2, Viana do Castelo; 3, Póvoa do Varzim; 4, Leixões; 5, Aveiro; 6, Figueira da Foz; 7, Nazaré; 8, Peniche; 9, Lisboa; 10, Sesimbra; 11, Setúbal; 12, Sines; 13, Sagres; 14, Portimão; 15, Quarteira; 16, Faro; 17, Olhão; 18, Tavira; 19, Vila Real de Santo António).

Feeding ecology

The relative importance of each item was evaluated by calculating the numerical composition (Cn%), frequency of occurrence (F%) and biomass (Cw%) (Hyslop, 1980). Differences in diet composition by sampling season and fish length (two length-classes: <250 mm and >250 mm total length) were evaluated by correspondence analysis (CA) that was performed using CANOCO software (ter Braack Smilauer, 1998).

Age and growth

Age was evaluated using otoliths. For each specimen, two counts of otolith annuli were made under a dissecting

Table 1. Sexual maturity stages of *Solea lascaris* (adapted from Andrade, 1990, and Cabral, 1998).

	Females	Males
1. Immature	Ovaries small and translucent	Testes small and translucent
2. Early development	Ovaries larger and opaque, small white eggs can be seen	Testes larger and opaque; whitish
3. Late development	Ovaries yellow, both white and translucent eggs can be seen	Testes swelling; light-brown
4. Spawning or partly spent	Hyaline eggs run from vent on slight pressure; or less swollen and with red spots but hyaline eggs are still numerous	Testes fully swollen; sperm can be extruded under light pressure
5. Spent	Ovaries flabby, red coloured	Testes flabby, residual sperm

microscope. Whenever the two readings of the same otolith resulted in different age estimates the data were not considered for further analysis.

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

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

where L_t is the total length at age t, L_∞ is the asymptotic length, k is the growth coefficient and t_o 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 females and males.

Sexual cycle

Gonads were observed macroscopically and a maturation stage was assigned to each individual, according to a five-stage scale (Table 1). For each season the proportion of fish in stages 2 to 5 was determined.

In order to evaluate gonadal development during the annual sexual cycle and to determine the spawning season, the gonadosomatic index (GSI) was calculated per sex for each season. The GSI was expressed as the percentage of the weight of gonads in relation to eviscerated weight of fish.

RESULTS

Feeding ecology

The diet spectrum of *Solea lascaris* was broad, consisting of a variety of Polychaeta, Crustacea, Mollusca, Echinodermata and Cephalochordata (Table 2). Crustacea was found to be the most important prey group according to all three indices (Cn = 80.7%; F = 67.3%; Cw = 73.8%). Amongst Crustacea, Mysidacea were the most important prey in both numbers and weight (values of Cn = 44.1% and Cw = 64.8%), while on occurrence alone Amphipoda was the most important group (F = 17.2%). Polychaeta also held a considerable importance in the *S. lascaris* diet: when considering occurrence in stomach contents (F = 18.8%) Polychaeta were more important than any subgroup of Crustacea and also scored a high value on the basis of weight (Cw = 20.5%).

The first two axes of all three CA that were performed explained a high percentage of the total observed variation in diet according to each of the three indices (85.9%, 90.6% and 88.7% for Cn, F and Cw data based analyses, respectively) (Figure 2).

Three groups can be identified based on the Cn ordination diagram: one group encompasses the samples relative to autumn diet of the length-class 1, that was strongly associated with Polychaeta; winter and spring diets of the length-class 1 and winter diet of the length-class 2 formed a second group associated to Amphipoda, Bivalvia and Isopoda; the third group consisted of the spring diet of length-class 1, the summer diet of length-classes 1 and 2, and the autumn diet of length-class 2, which was associated with Cumacea, Decapoda, Echinodermata and Mysidacea.

Table 2. Numerical composition (Cn), frequency of occurrence (F) and biomass composition (Cw) indices values of prey found in stomachs of *Solea lascaris* on the Portuguese coast (n, number of stomachs in which prey occurs; p, number of individuals of a specific prey).

Prey item	n	p	Cn	F	Cw
Polychaeta	139	364	8.4	18.8	20.5
Aphroditidae	1	3	0.1	0.1	0.2
Cirratulidae	2	2	0.1	0.2	0.2
Glycera spp.	1	10	0.3	0.1	1.2
Nereis spp.	7	19	0.5	0.8	0.7
Ophelia bicornis	7	49	1.3	0.9	2.7
Phyllodocidae	3	4	0.1	0.3	0.2
Ephesiella abyssorum	1	1	0.0	0.1	0.0
Syllidae	1	1	0.0	0.1	0.0
Polychaeta n.i.	116	275	6.1	16.1	15.3
Crustacea	413	3099	80.7	67.3	73.8
Cumacea	98	340	9.2	11.8	0.4
Iphinoe trispinosa	3	4	0.3	0.6	0.0
Iphinoe sp.	3	3	0.3	0.7	0.0
Bodotria scorpioides	14	61	1.6	1.6	0.0
Bodotriidae n.i.	5	4	0.1	0.4	0.0
Pseudocuma (Pseudocuma) longicorne	5	8	0.2	0.6	0.0
Diastylis rugosa	20	153	4.0	2.3	0.1
Diastylidae n.i.	9	18	0.5	1.0	0.1
Cumacea n.i.	38	87	2.3	4.7	0.1
Apseudes latreillii	1	2	0.1	0.1	0.0
Mysidacea	85	1689	44.1	12.2	64.8
Isopoda	29	35	0.9	3.2	0.1
Gnathiidae	1	1	0.0	0.1	0.0
Conilera cylindracea	1	1	0.0	0.1	0.0
Eurydice pulchra	3	3	0.1	0.3	0.0
Eurydice sp.	2	2	0.1	0.2	0.0
Idotea balthica	3	4	0.1	0.3	0.0
Idotea sp.	3	3	0.1	0.3	0.0
Isopoda n.i.	16	21	0.5	1.8	0.1
Amphipoda	121	411	10.7	17.2	1.3
Gammaridea	121	406	10.6	16.8	1.2
Amphipoda n.i.	4	5	0.1	0.4	0.1
Decapoda	97	410	11.1	12.8	5.5
Crangon crangon	66	358	9.7	9.3	5.0
Paguridae	2	3	0.1	0.3	0.0
Portunidae	10	15	0.4	1.1	0.1
Decapoda n.i.	19	34	0.9	2.1	0.4
Crustacea n.i.	79	214	4.7	9.8	1.6
Mollusca	88	245	6.4	10.2	4.7
Antalis entalis	2	5	0.1	0.2	0.0
Gastropoda	2	2	0.1	0.2	0.0
Bivalvia	84	238	6.2	9.7	4.6
Arca tetragona	1	3	0.1	0.1	0.1
Tapes rhomboides	1	4	0.1	0.1	0.1
Mactra sp.	3	6	0.2	0.3	0.1
Spisula solida	6	10	0.3	0.7	0.1
Tellina tenuis	5	31	0.8	0.7	0.5
Tellina fabula	21	63	1.6	2.5	1.7
Scrobicularia plana	6	9	0.2	0.7	0.6
Abra sp.	1	2	0.1	0.1	0.0
Solecurtinae	2	7	0.2	0.2	0.2
Solenidae	2	4	0.1	0.2	0.0
Bivalvia n.i.	36	99	2.6	4.1	1.3
Echinodermata	25	152	4.0	3.4	0.8
Asteroidea	1	1	0.0	0.1	0.0
Ophiuroidea	16	99	2.6	2.1	0.6
Echinocyamus pusillus	6	50	1.3	0.9	0.2
Echinodermata n.i.	2	2	0.1	0.2	0.0
Cephalochordata	2	17	0.4	0.2	0.2
Branchiostoma lanceolatum	2	17	0.4	0.2	0.2

n.i., not identified.

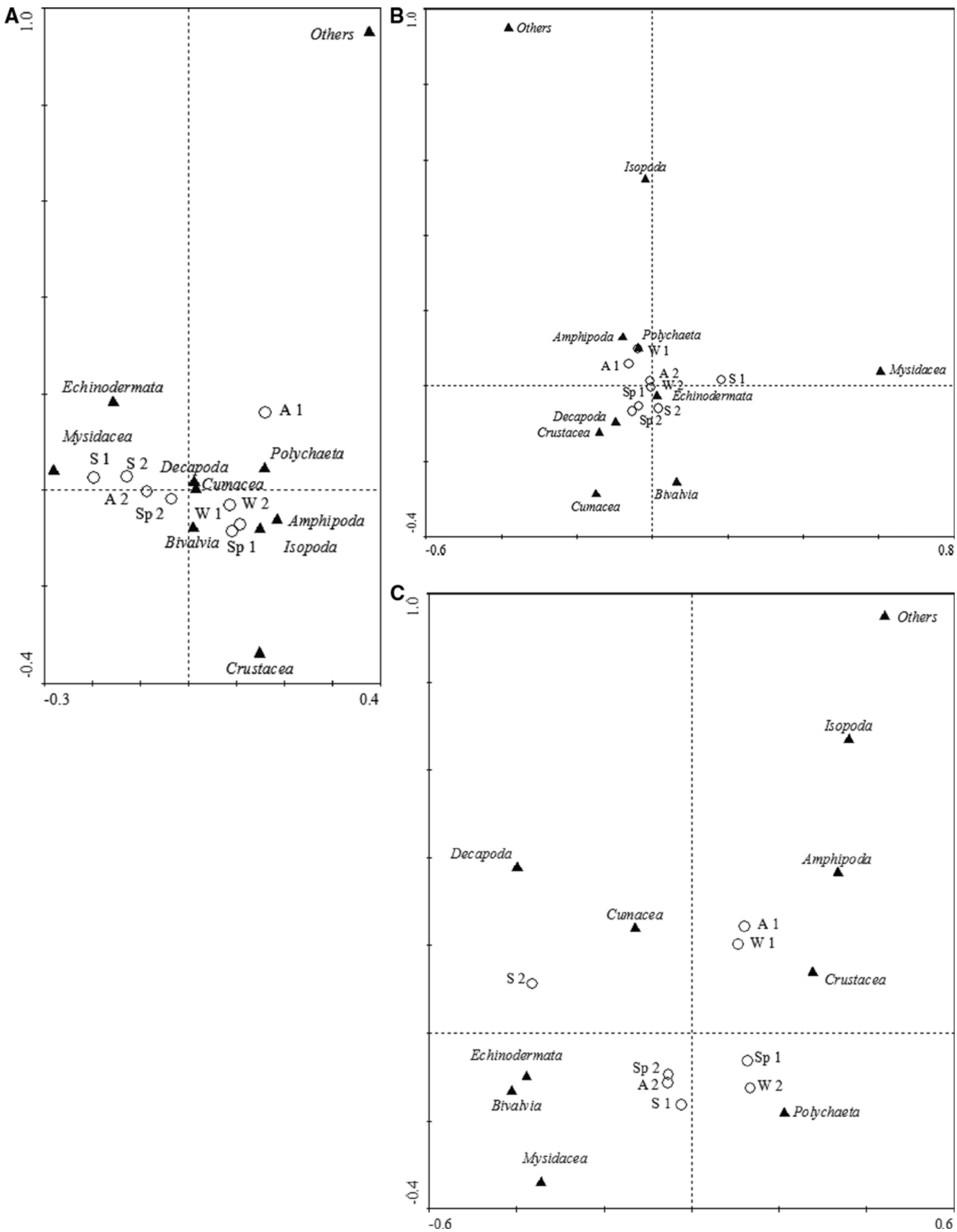

Fig. 2. Ordination diagrams of the correspondence analyses performed to numerical composition (A), frequency of occurrence (B) and biomass composition (C) of prey found in stomachs of *Solea lascaris* (1, length-class 1; 2, length-class 2; W, winter; Sp, spring; S, summer; A, autumn).

In the ordination diagram obtained for frequency of occurrence data can be seen one group relative to winter diet of length-class 1, autumn diet of length-classes 1 and 2, and summer diet of length-class 1, associated with Amphipoda and Polychaeta. The diet of individuals of length-class 1 in spring and of length-class 2 in winter, spring and summer were associated with Crustacea, Decapoda and Echinodermata.

When the Cw was considered in the ordination analysis, Polychaeta was strongly related to spring and winter diets of length-classes 2 and 1, respectively. Winter and autumn diets

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of length-class 1 were associated with Crustacea, Amphipoda and Isopoda; the summer diet of length-class 2 were associated with Cumacea and Decapoda; Echinodermata, Bivalvia and Mysidacea were associated with spring and autumn diets of length-class 2 and summer diet of length-class 1.

Overall, Amphipoda and Echinodermata were the most important element of the winter and summer diets, respectively, according to all three indices. Considering Cn and F, Decapoda were particularly important in spring. The Amphipoda were the major item of the autumn diet according to F and Cw. Winter and autumn diets were very similar according to F and Cw, and spring and summer diets were very similar according to F. Amphipoda were the most important prey item of length-class 1, according to all three indices. Length-class 2 fed mainly on Decapoda and Echinodermata, according to all three indices.

Age and growth

A total of 296 females and 113 males were analysed for age determination. The total length of fish analysed varied from 61 mm to 340 mm, for females, and from 61 mm to 310 mm, for males. The oldest fish was 6 years.

The von Bertalanffy growth equation parameters differed between sexes (Figure 3). The asymptotic length (L_∞) obtained for females was higher compared to the one obtained for males (342.3 mm and 264.5 mm, respectively), while the growth coefficient (k) estimated for females ($k = 0.50$) was lower than that determined for males ($k = 0.82$). The t_o estimates were -0.87 and 0.13 for females and males, respectively.

Sexual cycle

Percentage of individuals according to maturity stages was in agreement with GSI seasonal changes (Figures 4 & 5). The highest values of the GSI were obtained in winter and spring, the seasons when the highest percentage of individuals in spawning were recorded. The lowest GSI values (2.8% of eviscerated weight for females, 0.2% of eviscerated weight for males) were recorded in autumn, but a large proportion of partly spent females and spawning males indicated spawning was still taking place.

DISCUSSION

The diet composition determined for *Solea lascaris* along the Portuguese coast was similar to that described by Rodriguez (1996) for the west coast of Brittany. In both studies, it was found that *S. lascaris* feeds on a wide range of prey belonging to several taxa, the most important groups being Mysidacea, Polychaeta and Amphipoda. The *S. lascaris* diet reported by Cabral *et al.* (2002) and Marinaro & Bouabid (1983) is somewhat different: the prey-range is much smaller and Polychaeta are not an important prey. However, Cabral *et al.* (2002) studied the diet of juveniles and Marinaro & Bouabid (1983) had a small sample size (24 full stomachs), which could bias the estimation of prey importance.

The diet of *S. lascaris* is similar to that of *S. solea* and *S. senegalensis* differing mostly on Mollusca importance (e.g. Molinero & Flos, 1991; Garcia-Franquesa *et al.*, 1996; Cabral, 2000b; Darnaude *et al.*, 2001) that seem to be a preferential prey for the former species but not for *S. lascaris*. Overall, *S. lascaris* can be considered an opportunistic and generalist feeder, a status that has been recognized for several species of Soleidae (e.g. Cabral, 2000b; Darnaude *et al.*, 2001).

The differences found in the diet of *S. lascaris* in regards to season and length size were in agreement with Rodriguez (1996). These seasonal variations were a consequence of changes in space- and time-variation of benthic fauna composition, shifts due to life-history patterns of prey and feeding activity of the predator (Wootton, 1998). The diet variation according to fish length is consistent with the optimum foraging theory (Gerking, 1994), which states that larger predators tend to consume larger prey in order to maximize the energetic gain relative to capture effort.

The growth pattern found for *S. lascaris* in this study is quite different from what was previously described (e.g. Deniel, 1981; Dinis, 1986; Andrade, 1990). The observed longevities of 6 years for females and 5 years for males are lower than those found by Dinis (1986) (11 years, both for females and males), but similar to those reported by Andrade (1990) (7 and 6 years, respectively for females and males).

The observed pattern in the sexual cycle through the year is in accordance with expectations, and is similar to those reported by Dinis (1986), Andrade (1990) and Gomes (2002) for the Portuguese coast: *S. lascaris* has a winter–summer spawning

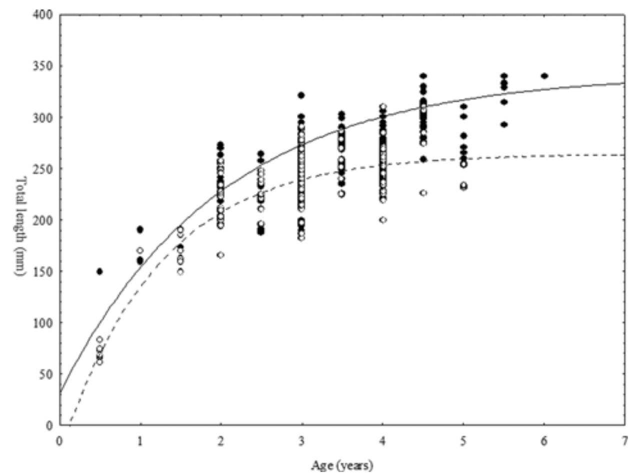

Fig. 3. von Bertalanffy growth curves fitted to length-at-age data of *Solea lascaris* (females. black circles and solid lines; males, empty circles and dashed lines).

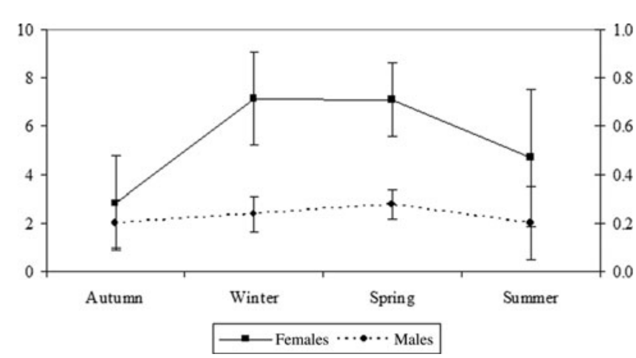

Fig. 4. Gonadosomatic index mean values season, determined for each sex (standard deviation is represented).

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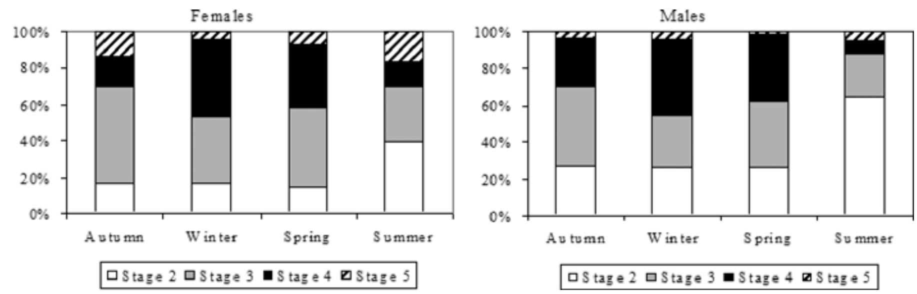

Fig. 5. Percentage of individuals in each maturation stage according to season, for females and males (maturation stages as in Table 2).

season and a latitudinal gradient that can be noticed. For the Douarnenez Bay (France), Deniel (1981) found a spawning season from May to September. Deniel (1981) reported a similar gradient for the *S. solea* spawning season.

The observed duration of the spawning period was longer than has been reported (7/8 months in this study against 5 months—Deniel, 1981; Dinis, 1986; Andrade, 1990; Gomes, 2002). These authors have noted that there is an asynchrony in the spawning of older and younger females, the second group spawns later, which could explain this long duration. This trend was not completely evident in this study (data not shown), and the long duration of the spawning season is due perhaps to serial spawning temporally spaced and/or to year fluctuations (e.g. Koutsikopoulos *et al.*, 1995).

Other Soleidae species have a winter–summer spawning season, namely *S. senegalensis* and *Dicologlossa cuneata* (Moreau, 1881) (Dinis, 1986): as *S. lascaris* these are subtropical species that attain maturity during the increasing daylight period.

Many aspects of *S. lascaris* biology remain to be studied, namely those regarding larvae and juvenile stages. These have been generally considered as very important life cycle phases, critical for individual survival, and so knowledge of these is of extreme importance, both for fisheries and aquaculture purposes.

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Correspondence should be addressed to:
Célia M. Teixeira
Universidade de Lisboa, Faculdade de Ciências
Centro de Oceanografia, Campo Grande
1749-016 Lisboa, Portugal
email: cmteixeira@fc.ul.pt