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Influence of season on the feeding habits of the common sole *Solea solea*

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Abstract. The object of the study was to determine whether the composition of the diet of sole *Solea solea* Linnaeus, 1758 throughout the year is influenced only by the presence and abundance of prey or whether in addition it is influenced by a selection procedure resulting from its energetic and nutritional needs. Feeding habits were established by examining the stomach contents of males and females throughout the year. We recorded the presence or absence of each prey item and identified dominant, occasional and accidental prey. Differences in the seasonal composition of the basic diet were analysed (chi-square). Throughout the year, the diet consisted mainly of crustaceans, except in autumn when polychaetes were the most abundant prey. Significant differences (chi-square) in feeding habits were established between seasons and between sexes in each season. Some of the dominant prey (Ampeliscidae and Callianassidae) live exclusively in estuaries and bays, and occur in highest abundance during winter, the season in which sole enter estuaries to spawn. These prey items were present in higher numbers in the stomach contents of the sole during this period, reflecting the dependence of its diet on prey availability.

Introduction

The composition of a species' diet can be influenced both by its own population dynamics and those of its prey. The former can display diet variations consistent with differences in energetic and nutritional needs such as during periods of active growth and reproduction, together with differences in capture strategies, the latter determine the presence or absence of a certain prey in the habitat as well as its relative abundance in each season.

The composition of the diet of *Solea solea* Linnaeus, 1758 has been studied by several authors (Braber and de Groot 1973, Quiniou 1978, Ramos 1981, Lagardère 1987). Similar prey species have been recorded in the sole diet both in the Atlantic Ocean and the Mediterranean Sea, and variations in the importance of the individual prey items probably arise from regional and seasonal variations in their relative abundance.

The purpose of the present study was to determine whether seasonal variations in the composition of the basic diet of Ebro sole are simply a consequence of prey selection resulting from energetic and nutritional requirements. Feeding habits were established by examining the stomach contents of males and females throughout the year. The presence or absence of each prey item was recorded, and dominant, occasional and accidental prey were identified. Differences in the seasonal composition of the sole's diet were statistically analysed.

Materials and methods

Solea solea Linnaeus, 1758 were collected from the Ebro estuary (40°37′–40°48′ N; 0°21′–0°40′ E) Tarragona, Spain, each month (January–December) throughout 1987; 461 individuals were examined. The fish were weighed, measured, and their sex was determined. Stomach and intestinal tracts were frozen at −40 °C. (Herein, "stomach" is defined as including the stomach and entire intestinal tract.) Stomachs were cut open under a stereoscopic microscope; empty stomachs were recorded for calculation of the vacuity index and were then discarded. Food items were divided into general groups, identified, assigned to taxonomic categories, and counted.

Prey items were identified to the family level only, since it was often impossible to identify some prey items beyond this category, and since calculation of the dominance index and subsequent comparisons must be made at hierarchically homogeneous levels. Although this resulted in less detailed information on prey consumed, the data were thus more valid in comparisons between different groups of samples.

Stomach contents were analysed for the sample as a whole and for males and females separately throughout the year using four indexes.

(1) Numerical abundance (%*N*): the number of each prey item in all non-empty stomachs in a sample, expressed as the percentage of the total number of food items in all stomachs in a sample.

(2) % frequency of occurrence (%*F*): based on the number of stomachs in which a food item occurred: this is expressed as a percentage of the total number of non-empty stomachs.

(3) Simpson's dominance index $(\lambda) = \Sigma Pi^2$, where Pi is the number of prey types (i) in any one stomach divided by the total number of prey items in that stomach. This index constitutes a measure of the expected commonness of a particular prey and provides an estimate of the dominance of a given prey category in the predator's diet (Pielou 1975, Ruiz and Jover 1981, 1983). In order to render the index independent of sample size, $\lambda' = (\lambda/z) \times 100$ was calculated (z = total number of non-empty stomachs). Finally, dominance values were expressed as a percentage $\lambda'' = (\lambda'/\Sigma \lambda') \times 100$. Simpson's dominance index gives an assessment of the predator's principal prey.

(4) Vacuity index (VI): number of empty stomachs divided by total number of stomachs $\times 100$.

In order to determine the size of the requisite sample, an analysis of diversity established the point ("t") at which the diversity value of prey in the stomach contents became stabilized, resulting in a saturation of information, which meant that the addition of another stomach would not add new information. The sample size (non-empty stomachs) was too small in some months, so fish were grouped according to season for this analysis.

Sex ratio and age-class composition were determined for each season, since preliminary studies (Molinero and Flos 1991) had revealed significant differences related to sex and age class.

The amount of any important prey item in the stomach contents or its absence for either sex or in any particular season will reveal significant differences in diet composition. In order to discover whether other differences exist, only common prey species present during all seasons were considered to constitute the basic diet.

Statistical analysis

Statistical differences ($P < 0.05$) in basic diet composition among seasons and statistical differences between sexes in each season were established by a chi-square test of the frequency of occurrence of common prey species for all seasons.

Results

In spring, both male and female *Solea solea* displayed their lowest vacuity index (VI=20%) (Fig. 1); in summer, autumn and winter the VI was similar for both sexes. The ratio females : males was: 1 : 1.7 in winter, 1 : 1.8 in spring, 1 : 1.3 in summer and 1 : 1.2 in autumn; however, for the non-empty stomachs alone, it was 1 : 1 in winter, spring and summer and 1.3 : 1 in autumn. Some prey items were present throughout the year (Table 1): Nereidae, Eunicidae, Glyceridae, Phyllodocidae, Terebellidae, Ampharetidae, Ampeliscidae, Leucothoidae, Corophiidae, Donacidae and Semelidae were present in the stomachs of at least one sex in all seasons. On the other hand, Nephthydidae, Paraonidae, Cirratulidae, Serpulidae, Aoridae, Ischyroceridae, Cumacea, Crangonidae, Turritellidae, Cardiidae and Trochidae were present only in stomachs in one season. Throughout the year, the diet of the whole sample (males and females) was based mainly on crustaceans, except in autumn when polychaetes were more abundant (cf. Tables 2–4 with Table 5). The Amphipoda and Tanaidacea were the most abundant crustaceans in stomachs, except in winter (Table 2), when the Decapoda were the most abundant crustacean group. Apseudidae disappeared from the stomach contents in winter. Errant polychaetes were more important than sedentary polychaetes in summer, but in spring and autumn the situation was reversed; in winter, the proportion of sedentary and errant polychaetes was similar. The numerical abundance of the molluscs increased in spring (Table 3). The basic diet was established on the presence of prey items common to all seasons: Nereidae, Eunicidae, Glyceridae, Phyllodocidae, Terebellidae, Ampharetidae, Ampeliscidae, Leucothoidae, Corophiidae,

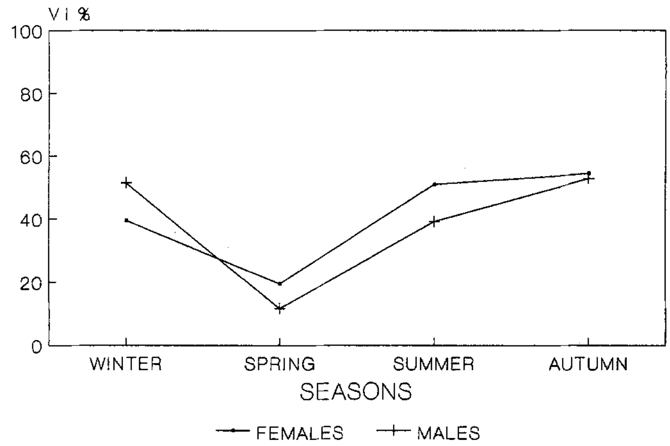

Fig. 1. *Solea solea.* Vacuity index (VI, %) of males and females as a function of season. VI = number of empty stomachs ÷ total number of stomachs $\times 100$

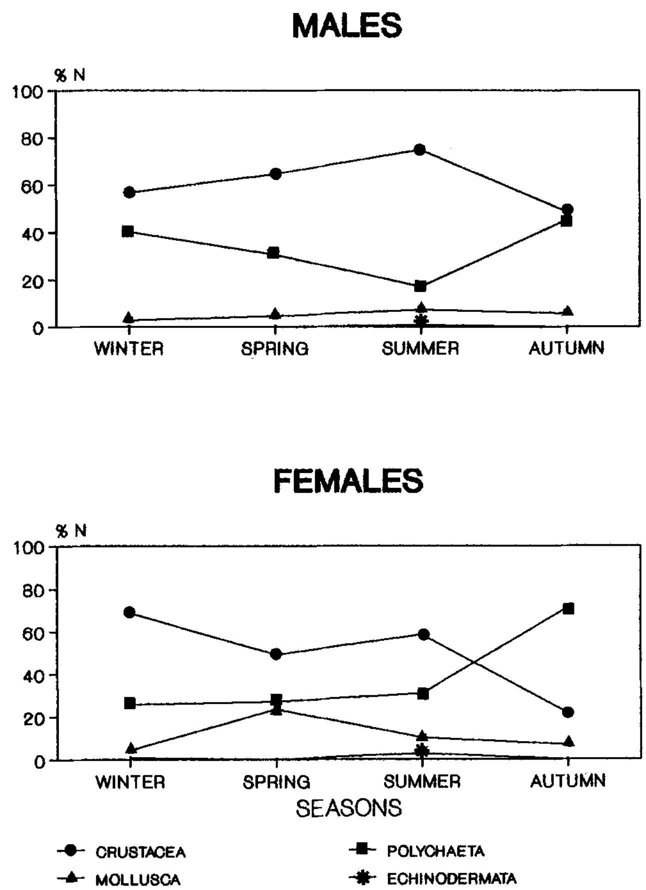

Fig. 2. *Solea solea.* Prey abundance as a function of sex and season, determined from contents of 291 non-empty stomachs

Table 1. *Solea solea.* Prey recorded in stomach contents as a function of sex and season. F: females; M: males; +: present; −: absent

Prey	Winter		Spring		Summer		Autumn	
	F	M	F	M	F	M	F	M
Polychaetes								
Neureidae	+	+	+	+	+	+	+	+
Eunicidae	+	+	+	+	+	+	+	+
Glyceridae	−	+	+	+	+	+	+	+
Phyllodocidae	+	−	+	+	+	+	+	+
Aphroditidae	−	−	−	+	+	+	+	−
Nephthydidae	+	−	−	−	+	−	−	−
Syllidae	−	−	+	−	+	−	−	−
Terebellidae	+	+	+	+	+	+	+	+
Sabellidae	−	−	+	+	+	−	+	−
Sternaspidae	+	+	−	−	+	−	−	−
Spionidae	−	−	−	+	−	−	+	+
Paraonidae	−	−	−	−	−	−	+	+
Cirratulidae	−	−	−	−	−	−	+	+
Serpulidae	−	−	−	−	−	−	+	−
Ampharetidae	−	+	+	+	+	+	+	−
Maldanidae	−	−	−	−	−	+	+	−
Crustaceans								
Ampeliscidae	+	+	+	+	+	+	+	+
Leucothoidae	+	+	+	+	+	+	+	+
Corophiidae	+	−	+	+	+	+	+	+
Aoridae	−	−	−	+	−	−	−	−
Ischyroceridae	−	−	−	−	−	−	+	+
Caprellidae	−	−	+	−	+	−	+	+
Apseudidae	−	−	+	+	+	+	+	+
Isopoda	+	+	−	+	+	+	−	−
Cumacea	−	−	−	−	−	−	+	+
Alpheidae	+	+	−	+	−	−	+	−
Callianassidae	+	+	+	+	+	+	−	−
Grapsidae	+	+	+	+	+	−	−	−
Processidae	+	+	−	+	−	−	+	+
Portunidae	+	−	+	+	−	−	−	−
Crangonidae	−	−	−	−	+	−	−	−
Molluscs								
Donacidae	+	−	+	+	+	−	+	−
Tellinidae	−	−	+	−	+	+	−	−
Turritellidae	+	+	−	−	−	−	−	−
Naticidae	+	−	+	−	−	−	−	+
Nassariidae	−	−	−	−	+	+	+	+
Cardiidae	+	−	+	−	+	+	−	−
Semelidae	+	+	+	+	+	+	+	−
Cardiidae	−	−	−	−	+	−	−	−
Philinidae	−	−	+	−	+	+	+	−
Pyramidellidae	−	−	−	+	−	+	−	−
Nuculidae	−	−	+	−	+	−	−	−
Nucularidae	−	−	+	−	+	−	−	−
Cerithiidae	−	−	−	−	−	+	+	−
Trochidae	−	−	−	−	−	−	+	−

Donacidae and Semelidae. A chi-square test was applied to the data to ensure that any differences did not arise merely from the presence or absence of a prey in the stomachs.

Influence of season on male diet

Season significantly affected the basic diet of males (chi-square test). The numerical abundance (%*N*) of crustaceans and polychaetes displayed an inverse relationship (Fig. 2): %*N* of crustaceans increased from winter to summer, diminishing in autumn, whereas that of polychaetes decreased from winter to summer, increasing in autumn – at which time it was at the same level as that of the crustaceans. %*N* of molluscs was fairly constant throughout the year, although slightly higher numbers were recorded in autumn. The importance of the individual crustacean groups varied during the year (Tables 2–5): decapods were more abundant in winter ($\%N = 43.7$), Amphipoda in spring ($\%N = 35.9$) and summer ($\%N = 60.9$), and Amphipoda ($\%N = 25.0$) and Tanaidacea ($\%N = 16.2$) in autumn.

Influence of season on female diet

Season also significantly affected the basic diet of females (chi-square test). %*N* of crustaceans fluctuated throughout the year (Fig. 2). Polychaetes were constant in abundance throughout the year except in autumn, when their numbers increased steeply, %*N* of molluscs was also quite constant throughout the year, except in spring, when numbers increased. Among the crustaceans, the Decapoda were most abundant in winter ($\%N = 62.5$); thereafter, they decreased, being replaced in dominance by Tanaidacea in spring ($\%N = 22.8$) and by Amphipoda in summer ($\%N = 42.8$). Molluscs were more abundant (%*N*) in the female than in the male diet.

Comparison of male and female diet as a function of season

Winter

The chi-square test revealed significant differences ($P < 0.001$) between male and female diets in winter. Simpson's dominance index showed Nereidae, Terebellidae and Callianassidae to be the dominant prey items for both sexes, but with different dominance-index values for each sex (Table 2). Ampeliscidae and Alpheidae were dominant in the male diet ($\lambda'' = 12.1$ and 6.5%, respectively), but not in the female diet ($\lambda'' = 0.83$ and 3.2%, respectively). Their frequency of occurrence (%*F*) in stomach contents was similar, but their numerical abundance (%*N*) differed. As a result, their dominance indexes (λ'') were different.

Spring

Significant differences ($P < 0.001$) were found between the basic diet of males and females in spring (Table 3). Callianassidae was again the dominant prey, with similar λ'' values for male (44.23%) and female (45.6%) diets. Apseudidae had become dominant in the male ($\lambda'' = 19.8\%$) and female ($\lambda'' = 12.7\%$) diets. Terebellidae again constituted a numerically dominant prey, but with a lower dominance index than in winter.

Table 2. *Solea solea.* Prey recorded in stomach contents in winter. *N*: total numbers counted; %*N*: number of prey items in all non-empty stomachs as % of total number of food items; %*F*: percentage of frequency of occurrence; λ″: Simpson's dominance index; –:absent

Prey	Females				Males			
	N	%*N*	%*F*	λ″	*N*	%*N*	%*F*	λ″
Polychaetes								
Errant								
Nereidae	12	6.4	23.5	5.76	18	12.6	22.8	17.06
Eunicidae	9	4.9	14.7	1.11	2	1.3	5.7	0.27
Glyceridae	–	–	–	–	4	2.7	11.4	1.25
Phyllodocidae	5	2.7	11.6	2.58	–	–	–	–
Aphroditidae	–	–	–	–	–	–	–	–
Nephthydidae	1	0.5	2.9	0.07	–	–	–	–
Syllidae	–	–	–	–	–	–	–	–
(total errant)	(27)	14.5			(24)	16.6		
Sedentary								
Terebellidae	19	10.3	23.5	6.74	29	20.1	51.4	25.16
Sabellidae	–	–	–	–	–	–	–	–
Sternaspidae	2	1.0	5.8	0.20	3	2.0	5.7	4.12
Spionidae	–	–	–	–	–	–	–	–
Paraonidae	–	–	–	–	–	–	–	–
Cirratulidae	–	–	–	–	–	–	–	–
Serpulidae	–	–	–	–	–	–	–	–
Ampharetidae	–	–	–	–	2	1.3	5.7	0.16
Maldanidae	–	–	–	–	–	–	–	–
(total sedentary)	(21)	11.3			(34)	23.4		
Total polychaetes	48	25.9			58	40.1		
Crustaceans								
Amphipoda								
Ampeliscidae	5	2.7	8.8	0.83	16	11.1	17.1	12.16
Leucothoidae	3	1.6	8.8	4.92	2	1.3	2.8	0.25
Corophiidae	1	0.5	2.9	0.09	–	–	–	–
Aoridae	–	–	–	–	–	–	–	–
Ischyroceridae	–	–	–	–	–	–	–	–
Caprellidae	–	–	–	–	–	–	–	–
(total amphipods)	(9)	4.8			(18)	12.5		
Tanaidacea	–	–	–	–	–	–	–	–
Apseudidae	–	–	–	–	–	–	–	–
Isopoda	2	1.1	5.8	1.0	1	0.6	2.8	0.25
Cumacea	–	–	–	–	–	–	–	–
Decapoda								
Alpheidae	9	4.9	23.5	3.2	12	8.3	25.7	6.50
Callianassidae	94	51.9	67.6	62.5	47	32.6	34.2	32.25
Grapsidae	4	2.2	8.8	2.30	2	1.3	5.7	0.11
Processidae	3	1.6	8.8	0.22	2	1.3	5.7	0.09
Portunidae	2	1.5	2.9	0.29	–	–	–	–
(total decapods)	(112)	62.5			(63)	43.7		
Total crustaceans	123	68.7			82	57.0		
Molluscs								
Bivalvia								
Donacidae	1	0.5	2.9	1.17	–	–	–	–
Tellinidae	–	–	–	–	–	–	–	–
Cardiidae	2	1.7	2.9	1.17	–	–	–	–
Semelidae	3	2.2	8.8	0.38	3	2.0	8.5	0.03
Nuculidae	–	–	–	–	–	–	–	–
Nucularidae	–	–	–	–	–	–	–	–
(total bivalves)	(6)	3.3			(3)	2.0		
Gastropoda								
Turritellidae	1	0.5	2.9	0.13	1	0.6	2.8	0.03
Naticidae	–	–	–	–	–	–	–	–
Nassariidae	–	–	–	–	–	–	–	–
Philinidae	–	–	–	–	–	–	–	–
Barleiidae	–	–	–	–	–	–	–	–
Pyramidellidae	–	–	–	–	–	–	–	–
Cerithiidae	–	–	–	–	–	–	–	–
Trochidae	–	–	–	–	–	–	–	–
(total gastropods)	(2)	1.1			(1)	0.6		
Total molluscs	8	4.4			4	2.7		

Table 3. *Solea solea.* Prey recorded in stomach contents in spring. *: $P<0.01$, Further details as in Table 2

Prey	Females				Males			
	N	$\%N$	$\%F$	λ''	N	$\%N$	$\%F$	λ''
Polychaetes								
Errant								
Nereidae	13	1.1	11.1	3.33	3	0.3	4.6	0.23
Eunicidae	13	1.1	4.7	1.61	23	2.4	9.2	3.28
Glyceridae	6	0.5	9.5	0.12	9	0.9	12.3	1.23
Phyllodocidae	19	1.6	15.8	0.58	9	0.9	6.1	0.84
Aphroditidae	–	–	–	–	1	0.1	1.5	0.28
Nephthydidae	–	–	–	–	–	–	–	–
Syllidae	2	0.1	3.1	0.04	–	–	–	–
(total errant)	(53)	4.4			(45)	4.8		
Sedentary								
Terebellidae	103	8.9	42.8	8.00	138	14.8	35.3	8.85
Sabellidae	3	0.2	3.1	0.01	3	0.3	1.5	0.07
Sternaspidae	–	–	–	–	–	–	–	–
Spionidae	–	–	–	–	1	0.1	1.5	*
Paraonidae	–	–	–	–	–	–	–	–
Cirratulidae	–	–	–	–	–	–	–	–
Serpulidae	–	–	–	–	–	–	–	–
Ampharetidae	153	13.3	22.2	6.15	97	10.4	16.9	2.76
Maldanidae	–	–	–	–	–	–	–	–
(total sedentary)	(259)	22.5			(239)	25.7		
Total polychaetes	312	27.1			284	30.6		
Crustaceans								
Amphipoda								
Ampeliscidae	174	15.1	33.3	6.89	77	8.2	24.6	3.59
Leucothoidae	5	0.4	4.7	0.40	13	1.4	9.2	1.23
Corophiidae	12	1.0	6.3	4.39	241	25.9	3.0	4.57
Aoridae	–	–	–	–	3	0.3	3.0	*
Ischyroceridae	–	–	–	–	–	–	–	–
Caprellidae	3	0.2	3.1	0.03	–	–	–	–
(total amphipods)	(194)	16.8			(334)	35.9		
Tanaidacea								
Apseudidae	263	22.8	38.1	12.79	178	19.1	44.6	19.84
(total tanaids)	(263)	22.8			(178)	19.1		
Isopoda	–	–	–	–	2	0.2	3.0	0.01
Cumacea	–	–	–	–	–	–	–	–
Decapoda								
Alpheidae	–	–	–	–	1	0.1	1.5	2.53
Callianassidae	95	8.3	42.8	45.61	83	8.9	43.0	44.23
Grapsidae	2	0.1	3.1	0.07	2	0.2	3.0	0.63
Processidae	–	–	–	–	1	0.1	1.5	0.15
Portunidae	12	1.0	12.7	0.49	1	0.1	1.5	0.05
(total decapods)	(109)	9.4			(88)	9.4		
Total crustaceans	566	49.2			602	64.8		
Molluscs								
Bivalvia								
Donacidae	1	*	1.5	0.07	1	0.1	1.5	0.15
Tellinidae	2	0.1	1.5	*	–	–	–	–
Cardiidae	1	*	1.5	0.02	–	–	–	–
Semelidae	242	21.0	26.9	8.09	40	4.3	30.7	5.33
Nuculidae	1	*	1.5	*	–	–	–	–
Nucularidae	1	*	1.5	*	–	–	–	–
(total bivalves)	(248)	21.5			(41)	4.4		
Gastropoda								
Turritellidae	–	–	–	–	–	–	–	–
Naticidae	1	*	1.5	*	–	–	–	–
Nassariidae	–	–	–	–	–	–	–	–
Philinidae	23	2.0	7.9	0.99	–	–	–	–
Barleiidae	–	–	–	–	–	–	–	–
Pyramidellidae	–	–	–	–	1	0.1	1.5	*
Cerithiidae	–	–	–	–	–	–	–	–
Trochidae	–	–	–	–	–	–	–	–
(total gastropods)	(24)	2.0			(1)	0.1		
Total molluscs	272	23.6			42	4.5		

Table 4. *Solea solea.* Prey recorded in stomach contents in summer. Further details as in Tables 2 and 3

Prey	Females				Males			
	N	$\%N$	$\%F$	λ''	N	$\%N$	$\%F$	λ''
Polychaetes								
Errant								
Nereidae	33	7.9	21.5	6.34	24	4.4	26.5	2.69
Eunicidae	13	3.1	17.6	6.58	13	2.3	14.2	2.40
Glyceridae	14	3.3	17.6	6.74	5	0.9	8.1	1.05
Phyllodocidae	13	3.0	13.7	2.12	20	3.6	14.2	1.67
Aphroditidae	32	7.8	1.9	2.90	1	0.1	2.0	0.83
Nephthydidae	2	0.4	3.9	3.21	–	–	–	–
Syllidae	2	0.4	3.9	0.10	–	–	–	–
(total errant)	(109)	26.7			(63)	12.4		
Sedentary								
Terebellidae	11	2.6	15.6	7.82	24	4.7	18.3	6.98
Sabellidae	1	0.2	1.9	0.77	–	–	–	–
Sternaspidae	2	0.4	1.9	0.08	–	–	–	–
Spionidae	–	–	–	–	–	–	–	–
Paraonidae	–	–	–	–	–	–	–	–
Cirratulidae	–	–	–	–	–	–	–	–
Serpulidae	–	–	–	–	–	–	–	–
Ampharetidae	4	0.9	5.8	0.43	3	0.5	2.0	0.83
Maldanidae	–	–	–	–	1	0.1	2.0	0.70
(total sedentary)	(18)	4.4			(28)	5.3		
Total polychaetes	127	31.1			91	17.7		
Crustaceans								
Amphipoda								
Ampeliscidae	132	31.8	31.3	24.02	245	48.3	48.9	37.44
Leucothoidae	41	9.6	33.3	5.09	64	12.6	34.6	9.35
Corophiidae	1	0.2	1.9	0.04	–	–	–	–
Aoridae	–	–	–	–	–	–	–	–
Ischyroceridae	–	–	–	–	–	–	–	–
Caprellidae	1	0.2	1.9	0.08	–	–	–	–
(total amphipods)	(175)	42.8			(309)	60.9		
Tanaidacea								
Apseudidae	10	2.4	11.7	0.63	39	7.7	32.6	7.30
(total tanaids)	(10)	2.4			(39)	7.7		
Isopoda	15	3.6	3.9	2.28	7	1.3	8.1	0.97
Cumacea	–	–	–	–	–	–	–	–
Decapoda								
Alpheidae	–	–	–	–	–	–	–	–
Callianassidae	25	6.8	17.6	12.87	25	4.9	16.3	7.54
Grapsidae	5	1.1	1.9	0.19	–	–	–	–
Processidae	–	–	–	–	–	–	–	–
Portunidae	–	–	–	–	–	–	–	–
Crangonidae	9	2.1	1.9	0.05	–	–	–	–
(total decapods)	(39)	9.5			(25)	4.9		
Total crustaceans	239	58.5			380	74.9		
Molluscs								
Bivalvia								
Donacidae	1	0.4	1.9	0.34	–	–	–	–
Tellinidae	8	1.8	7.8	3.42	20	6.9	12.2	9.99
Cardiidae	8	1.6	5.8	1.03	–	–	–	–
Semelidae	1	1.4	1.9	0.08	1	0.4	2.0	0.05
Nuculidae	1	0.8	1.9	0.12	–	–	–	–
Nucularidae	1	0.9	1.9	0.01	–	–	–	–
(total bivalves)	(31)	7.5			(25)	4.9		
Gastropoda								
Turritellidae	–	–	–	–	–	–	–	–
Naticidae	–	–	–	–	–	–	–	–
Nassariidae	6	1.9	9.8	1.25	6	0.4	4.0	0.03
Philinidae	5	2.9	5.8	0.44	5	1.6	8.1	5.26
Barleiidae	–	–	–	–	–	–	–	–
Pyramidellidae	–	–	–	–	1	0.3	2.0	*
Cerithiidae	–	–	–	–	3	0.6	2.0	0.05
(total gastropods)	(11)	2.6			(11)	2.1		
Total molluscs	42	10.2			36	7.1		

Table 5. *Solea solea.* Prey recorded in stomach contents in autumn. Further details as in Tables 2 and 3

Prey	Females				Males			
	N	$\%N$	$\%F$	λ''	N	$\%N$	$\%F$	λ''
Polychaetes								
Errant								
Nereidae	37	7.2	19.5	3.96	31	18.0	37.0	11.97
Eunicidae	3	0.5	4.8	0.01	2	1.2	7.4	0.75
Glyceridae	12	2.3	17.0	3.16	3	1.7	11.1	0.79
Phyllodocidae	8	1.5	14.6	4.50	3	1.7	11.1	3.32
Aphroditidae	7	1.3	2.4	0.06	–	–	–	–
Nephthydidae	–	–	–	–	–	–	–	–
Syllidae	–	–	–	–	–	–	–	–
(total errant)	(67)	13.2			(39)	22.6		
Sedentary								
Terebellidae	8	1.5	14.6	4.04	7	4.0	14.8	2.84
Sabellidae	31	6.1	7.6	1.24	–	–	–	–
Sternaspidae	–	–	–	–	–	–	–	–
Spionidae	1	0.2	2.4	*	1	0.6	3.7	0.03
Paraonidae	15	2.9	14.6	1.35	12	6.9	11.1	4.40
Cirratulidae	4	0.7	4.8	0.13	2	1.2	3.7	0.15
Serpulidae	1	0.2	2.4	*	–	–	–	–
Ampharetidae	229	45.5	24.3	23.71	17	9.9	18.5	12.63
Maldanidae	5	0.9	7.3	0.10	–	–	–	–
(total sedentary)	(294)	58.1			(39)	22.6		
Total polychaetes	361	71.3			78	45.3		
Crustaceans								
Amphipoda								
Ampeliscidae	35	6.8	36.5	16.22	17	9.8	33.3	8.23
Leucothoidae	10	1.9	19.5	3.22	16	9.3	29.6	3.50
Corophiidae	21	4.1	7.3	4.87	2	1.2	7.4	0.05
Aoridae	–	–	–	–	–	–	–	–
Ischyroceridae	1	0.2	2.4	0.03	9	5.2	7.4	3.62
Caprellidae	4	0.7	7.3	0.83	2	1.1	3.7	6.39
(total amphipods)	(71)	14.0			(46)	26.7		
Tanaidacea								
Apseudidae	33	6.5	26.8	10.93	28	16.2	44.4	28.78
(total tanaids)	33	6.5			28	16.2		
Isopoda	–	–	–	–	–	–	–	–
Cumacea	3	0.5	7.3	4.16	9	5.2	14.8	1.72
Decapoda								
Alpheidae	1	0.2	2.4	4.04	–	–	–	–
Callianassidae	–	–	–	–	–	–	–	–
Grapsidae	–	–	–	–	–	–	–	–
Processidae	2	0.3	4.8	8.08	1	0.5	3.7	6.39
Portunidae	–	–	–	–	–	–	–	–
(total decapods)	(3)	0.5			(1)	0.5		
Total crustaceans	110	21.7			84	48.8		
Molluscs								
Bivalvia								
Donacidae	1	0.1	2.4	0.02	–	–	–	–
Tellinidae	–	–	–	–	–	–	–	–
Cardiidae	–	–	–	–	–	–	–	–
Semelidae	4	0.7	4.8	0.56	–	–	–	–
Nuculidae	–	–	–	–	–	–	–	–
Nucularidae	–	–	–	–	–	–	–	–
(total bivalves)	(5)	0.9			–	–		
Gastropoda								
Turritellidae	–	–	–	–	–	–	–	–
Naticidae	–	–	–	–	1	0.8	3.7	0.02
Nassariidae	11	2.1	12.2	0.56	9	5.2	7.4	4.05
Philinidae	2	0.4	4.8	4.07	–	–	–	–
Barleiidae	–	–	–	–	–	–	–	–
Pyramidellidae	–	–	–	–	–	–	–	–
Cerithiidae	4	0.7	4.8	0.04	–	–	–	–
Trochidae	13	2.5	4.8	0.34	–	–	–	–
(total gastropods)	(30)	5.9			(10)	5.8		
Total molluscs	35	6.9			10	5.8		

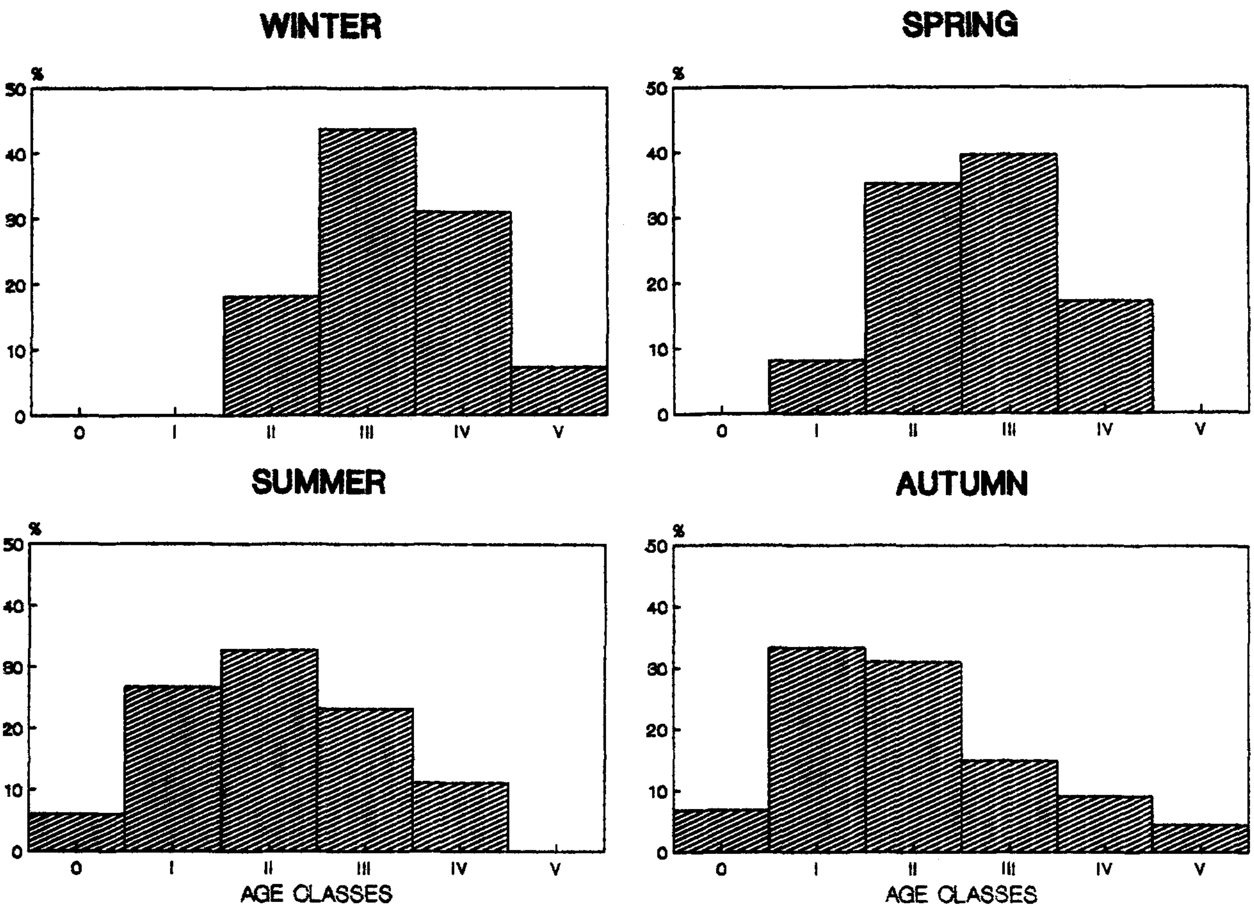

Fig. 3. *Solea solea*. Age distribution (% of total individuals in each age class) as a function of season

Summer

The chi-square test revealed significant differences in the basic diets of males and females in summer (Table 4). Four families were predominant in both male and female diets: Terebellidae, Ampeliscidae, Leucothoidae and Callianassidae. In the female stomachs, Nereidae, Eunicidae, and Glyceridae were the other dominant prey items, whereas Apseudidae, Tellinidae and Philinidae were the other dominants in males. It is worthy of note that some dominant prey in male stomachs, e.g. Apseudidae and Philinidae, were only accidental prey items in female stomachs.

Autumn

There were significant differences in the basic diets of males and females in autumn (Table 5). Ampharetidae, Ampeliscidae, Apseudidae and Processidae were the numerical dominant prey items in both sexes, albeit with differences in their dominant indexes. Nereidae and Caprellidae were other dominant prey of males, whereas in female stomachs Nereidae were only occasional and Caprellidae only accidental prey items. In females, there were no further dominant prey items.

Seasonal influences were also examined as a function of age (Fig. 3). In winter, 74.5% of the sole in our sample were in Age Classes III and IV (Age 0 = 1 to 12 mo, Age I = 13 to 24 mo, Age II = 25 to 36 mo, Age III = 37 to 48 mo, Age IV = 49 to 60 mo); their diet consisted mainly of crustaceans ($\%N = 63.4$). This is in accordance with the results of Molinero and Flos (1991), who reported a diet based mainly (50%) on crustaceans, principally decapods, for these age classes. Hence, diet composition, age and season are related. In spring, 74.4% of our sample consisted of Ages Classes II and III, with a diet based mainly on crustaceans (principally amphipods). In summer and autumn, similar age classes predominated (82.6 and 79.2% of Age Classes I, II and III in summer and autumn, respectively). However, the basic diet was different in these seasons: in summer it was based mainly on crustaceans ($\%N = 67.6$) (principally amphipods) and a few polychaetes ($\%N = 23.8$); in autumn it was based on polychaetes ($\%N = 64.7$) and a few crustaceans ($\%N = 28.6$).

Discussion

The vacuity index (*VI*) of stomachs of *Solea solea* is estimated as ~50%. The lower *VI* value in both males and females in spring could be due to an increased abundance of prey as a consequence of favourable environmental factors such as temperature and photoperiod resulting in a higher availability of food for the prey. Also, having completed the process of reproduction, which takes place principally in winter in the Ebro estuary, females must recuperate their energetic resources. Since their gonad volume will have decreased, the entire capacity of their intestinal tract is available for food. Ramos (1981), in a study on the diet of the sole, reported similar results for the vacuity index: decreasing *VI* values after the period of reproduction. Similar data have been reported for other flatfishes with similar modes of reproduction (Pitt 1973).

Some assumptions have been made in interpreting the results: (1) Since the diet composition presumably reflects environmental changes in prey availability, the most frequent and abundant prey in the stomach contents should be among the most abundant species in the environment. (2) Size or other morphological/physiological predator-prey characteristics can also restrict or facilitate predation in some seasons. (3) Age influences the feeding habits of *Solea solea* (Molinero and Flos 1991), and therefore age composition must be taken into consideration when evaluating differences in diet. These are discussed below:

Prey availability. The life cycles of some of the dominant prey items such as Ampeliscidae (*Ampelisca typica*) or Callianassidae (*Upogebia* sp.) do indeed reflect their abundance in the environment and in the stomach contents of the sole. For example, *Upogebia* sp. lives exclusively in protected environments such as estuaries and bays (Dworschak 1987) and is very abundant in winter; it is frequently found in sole stomachs in this season. Sole in Age Classes I, II and III live in estuarine areas near the coast, whereas Age Class IV individuals live some distance from the coast, coming into the estuaries in winter to spawn (Molinero 1986). Hence, the higher abundance of *Upogebia* sp. in sole stomachs in winter can be explained by the higher availability of this prey at a time in the predator's life cycle when the distributions of predator and prey coincide. A similar situation was noted for Ampeliscidae by Lagardère (1987), who mentioned the studies of Kaim Malka (1969) and Fincham (1971) concerning the population dynamics of the Ampeliscidae. He reported that their population increases in summer, and it is in this season when Ampeliscidae were found more abundantly in the stomach contents of sole from the Ebro estuary (present study).

Morphological/physiological predator-prey interactions. In a previous study (Molinero and Flos 1991), we reported differences in the diets of sole as a function of sex and age. Such differences emerge when the data for males and females are examined separately. Thus, if a prey item is present in the stomach of one sex only, this indicates its presence in the habitat, and the possibility of selective capture. This is however relevant only when the prey is dominant or occasional; accidental prey must be considered as casual. In the present study, Ampeliscidae were dominant in the diet of males in winter, but were merely accidental in the female diet, indicating that Ampeliscidae are actively selected by males because of some unknown requirement by males for this particular dietary item. Terebellidae and Corophiidae had similar dominance indexes (λ'') in both sexes but were more abundant ($\%N$) in males, although occurring more frequently in females ($\%F$). These data indicate an abundance of these prey items in the environment, with the higher frequency ($\%F$) in females suggesting an increased requirement for these particular prey items by the females.

Feeding habits as a function of age. In spring and winter, the basic diet would seem to be a function of age of the sole. This is not so for summer and autumn, where differences in the basic diet occurred between individuals of the same age. The abundance of crustaceans in the habitat may have decreased in autumn, since Callianassidae were not found in any stomach during this season; instead, a higher number of polychaetes was recorded.

During each season, diet was a function of the presence or absence of prey in the habitat, but also of the age distribution of the sole. Thus, a relationship exists between the basic diet of the sole and its age. The basic diet is also a function of the energetic and nutritional requirements of each particular age group as well as a function of the strategy and capacity of capture.

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Literature cited

Braber, L., De Groot, S. J. (1973). The food of five flatfish species (Pleuronectiformes) in the northern North Sea: Neth. J. Sea Res. 6: 163–172

Dworschak, P. C. (1987). The biology of *Upogebia pusilla*. Mar. Ecol. 8: 337–358

Fincham, A. A. (1971). Ecology and population studies of some intertidal and sublittoral sand-dwelling amphipods. J. mar. Biol. Ass. U.K. 51: 471–488

Kaim Malka, R. A. (1969). Biologie el ecologie de quelques *Ampelisca* (Crustacea Amphipoda) de la region de Marseille. Téthys 1: 977–1022 (*in* Lagardère 1987)

Lagardère, J. P. (1987). Feeding ecology and daily food consumption of common sole, *Solea vulgaris* Quensel, juveniles on the French Atlantic coast. J. Fish Biol 30: 91–104

Molinero, A. (1986). Contribucion al conocimiento de la biología de la F. Soleidae del delta del Ebro. Tesis doctoral. Universidad de Barcelona

Molinero, A., Flos, R. (1991). Influence of sex and age on the feeding habits of the common sole *Solea solea*. Mar. Biol. 111: 493–501

Pielou, C. (1975). Ecological diversity. Wiley, New York

Pitt, T. K. (1973). Food of American plaice (*Hippoglossoides platessoides*) from the Grand Bank, Newfoundland. J. Fish. Res. Bd Can. 30: 1261–1273

Quiniou, L. (1978). Les poissons démerseaux de la baie de Douarnenez; alimentation et écologie. Thèse 3ème cycle. Université de Bretagne Occidentale, Brest

Ramos, J. (1981). Règimen y comportamiento alimentario del lenguado (*Solea solea* L.) Infmes téc. inst. Invest. pesq. 83: 3–15

Ruiz, J., Jover, L. (1981). Sobre la alimentación otoñal de la garcilla bueyera – *Bubulcus ibis* – en el delta del Ebro, Tarragona. Publnes Dep. Zool. Univ. Barcelona 6: 65–72

Ruiz, J., Jover, L. (1983). Tipificación trófica de poblaciones mediante estimas de la dominancia y la diversidad. Trans. 15th int. Congr. Game. Biol. 695–707 (Sevilla)