J. Mar. Biol. Ass. U.K. (2000), **80**, 95–102
Printed in the United Kingdom

Feeding of the spider crab *Maja squinado* in rocky subtidal areas of the Ría de Arousa (north-west Spain)

C. Bernárdez, J. Freire* and E. González-Gurriarán

Departamento de Bioloxía Animal, Bioloxía Vexetal e Ecoloxía, Universidade da Coruña, Campus da Zapateira s/n, 15071 A Coruña, Spain. *E-mail: jfreire@udc.es

The diet of the spider crab, *Maja squinado*, was studied in the rocky subtidal areas of the Ría de Arousa (Galicia, north-west Spain), by analysing the gut contents of crabs caught in the summer and winter of 1992. The highly diverse diet was made up primarily of macroalgae and benthic invertebrates that were either sessile or had little mobility. The most important prey were the seaweeds Laminariaceae (43% of the frequency of occurrence and 15% of the food dry weight), *Corallina* spp. (38% and 3%), molluscs [the chiton *Acanthochitona crinitus* (15% and 1%), the gastropods *Bittium* sp. (30% and 2%), Trochiidae and others and the bivalve *Mytilus* sp. (32% and 12%)], echinoderms [the holothurian *Aslia lefevrei* (32% and 18%) and the echinoid *Paracentrotus lividus* (16% and 7%)] and solitary ascidians (18% and 6%). The variability in diet composition was determined by the season (Laminariaceae, *Corallina* spp., *P. lividus*, *Mytilus* sp., gastropods and chitons appeared in greater frequency in winter, while the solitary ascidians and *A. lefevrei* were consumed to a greater extent in summer) in addition to sexual maturity (prey such as *Bittium* sp. or Trochiidae were more common in juveniles). Moreover, the changes in the food consumption rate were linked primarily to the moult stage. Feeding activity plummeted during the phases immediately preceding and following ecdysis (stages D_0–D_{3-4} and A), and the diet was less diverse during these phases. No feeding differences were found that could be linked to sex. The composition of the diet of *Maja squinado* appears to be determined by the seasonal abundance of the different prey in subtidal rocky areas and by their availability (depending on their behavioural and anatomical characteristics, mainly mobility and the presence of hard external structures). Moreover, life history factors have little importance in the variability of the diet composition and only the moult cycle has a considerable effect on feeding rate.

INTRODUCTION

The spider crab *Maja squinado* (Herbst, 1788) (Crustacea: Decapoda: Majidae) is a species of great commercial importance which is distributed along the north-west Atlantic coast and in the Mediterranean, from the subtidal level down to depths of 90 m (Kergariou, 1984). Due to the importance to fisheries of this species in the waters off the coast of Galicia (north-west Spain), studies focusing on reproduction, growth, migration and fisheries have been carried out to date (González-Gurriarán et al., 1993, 1995, 1998; González-Gurriarán & Freire, 1994; Hines et al., 1995; Freire & González-Gurriarán, 1998; Freire et al., 1998).

In the Ría de Arousa juveniles of the spider crab inhabit shallow areas (up to 15 m deep), with mixed rocky and sandy bottoms and their movements are non directional and slow (less than about 10 m per day). Immediately after the onset of sexual maturity and the terminal moult, these animals begin moving somewhat faster. From one to three months after the terminal moult, they begin to migrate towards deeper waters (González-Gurriarán & Freire, 1994; Hines et al., 1995; Freire & González-Gurriarán, 1998). This paper examines diet composition and gut fullness (as an indicator of feeding rate) of individuals caught in shallow areas, that is, juveniles and adults that have just undergone the pubertal moult.

There is little information available on the feeding habits of *M. squinado* based on direct observations in the field (Carlisle, 1957; Kergariou, 1974). Laboratory experiments done by Stevcic (1967) indicate that the spider crab has an omnivorous diet. Data from studies based on gut contents are scarce (Brosnan, 1981; Kergariou, 1974; Stevcic, 1967, 1968), but they also point to an omnivorous diet based on the consumption of prey common in the habitat.

MATERIALS AND METHODS

Sampling area

The crabs were caught in the Ría de Arousa, on the north coast of the O Grove Peninsula (42°29′N 09°56′W, Galicia, north-west Spain). The capture areas were shallow waters (<10 m deep), with rocky vegetated bottoms alternating with sandy bottoms. This type of habitat is typical of juveniles and adults that have just undergone the pubertal moult (González-Gurriarán & Freire, 1994; unpublished data). The crabs were caught only on rocky bottoms.

Two samplings were carried out in summer (20 July and 7 August 1992) and one in winter (22 December 1992) in which 132, 158 and 97 specimens of *Maja squinado* were caught respectively. The glass-box, which allows direct observation of shallow bottoms (<10 m), was used to locate the crabs, that were caught from the vessel with a boat-hook.

After the crabs were caught, the carapace length (CL, in mm) was measured in all specimens and the right cheliped length in males. The relationship between cheliped size and carapace length was used to determine morphometric maturity in males by means of a discriminant equation that was calculated for the population in the sampling area (Sampedro et al., 1999). Also determined were abdomen morphology, gonad development stage (González-Gurriarán et al., 1993, 1998) and the presence of a brood in females. Sexual maturity in females was determined by following morphological criteria: flat abdomen in juveniles and domed abdomen with developed pleopods in adults.

The stage of the intermoult cycle was determined by examining the endite of the second maxilla according to the criteria of González-Gurriarán et al. (1995) [adapted from Drach & Tchernigovtzeff (1967)], and using the nomenclature of Moriyasu & Mallet (1986) (immediate postecdysis, A; postmoult, B; intermoult, C; premoult, D_0, $D_{1'}$, $D_{1''}$, $D_{1'''}$, D_{3-4}).

The cardiac stomach was extracted from each specimen and fixed in a solution of 4% formaldehyde in seawater. After 48–72 h they were changed to 70% alcohol in which the gut was preserved until analysed.

Analysis of gut contents

Gut fullness was determined by visually estimating the percentage of gut volume occupied by the contents (the points method) (Williams, 1981; Freire & González-Gurriarán, 1995; Freire, 1996). Each prey was determined at the lowest possible taxonomic level. Next, each one was assigned a score in terms of its relative importance, estimated visually, as compared to the total level of fullness. The fragmented state in which the prey are found in the gut contents of the decapods makes them impossible to sort, which would be necessary to obtain other quantitative indices such as weight (Williams, 1981). The dry weight of the contents of each gut was found (at 60°C for 24–48 h).

Data analysis

For data analysis, the 100 types of prey first determined were grouped into 30 categories exclusive of each other. The standardized food dry weight (DW_{st}, which is equivalent to the weight of the gut contents of an individual with the same fullness and carapace length identical to the sample average, 115.2 mm.) was used to measure gut fullness. The food dry weight (DW) was standardized in terms of body size (CL), based on the regression relating the food dry weight (DW) to the CL:

$$\log_{10} DW_{st} = 2.602 + \log_{10} DW - 1.262 \log_{10} CL \quad (1)$$

In order to quantify the importance of the different prey in the diet, two indices were used: (i) frequency of occurrence, based on the presence of a particular prey in the gut:

$$F_i = \frac{n_i}{N} \quad (2)$$

where n_i is the number of occurrences (number of guts in which the prey i is present) and N is the total number of guts containing food. (ii) Dry weight index (DWI): percentage of standardized dry weight of the gut contents corresponding to each prey. To calculate this index, it is necessary to have previously estimated the dry weight of each prey in each gut (DW_{ij}), depending on its estimated importance determined by the point method:

$$DW_{ij} = DW_{st,j} \times \frac{PI_{ij}}{PI_j} \quad (3)$$

where PI_{ij} are the points assigned to prey i in gut j, and PI_j are the total points assigned to gut j, and DW_{st}, j is the standardized dry weight of contents of gut j.

$$DWI_i = \left(\sum_{j=1}^{n} DW_i / \sum DW_{st} \right) \times 100 \quad (4)$$

This index provides information on the importance of a particular prey in the diet in terms of biomass. There could be an overestimation of prey having hard parts, which are slower to evacuate, than softer prey. However this bias would be partially compensated because the contribution of each gut to the index increases with the fullness level. The guts having a greater fullness are those from crabs which had ingested food most recently, and are, therefore, more representative of the true proportions of the prey in the diet.

The analysis of seasonal and life history (sex, maturity and moult stage) variations in the consumption of the different prey was carried out by means of analysis of variance (ANOVA, using the DWI) and fitting of contingency tables using log-linear models (using frequency of occurrence). Only guts with food were used. In the cases where there were significant differences in the consumption of a prey category between the different stages of the moult cycle (the only factor having more than two categories), paired comparisons between these categories were carried out *a posteriori* by means of Tukey tests of multiple comparisons (Day & Quinn, 1989).

Diet diversity was estimated by the Shannon–Wiener (H′) index:

$$H' = -\sum_{i=1}^{n} p_i \log_2 p_i \quad (5)$$

where p_i is the proportion of prey i in the diet, and n the total number of prey categories present in the group of crabs analysed.

The variations in fullness level (standardized food dry weight) between seasons, sex, maturity and moult stages were analysed by ANOVA and, where necessary, Tukey tests.

A preliminary comparison between the July and August samples did not show significant differences in the consumption of any one prey ($P > 0.05$). Therefore, for the purpose of analysis, they were pooled (designated as summer).

Table 1. Maja squinado*: the importance of different prey categories in the gut contents. Frequency of occurrence (in percentage out of the total number of guts with food,* N=*308) and the dry weight index (DWI) are indicated. Included are the different diet components identified in each category.*

Prey category	Frequency	DWI
Corallina[1]	38.0	2.6
Cystoseira sp.	10.4	1.0
Epiphytes of Laminariaceae[2]	2.6	0.2
Laminaiaceae	42.9	14.8
Phaeophyta[2]	6.2	0.6
Rhodophyta[4]	2.6	0.0
Porifera	13.3	2.4
Polychaeta[5]	8.1	0.8
Bryozoa[6]	3.6	0.5
Acanthochitona	14.6	1.4
Bittium sp.	30.2	1.7
Bivalvia[2]	19.5	3.2
Mytilus (byssus)	15.6	1.4
Mytilus (shell)	16.6	11.1
Gastropoda[8]	20.1	0.6
Trochiidae (shell)[9]	18.8	0.8
Trochiidae (operculum)	33.4	0.4
Operculum indet.	12.7	0.0
Anomura and Brachyura[10]	16.2	3.8
Balanida	6.2	0.2
Aslia lefevrei (calceous deposits)	5.5	0.8
Aslia lefevrei (soft tissue)	28.6	17.3
Paracentrotus lividus	15.6	6.8
Echinoidea[11]	3.9	4.2
Ophiuroidea[12]	1.6	0.3
Solitary ascidians	18.2	6.3
Didemnun sp.	3.2	1.9
Teleostei[13]	6.8	1.4
Others[14]	4.2	13.3
Organic matter indet.	46.8	0.2

1, *Corallina officinalis*, *C. mediterranea*, *C. elongata*, *Jania rubens*; 2, *Sphacelaria plumosa*, *Pterosiphonia complanata*, *Heterosiphonia* spp., *Ectocarpus* spp., *Hinksia* spp.; 3, *Sargassum muticum*; 4, *Polysiphonia* spp., *Ceramium* spp.; 5, Spionidae, Arabellidae, Polyoniae, Cirratulidae, *Nereis* sp., Nereidae; 6, *Amanthia lendigera*, *Scrupocellaria* spp.; 7, *Dosinia exolata*, Tellinidae; 8, *Rissoa* sp., Rissoidae, *Diodora reticulata*, *Diodora* spp., Fissurellidae, *Patella* spp., *Littorina* spp., Nassidae spawns, *Hinia* spp., *Patina pellucida*, *Onoba semicostata*, radulae indet; 9, *Jujubinus exasperatus*, *Calliostoma ziziphynum*, *Gibbula* spp.; 10, *Pisidia longicornis*, Galatheidae, *Liocarcinus arcuatus*, *Necora puber*, Portunidae, *Pilumnus hirtellus*, *Xantho incisus*, Xanthidae, Brachyura indet., Decapoda indet; 11, *Echinocardium cordatum*; 12, Ascididae, Molgulidae, solitary ascidians indet; 13, Labridae; 14, *Elphidium crispum*, *Sertullariella meditarranea*, Hydroidea indet., *Nymphon* sp., Isopoda indet., Caprellidea indet., Amphipoda indet.

RESULTS

Analysis of gut contents

In the analysis of the gut contents of *Maja squinado* a total of 100 diet components were found (Table 1). In most cases the prey were highly fragmented. The fragments of kelp are regular in form and are sometimes accompanied by epiphytes. As far as animal remains are concerned, they were often identified by hard structures that take longer to digest: sponge spicules, polychaete jaws, shells and opercula of molluscs, crustacean exoskeleton, etc. The individuals of the holothurian *Aslia lefevrei* (Barrois) ingested were found whole and the solitary ascidians were almost always found with unbroken tunics.

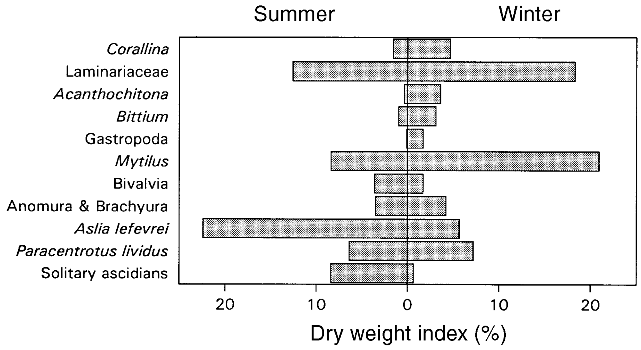

Figure 1. *Maja squinado*: dietary importance (as dry weight index, DWI), of the main prey in summer and winter.

Maja squinado was found to have a diverse diet, containing a large number of frequent prey. The most common diet components with the greatest quantitative importance were the Laminariaceae (appearing in 43% of the guts and accounting for 15% of the DWI) (Table 1). Of the rest of the seaweeds, only *Corallina* (different species of the genus *Corallina* and *Jania rubens* (L.) Lamour were included in this category), reached a high frequency of occurrence (38%, with a DWI of 3%). Other prey with a considerable quantitative importance were the holothurian *Aslia lefevrei* (frequency of occurrence of 32% and 18% DWI), the solitary ascidians (16% and 6%, respectively), the echinoid *Paracentrotus lividus* (Lamarck) (16% and 7% respectively) and the brachyuran crustaceans and anomurans (16% and 4% respectively). Some prey having a high frequency of occurrence, such as the gastropods, sponges and bivalves, had little quantitative importance due to their small body size. Organic matter unidentified because of the advanced state of digestion appeared frequently in the gut contents (47%), although its quantitative importance was minimal (0.2% DWI).

Seasonal variations in diet composition and feeding

Seasonal differences were found in the consumption of *Mytilus* and *Corallina*, whose DWI and frequency of occurrence were greater in winter (Figure 1). Seasonal differences were also observed in the consumption of *Paracentrotus lividus*, *Mytilus* sp., the gastropods and chitons (Tables 2 & 3), which were also more common in winter. The opposite trend (increase in frequency of occurrence and DWI in summer) was exhibited by solitary ascidians and the holothurian *Aslia lefevrei*. Diet diversity was very similar in summer and winter (H′= 3.69 and 3.67, respectively). The seasonal changes in fullness were not statistically significant (ANOVA, $F_{1,364}=1.06$, $P=0.304$), although there was an increase in the dry weight of the gut contents in winter (Figure 2).

Diet composition and feeding related to life history

No significant differences ($P>0.05$) were found in diet composition between males and females (Tables 2 & 3), except in the case of *Paracentrotus lividus*, which made up a

Table 2. Maja squinado*: results of the analysis variance (*F*-statistic and significance level in parentheses) used to test the differences in the consumption of the different categories of prey (based on the DWI index) between seasons, sexes, maturity stages and intermoult stages. The comparisons between maturity and intermoult stages were carried out on both crabs caught in summer and on all specimens (summer and winter). In cases where the comparisons between the intermoult stages presented significant differences, the results of the paired comparisons with the Tukey test are given (the groups not having significant differences between each other are underlined).*

Factor comparison	Season summer/winter		Sex males/females		Maturity juveniles/adults				Moult B/C/D_0			
					(summer/winter)		(summer)		(summer/winter)		(summer)	
d.f.	1306		1306		1306		1355		2257		2288	
Corallina	9.26	(0.003)	0.13	(0.718)	0.03	(0.865)	3.16	(0.766)	1.34	(0.263)	0.57	(0.565)
Cystoseira	1.50	(0.222)	0.19	(0.891)	1.95	(0.163)	1.07	(0.303)	4.13	(0.017)	3.86	(0.023)
Laminariaceae	3.55	(0.036)	0.37	(0.543)	0.47	(0.494)	3.85	(0.051)	3.35	(0.037)	4.98	(0.008)
Phaeophyta	2.18	(0.141)	2.38	(0.124)	0.21	(0.644)	0.52	(0.472)	0.01	(0.992)	0.00	(0.996)
Porifera	5.34	(0.021)	0.50	(0.482)	0.09	(0.762)	0.51	(0.476)	2.10	(0.125)	1.50	(0.226)
Polychaeta	1.48	(0.224)	1.26	(0.263)	0.58	(0.448)	0.57	(0.018)	0.12	(0.885)	0.23	(0.797)
Acanthochitona	23.39	(0.000)	3.82	(0.051)	2.75	(0.098)	0.11	(0.743)	0.58	(0.558)	0.34	(0.713)
Bittium	9.66	(0.002)	0.22	(0.6.39	3.85	(0.051)	1.88	(0.172)	1.56	(0.316)	0.95	(0.389)
Trochiidae (shell)	0.27	(0.610)	0.03	(0.862)	2.53	(0.171)	2.61	(0.108)	1.00	(0.368)	0.66	(0.520)
Trochiidae (operculum)	0.58	(0.446)	2.74	(0.099)	1.89	(0.460)	2.02	(0.157)	0.93	(0.397)	0.95	(0.390)
Gastropoda	20.33	(0.000)	1.06	(0.303)	3.19	(0.0.75)	0.94	(0.334)	1.07	(0.344)	0.09	(0.917)
Operculum indet.	1.85	(0.175)	0.55	(0.461)	0.44	(0.510)			0.11	(0.896)		
Mytilus (byssus)	1.48	(0.225)	2.85	(0.093)	1.26	(0.262)	1.63	(0.203)	0.14	(0.871)	0.18	(0.837)
Mytilus (shell)	4.34	(0.038)	0.93	(0.336)	1.30	(0.255)	0.69	(0.409)	0.01	(0.987)	0.47	(0.629)
Bivalvia	0.46	(0.500)	0.16	(0.691)	0.21	(0.647)	0.14	(0.711)	1.80	(0.168)	1.43	(0.241)
Anomura and Brachyura	0.32	(0.573)	0.91	(0.341)	0.55	(0.460)	1.27	(0.262)	2.83	(0.061)	0.75	(0.474)
Balanida	1.16	(0.281)	0.70	(0.404)	0.06	(0.808)	0.00	(0.989)	0.08	(0.925)	0.10	(0.904)
Aslia lefevrei (dermic plates)	1.81	(0.180)	0.03	(0.865)	0.59	(0.444)	0.95	(0.330)	0.14	(0.872)	0.19	(0.827)
Aslia lefevrei (soft tissue)	8.00	(0.005)	0.37	(0.542)	12.72	(0.000)	0.86	(0.004)	1.94	(0.146)	2.23	(0.111)
Echinoidea	0.81	(0.776)	0.04	(0.848)	0.04	(0.832)	0.12	(0.728)	0.98	(0.378)	1.27	(0.285)
Paracentrotus lividus	0.12	(0.730)	7.27	(0.007)	0.04	(0.844)	0.25	(0.620)	0.54	(0.586)	0.47	(0.625)
Solitary ascidians	6.55	(0.011)	0.18	(0.672)	11.28	(0.001)	7.20	(0.008)	0.36	(0.695)	0.44	(0.643)
Didemnum	0.44	(0.506)	1.49	(0.224)	1.40	(0.238)	1.29	(0.257)	3.68	(0.027)	2.93	(0.056)
Teleostei	9.93	(0.002)	0.00	(0.959)	0.78	(0.379)	0.94	(0.334)	0.51	(0.604)	0.32	(0.728)
Other	0.37	(0.542)	0.04	(0.831)	0.91	(0.341)	0.63	(0.430)	1.18	(0.310)	2.39	(0.094)
Organic matter indet.	0.16	(0.686)	0.05	(0.836)	1.78	(0.183)	2.05	(0.154)	1.17	(0.312)	0.90	(0.410)

Tukey test	Moult	(B/C/D0)	
Cystoseira	B	D0	C
Didemnum	B	C	
Laminariaceae	B	C	D0

higher percentage of DWI in males. Fullness and diet diversity were also quite similar between both sexes (Figure 2; H′ = 3.76 and 3.80, for males and females) (fullness comparison, ANOVA, $F_{1,364}$ = 0.43, P = 0.511).

The analysis of the diet as related to maturity was carried out using only data from the summer samplings, since practically all of the crabs that were caught in winter were juveniles. The Laminariaceae, solitary ascidians and *Aslia lefevrei* were more abundant and more frequent in adults (Figure 3). In contrast, prey such as *Bittium* sp., opercula and shells of trochids, other gastropods, *Mytilus* sp. and undetermined opercula, appeared more frequently in the diet of juveniles, although these differences were only significant in the first two ($P < 0.01$). There was a similar pattern, although less pronounced in quantitative terms, in sponges, bivalves, chitons, crustaceans and barnacles. No significant differences were found in fullness (Figure 2; ANOVA, $F_{1,364}$ = 0.218, P = 0.572) and diversity proved to be slightly higher in juveniles (H′ = 3.82 in juveniles and 3.12 in adults).

The most important differences in the diet of the spider crab between life history phases occur in relation to the moult cycle. The fullness level was significantly different in moult stages B, C, D_0 and D (Figure 2; ANOVA, $F_{3,311}$ = 6.259, $P < 0.001$; Tukey test, $P < 0.01$ in all cases). Phase A was not included in the analyses and stages $D_{1'}$, $D_{1''}$, $D_{1'''}$ and D_{3-4} were grouped into stage D because of the small number of specimens analysed

Table 3. Maja squinado*: results of the log-linear model fit for the analysis of prey consumption. The model is made up of the factors Prey (presence/absence)×Sex (males/females)×Maturity (Mat, juveniles/adults)×Moult (Mou, B/C/D_0)×Season (Sea, summer/winter). The significance level of statistic χ^2 of partial association between factors is given. Third order interactions have been omitted since in all cases the effects were not significant (*$P>0.1$*).*

	Effect of prey× Sex×Mat	Sex×Mou	Sex×Sea	Mat×Mou	Mat×Sea	Mou×Sea	Sex	Mat	Mou	Sea
Corallina	0.214	0.579	0.912	0.465	0.224	0.759	0.607	0.530	0.231	0.292
Cystoseira	0.253	0.059	0.678	0.867	0.489	0.670	0.518	0.049	0.008	0.581
Laminariaceae	0.117	0.910	0.755	0.610	0.014	0.257	0.964	0.385	0.776	0.026
Phaeophyta	0.994	0.698	0.963	0.832	0.324	0.629	0.369	0.121	0.001	0.971
Porifera	0.408	0.720	0.811	0.471	0.088	0.256	0.466	0.527	0.401	0.698
Polychaeta	0.732	0.810	0.219	0.586	0.379	0.951	0.595	0.509	0.062	0.003
Acanthochitona	0.153	0.780	0.548	0.888	0.052	0.513	0.328	0.978	0.053	0.000
Bittium	0.559	0.415	0.447	0.209	0.636	0.613	0.697	0.006	0.421	0.940
Trochiidae (shell)	0.689	0.801	0.818	0.381	0.084	0.748	0.662	0.053	0.505	0.185
Trochiidae (operculum)	0.408	0.637	0.625	0.499	0.002	0.418	0.333	0.000	0.276	0.408
Gastropoda	0.206	0.648	0.667	0.306	0.592	0.463	0.833	0.269	0.414	0.001
Operculum indet.	0.336	0.817	0.433	0.347	0.774	0.444	0.296	0.351	0.387	0.011
Mytilus (byssus)	0.544	0.961	0.145	0.345	0.873	0.301	0.653	0.370	0.280	0.006
Mytilus (shell)	1.000	0.866	0.394	0.437	0.595	0.545	0.690	0.449	0.356	0.000
Bivalvia	0.790	0.630	0.479	0.812	0.878	0.162	0.510	0.914	0.707	0.869
Anomura and Brachyura	0.269	0.543	0.316	0.879	0.063	0.774	0.195	0.970	0.082	0.158
Balanida	0.309	0.895	0.687	0.690	0.263	0.654	0.167	0.788	0.153	0.833
Aslia lefevrei (dermic plates)	0.215	0.929	0.722	0.728	0.484	0.802	1.000	0.191	0.018	0.596
Aslia lefevrei (soft tissue)	0.618	1.000	0.651	0.689	0.408	0.309	0.171	0.098	0.480	0.002
Echinoidea	0.369	0.646	0.266	0.833	0.018	0.849	0.514	0.109	0.097	0.113
Paracentrotus lividus	0.400	0.944	0.417	0.546	0.613	0.877	0.053	0.564	0.865	0.017
Solitary ascidians	0.060	0.725	0.630	0.421	0.323	0.313	0.627	0.251	0.510	0.003
Didemnum	0.344	0.707	0.589	0.967	0.620	0.994	0.513	0.204	0.010	0.074
Teleostei	0.861	0.938	1.000	0.884	0.097	0.632	0.502	0.120	0.138	0.001
Other	0.860	0.726	0.405	0.795	0.171	0.888	0.708	0.883	0.016	0.522
Organic matter indet.	0.955	0.636	0.726	0.940	0.069	0.920	0.442	0.462	0.550	0.149
d.f.	1	2	1	2	1	2	1	1	2	1

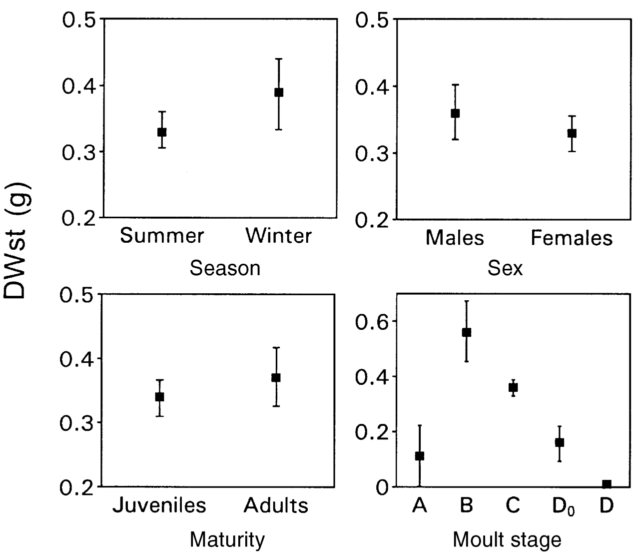

Figure 2. *Maja squinado*: fullness (DW_{st}, standardized dry weight of gut contents, in g) in terms of season, sex, maturity and stage of the intermoult cycle. The mean value standard error is shown. In the intermoult cycle stage D groups crabs in phases $D_{1'}$ to $D_{3\text{–}4}$.

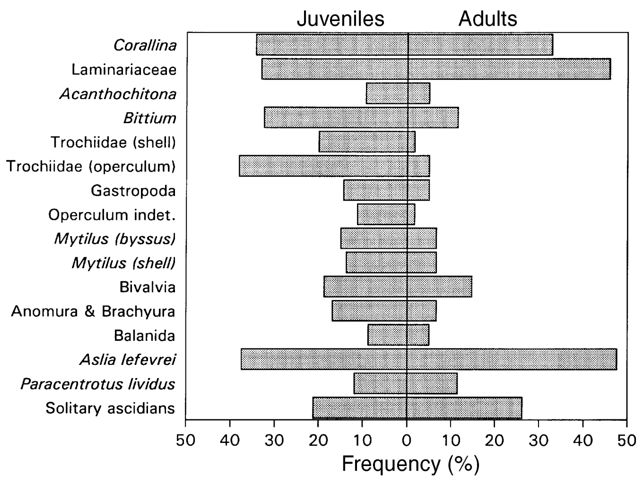

Figure 3. *Maja squinado*: dietary importance (as frequency of occurrence) of the main prey in juveniles and adults.

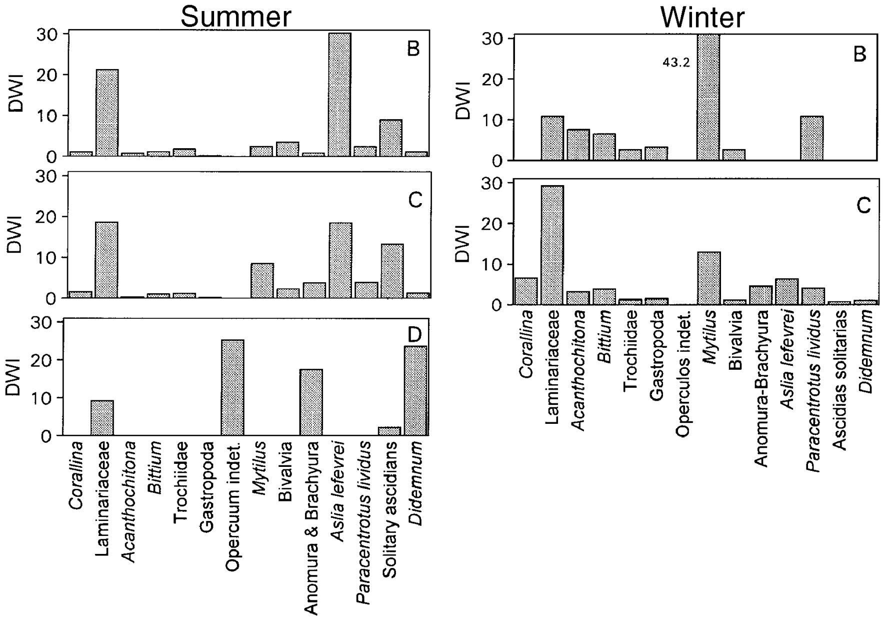

Figure 4. *Maja squinado*: dietary importance (as the dry weight index, DWI) of the main prey throughout the intermoult cycle. Stage D groups crabs in phases D_0 to D_{3-4}.

(N<8 in all cases). Stage B was observed to have a maximum fullness level (0.56 g DW_{st}), while in stage C the fullness level underwent a slight decrease as compared to the previous stage (0.36 g DW_{st}). Phase D_0 had a very low fullness level which became null in the following stages (from D_1 on).

As regards diet composition, there were differences that could be linked to the moult cycle in the DWI of the Laminaraiceae, *Cystoseira* sp. and *Didemnum* sp. (Table 2, Figure 4), and in the frequency of occurrence of prey with little quantitative importance (Phaeophyta, dermic plates of *Aslia lefevrei*, *Didemnum* sp. (Table 3)). There were no clear patterns observed in these changes.

Diet diversity followed a cyclic pattern, similar to that of fullness and was highest in stages B (H'=3.58) and C (3.80) and lowest in the premoult stages D_0 (2.52) and following D stages (0.75).

DISCUSSION

The studies on the diet of decapods have generally found that these animals tend to consume prey which are abundant in the habitat rather than a selective capture of their prey (Freire, 1996; Freire & González-Gurriarán, 1995; Woods, 1993). Our study also points to a close link between the diet of *Maja squinado* and the abundance and availability of the prey in the habitat. A number of studies on feeding of majid crabs have been carried out in the rocky, shallow bottoms characterized for the most part by kelp forests, which highlight the importance of the seaweeds in the diet of the majids living in these areas (Hines, 1982; Stevcic, 1990; Woods, 1993). The diet of the species of this family living on soft bottoms at greater depths, in contrast, is dominated by bivalve molluscs, crustaceans, polychaetes, sponges and echinoderms, which are common prey in these habitats (Lefebvre & Brêthes, 1989; Wieczorek & Hooper, 1995).

Studies on species from the genus *Maja* in rocky subtidal areas highlight the importance of the habitat in diet composition. Stevcic (1985) found echinoderms, chitons, crustaceans, seaweeds and bivalves in the gut contents of *M. crispata* Risso in the Adriatic Sea. Brosnan (1981) reported asteroids, brachyurans and seaweeds in the gut contents of *M. squinado* on the west coast of Ireland. Kergariou (1974) described a diet consisting mainly of seaweeds, molluscs, echinoderms and crustaceans for this species in the English Channel; all of these prey were common in the study areas.

From field observations made by divers (Kergariou, 1974), it was found that *M. squinado* preys on asteroids of the genus *Marthasterias*, mussels, and red seaweeds that grow on the rocky walls. In experiments on food preference (Brosnan, 1981), these crabs consumed *Carcinus maenas* L. recently killed, the seastars *Asterias* and *Marthasterias*, as well as previously opened *Mytilus edulis* L.

The diet composition of *Maja squinado* in the Ría de Arousa is dominated by the macroalgae (chiefly Laminariaceae) and benthic invertebrates sessile (*Mytilus* sp., solitary ascidians) or having little mobility (*Acanthochitona crinitus* (Pennant), *Bittium* sp., *Aslia lefevrei*). The diet appears to be determined by the availability of the prey, which is in turn, conditioned by both the abundance of these prey (that is, by habitat) and by behavioural (mobility) and anatomical (the presence and hardness of the exoskeleton, shell or other rigid structures) characteristics of the potential prey.

Similarly, the seasonal changes in the environment also give rise to variations in food abundance and availability as the life cycles of many prey present fluctuations which make them optimum for consumption (because of their size, etc.) during specific periods (Abelló & Cartes, 1987; Choy, 1986; Freire, 1996). In this paper the seasonal changes in the consumption of kelp may be related to the information from these seaweed communities associated with mussel raft culture (Lapointe et al., 1981), which is of enormous importance in zones near our study areas. These seaweeds achieve peak biomass in the summer months, whereas in autumn, when the plants die and accumulate on the bottom, they are probably more accessible to the spider crab, which might be related to the increase in their frequency of occurrence in the diet during the winter.

The variations in the frequency of occurrence of *Aslia lefevrei* may also be linked to the life cycle of the prey. This holothurian has only one breeding season annually in the Ría de Arousa, between February and March (Costelloe, 1988). The size of the specimens (5–8 mm body length), which are swallowed whole by the spider crab, is probably reached in summer, which coincides with an increase in the frequency of occurrence of this prey in the gut contents. The increase in the frequency of occurrence of the colonial ascidians (*Didemnum* sp.) in summer may be attributed to its abundance in the habitat, since several species of this genus only appear in the spring and summer (Hayward & Ryland, 1990). The influence of the cycles of natural populations of *Mytilus* sp. attached to the rocks in shallow zones may give rise, during a specific period, to an optimum size prey for consumption, taking into account the life cycle of this species in nearby areas devoted to mussel culture (Mariño et al., 1982). This may cause the increase in the consumption of *Mytilus* sp. and other prey in winter.

The changes in the fullness levels found in relation to season may be explained by the seasonality of the moult and by the changes in activity that this entails. Thus, the drop in fullness reported in summer is related to the most important peak in moulting of the year, when the pubertal moult takes place (González-Gurriarán et al., 1995; unpublished data). In the intermoult stages close to the moult (from D_0 on), the crabs reduce their activity to a minimum, thus also minimizing the risk of predation and the energy invested in other functions. Studies carried out on other decapods report that during the time ecdysis lasts, as well as the stages immediately preceeding it, this lack of activity translates to a low level of gut fullness (Abelló & Cartes, 1987; Freire, 1996).

Studies on other majids (Wieczorek & Hooper, 1995) as well as on *Maja squinado* (Hartnoll, 1963; Kergariou, 1974) do not exhibit differences in diet composition in terms of body size or sexual maturity. In the present comparison of the diet of juveniles and adults it was found that the diet of *M. squinado* had a slight trend to be more diversified in juveniles. The frequency of occurrence of most of the prey was also greater in juveniles, although this pattern is not important in quantitative terms.

The quantitative changes associated with maturity in the crabs appear to be related to the demand for certain nutrients required during the intermoult phase, since ecdysis implies a strong need for calcium and other materials to form the new exoskeleton. The use of calcium from the diet in the process of calcification has been reported for other species of decapods (Vigh & Dendinger, 1982; Sardá & Cros, 1984). Juveniles carry out frequent ecdyses, thus, the need to build up calcium reserves may imply a greater consumption of gastropods and other prey having a high content of calcium carbonate. This requirement would decrease after the terminal pubertal moult.

Kergariou (1974) found differences in the diet between males and females of *M. squinado* which he attributed to an uneven bathymetric distribution in certain seasons, thus, the actual reason for these differences would, once again, be habitat and availability of prey. Our data follow the same pattern, resulting in significant differences only in the consumption of one prey, *Paracentrotus lividus*.

The biological factor appearing as the greatest source of variation in the diet is the intermoult cycle, whose effect on diet composition in decapods and especially on feeding rate, has already been reported by a number of researchers (Abelló & Cartes, 1987; Choy, 1986; Drach, 1939; Freire, 1996; Sardá & Cros, 1984). The specimens of *M. squinado* found to be in recent postmoult (stage A) consume little food, which is associated with decreased activity. In a more advanced phase (stage B), the individuals begin a stage of active feeding needed for the gradual hardening of the newly formed carapace, which would explain the high levels of fullness and diversity found. In stage D_0 the crabs show the first signs of the impending ecdysis, and some diet changes may already be noticeable, again, as a result of the decrease in general activity. In terms of diet, this could be considered a transitional stage. During the phases following stage D, the crabs reduce their activity and stop feeding.

This study is part of research projects funded by the Consellería de Pesca, Marisqueo e Acuicultura, Dirección Xeral de Formación Pesqueira e Investigación of the Xunta de Galicia. We thank J. Parapar, M.E. Vázquez, C. Olabarría and A. Veiga for their collaboration in the identification of different taxonomic groups in gut contents, and the fishermen J.F. Silva and F. Vidal who collaborated in the sampling.

REFERENCES

Abelló, P. & Cartes, J., 1987. Observaciones sobre la alimentación *de Liocarcinus depurator* (L.) (Brachyura: Portunidae) en el Mar Catalán. *Investigación Pesquera*, **51**, 413–419.

Brosnan, D.M., 1981. *Studies on the biology, ecology, and fishery of the spider crab* Maja squinado *Herbst (1788) off the west coast of Ireland.* MSc thesis, Department of Zoology, University College Galway, Ireland.

Carlisle, D.B., 1957. On the hormonal inhibition of moulting in decapod Crustacea. II. The terminal anecdysis in crabs. *Journal of the Marine Biological Association of the United Kingdom*, **36**, 291–307.

Costelloe, J., 1988. Reproductive cycle, development and recruitment of two geographically separated populations of the dendrochirote holthurian *Aslia lefevrei. Marine Biology,* **99**, 535–545.

Choy, S.C., 1986. Natural diet and feeding habits of the crabs *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae). *Marine Ecology Progress Series*, **31**, 87–99.

Day, R.W. & Quinn, G.P., 1989. Comparison of treatments after an analysis of variance in ecology. *Ecological Monographs*, **59**, 433–463.

Drach, P., 1939. Mue et cycle d'intermue chez les crustacés décapodes. *Annales de l'Institut d'Océanographie,* **19**, 103–391.

Drach, P. & Tchernigovtzeff, C., 1967. Sur le méthode de détermination des states d'intermue et son application générale aux Crustacés. *Vie et Milieu*, **18**, 596–610.

Freire, J., 1996. Feeding ecology of *Liocarcinus depurator* (Decapoda: Portunidae) in the Ría de Arousa (Galicia, north-west Spain): effects of habitat, season and life history. *Marine Biology*, **126**, 297–311.

Freire, J. & González-Gurriarán, E., 1998. New approaches to the behavioural ecology of decapod crustaceans using telemetry and electronic tags. *Hydrobiology*, **371/372**, 123–132.

González-Gurriarán, E., Fernández, L., Freire, J., Muiño R. & Parapar, J., 1993. Reproduction of the spider crab *Maja squinado* (Brachyura: Majidae) in the southern Galician coast (NW Spain). *International Council for the Exploration of the Sea (CM Papers and Reports)*, Shellfish Committee, CM 1993/K:19, 17 pp.

González-Gurriarán, E., Fernández, L., Freire, J., Muiño, R., 1998. Mating and role of seminal receptacles in the reproductive biology of the spider crab *Maja squinado* (Decapoda, Majidae). *Journal of Experimental Marine Biology and Ecology*, **220**, 269–285.

González-Gurriarán, E. & Freire, J., 1994. Movement patterns and habitat utilization in the spider crab *Maja squinado* (Herbst) (Decapoda, Majidae) measured by ultrasonic telemetry. *Journal of Experimental Marine Biology and Ecology*, **184**, 269–291.

González-Gurriarán, E., Freire, J., Parapar, J., Sampedro, M.P. & Urcera, M., 1995. Growth at moult and moulting seasonality of the spider crab, *Maja squinado* (Herbst) (Decapoda: Majidae) in experimental conditions: implications for juvenile life history. *Journal of Experimental Marine Biology and Ecology*, **189**, 183–203.

Hartnoll, R.G., 1963. The biology of Manx spider crabs. *Proceedings of the Zoological Society of London*, **141**, 423–496.

Hayward, P.J. & Ryland, J.S., ed., 1990. *The marine fauna of the British Isles and north-west Europe.* Oxford: Clarendon Press.

Hines, A.H., 1982. Coexistence in a kelp forest: size, population dynamics, and resource partitioning in a guild of spider crabs (Brachyura, Majidae). *Ecological Monographs,* **52**, 179–198.

Hines, A.H., Wolcott, T.G., González-Gurriarán, E., González-Escalante, J.L. & Freire, J., 1995. Movement patterns and migrations in crabs: telemetry of juvenile and adult behaviour in *Callinectes sapidus* and *Maja squinado. Journal of the Marine Biological Association of the United Kingdom*, **75**, 27–42.

Kergariou, G. de, 1974. Régime alimentaire de *Maia squinado. International Council for the Exploration of the Sea (CM Papers and Reports)*, comité des crustacés, coquillages et benthos, CM 1974/K:36, 6 pp.

Kergariou, G. de, 1984. L'araignée de mer, *Maia squinado* L., sur le littoral de Bretagne. *Science et Pêche, Bulletin de l'Institut de Pêches Maritimes*, **205**, 11–19.

Lapointe, B.E., Niell, F.X. & Fuentes, J.M., 1981. Community structure, succession and production of seaweeds associated with mussel-rafts in the Ría de Arosa, NW Spain. *Marine Ecology Progress Series*, **5**, 243–253.

Lefebvre, L. & Brêthes, J.C.F., 1989. Food of early benthic stages of snow crab (*Chionoecetes opilio*) in the southwestern Gulf of St. Lawrence. *Proceedings of the International Symposium on King & Tanner Crabs, November 1989, Anchorage, Alaska.*

Mariño, J., Pérez, A. & Román, G., 1982. El cultivo del mejillón (*Mytilus edulis* L.) en la Ría de Arosa. *Boletín del Instituto Español de Oceanografía*, **7**, 297–308.

Moriyasu, M. & Mallet, P., 1986. Reading moult stages of the snow crab (*Chionoecetes opilio*) by the observation of the maxilla. *Journal of Crustacean Biology*, **6**, 709–718.

Sampedro, M.P., González-Gurriarán, E., Freire, J. & Muiño, R., 1999. Morphometry and sexual maturity in the spider crab *Maja squinado* (Decapoda: Majidae) in Galicia (NW Spain). *Journal of Crustacean Biology*, **19**, 578–592.

Sardá, F. & Cros, L., 1984. El metabolismo del calcio y el magnesio en la cigala *Nephrops norvegicus* (L.) durante las etapas del ciclo de intermuda. *Investigación Pesquera*, **48**, 377–397.

Stevcic, Z., 1967. Le complex de la norriture de l'araignée de mer *Maja squinado. Helgoländer Wissenschaftliche Meeresuntersuchungen*, **15**, 630–636.

Stevcic, Z., 1968. Relations interespécifiques de l'araignée de mer. *Rapports de la Commision Intérnational de la Mer Méditerranée*, **19**, 147–149.

Stevcic, Z., 1985. Contribution à la connaisance sur la norriture du crabe *Maja crispata*. *Rapports de la Commision Intérnational de la Mer Méditerranée*, **29**, 315–316.

Stevcic, Z., 1990. Note on the autoecology of the spider crab *Macropodia rostrata*. *Rapports de la Commision Intérnational de la Mer Méditerranée*, **32**, 34.

Vigh, D.A. & Dendinger, J.E., 1982. Temporal relationship of post-molt deposition of calcium, magnesium, chitin and protein in the cuticle of the Atlantic blue crab, *Callinectes sapidus* Rathbun. *Comparative Biochemistry and Physiology*, **72A**, 365–369.

Wieczorek, S.K. & Hooper, R.G., 1995. Relationship between diet and food availability in the snow crab *Chionoecetes opilio* (O. Fabricius) in Bonne Bay, Newfoundland. *Journal of Crustacean Biology*, **15,** 236–247.

Williams, M., 1981. Methods for analysis of natural diet in portunid crabs (Crustacea: Decapoda: Portunidae). *Journal of Experimental Marine Biology and Ecology*, **52**, 103–113.

Woods, C.M.C., 1993. Natural diet of the *Notomithrax ursus* (Brachyura: Majidae) at Oaro, South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, **27**, 309–315.

Submitted 22 April 1998. Accepted 23 June 1999.