Influence of morphometry and biomechanics on diet selection in three portunid crabs

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ABSTRACT: Morphometric and biomechanical characteristics [size, mechanical advantages (MAs), muscle mass ratio (MR)] of the chelipeds of *Necora puber*, *Liocarcinus depurator* and *Liocarcinus arcuatus* (Crustacea, Decapoda, Portunidae) were analyzed to investigate their relation to diet selection patterns observed from gut content analysis of crabs from the Ría de Arousa (Galicia, NW Spain). The size of the chelipeds relative to body size is similar in the 3 species, but there are important differences in biomechanical parameters. Both males and females demonstrate an interspecific morphometric gradient where there is an inverse relationship between MA and MR of the chelipeds. The prey consumed by portunids in the Ría de Arousa was classified according to its mobility and presence of a hard exoskeleton. The diet of *L. depurator* had a high morphological diversity as the functional structure of the chelipeds is more versatile than in the other species. Chelipeds of *L. depurator* are highly mobile because the MAs are relatively low, but the decrease in force produced is compensated by a relative increase in muscle mass. *L. arcuatus* has a lower MR but the highest MA, hence the force produced depends more on the design of the chelipeds. These characteristics give rise to appendages with little mobility, which is reflected in a diet made up mainly of sedentary prey without an exoskeleton. *N. puber* has intermediate trophic and biomechanical characteristics; its prey are primarily mobile and have hard exoskeletons. Ontogenetic changes are the main factor reponsible for life history variation in the diet, and they are related to biomechanical factors due to the absolute growth of the chelipeds. Growth gives access to prey with hard exoskeletons, especially in the case of *L. depurator*, whereas the changes in relative growth are associated with the onset of sexual maturity and reproductive behaviour. Within a species, the morphometric patterns observed may be attributed to non-trophic selection processes, and they have no major influence on the diet, which is conditioned mainly by the absolute growth of the chelipeds and muscle mass. On a longer evolutionary scale, the interspecific diversity in feeding habits and morphometry are correlated, although the causal mechanism could not be determined.

KEY WORDS: Biomechanics · Diet selection · Feeding · Morphometry · Decapoda · Portunidae

INTRODUCTION

Decapod crustaceans are the dominant epibenthic invertebrates in the Ría de Arousa (Galicia, NW Spain), especially in the extensive soft-bottom areas devoted to the raft culture of mussel *Mytilus galloprovincialis* (Tenore et al. 1982). The density and biomass of decapods are higher in the Ría de Arousa than in other rías, and in raft areas compared to zones that are not used for mussel culture (González-Gurriarán 1982, Romero et al. 1982). In particular, food provided by mussels and the associated epifauna on rafts have determined the changes in the abundance and distribution patterns observed for the epibenthic decapods in the Ría de Arousa (González-Gurriarán et al. 1989, Freire et al. 1990, Freire 1993, in press, Freire & González-Gurriarán 1995). Portunids (*Necora puber*, *Liocarcinus depurator* and *Liocarcinus arcuatus*) are the most abundant decapods in the Ría de Arousa, and their population dynamics are linked to new habitats created by mussel culture (González-Gurriarán 1985, Fernández et al. 1991, Freire et al. 1991).

There are major differences in the size and morphology of chelipeds in brachyuran crustaceans, as well as in the degree of sexual dimorphism and heterochely

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(Schäfer 1954, Hartnoll 1974, 1978, Vermeij 1977) In the portunids the morphological structure of chelae has been analyzed because of their importance in predation techniques and prey selection mechanisms (Elner 1980, Hughes & Seed 1981, Blundon & Kennedy 1982, ap Rheinallt & Hughes 1985, ap Rheinallt 1986). Chelipeds are relatively simple lever systems in which the mobility and the force produced are inversely related. They generate forces that are applied by means of occlusive surfaces, facilitating the handling of resistant prey with hard exoskeletons or a shell (Warner & Jones 1976).

This study examines morphometrical and biomechanical aspects of the chelipeds of *Necora puber, Liocarcinus depurator* and *Liocarcinus arcuatus* in order to test the hypothesis that these characteristics cause differences in diet selection, both interspecifically and between life history stages within species.

MATERIALS AND METHODS

Diet composition. A detailed description of the sampling areas, methodology and diet composition and its spatial and seasonal changes and variability related to life history is given elsewhere (Freire 1993, in press, Freire & González-Gurriarán 1995), and only a brief summary is presented here. Diet composition was examined in approximately 10000 gut contents of *Necora puber, Liocarcinus depurator* and *Liocarcinus arcuatus*. Specimens were caught monthly from July 1989 to June 1990 in different sampling stations located in 3 types of soft-bottom habitat: mussel culture areas inhabited by the 3 species, the central channel of the ría where only *L. depurator* was present, and a beach area where only *L. arcuatus* was present (*N. puber* is a species typical of subtidal rocky areas, inhabiting only soft bottoms in mussel culture areas, González-Gurriarán 1985). The prey consumed by portunids in the Ría de Arousa was classified according to the following characteristics: mobility (sessile or slow moving and mobile) and presence or absence of a hard exoskeleton (non-articulated or articulated as in ophiuroids, where the handling and ingestion of the prey is carried out by crushing the articulated areas and not the exoskeleton itself) (Lawton & Elner 1984).

Morphometry and biomechanics. Morphometrics were studied in specimens fixed in 4 % formaldehyde for 24 to 48 h and preserved in 70 % alcohol. Males and females in intermoult stage with body sizes (carapace width between the tips of the fifth anterolateral spines, CW) covering the

typical range for each species and sex (*Necora puber* 20 to 80 mm, *Liocarcinus depurator*: 10 to 60 mm, *L. arcuatus*: 10 to 40 mm) were selected. The specimens used did not show any signs of regeneration or malformation of the chelae and presented the typical heterochely of the species studied (with a right crusher chela and a left pincer chela). The heterochely of portunids is defined by the different morphology of the dentition in both chelipeds, although their sizes are similar. The crusher chela, usually the right one, is larger and has blunt molar shaped teeth, with an ample contact surface and a greater sized molar process at the base of the dactylus. The pincer chela has sharp teeth with triangular sections.

The following variables were measured (to the nearest 0.1 mm) for each specimen using a digital caliper (Fig 1): CW; length, width and height (excluding the spine located in the dactylus insertion in the case of *Necora puber* and *Liocarcinus depurator*) of the propodius of both chelipeds. The following data were recorded for the study of the mechanical advantages (MAs) in chelipeds (Warner & Jones 1976): L_1, distance between the pivot (point of articulation between the dactylus and propodius) and the point of insertion on the dactylus of the closer apodeme muscle; L_{2a}, dactylus length (distance between the pivot and the tip of the dactylus); L_{2b} (only in the crusher chela), distance between the pivot and the molar process at the base of the dactylus. The apodeme of the closer muscle, muscle and tegument from the propodius and dactylus were separated and the dry weight was obtained for each component after 48 h at 70°C. The proportion of the weight of the cheliped which is made up of muscle was estimated: muscle mass ratio (MR) = muscle dry weight/(muscle dry weight + tegument dry weight). Due to the small size of some individuals, the apodemes could not be completely removed to obtain their dry weight; for this reason these variables were not included in the multivariate analyses.
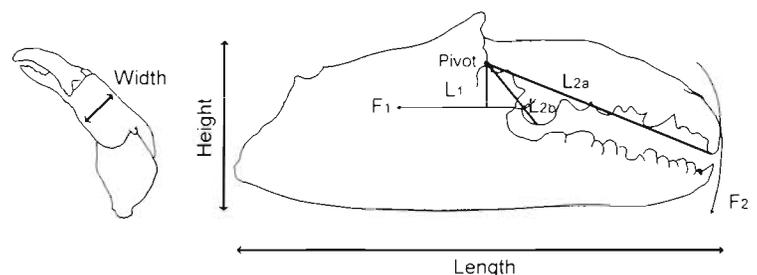

Fig. 1. Diagram of a crusher cheliped showing the morphometric variables measured (length, height and width of the propodius), location of pivot (point of articulation between dactylus and propodius), parameters of the ideal mechanical advantages (L_1, L_{2a} and L_{2b}) and directions through which the force applied F_1 and the force produced F_2 act. In a system with frictionless pivots: $F_1 \times L_1 = F_2 \times L_2$ or $F_2/F_1 = L_1/L_2$ = mechanical advantage

A series of ideal MAs were estimated, defined by the ratio of the lever lengths: $MA_a = L_1/L_{2a}$, and $MA_b = L_1/L_{2b}$ (only in the right chela). Moreover, the estimate of the functional MA is based on the direct measurement of the force applied (F_1) and the force produced (F_2) ($MA = F_2/F_1$). In a system with frictionless pivots: $F_1 \times L_1 = F_2 \times L_2$ or $F_2/F_1 = L_1/L_2$; which means that the force produced by the system increases with the ideal MA (L_1/L_2). However the speed of the resultant movement and the distance moved both decrease in proportion (Warner & Jones 1976). L_2 depends on the position along the axis of the dactylus, which is why maximum (L_{2a}) and minimum (L_{2b}) levers have been defined.

The MAs and MR of each cheliped were compared between sexes for each species and between species for each sex using analysis of variance (ANOVA) followed by pairwise comparisons using HSD-Tukey tests. In order to analyze the ontogenetic changes in the morphometrical and biomechanical characteristics of chelipeds, the linear correlation of CW with MAs and MRs for each sex and species was obtained, and a series of allometric equations which relate CW to the different variables obtained to determine the mechanical advantages and dry weights of the muscle, tegument and apodeme for both chelipeds ($y = aCW^b$) were fitted using minimum square linear regression after $\log_{10}$-transformation. The parameters for the equations obtained for each sex and species were compared between sexes within each species and between species for each sex using analysis of covariance (ANCOVA). In comparisons between species, multiple pairwise comparisons were carried out when differences were found between slopes (p < 0.05), applying the Bonferroni correction to maintain a probability level of p = 0.05. For the description of the patterns of interspecific morphometrical variability, principal component analyses for each sex were carried out on the correlation matrix of the log-transformed variables (CW, length, width, height, MAs and MRs of both chelipeds).

RESULTS

Morphometry and biomechanics

The mean MAs and MRs of chelipeds for each species and sex are shown in Table 1. No significant differences were found between males and females for *Liocarcinus depurator*, while for *Necora puber* only the MA_a of the crusher cheliped was significantly larger in males than in females. For *Liocarcinus arcuatus* there were no significant differences in the MRs between sexes, however both MAs of

Table 1. Mean (SD) of mechanical advantages (MA) and muscle mass ratio (MR) of chelipeds for males and females of 3 species. *F*-statistics (significance level) of ANOVA carried out to compare these parameters between sexes for each species are shown (n = sample size). See 'Materials and methods' for equation used to derive MA and MR

	Males	Females	F (p)
Necora puber			
Crusher cheliped	n = 45	n = 34	
MA_a	0.294 (0.030)	0.275 (0.015)	11.10 (0.001)
MA_b	0.843 (0.079)	0.845 (0.049)	0.03 (0.865)
MR	0.206 (0.054)	0.201 (0.048)	0.21 (0.645)
Pincer cheliped			
MA_a	0.254 (0.046)	0.246 (0.018)	0.28 (0.598)
MR	0.218 (0.100)	0.189 (0.089)	1.68 (0.199)
Liocarcinus depurator			
Crusher cheliped	n = 89	n = 18	
MA_a	0.271 (0.020)	0.276 (0.032)	0.51 (0.478)
MA_b	0.782 (0.066)	0.791 (0.061)	0.28 (0.597)
MR	0.231 (0.039)	0.227 (0.037)	0.16 (0.694)
Pincer cheliped			
MA_a	0.225 (0.020)	0.233 (0.019)	2.54 (0.114)
MR	0.233 (0.048)	0.225 (0.043)	0.35 (0.556)
Liocarcinus arcuatus			
Crusher cheliped	n = 62	n = 52	
MA_a	0.310 (0.022)	0.288 (0.027)	17.28 (0.000)
MA_b	0.865 (0.094)	0.824 (0.068)	6.85 (0.010)
MR	0.191 (0.064)	0.201 (0.058)	0.61 (0.437)
Pincer cheliped			
MA_a	0.261 (0.037)	0.259 (0.027)	0.00 (0.954)
MR	0.189 (0.116)	0.190 (0.067)	0.02 (0.900)

the right cheliped were larger in males. The interspecific differences of the MAs and MRs were sex-dependent (Table 2). In males all the MAs for both chelipeds were lowest in *L. depurator* (p < 0.001); however, only MA_a of the crusher cheliped was significantly higher in *L. arcuatus* than in *N. puber* In contrast, the differences were not as important in females and only MA_b

Table 2. *F*-statistic (significance level) of ANOVA carried out to compare the mechanical advantages (MA) and muscle ratio (MR) of chelipeds between species for males and females. In cases where p < 0.05, pairwise comparisons were made using the HSD-Tukey test (underlined species were not significantly different, p > 0.05). NPU: *Necora puber*; LDE: *Liocarcinus depurator*, LAR: *L. arcuatus*

	Males		Females	
	F (p)	HSD-Tukey test	F (p)	HSD-Tukey test
Crusher cheliped				
MA_a	51.08 (0.000)	LDE NPU LAR	3.49 (0.034)	NPU LDE LAR
MA_b	20.72 (0.000)	LDE NPU LAR	4.75 (0.011)	LDE LAR NPU
MR	11.45 (0.000)	LAR NPU LDE	1.94 (0.149)	
Pincer cheliped				
MA_a	24.21 (0.000)	LDE NPU LAR	0.62 (0.503)	
MR	4.72 (0.010)	LDE NPU LAR	1.75 (0.179)	

showed significant differences between species. The MR of chelipeds was similar in males and females of each species (Table 1). There were no interspecific differences for females, but in the case of males both appendages presented greater MRs in *L. depurator* than in *N. puber* and reached minimum values for *L. arcuatus* (Table 2).

The MAs and MRs for *Necora puber* were independent of body size, except in the case of MA_a of the crusher cheliped in males, which presented a significant positive correlation with CW (Table 3). As *Liocarcinus depurator* grew in size MAs decreased significantly (except MA_a of the crusher cheliped in females) in both chelae. *L. arcuatus* had a different pattern of ontogenetic variability in that the correlations observed between MR and CW were higher than the correlations between MAs and CW. All the MAs in females of this species decreased with growth, whereas in males there were only significant correlations in the case of the right chela (negative for MA_b and positive for MA_a). The MRs had a high negative correlation with body size, which implies that the cheliped grows more in size than in muscle mass.

Ontogenetic changes in the morphology of the appendages and the relationship between mechanical parameters and body size were analyzed fitting allometric equations for the variables used to calculate MAs and MR (Table 4). The levers of chelipeds, and the apodeme, muscle and tegument dry weights showed high coefficients of determination ($r^2 > 0.8$, $p < 0.01$, with the exception of the apodemes of *Liocarcinus arcuatus* females due to the small sample size). There were major sexual differences in the relative growth of the chelipeds, and especially of the levers used in the estimation of the MAs (Table 5), which points to a divergence between males and females in biomechanical characteristics with growth. With reference to the crusher cheliped in males, the allometry of *L. arcuatus* was greater than in the other species for all the variables, while the differences between *L. depu-*

rator and *Necora puber* were restricted to L_{2a} (Table 6). In females, on the other hand, the slopes of the equations corresponding to *N. puber* were higher in all cases than for *L. arcuatus*; however *L. depurator* had a greater variability, due in part to the smaller number of specimens analyzed. Interspecific differences for the left cheliped were not significant, except in the case of L_1, which has a relative growth characterized by a larger slope in *L. arcuatus*. The differences in the allometry coefficient of the different levers (L_1, L_{2a} and L_{2b}) for each species and sex were generally more important for the species of the genus *Liocarcinus*, which resulted in higher correlations between the MAs of the chelipeds and body size than in the case of *N. puber*.

In males the slope of the equation for muscle dry weight in both chelipeds was greater for *Liocarcinus depurator* and similar in *Necora puber* and *L. arcuatus* (although significant differences did exist in the case of the right chela) (Table 6). In contrast, the allometry of tegument dry weight was greater in *L. arcuatus* ($b > 4$) than in *L. depurator* and especially in *N. puber*. In females the quantitative importance of the differences between species was smaller, especially in tegument weight; although, as is the case in males, the slope of the relationships corresponding to muscle weight was greater in *L. depurator*. For each species and sex, the allometry coefficients of tegument and muscle dry weights were similar, except in the case of *L. arcuatus*, which showed a negative correlation between MR and body size. The apodeme of the closer muscle had a similar growth pattern in males and females (Table 5). The slopes were higher for the right apodeme than for the left, except for *L. arcuatus*; in general interspecific variability was scarce (Table 6).

The results of the principal component analyses carried out to describe the morphometric variability between species were similar for males and females, in the correlation of the different variables with the axes extracted as well as in the proportion of variance explained (Fig. 2). Axis 1 represented body size, pre-

Table 3. Linear correlation, r (significance level), between carapace width (CW) and mechanical advantages (MA) and between CW and muscle mass ratio (MR) of chelipeds for males and females of the 3 species studied (analysis based on $\log_{10}$-transformed data)

| | *Necora puber* | | *Liocarcinus depurator* | | *Liocarcinus arcuatus* | |
	Males	Females	Males	Females	Males	Females
Crusher cheliped						
MA_a	0.332 (0.021)	−0.287 (0.100)	−0.401 (0.000)	0.231 (0.357)	0.226 (0.078)	−0.470 (0.000)
MA_b	−0.087 (0.557)	−0.321 (0.064)	−0.415 (0.000)	−0.486 (0.041)	−0.486 (0.000)	−0.238 (0.096)
MR	−0.205 (0.163)	0.007 (0.968)	−0.117 (0.275)	−0.385 (0.115)	−0.758 (0.000)	−0.639 (0.000)
Pincer cheliped						
MA_a	0.088 (0.550)	0.083 (0.642)	−0.432 (0.000)	−0.568 (0.014)	0.167 (0.195)	−0.243 (0.083)
MR	0.064 (0.665)	−0.128 (0.501)	0.055 (0.610)	−0.002 (0.993)	−0.562 (0.000)	−0.709 (0.000)

Table 4. Parameters of the allometric equations (intercept log a and slope b) fitted for males and females of each species that relate carapace width and the different variables obtained to determine the mechanical advantages and dry weights (DW) of muscle, tegument and apodeme of the propodius of both chelipeds. The coefficients of determination (r^2) were significant ($p < 0.01$) in all except the case of the apodeme of the pincer cheliped of the females of *Liocarcinus arcuatus* (results not shown). See 'Materials and methods' for definitions of L_1, L_{2a} and L_{2b}

	Males			Females		
	Intercept (SE)	Slope (SE)	r^2	Intercept (SE)	Slope (SE)	r^2
Necora puber						
Crusher cheliped						
Muscle DW	−6.20 (0.32)	3.15 (0.18)	0.86	−6.29 (0.53)	3.14 (0.31)	0.77
Tegument DW	−5.97 (0.16)	3.36 (0.09)	0.97	−5.79 (0.34)	3.21 (0.20)	0.90
L_1	−1.10 (0.07)	1.07 (0.04)	0.93	−1.09 (0.12)	1.04 (0.07)	0.87
L_{2a}	−0.38 (0.07)	0.96 (0.04)	0.93	−0.64 (0.10)	1.10 (0.06)	0.91
L_{2b}	−1.07 (0.08)	1.10 (0.05)	0.92	−1.15 (0.12)	1.12 (0.07)	0.89
Apodeme DW	−7.73 (0.55)	3.40 (0.32)	0.90	−8.03 (0.79)	3.55 (0.45)	0.91
Pincer cheliped						
Muscle DW	−6.37 (0.33)	3.15 (0.19)	0.86	−6.13 (0.46)	2.98 (0.27)	0.82
Tegument DW	−5.53 (0.29)	3.01 (0.17)	0.87	−5.78 (0.14)	3.13 (0.08)	0.98
L_1	−1.05 (0.08)	0.99 (0.05)	0.90	−1.05 (0.12)	0.97 (0.07)	0.87
L_{2a}	−0.39 (0.11)	0.95 (0.06)	0.83	−0.27 (0.34)	0.86 (0.20)	0.37
Apodeme DW	−7.06 (0.51)	2.83 (0.30)	0.78	−5.86 (0.72)	2.12 (0.42)	0.60
Liocarcinus depurator						
Crusher cheliped						
Muscle DW	−6.50 (0.13)	3.40 (0.08)	0.95	−5.90 (0.44)	3.00 (0.28)	0.87
Tegument DW	−6.10 (0.10)	3.48 (0.06)	0.98	−6.06 (0.36)	3.45 (0.23)	0.94
L_1	−1.02 (0.04)	1.02 (0.03)	0.95	−0.99 (0.16)	0.98 (0.10)	0.86
L_{2a}	−0.58 (0.03)	1.10 (0.02)	0.98	−0.22 (0.20)	0.85 (0.13)	0.73
L_{2b}	−1.06 (0.03)	1 11 (0.02)	0.97	−1.19 (0.02)	1.18 (0.11)	0.89
Apodeme DW	−7.21 (0.37)	3.26 (0.23)	0.88	−8.33 (1.13)	3.94 (0.71)	0.89
Pincer cheliped						
Muscle DW	−6.93 (0.16)	3.54 (0.10)	0.94	−6.45 (0.45)	3.23 (0.29)	0.89
Tegument DW	−6.35 (0.08)	3.50 (0.05)	0.98	−5.92 (0.22)	3.24 (0.14)	0.97
L_1	−1.12 (0.04)	1.01 (0.03)	0.95	−0.74 (0.12)	0.77 (0.08)	0.86
L_{2a}	−0.64 (0.02)	1.12 (0.01)	0.99	−0.50 (0.07)	1.02 (0.05)	0.97
Apodeme DW	−6.85 (0.38)	2.85 (0.24)	0.80	−4.32 (0.45)	1.19 (0.29)	0.68
Liocarcinus arcuatus						
Crusher cheliped						
Muscle DW	−6.29 (0.18)	3.32 (0.12)	0.92	−5.62 (0.17)	2.73 (0.12)	0.91
Tegument DW	−6.79 (0.16)	4.14 (0.11)	0.96	−5.79 (0.13)	3.31 (0.10)	0.96
L_1	−1.27 (0.04)	1.23 (0.03)	0.97	−0.86 (0.05)	0.88 (0.04)	0.92
L_{2a}	−0.70 (0.02)	1.19 (0.02)	0.99	−0.48 (0.03)	1.00 (0.02)	0.98
L_{2b}	−1.36 (0.06)	1.35 (0.04)	0.95	−0.86 (0.05)	0.95 (0.04)	0.94
Apodeme DW	−6.69 (0.48)	3.03 (0.33)	0.81	−4.54 (0.53)	1.34 (0.39)	0.50
Pincer cheliped						
Muscle DW	−6.41 (0.19)	3.25 (0.14)	0.90	−5.56 (0.19)	2.57 (0.14)	0.88
Tegument DW	−6.81 (0.22)	4.01 (0.16)	0.92	−5.96 (0.15)	3.35 (0.11)	0.95
L_1	−1.31 (0.03)	1.19 (0.02)	0.98	−1.01 (0.05)	0.94 (0.04)	0.93
L_{2a}	−0.53 (0.14)	1.05 (0.10)	0.64	−0.52 (0.04)	1.01 (0.03)	0.97
Apodeme DW	−7.04 (0.76)	3.03 (0.51)	0.68			

senting correlations higher than 0.98 with CW and length, height and width of the chelipeds (these variables showed minimum correlations with the other axes obtained). The correlations between MAs and MRs and axis 1 were always negative and low (−0.43 < r < 0). Axis 2 differentiated individuals of *Liocarcinus arcuatus* and *L. depurator*, which were associated with high MAs and MRs respectively, whereas the scores of individuals of *Necora puber* with this axis were small. Axis 3 had a positive correlation with both MAs and

MRs, and set *N. puber*, which had positive scores, in opposition to the 2 species of *Liocarcinus*. Together, axes 2 and 3 defined the biomechanical variability among the portunid species analyzed, which may be interpreted as a gradient presenting *L. depurator* on one end (having chelipeds with a high MR and great mobility, low MAs) and *L. arcuatus* on the other end (which has less mobile chelae with a low MR). *N. puber* presented intermediate biomechanical characteristics.

Table 5. Results of ANCOVA carried out to compare the parameters of the allometric equations (slope b and intercept $\log a$) that relate carapace width and the different variables obtained to determine the mechanical advantages and dry weight (DW) of the muscle, tegument and apodeme of the propodius of both chelipeds between sexes for each species. F-statistic and significance level are shown ($^*p < 0.05$, $^{**}p < 0.01$, $^{ns}p > 0.05$). Intercepts were compared only when slopes were not significantly different ($p > 0.05$)

	Necora puber Slope	Intercept	*Liocarcinus depurator* Slope	Intercept	*Liocarcinus arcuatus* Slope	Intercept
Crusher cheliped						
Muscle DW	6.04^*	–	1.81^{ns}	0.55^{ns}	32.18^{**}	–
Tegument DW	12.97^{**}	–	0.23^{ns}	0.22^{ns}	62.18^{**}	–
L_1	18.39^{**}	–	3.26^{ns}	2.67^{ns}	159.59^{**}	–
L_{2a}	7.58^{**}	–	15.36^{**}	–	153.98^{**}	–
L_{2b}	18.29^{**}	–	6.98^{**}	–	81.45^{**}	–
Apodeme DW	0.30^{ns}	0.29^{ns}	0.46^{ns}	0.32^{ns}	17.90^{**}	
Pincer cheliped						
Muscle DW	1.92^{ns}	1.80^{ns}	0.52^{ns}	0.00^{ns}	17.81^{**}	–
Tegument DW	1.98^{ns}	1.09^{ns}	2.21^{ns}	0.67^{ns}	15.82^{**}	–
L_1	10.83^{**}	–	5.00^*	–	80.01^{**}	–
L_{2a}	2.59^{ns}	2.36^{ns}	8.98^{**}	–	8.02^*	–
Apodeme DW	1.79^{ns}	0.20^{ns}	3.90^{ns}	0.78^{ns}		

Table 6. Results of ANCOVA carried out to compare the parameters of the allometric equations (slope b and intercept $\log a$) relating carapace width and the different variables obtained in order to determine the mechanical advantages and the dry weight (DW) of the muscle, tegument and apodeme of the chelipeds between species for each sex. F-statistic and significance level are shown ($^*p < 0.05$, $^{**}p < 0.01$). In cases where significant differences existed ($p < 0.05$), pairwise *a posteri* comparisons were made using the Bonferroni correction to maintain a probability level of $p = 0.05$ (underlined species were not significantly different). NPU: *Necora puber*. LDE: *Liocarcinus depurator*, LAR: *L. arcuatus*

	Slope				Intercept			
Males								
Crusher cheliped								
Muscle DW	31.88^{**}	NPU	LAR	LDE				
Tegument DW	264.06^{**}	NPU	LDE	LAR				
L_1	126.39^{**}	LDE	NPU	LAR	NPU	LDE		
L_{2a}	92.42^{**}	NPU	LDE	LAR				
L_{2b}	97.71^{**}	NPU	LDE	LAR	NPU	LDE		
Apodeme DW	34.06^{**}	LAR	LDE	NPU				
Pincer cheliped								
Muscle DW	18.74^{**}	NPU	LAR	LDE	LAR	NPU		
Tegument DW	125.49^{**}	NPU	LDE	LAR				
L_1	111.97^{**}	NPU	LDE	LAR	LDE	NPU		
L_{2a}	7.17^{**}	NPU	LAR	LDE	LAR	NPU		
Apodeme DW	19.88^{**}	NPU	LDE	LAR	LAR	LDE		
Females								
Crusher cheliped								
Muscle DW	13.32^{**}	LAR	NPU	LDE	NPU	LAR		
Tegument DW	23.28^{**}	NPU	LAR	LDE	LDE	LAR		
L_1	8.46^{**}	LAR	LDE	NPU	NPU	LDE	LAR	
L_{2a}	12.28^{**}	LDE	LAR	NPU	LAR	LDE	NPU	LAR
L_{2b}	19.97^{**}	LAR	NPU	LDE	NPU	LDE		
Apodeme DW	17.68^{**}	NPU	LDE					
Pincer cheliped								
Muscle DW	11.85^{**}	LAR	NPU	LDE	NPU	LAR	LDE	NPU
Tegument DW	26.68^{**}	NPU	LDE	LAR	LDE	NPU		
L_1	3.23^*	LDE	LAR	NPU	NPU	LAR	LDE	
L_{2a}	5.31^{**}	LAR	NPU	LDE	NPU	LDE	LAR	
Apodeme DW	4.58^*	LDE	NPU		NPU	LDE		

Diet composition

Gut-contents analysis indicated that portunid crabs in the Ría de Arousa have generalist diets, preying mainly on macroinvertebrates (crustaceans, molluscs and echinoderms) which are sessile or have little mobility; only in the case of *Liocarcinus arcuatus* did seaweeds have a high importance in the food composition (Table 7, see also Freire 1993, in press, Freire & González-Gurriarán 1995). Interspecific and spatial differences determine most of the trophic diversity among these decapods, and ontogenetic changes are responsible for most of the intraspecific trophic variability. Taking the mobility and morphology (presence and type of exoskeleton) of the prey into account, the diet composition in the different habitats was sim-
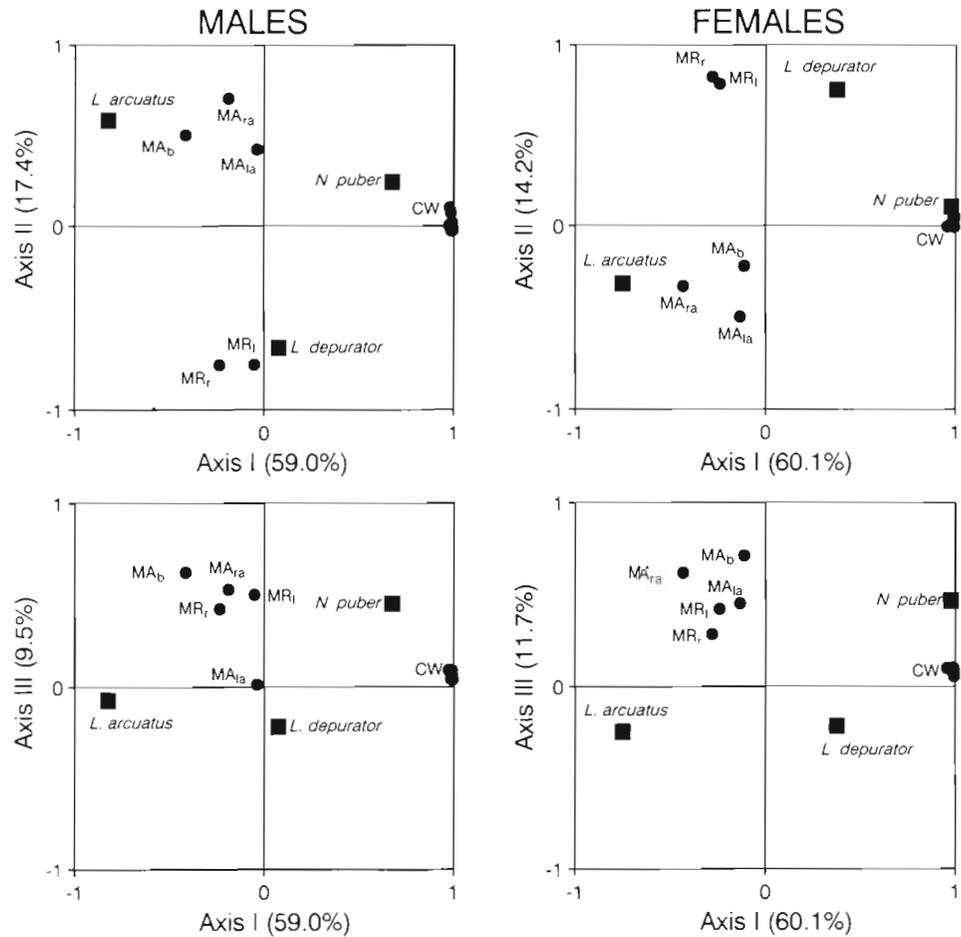
Fig. 2. Interspecific principal component analysis carried out for each sex. Ordination of the morphometric and biomechanical variables and centroids of the scores for each species on the axes 1, 2 and 3 (the identification of length, width and height of both chelipeds is omitted because they are distributed very closely to carapace width, CW). The percentage of variance explained by each axis is shown in parenthesis. MA_{ra}, MA_b: mechanical advantages of the right cheliped; MA_{la}: mechanical adavantage of the left cheliped; MR_r, MR_l: muscle ratio of the right and left chelipeds respectively

ilar for each species (Table 7, Fig. 3). Between-habitat differences appeared in the raft zones and areas not devoted to mussel culture and corresponded with differences in the epifaunal and infaunal prey communities (Freire 1993, in press, Freire & González-Gurriarán 1995). Thus, L. depurator increased its consumption of slow-moving prey without an exoskeleton (mainly polychaetes) in the central channel and reduced its predation on mobile prey with exoskeletons. In the case of L. arcuatus, soft-bodied prey, both mobile and sessile, were more important on the beach than in the raft area. The prey consumed by L. depurator presented high morphological diversity, as all the types of food items mentioned above make up an important part of its diet. L. depurator showed an ontogenetic increase in the consumption of prey having hard exoskeletons (Fig. 4). In the early life stages, between 10 and 30 mm CW, mobile prey increased their importance in the diet, while crabs with CW >30 mm preyed more on sessile organisms. In Necora puber and L. arcuatus there was little ontogenetic variability in the diet composition when considering prey morphology and mobility.

DISCUSSION

The morphology and biomechanical characteristics of chelipeds may determine, at least in part, predation techniques and prey selection mechanisms of decapod crustaceans. The findings of this morphometric analysis show that although the size of the chelipeds relative to body size is similar in Necora puber, Liocarcinus depurator and Liocarcinus arcuatus, the biomechanical parameters vary greatly. In this sense both sexes show an interspecific morphometric gradient with an inverse relationship between mechanical advantages (MAs) and muscle mass ratio (MR) of the chelipeds.

The functional structure of the chelipeds of Liocarcinus depurator, the species with the highest morphological diversity of prey, is more versatile. MAs are relatively low, giving the chelipeds greater mobility, and the decrease in force produced is probably compensated for by an increase in muscle mass. L. arcuatus, on the other hand, has a lower MR, for which reason the force produced depends more on the design of the chelipeds, with MAs higher than those of the other species studied. These characteristics give rise to appendages

Table 7. Diet composition of *Necora puber*, *Liocarcinus depurator* and *Liocarcinus arcuatus* from different sampling stations in the Ría de Arousa, NW Spain (B1, B5 and B6: mussel raft culture areas, M1 and M2: central channel areas, P3: beach area). Data from Freire (1993, in press) and Freire & González-Gurriarán (1995) based on the analysis of gut contents (the importance of each prey was estimated by its dry weight in the stomach). Mobility (S: sessile, SM: slow moving, M: mobile), presence of hard exoskeleton (E: exoskeleton not articulated, EA: articulated exoskeleton, N: no exoskeleton) and habitat (E: epibenthic megafauna, R: raft epifauna, I: benthic macroinfauna) are indicated for each prey. –: prey absent

Prey		Prey characteristics			*Necora puber* Raft			*Liocarcinus depurator* Raft		Channel		*Liocarcinus arcuatus* Raft	Beach
		Mobility	Exoskeleton	Habitat	B1	B5	B6	B1	B5	M1	M2	B6	P3
Fishes	Teleosts	M	N	E	5.9	2.2	2.5	6.6	1.2	–	4.1	0.7	1.5
Crustaceans	Natantia	M	N	E	0.8	0.2	4.3	3.1	2.6	–	0.9	1.5	2.0
	Brachyura	M	E	E	3.5	1.5	21.3	2.8	2.9	0.8	1.0	2.7	4.6
	Anomura: *Pisidia longicornis*	M	E	R	68.9	80.6	49.5	30.7	51.9	52.4	14.7	8.9	1.4
	Amphipods	M	N	R	0.0	0.3	–	1.3	1.8	0.4	3.4	0.8	3.4
	Other non-decapod crustaceans	M	N	I	–	0.1	–	2.3	1.1	–	0.8	1.0	4.6
Molluscs	*Mytilus galloprovincialis*	S	E	R	8.7	1.8	2.7	12.5	8.9	2.1	2.5	4.1	0.1
	Other bivalves	S	E	I	0.9	0.2	2.3	10.5	2.0	3.2	6.1	5.4	2.2
	Gastropods	SM	E	R	1.5	1.6	0.9	7.2	1.3	5.6	6.7	1.0	1.1
	Egg cases of *Nassa* spp.	S	N	R	4.2	2.2	–	2.2	9.1	–	0.6	2.1	2.1
Echinoderms	Ophiuroids	SM	AE	I	–	0.6	1.9	–	9.1	23.4	5.4	2.1	0.0
	Crinoids: *Antedon bifida*	S	AE	R	–	–	–	–	–	–	–	6.3	–
	Echinoids: *Psammechinus miliaris*	SM	E	E	2.4	5.8	3.5	3.2	1.3	–	–	–	–
	Holothuroids: *Aslia lefevrei*	S	N	E/R	0.7	0.3	4.5	5.6	2.2	9.3	1.5	–	7.7
Polychaetes		SM	N	I	0.2	0.5	2.9	1.1	7.3	–	33.7	10.4	–
Plants		SM	N		1.1	1.4	3.1	0.0	1.7	–	6.1	3.2	60.4
Sponges		S	N		1.0	0.3	0.4	0.1	0.1	–	2.0	37.8	0.1
Others		S	N	R	0.2	0.5	0.2	0.1	0.0	–	1.0	4.7	8.8
Unidentified animal remains					–	–	–	10.9	4.2	2.8	9.4	7.3	–

that are relatively immobile, which is reflected in a diet made up chiefly of sedentary soft-bodied prey. *Necora puber* has intermediate trophic and biomechanical characteristics; its prey are primarily mobile, and organisms with hard exoskeletons are dominant both in the mobile and the sessile or slow-moving prey groups.

Ontogenetic changes in the diet are related to the absolute growth of the chelipeds and partially determined by biomechanical factors. Brown et al. (1979) reported an increase in the absolute force produced as body size increases in decapods, independent of the morphological differences between species. *Liocarcinus depurator* shows a negative correlation between the MAs of the chelipeds and carapace width (CW), while the MR remains constant, causing a negative allometry in the force produced and an increase in the mobility of the appendages throughout growth. In spite of these changes in relative growth, there is an absolute increase in muscle mass and cheliped size, which causes an increase in the consumption of prey with hard exoskeletons. Our results suggest that the ontogenetic changes in the diet are linked to the absolute growth of the chelipeds, giving access to the more resistant prey, whereas Abelló et al. (1990) showed that the changes in relative growth are associated with sexual maturity and reproductive behaviour. In *Necora puber* and *L. arcuatus*, which did not show important diet changes with growth, the correlations between MAs and body size are generally low; however, the latter undergoes a sharp drop in the MR with growth due to a strong positive allometry in cheliped size (and tegument weight). The ontogenetic morphometrical variability of the chelipeds is related to the onset of the sexual maturity in both species (González-Gurriarán & Freire 1994, unpubl. data), and it does not have a direct influence on feeding. Sexual variability in the diet is minimal for the 3 species (Freire 1993, in press, Freire & González-Gurriarán 1995); this is related to the lack of significant differences in MAs and MRs between males and females, although cheliped size differs slightly.

It has been suggested that the evolution of the morphometric and functional diversity of the chelipeds in decapods (Schäfer 1954) is an adaptive response to the diversity of the prey communities characteristic of the habi-
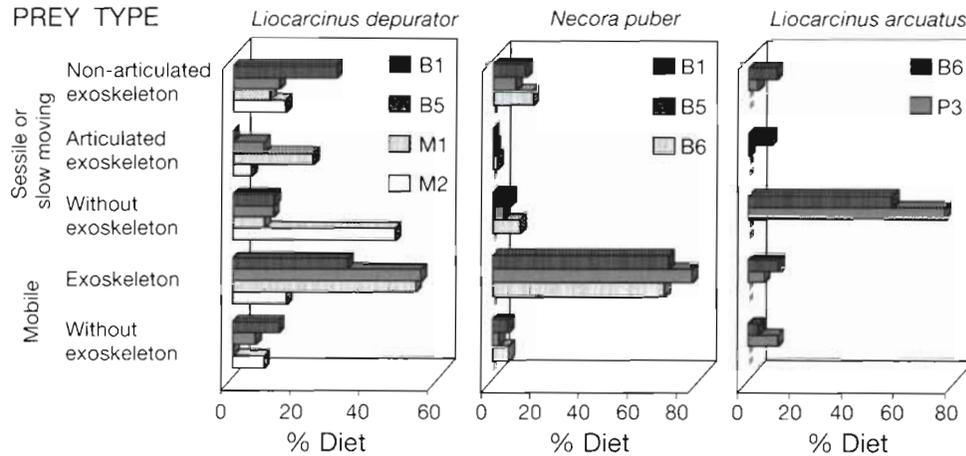
Fig. 3. Diet composition of *Necora puber*, *Liocarcinus depurator* and *Liocarcinus arcuatus* in terms of mobility and morphological characteristics (presence and type of exoskeleton) of the prey consumed in different sampling stations in the Ría de Arousa, NW Spain (B1, B5 and B6: mussel raft culture areas; M1 and M2: central channel areas; P3: beach area). The importance of each prey type was estimated by its dry weight in the gut contents analyzed

tats occupied by these species (Vermeij 1977, Zipser & Vermeij 1978, Lawton & Elner 1984). Morphological and morphometric diversity observed in different groups of decapods is due to the evolution of reproductive behaviour and intra- and interspecific agonistic interactions (Orensanz & Galluci 1988, Kaiser et al. 1990, Lee & Seed 1992): these processes generate chelipeds with different biomechanical characteristics, which secondarily modifies prey selection and ultimately diet composition (Kaiser et al. 1990, Lee & Seed 1992), although probably the behavioural, physiological and habitat changes associated with sexual maturity have a stronger effect on the diet. Several authors have proven the existence of physiological adaptations

in cheliped muscles related to mating (Govind et al. 1992), social hierarchy (Govind & Pearce 1993) or feeding (Warner & Jones 1976, Smith & Palmer 1994).

ap Rheinallt & Hughes (1985) and ap Rheinallt (1986) described the mechanical factors and predation techniques used by *Necora puber* to select different prey types and sizes. The morphology of the chelipeds in *N. puber* have a design which is more appropriate for predation on mobile prey such as crustaceans than on sessile prey such as molluscs (ap Rheinallt & Hughes 1985). These experimental predictions are corroborated by our findings (Freire & González-Gurriarán 1995), which show a diet dominated by the anomuran decapod *Pisidia longicornis*, while molluscs are a sec-
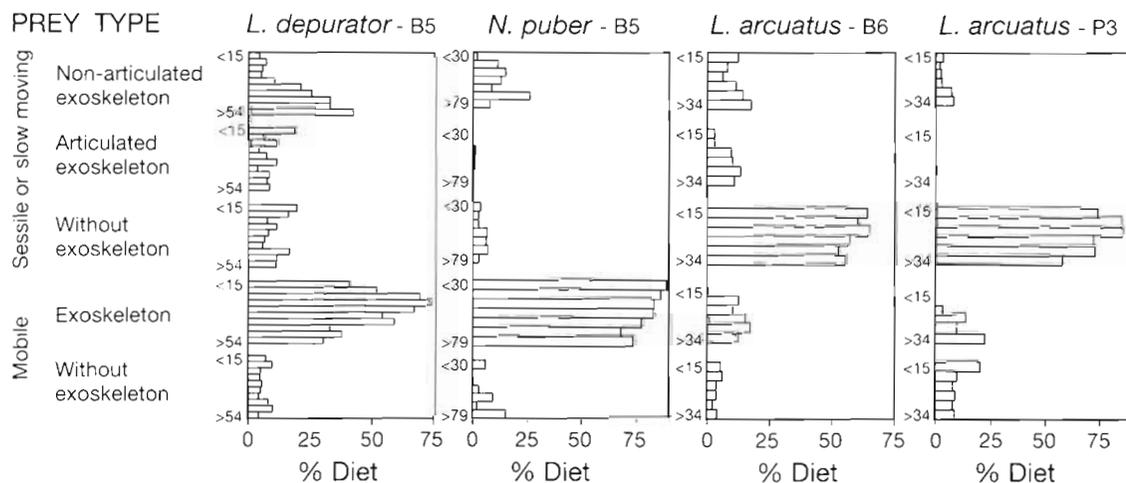

Fig. 4. Ontogenetic changes in diet composition of *Necora puber*, *Liocarcinus depurator* and *Liocarcinus arcuatus* in different sampling stations in the Ría de Arousa (B1 and B6: mussel raft culture areas; P3: beach area) in terms of mobility and morphological characteristics (presence and type of exoskeleton) of the prey consumed. For each species and group of prey only the first and last body size classes (carapace width) are shown (range of size classes: 5 mm for *L. depurator* and *L. arcuatus*, 10 mm for *N. puber*). The importance of each prey type was estimated by its dry weight in the gut contents analyzed

ondary component. On the other hand, both the mussel and other bivalves and gastropods are of relatively more importance in the diet of *Liocarcinus depurator* and *L. arcuatus* in the same areas of the Ría de Arousa (Table 7, Freire 1993, in press). In relation to prey size selection, in the Ría de Arousa, a positive correlation between the size of the predator and its crustacean prey (especially in the case of specimens of *P. longicornis* consumed by *L. depurator* and *N. puber*) which agrees with the experimental predictions has been observed (Freire 1993).

In conclusion, the comparative morphological analysis carried out on the 3 species of portunids points to the existence of an interspecific variability that is largely associated with differences in the morphology and mobility of the prey consumed. Secondly, on an intraspecific level, the sexual and ontogenetic variability is lower and appears to be linked to the onset of sexual maturity and reproductive behaviour Within a species, the morphometric and biomechanical changes observed may be attributed to non-trophic selection processes (Hartnoll 1974, 1978, Orensanz & Galluci 1988), and they have no major influence on the diet, which is conditioned mainly by the absolute growth of the chelipeds and muscle mass (Brown et al. 1979). On a longer evolutionary scale, the interspecific diversity in feeding habits and morphometry are correlated (Lawton & Elner 1984), although the causal mechanism could not be determined due to a lack of sufficient information on mating systems and social interactions in these species.

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