

Feeding ecology of the velvet swimming crab *Necora puber* in mussel raft areas of the Ría de Arousa (Galicia, NW Spain)

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ABSTRACT: The feeding ecology of the velvet swimming crab *Necora puber* (Decapoda: Portunidae) in 3 mussel raft culture areas of the Ría de Arousa (Galicia, NW Spain) was studied through the analysis of stomach contents. The dominant prey was *Pisidia longicornis* (50 to 81 % of the diet in the different areas), a small epifaunal anomuran crab that inhabits culture ropes. Other important food components were brachyuran crabs, the mussel *Mytilus galloprovincialis* and other bivalves, gastropods, egg cases of the gastropod *Nassa* spp., the echinoid *Psammechinus miliaris* and fishes. Plants (both eelgrass and seaweeds), sponges and polychaetes constituted secondary prey, with low quantitative importance. Habitat was the most important factor in diet variability within the ría, related to the spatial differences in abundance and structure of the benthic and raft epifaunal communities. Also, important differences were observed between the diet in soft bottom areas of the Ría de Arousa and rocky zones in other geographical areas, where the importance of seaweeds was higher. The diet of *N. puber* was dominated by raft epifauna and mussels, and also by the megabenthos. Macroinfauna and plants showed little quantitative importance. For the epifaunal prey, *P. longicornis* was selected positively and amphipods negatively; in the case of the infauna, bivalves and ophiuroids were selected positively, and polychaetes negatively. Diet variability related to life history was due mainly to ontogenetic changes. Fishes, brachyurans, mussels, echinoids and sponges increased their contribution to the diet with growth, but *P. longicornis*, egg cases of *Nassa* spp., and the holothurian *Aslia lefevrei* presented the opposite pattern. The relationship between body size and gut fullness presented a negative allometry, but absolute food consumption increased with size. Food consumption variability was linked mainly to intermoult stage and season. During the immediate premoult and postmoult, there was no food ingestion; however, gut fullness was higher in the recent postmoult compared to intermoult animals. Seasonal changes were due to higher food consumption in autumn and winter.

KEY WORDS: Feeding · Diet · Mussel culture · Ría de Arousa · *Necora puber* · Portunidae

INTRODUCTION

The velvet swimming crab *Necora puber* (Decapoda: Portunidae) is an abundant species in the subtidal rocky zones of the northeast Atlantic (González-Gurriarán & Méndez 1985), where it may be one of the dominant epibenthic predators regulating the abundance and distribution of the prey populations (Kitching et al. 1959, Muntz et al. 1965, Aronson 1989, 1992). Earlier studies in rocky intertidal and subtidal zones indicate that the diet composition and food consumption of this species are highly variable, both spatially (along the

depth gradient) and seasonally, as well as over the crab's life history (reproductive and intermoult cycles) (Choy 1986, Norman & Jones 1992).

Mussel culture is becoming increasingly important worldwide, causing major changes in the ecosystem (Veer 1989, Smaal 1991). In the rías of the coast of Galicia (NW Spain), the culture of *Mytilus galloprovincialis* on rafts has brought about changes in the structure of the pelagic (Corral & Alvarez-Ossorio 1978) and benthic (Tenore et al. 1982) food webs. The production of pseudofaeces by the mussel and the 3-dimensional habitat made up of the culture ropes has led to the

development of an epifaunal and macroalgal community that reaches a high biomass (Lapointe et al. 1981, González-Sanjurjo 1982, Román & Pérez 1982, Fernández et al. 1990). On the other hand, the accumulation of biodeposits on the bottom has modified the characteristics of the sediment and has led to a decrease in infaunal diversity and biomass (López-Jamar 1982, Tenore et al. 1982). The production and biomass of the megabenthos, particularly of decapod crustaceans, are higher in the culture areas, as compared to other rías and other habitats within the Ría de Arousa (Chesney & Iglesias 1979, Iglesias 1981, González-Gurriarán 1982, Olaso 1982, Romero et al. 1982).

There is an important trap fishery for *Necora puber* on the rocky subtidal zones of Galicia. However, the new soft substrate habitats created in the mussel culture zones have been occupied by the velvet swimming crab, giving rise to high population densities and to the creation of a new trawl fishery (González-Gurriarán 1981, 1985a, b). *N. puber* is one of the dominant species within the megabenthic community, especially in the outer area of the Ría de Arousa. Preliminary studies pointed to the influence that the culture has on diet composition (González-Gurriarán 1978); these studies do not, however, deal with the different aspects of *N. puber* feeding ecology.

This study examines the feeding ecology of *Necora puber* in the mussel culture areas in the Ría de Arousa, based on the hypothesis that distribution and abundance patterns are associated with changes in diet

composition. The crab's feeding habits, its seasonal and spatial changes, and the variability related to the life history are determined through the analysis of stomach contents.

MATERIAL AND METHODS

Study area. Three mussel culture areas which are characteristic of the biotic and environmental variability that exists in the ría within the raft polygons were sampled (Fig. 1) (González-Gurriarán 1982, López-Jamar 1982, Román & Pérez 1982, Tenore et al. 1982). The bottoms of the culture areas receive a great amount of material and organisms from the rafts (mussel and associated epifauna, macroalgae, remains of culture ropes, etc.), which generate shelter and microhabitats for the mobile epifauna. Stn B1, which is found in the inner ría area, is 10 to 15 m deep, has salinity fluctuations due to the river runoff, and a muddy bottom which is sometimes anoxic (López-Jamar 1982). Stn B5 is located in the mid-outer zone which is subject to oceanic influence, with a depth of 20 to 30 m and a sandy-muddy bottom. Stn B6 is located on the southeast side of the ría and is mainly used for mussel culture, although some of the rafts are used to culture oysters. The depth in this zone ranges between 10 and 20 m, with a sandy-muddy bottom and a great abundance of green seaweeds in spring and summer. This area has a mixture of characteristics typical of the beach areas and raft culture zones.

Sampling. Samples were taken using a beam trawl having an opening of 4 m and a cod-end mesh of 10 mm (González-Gurriarán 1982). A preliminary study was carried out to analyze the diel pattern of feeding activity and to determine the subsequent sampling strategy. Sampling was carried out over a 24 h cycle in April 1989 at Stns B1 and B5. At each station three 10 min tows were taken at 6 h intervals. The 3 stations were sampled monthly from July 1989 to June 1990 with the exception of December due to inclement weather conditions. Each month 3 to 5 tows were carried out at each station over a 2 d period (between 08:00 and 15:00 h). After each tow the samples were fixed in 4% neutralized formalin, and after 24 to 48 h were stored in 70% alcohol.

Laboratory methods. The following data were recorded for each crab: carapace width (CW, from the extremes of the fifth pair of anterolateral spines of the

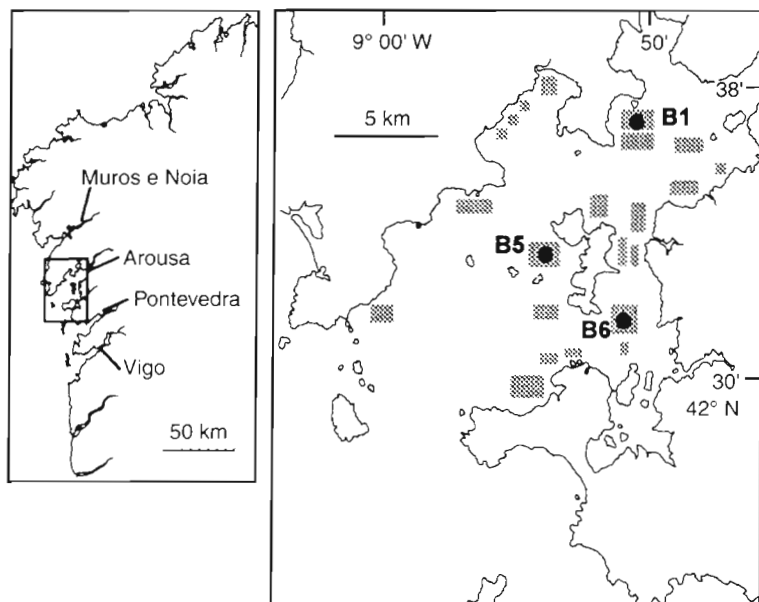


Fig. 1. Coast of Galicia (NW Spain). Ría de Arousa. Location of sampling stations (●) and areas where mussel raft culture is carried out within the ría (shaded areas)

cephalothorax); wet weight (dry weight was calculated using the conversion factor obtained by González-Gurriarán 1982); sex; and in females, the presence of eggs in the abdomen was determined, as well as the gonad maturity stage following criteria of González-Gurriarán (1985a) and Choy (1988) (stage I, ovaries at rest; stage II, beginning of maturation; stage III, mature ovaries in active development; stage IV, fully developed ovaries, immediately prior to spawning). The stage of the intermoult cycle was determined based on the calcification level in the exoskeleton: stage A, immediate postmoult, very soft exoskeleton (stage A₁ from Drach & Tchernigovtzeff 1967); stage B, when calcification begins and the exoskeleton has a paper-like consistency (A₂ to B₂); stage C, advanced postmoult, where the exoskeleton is only flexible in the pterigostomial region of the carapace (C₁ and C₂); stage IM, intermoult, the exoskeleton is rigid and hard (C₃ to D₁); and stage D, premoult, the new exoskeleton is almost completely formed underneath the old one (D₂ to D₄).

The different prey found in the stomach contents were determined at the lowest taxonomic level possible under a binocular microscope. In cases where more than 1 food component was found in the stomach contents, the relative importance of the different prey was determined using the points method. This method estimates the food volume with respect to the total stomach volume (maximum 100) and the assigned value is divided among the different prey in terms of the volume of the stomach content that they occupy (Williams 1981). Given the fragmentation of the prey, it was only possible to determine the number of specimens of each prey per stomach in part of the contents analyzed. Stomach fullness was estimated by means of both the points method and dry weight of the food (to the nearest 1 mg).

Data analysis. Stomach fullness is described by the percentage of stomachs with food, points index, and the BDW index: $BDW = (\text{Food dry weight} / \text{Body dry weight}) \times 100$. The importance of the different food components in the diet was estimated by means of the following indices:

- Frequency of appearance index: $F_i = (n_i / N) \times 100$, where n_i is the number of stomachs containing prey i and N is the number of stomachs with food analyzed;
- Points index: $IP_i = (\Sigma P_{ij} / \Sigma P_j) \times 100$, where P_{ij} is the value in points of prey i in stomach j , and P_j is the total number of points for stomach j ; and
- Percentage of the BDW fullness index corresponding to each prey: $BDW_i = (\Sigma BDW_{ij} / \Sigma BDW_j) \times 100$, where BDW_{ij} is the percentage of body dry weight corresponding to prey i in stomach j , and BDW_j is the percentage of body dry weight corresponding to the total food for specimen j . Where stomachs showed more

than 1 prey, BDW_{ij} was estimated from BDW_j and the value in points assigned to each prey.

In the study of the diel cycle, the differences in fullness level between hours at each station were tested using analysis of covariance (ANCOVA) [variable: $\log_{10}(\text{Food dry weight} + 0.001)$; covariate: $\log_{10}(\text{Body dry weight})$]. The diel differences in the consumption of the different prey (measured as BDW) were analyzed using Kruskal-Wallis tests.

The analysis of the influence of different factors on the consumption of each prey was carried out by fitting log-linear models by the maximum likelihood method to contingency tables made up of the following variables: prey (presence/absence), station, sex, intermoult stage (B, C and IM) and body size classes. Log-linear models have also been used to analyze the variability in the number of different food components per stomach. Diet diversity was estimated using the Shannon-Wiener index (H') and the variance was calculated according to Magurran (1989).

The relationships between diet composition and variables linked to the life history and environmental variables ('external variables') were determined using canonical correspondence analysis (CCA) (Ter Braak 1986, Ter Braak & Prentice 1988). For this purpose matrices of prey and external variables were analyzed, which included data from crabs having food in the stomach. The variables for the prey matrix are the diet components, presenting information on the presence or absence in each stomach. The matrix of external variables is composed of body size, sex (coded as a nominal variable with 3 categories: M, males; F, non-ovigerous females; O, ovigerous females), intermoult stage (coded as a nominal variable with 3 classes B, C and IM), and sampling station (each station is represented by a nominal variable). Partial CCAs were also carried out (Ter Braak 1987, Walker et al. 1991, Kingston et al. 1992) to test the influence of each external variable on diet composition, after eliminating the effect of the other variables introduced into the analysis as covariates (stomach fullness was also included, represented by the points index and food dry weight). The statistical significance of the effect of the variable tested was analyzed by Monte-Carlo randomization tests, in which 99 unrestricted permutations were carried out on the original matrices. The multivariate analyses were done with the software CANOCO v. 3.12 (Ter Braak 1988).

The Ivlev index of electivity was used to compare the importance of the different prey in the stomach contents and in the field (Ivlev 1961): $E = (d - c) / (d + c)$, where d is the proportion of the diet made up of a given prey, and c is the importance in number or biomass of the same prey in the field.

The relationship between body size and fullness was analyzed fitting the log-transformed allometric equation by least squares regression: Food dry weight = aCW^b . The differences in stomach fullness [$\log_{10}(\text{Food dry weight} + 0.001)$] between sexes, intermoult stages and stations were analyzed by means of ANCOVAs.

RESULTS

Diet composition and spatial changes

Forty-eight different prey taxa were identified in the stomach contents of *Necora puber*, which were grouped into 19 categories in terms of importance in the diet and by morphological and biological characteristics (Table 1). Habitat was the most important factor in the diet variability of *N. puber*; the frequency of appearance of the dominant diet components showed

significant differences between stations (Table 2; the results of the fitting of the log-linear models suggest that the factors analyzed represented effects which are independent, since only *Brachyura* and *Pisidia longicornis* have significant third order associations, although the significance level is generally lower than in second order interactions, $0.01 < p < 0.05$). The anomuran decapod *P. longicornis* was the main prey in all of the areas studied. The consumption of this prey exhibits significant differences between stations ($p < 0.001$), reaching 81% BDW at Stn B5. Brachyuran crabs were rather important at Stn B6, showing significant differences between stations ($p < 0.05$). Within the molluscs, *Mytilus galloprovincialis* was the most important prey, especially at Stn B1 where it appeared in 24% of stomachs with food ($p < 0.05$). The egg cases of the gastropod *Nassa* spp. were another important item in the diet at Stns B1 and B5; they were not consumed, however, at Stn B6. Teleost fishes make up

Table 1. *Necora puber*. Diet composition at the different sampling stations using the indices BDW, points (IP) and frequency of appearance (F); see 'Materials and methods: Data analysis'. Diet diversity for each station and index is shown. Number analyzed vs number with food given in parentheses after station number

Prey category	Code	Stn B1 (228/132)			Stn B5 (622/386)			Stn B6 (110/57)		
		BDW	IP	F	BDW	IP	F	BDW	IP	F
Fishes ^a	Fish	5.9	7.4	9.1	2.2	3.8	4.4	2.5	3.0	5.3
Natantia	Nata	0.8	0.5	0.8	0.2	0.6	0.8	4.3	2.6	1.8
Brachyura ^b	Brac	3.5	5.3	6.1	1.5	2.0	2.1	21.3	23.6	19.3
<i>Pisidia longicornis</i>	Pisi	68.9	53.6	66.7	80.6	70.9	77.7	49.5	32.5	40.4
Amphipods ^c	Amph	0.0	0.1	0.8	0.3	0.3	0.5	0.0	0.2	1.8
Barnacles ^d	—	—	—	—	0.1	0.3	0.3	0.0	0.2	1.8
<i>Mytilus galloprovincialis</i>	Myti	8.7	11.0	23.5	1.8	3.2	8.5	2.7	7.1	12.3
Other bivalves ^e	Biva	0.9	1.2	3.8	0.2	0.2	1.3	2.3	3.7	8.8
Trochiidae	Troc	0.4	0.2	0.8	0.6	0.7	4.1	0.3	0.8	3.5
Other gastropods	Gast	1.1	1.3	3.0	1.0	1.4	6.0	0.6	2.5	1.8
Egg cases of <i>Nassa</i> spp.	Nass	4.2	8.9	12.9	2.2	4.3	6.2	—	—	—
Ophiuroids ^f	Ophi	—	—	—	0.6	1.0	1.8	1.9	1.9	1.8
<i>Psammochinus miliaris</i>	Psam	2.4	1.9	3.0	5.8	5.4	11.1	3.5	3.5	10.5
<i>Aslia lefevrei</i>	Asli	0.7	0.9	3.0	0.3	0.2	0.5	4.5	7.2	8.8
Polychaetes ^g	Poly	0.2	0.5	0.8	0.5	0.8	1.3	2.9	6.7	5.3
Laminariales	Lami	—	—	—	0.9	1.8	3.6	0.0	0.4	1.8
Other seaweeds ^h	Seaw	1.0	0.9	3.0	0.3	0.5	1.3	0.6	0.9	3.5
<i>Zostera nana</i>	Zost	0.1	0.3	0.8	0.2	0.4	1.3	2.5	1.4	8.8
Sponges	Spon	1.0	5.1	6.8	0.3	1.1	2.1	0.4	1.5	3.5
Unidentified animal remains	Unid	0.2	0.9	2.3	0.5	1.2	2.8	0.2	0.4	1.8
Diversity H'		1.859	2.447	2.778	1.380	1.933	2.608	2.493	3.086	3.530
(SD)		0.150	0.135	0.128	0.098	0.101	0.093	0.202	0.174	0.152

^aGobiidae (*Gobius niger*, *Pomatoschistus minutus*, *Lesueurigobius friesii*), *Trisopterus* sp.
^b*Liocarcinus arcuatus*, Portunidae unidentified, *Atelecycclus* spp.
^c*Eurysteus maculatus*, Gammaridea unidentified
^d*Balanus* spp.
^e*Nucula* spp., Cardiacea
^f*Amphiura* spp., *Ophiocomina nigra*, *Ophiothrix fragilis*
^gNereidae, *Harmothoe* spp.
^hChlorophyta (*Ulva* spp., *Chaetomorpha* spp., *Cladophora* spp.), Rhodophyta (*Polysiphonia* spp., *Callithamnium* spp., *Porphyr* spp.)

Table 2. *Necora puber*. Analysis of the consumption of the different prey using log-linear models fitted to contingency tables. Model design is Prey (2) \times Station (3) \times Intermoult stage (3) \times Sex (3) \times Size (7) (the number of levels is indicated in parentheses). Statistical significance (p) of the χ^2 statistic for partial association between factors is shown (in bold the effects with $p < 0.05$). Fourth order interactions have been omitted as they presented non-significant effects in all cases ($p > 0.05$). Prey codes given in Table 1

	df	Fish	Nata	Brac	Pisi	Myti	Biva	Troc	Gast
Prey \times Station \times Intermoult	4	0.932	1.000	0.535	0.093	0.214	0.085	0.230	1.000
Prey \times Station \times Sex	4	0.724	0.632	0.035	0.212	0.717	0.683	0.164	0.090
Prey \times Intermoult \times Sex	4	0.996	1.000	0.248	0.882	0.545	0.625	0.732	0.714
Prey \times Station \times Size	12	0.530	0.865	0.021	0.187	0.733	0.238	0.682	0.161
Prey \times Intermoult \times Size	12	0.985	1.000	0.592	0.011	0.895	0.661	0.932	0.645
Prey \times Sex \times Size	12	0.999	0.994	0.999	0.097	0.817	0.999	0.911	0.159
Prey \times Station	2	0.267	0.792	<0.001	<0.001	0.011	0.011	0.151	0.127
Prey \times Intermoult	2	0.006	0.138	0.419	0.184	0.072	0.677	0.548	0.269
Prey \times Sex	2	0.283	0.744	0.003	0.023	0.936	0.838	0.594	0.379
Prey \times Size	6	0.004	0.546	0.024	<0.001	<0.001	0.748	0.130	0.063
	df	Nass	Psam	Asli	Poly	Lami	Seaw	Zost	Spon
Prey \times Station \times Intermoult	4	0.749	0.217	0.671	0.991	0.759	0.437	0.999	1.000
Prey \times Station \times Sex	4	0.905	0.200	0.799	0.967	1.000	0.246	0.946	0.165
Prey \times Intermoult \times Sex	4	0.369	0.791	1.000	0.668	0.310	0.844	1.000	1.000
Prey \times Station \times Size	12	0.898	0.691	0.998	0.930	0.988	0.946	0.794	0.596
Prey \times Intermoult \times Size	12	0.351	0.643	0.607	0.785	0.817	0.996	0.993	1.000
Prey \times Sex \times Size	12	0.211	0.888	1.000	0.992	0.992	0.999	0.732	1.000
Prey \times Station	2	0.001	0.010	0.001	0.106	0.018	0.213	0.002	0.548
Prey \times Intermoult	2	0.272	0.245	0.405	0.963	0.003	0.248	<0.001	0.001
Prey \times Sex	2	0.310	0.085	0.007	0.637	0.840	0.434	0.117	0.071
Prey \times Size	6	0.038	0.560	0.134	0.073	0.234	0.052	0.755	0.006

between 2 and 6% BDW at the different stations. The echinoid *Psammechinus miliaris* was one of the main prey at Stn B5, showing significant differences between areas ($p = 0.01$). The holothuroid *Aslia lefevrei* had some quantitative importance at Stn B6, whereas at Stns B1 and B5 it did not exceed 1% BDW ($p = 0.001$). The following prey were secondary components in the diet ($<3\%$ BDW): polychaetes and the eelgrass *Zostera nana* (both consumed mainly at Stn B6), seaweeds and sponges. The remains of unidentifiable food in the stomachs constituted 0.2 to 0.5% BDW of the diet (appearing in $<3\%$ of stomachs). Stn B5 had lower diversity values than those at Stns B1 and B6, which may be attributed to the greater importance of *P. longicornis* at Stn B5 (Table 1).

Diel patterns of feeding activity

The stomach fullness of *Necora puber* throughout the diel cycle ranged between 0.24 and 0.35% BDW (26 to 32% points) at Stn B5 and between 0.16 and 0.54% BDW (27 to 43% points) at Stn B1 (Fig. 2). There was high variability within each sample and no significant differences in repletion level were observed between

times at any of the stations (ANCOVA, $p > 0.1$ for the effects of time and body dry weight at Stns B1 and B5). On the other hand, no significant differences were found in the diet composition throughout the diel cycle (Kruskal-Wallis tests, $p > 0.05$), except in the case of the egg cases of *Nassa* spp. at Stn B5, which were consumed to a greater extent during the day ($p < 0.001$).

Number of food components and prey specimens per stomach

Of the stomach contents analyzed, 68.5% showed 1 type of prey, 22.5% exhibited 2 types, and 8.0% exhibited 3 and 4 types (only in 3 cases) (mean number of different prey per stomach: 1.41). The prey diversity per stomach varied according to the intermoult stage and size (log-linear model, $p < 0.05$), but not between stations or sexes ($p > 0.05$). Growth was associated with an increase in the diversity per stomach; crabs smaller and larger than 50 mm CW had an average of 1.25 and 1.51 prey per stomach respectively. During the intermoult cycle the number of prey per stomach increased in stage C (1.61) as compared to stages B and IM (1.35 and 1.37 respectively).

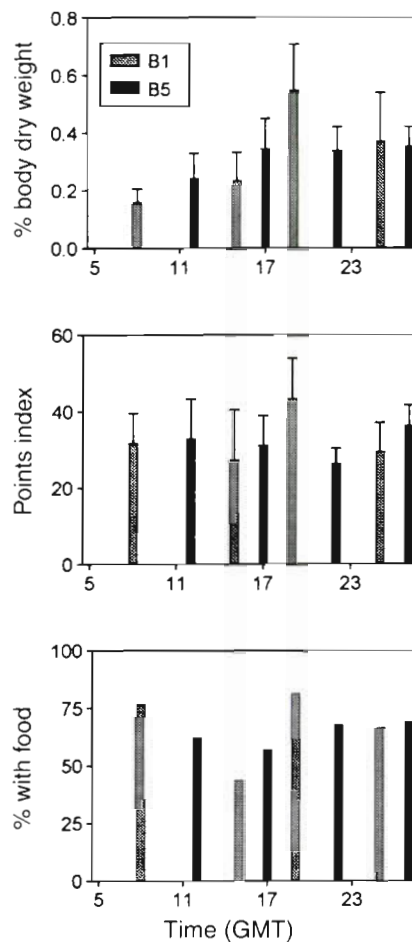


Fig. 2. *Necora puber*. Diel evolution of stomach fullness (estimated as BDW, points index and percentage of stomachs with food) at Stns B1 and B5. Standard error is shown for the points and BDW indices

Only in 27% of the cases was it possible to identify the number of specimens of each prey per stomach (excluding seaweeds, sponges and holothurians). Of the prey, 91% were represented by 1 specimen only, 6% by 2, and 3.3% had 3 or more individuals. The

results were very similar for all prey, with a slight increase in the percentage of stomachs with only 1 specimen in components having a larger body size (such as the fishes, *Brachyura* or *Mytilus galloprovincialis*).

Comparative analysis of diet composition indices

Points and BDW indices give a similar description of diet composition, although the points index increases, generally, the importance of the prey representing <10% of the diet. However, there are major differences between the quantitative indices and frequency of appearance, especially in small-sized prey which are consumed on a regular basis but are of relatively minor quantitative importance (Table 1).

The points and BDW indices used in the quantitative estimate of diet composition were subjected to a comparative analysis. Seven dominant prey and stomach contents showing the remains of only 1 prey were chosen. The allometric equations fitted relating the 2 indices were significant in all cases and the slopes were always different from 1 (t -test, $p < 0.05$) (Table 3). Both the sponges and *Mytilus galloprovincialis* ($b < 1$) appear in the stomach contents as non-skeletal tissue (in the mussel the volume of shell ingested was small compared to the mantle), whereas the remains of *Psammechinus miliaris*, *Brachyura*, *Pisidia longicornis* and fishes ($b > 1.24$) had a large amount of hard elements with a high dry weight: volume ratio.

Differences in diet composition between sexes

There were only minor differences in the diet between sexes. Non-ovigerous females consumed more *Pisidia longicornis* than males at the 3 stations (Table 2, $p < 0.05$; Stn B1: 78% BDW in males and 62% in females; Stn B5: 86% and 75%; Stn B6: 65% and 34%). Males preyed largely on *Brachyura* especially at

Table 3. *Necora puber*. Relation between the BDW and points indices in terms of establishing the importance of the different prey in the diet. Parameters of the equation $\log_{10}(\text{BDW}_i) = \log_{10}a + b\log_{10}(\text{IP}_i)$, fitted for the different groups of prey, the regression coefficient (R^2) and their significance (p) are indicated. Data from crabs having only 1 type of prey in their stomach contents were used

Prey	$\log a$ (SE)	b (SE)	R^2	p	N
Fishes	-3.721 (0.382)	1.433 (0.236)	0.770	<0.001	13
Brachyura	-4.128 (0.444)	1.610 (0.259)	0.708	<0.001	18
<i>Pisidia longicornis</i>	-3.500 (0.097)	1.245 (0.060)	0.613	<0.001	278
<i>Mytilus galloprovincialis</i>	-3.163 (0.230)	0.896 (0.158)	0.617	<0.001	22
Egg cases of <i>Nassa</i> spp.	-3.568 (0.357)	1.090 (0.241)	0.612	0.001	15
<i>Psammechinus miliaris</i>	-3.481 (0.448)	1.399 (0.330)	0.750	0.005	8
Sponges	-2.835 (0.321)	0.675 (0.233)	0.433	0.015	13

Stns B1 and B6 ($p < 0.05$; in males, brachyuran remains represented 6% and 45% BDW at Stns B1 and B6 respectively, whereas in females, they were not present). The diet of ovigerous females did not show any major differences and the number of stomachs with food did not allow for a detailed analysis. The diversity of the diet was greater in males than females, especially at Stns B1 and B5, ranging from 1.64 to 2.14 for females at the different stations and from 1.08 to 1.91 for females.

Changes in diet composition linked to the intermoult cycle

There were significant changes between intermoult stages in the consumption of fishes, Laminariales, *Zostera nana* and sponges (Table 2, $p < 0.05$). A distinction can be made between those components consumed more by the recent postmoult stages B and C (fishes, Laminariales and *Z. nana*, and to a lesser extent, *Pisidia longicornis*), and those consumed more in intermoult (*Mytilus galloprovincialis*, sponges, egg cases of *Nassa* spp. and *Psammechinus miliaris*).

At Stn B1 the most important differences between intermoult stages were found in components that are of minor quantitative value in the diet. At Stn B6, *Necora puber* preyed during stage B on Brachyura, ophiuroids, *Aslia lefevrei*, fishes and polychaetes, with a sharp drop in the consumption of *Pisidia longicornis* compared to stages C and IM (21% BDW in stage B, 72% in C and 50% in IM). At Stn B5, the consumption of both Laminariales and *Zostera nana* gradually decreased over the postmoult period (3.9% BDW for plants in stage B, 1.2% in C and 0.5% in IM). As with plants, predation on fishes diminished during the intermoult period (maximum of 5.4% BDW in stage C and minimum of 1.1% in IM). Additionally, *Mytilus galloprovincialis*, egg cases of *Nassa* spp., and sponges appeared to increase their contribution to the diet throughout the intermoult cycle. The intermoult cycle did not modify the diversity of the diet in the different stations.

Ontogenetic changes in the diet

Consumption of fishes, Brachyura, *Mytilus galloprovincialis*, *Psammechinus miliaris* and sponges increased with growth, whereas the importance in the diet of *Pisidia longicornis*, egg cases of *Nassa* spp., and *Aslia lefevrei* diminished with predator body size (Fig. 3). *P. longicornis* had a similar pattern at the 3 stations; its contribution decreased as the crab grew (Table 2, $p < 0.001$), especially in specimens ≥ 70 mm

CW. At Stn B5 it varied between 89% BDW in crabs < 30 mm and 57% in sizes of 70 to 79 mm. Stns B1 and B6 present a more pronounced ontogenetic diet variability. In crabs ≤ 50 mm, *P. longicornis* accounted for $> 50\%$ of the diet, whereas in the ≥ 70 mm size class it was reduced to 37% at Stn B1 and as low as 10% in crabs > 80 mm at Stn B6. The consumption of fishes at Stn B1 as well as Stn B5 increased with predator growth ($p < 0.05$), and they appeared exclusively in the stomach contents of crabs with a CW ≥ 50 mm and reached their peak in individuals ≥ 80 mm. The Brachyura present in the stomach contents appeared in crabs with a CW ≥ 40 mm, and reached maximum values in individuals > 60 mm ($p < 0.05$). The mussel became more important in the diet with growth ($p < 0.001$) and it was consumed in individuals with CW > 40 mm (Stns B1 and B5) or 50 mm (Stn B6). However, in crabs within these size ranges, no clear trend was observed. *P. miliaris* appeared in the stomach contents of crabs between 56 and 79 mm CW at Stns B1 and B6. At Stn B5 it made up part of the diet of all the size classes, with values ranging between 2% BDW in individuals < 30 mm and 18% in those between 70 and 79 mm, although the differences are not significant ($p > 0.05$). The diet diversity increased with growth both at Stns B1 and B5, although at Stn B6 the Shannon index was similar in the different size classes, with the exception of an increase in the specimens of 70 to 79 mm (Fig. 4).

Seasonal changes in diet composition

The dominant food components did not show any major seasonal fluctuations. The seasonality of the catches of *Necora puber* did not allow us to carry out a detailed analysis of the temporal variation of the diet at Stns B1 and B6 (at Stn B1 catches in winter were very small, whereas at Stn B6 most of the crabs analyzed were caught from September to November, and to a lesser extent in March). The importance of *Pisidia longicornis* in the diet at Stn B1 ranged between 65% BDW in May and 92% in March, however there was no seasonal pattern. The predation on molluscs increased in summer, both for bivalves and gastropods. *Mytilus galloprovincialis* was of maximum importance in the diet from July to October (reaching 6% BDW in August) and the minimum was reached from February to April ($< 1.0\%$). Similarly, gastropods only made up part of the diet of *N. puber* in summer and spring at Stn B1, while at Stn B5 they had minimum values in winter, reaching 7% BDW in May. Egg cases of *Nassa* spp. were only consumed from April to October, reaching maximums in July and September. *Psammechinus miliaris* presented minimum contributions in the diet in

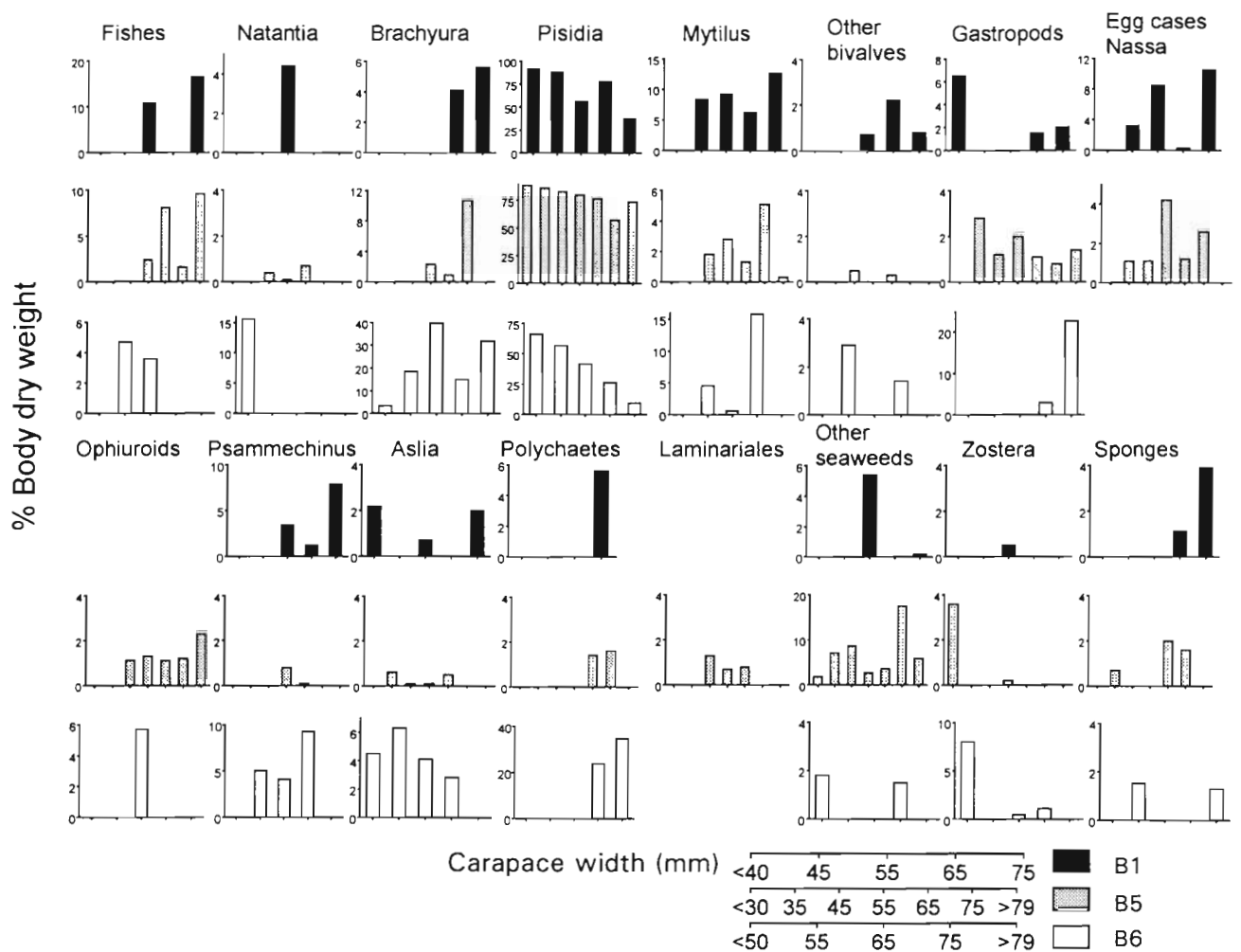


Fig. 3. *Necora puber*. Diet composition (BDW index) by body size class at Stns B1, B5 and B6. Note that the scales for each prey and station are different

winter and reached 19% BDW in November. The brown seaweeds were clearly seasonal, making up part of the diet between November and April, with maximum values in January.

Relation between sizes of predator and prey

In general, the fragmentation of prey in the stomachs prevents the determination of their size. The size of *Pisidia longicornis* was estimated by the maximum width of its abdomen, which appeared either intact or fragmented in 2 pieces; maximum thickness of the shell remains of *Mytilus galloprovincialis* was estimated; the size of the gastropods of the family Trochiidae consumed was estimated by the diameter of the operculum which appears either intact or slightly fragmented. There was a significant positive relationship

between predator (carapace width, x) and prey (y) size in the case of *P. longicornis* ($y = 0.092x^{0.861}$, $N = 29$, $r = 0.54$, $p < 0.01$) and *M. galloprovincialis* ($y = 0.009x^{1.340}$, $N = 32$, $r = 0.50$, $p < 0.01$) but not for Trochiidae ($N = 9$, $r = 0.325$, $p > 0.05$).

Multivariate analysis of diet composition

The variance of the prey matrix explained by the axes extracted using the CCA was low (axis 1: 1.4%) due to the fact that stomachs contained few and generally only 1 type of prey; however, the correlation between prey and external variables was high. Axis 1 ($r = 0.468$; 36.4% of the variance of the prey-external variables relationship) correlates positively with size, and contrasts Stn B5 with Stns B1 and B6. Brachyura and sponges present positive scores, whereas the ophi-

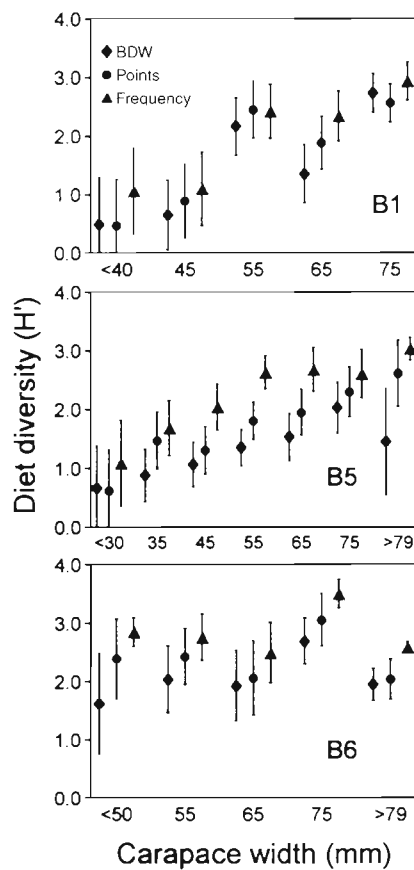


Fig. 4. *Necora puber*. Diet diversity (index H' and 95% confidence interval) in the different size classes at each station, using different diet composition indices (BDW, points and frequency of appearance)

uroids, *Natantia* and *Pisidia longicornis* are arranged on the negative part of the axis (Fig. 5). Axis 2 ($r = 0.428$; 30.0% variance) explains the changes in the diet which are linked to the intermoult cycle, with stage B and prey such as *Zostera nana*, *Aslia lefevrei* and the Laminariales being on the positive end and others, such as the sponges, *Mytilus galloprovincialis*, gastropods or egg cases of *Nassa* spp., which are associ-

ated with stage IM, on the negative part. Axis 3 (which corresponds only to 16.0% of the prey - external variables relationship) is associated mainly with the station, although the correlations are lower than in axes 1 and 2. Axis 3 differentiates, on the one hand, Stn B5 and components such as Laminariales and *Psammechinus miliaris* and, on the other hand, Stn B1 and, to a lesser extent, Stn B6 which have prey such as *Natantia*, *A. lefevrei* or other bivalves.

The partial CCAs show that all the factors analyzed have a significant effect on diet composition ($p = 0.01$), with the exception of sex ($p = 0.15$). Eigenvalues of canonical axes show that station is the most important factor, and next in importance is size and the intermoult stage (Table 4). The partial CCA carried out to test the importance of stomach fullness on diet composition points to the existence of a significant effect; in any case, the dominant prey do not present important scores on axis 1. The prey having negative scores such as the group of other food items and unidentified remains, sponges, plants, gastropods and amphipods become less important in the diet as the fullness decreases, and therefore in stomachs in advanced stages of digestion. In contrast, Brachyura, ophiuroids, fishes, *Psammechinus miliaris* and Trochiidae continue to make up part of the stomach contents for a longer period of time.

Stomach fullness

There was a significant correlation between the level of stomach fullness, measured as food dry weight, and body size ($p < 0.05$, analyzing crabs with food in the stomach, except in ovigerous females) (Table 5). The slope of the fitted equations are always < 2 , which points to a negative allometric relationship, given that the slope of the size-weight relation for *Necora puber* in the Ría de Arousa is 2.96 in males and 2.88 in females (González-Gurriarán 1985b). Although the absolute fullness increased with body size, the relative BDW index decreased (Fig. 6). Significant differences

Table 4. *Necora puber*. Results of partial CCA in which the effect of the different external variables in the diet composition is tested after the other variables are introduced as covariates. E_1 , E_2 : eigenvalues of canonical axes 1 and 2; r : correlation between the variables tested and the axis; E_c/E_{nc} : relation between the sum of the eigenvalues for the canonical axes and the first non-canonical axis; $p_{axis 1}$, p_{global} : significance levels of the Monte Carlo tests for axis 1 and for all canonical axes

Variable	Covariates	E_1 (r)	E_2 (r)	E_c/E_{nc}	$p_{axis 1}$	p_{global}
Size	Station, Sex, Intermoult	0.078 (0.345)	–	0.085	0.01	–
Sex	Size, Station, Intermoult	0.041 (0.251)	0.009 (0.122)	0.054	0.03	0.15
Intermoult stage	Size, Station, Sex	0.076 (0.350)	0.015 (0.152)	0.099	0.01	0.01
Station	Size, Sex, Intermoult	0.117 (0.421)	0.051 (0.305)	0.182	0.01	0.01
Gut fullness	Size, Sex, Intermoult, Station	0.057 (0.283)	0.033 (0.234)	0.099	0.01	0.01

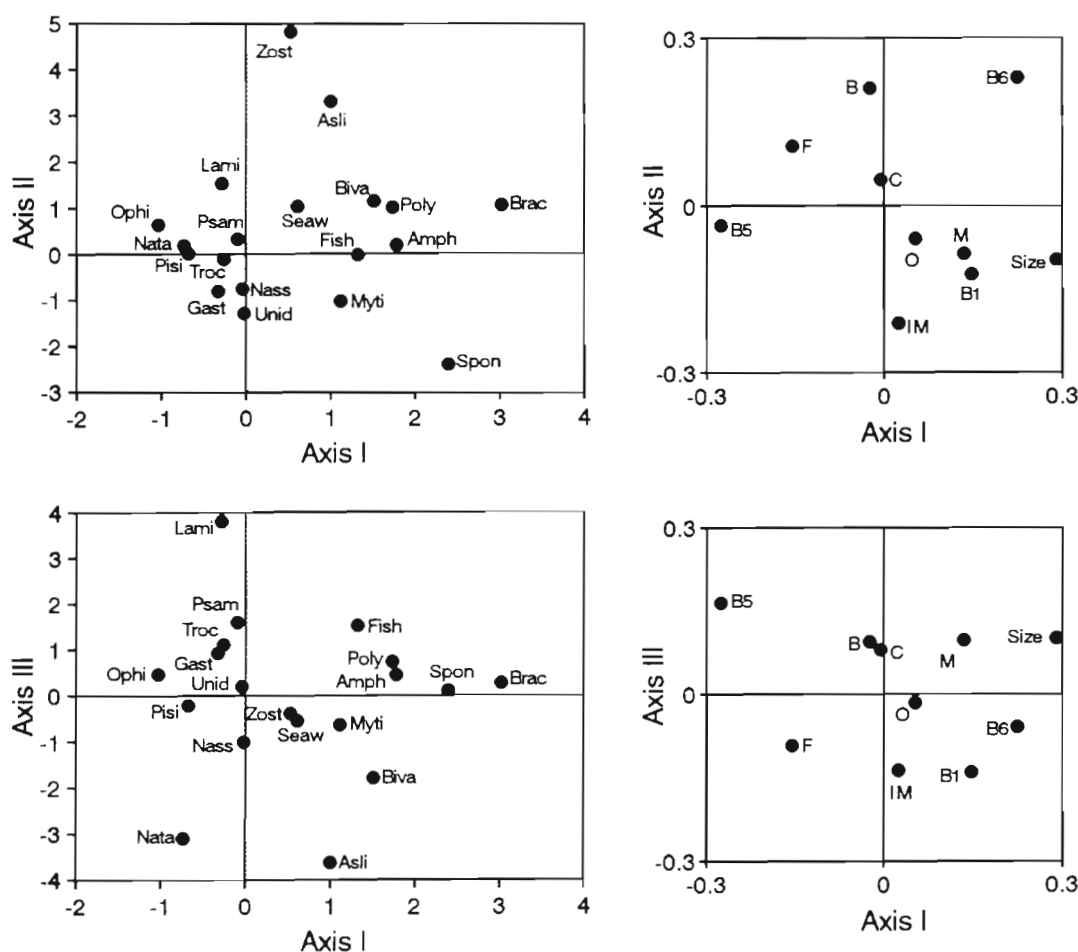


Fig. 5. *Necora puber*. Distribution of prey and 'external variables' (size; sex: M, F, O; station: B1, B5, B6; and intermolt cycle stage: B, C, IM) on the first 3 axes extracted from the CCA (prey codes are given in Table 1); see 'Materials and methods' for sex and intermolt stages

Table 5. *Necora puber*. Parameters of the allometric equation, $\log_{10}(\text{Food dry weight}) = \log_{10}a + b\log_{10}\text{CW}$, fitted for each station, sex and intermolt cycle stage and for specimens having maximum repletion (points index = 100). Regression coefficient (R^2), number of crabs (N) and significance level (p) are shown. The equations were fitted using data from crabs having food in their stomachs

	$\log a$ (SE)	b (SE)	R^2	p	N
Station					
B1	-3.922 (0.676)	1.360 (0.378)	0.091	0.001	132
B5	-3.724 (0.393)	1.265 (0.228)	0.074	<0.001	386
B6	-3.826 (0.967)	1.365 (0.543)	0.103	0.015	57
Sex					
Males	-3.765 (0.391)	1.272 (0.223)	0.094	<0.001	313
Non-ovigerous females	-4.043 (0.507)	1.473 (0.293)	0.092	<0.001	252
Ovigerous females	1.821 (5.597)	-1.837 (3.052)	0.024	0.556	17
Intermolt cycle stage					
B	-4.575 (0.858)	1.715 (0.492)	0.099	0.001	113
C	-4.775 (0.876)	1.988 (0.500)	0.178	<0.001	75
IM	-3.366 (0.338)	1.047 (0.194)	0.070	<0.001	391
Maximum fullness (Points index = 100)	-4.341 (0.530)	1.956 (0.306)	0.383	<0.001	68

in fullness were found between the different intermolt stages and seasons (ANCOVA; covariate effect: predator size, $p > 0.1$ for analyses including crabs without food and $p < 0.001$ for analyses restricted to crabs with food; intermolt stage, $p < 0.001$ for both analyses; season, $p > 0.01$ for gut fullness ≥ 0 and $p < 0.05$ for fullness > 0); this, however, was not the case between stations or sexes ($p > 0.1$). Stn B5 had a lower percentage of empty stomachs (31.4%) than Stn B1 (41.2%) or Stn B6 (46.4%); however, fullness levels are quite similar in the different areas studied. The BDW index at Stn B5 was higher than at Stns B1 and B6, since the mean size of the crabs caught and analyzed at Stn B5 (males: 57.2 mm CW, SD = 14.6; females: 53.8 mm \pm 11.3) was lower than at Stn B1 (males: 66.6 mm \pm 15.1; females: 61.4 mm \pm 10.9) and at Stn B6 (males: 66.1 mm \pm 15.1; females: 57.1 mm \pm 11.1).

The stomach fullness appeared lower in the case of ovigerous females, although because of the small sample size this could not be verified, and similar between males and non-ovigerous females, although the latter always presents slightly higher values (Fig. 6). The changes in fullness in females appear to be linked to the reproductive cycle, showing a drop throughout the maturation process. The differences in fullness observed during the intermolt cycle point to the existence of 4 clearly defined periods of feeding activity (Fig. 6). In the stages immediately before and after ecdysis (stages D and A respectively) there was practically no ingestion of food (96% and 95%, respectively, of the crabs analyzed had empty stomachs). Food consumption began after ecdysis during stage B (28.5% of the stomachs were empty), and increased during intermolt period C (19.8% empty stomachs), to decrease to lower levels in stage IM (38% empty stomachs). There were important seasonal changes in food consumption which were reflected in an increase in stomach fullness in autumn and especially in winter (Fig. 6), with low values in July and August.

Predation on infauna and raft epifauna: prey selection

From a functional point of view, different groups of prey can be distinguished among the benthos and organisms associated with mussel culture (Fig. 7). The raft epifauna and the mussel made up the dominant group

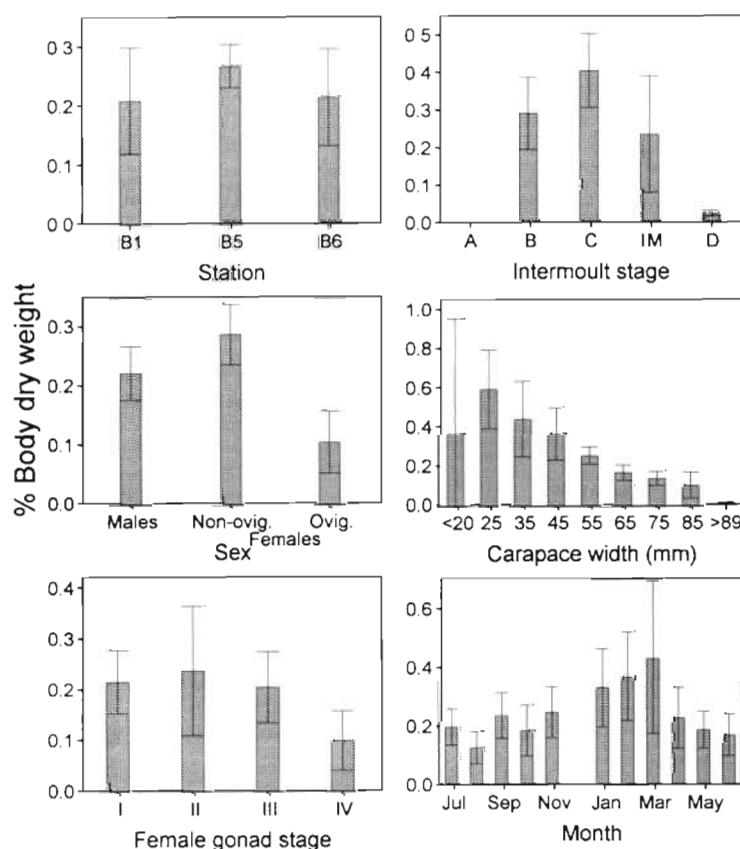


Fig. 6. *Necora puber*. Stomach fullness (mean and 95% confidence interval of the BDW index are shown) for the different sampling stations, sexes, stage of gonad development in females, intermolt cycle stage, body size, and monthly evolution throughout the yearly cycle

of prey in the diet of *Necora puber*. Spatial differences did exist, however, with these organisms showing maximum importance in the diet at Stns B1 and B5 (>80% BDW), while at Stn B6 predation on the epifauna and mussel decreased to approximately 50%. Macroinfauna

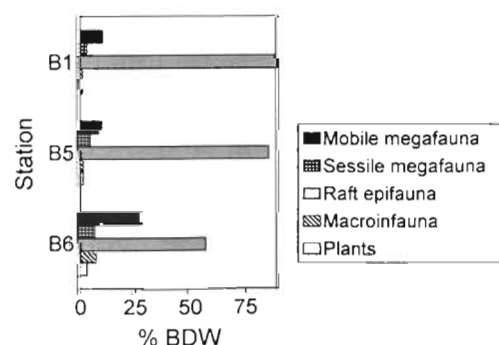


Fig. 7. *Necora puber*. Diet composition at the different sampling stations located in the Ría de Arousa. Original prey are grouped in terms of habitat, biological characteristics and mobility

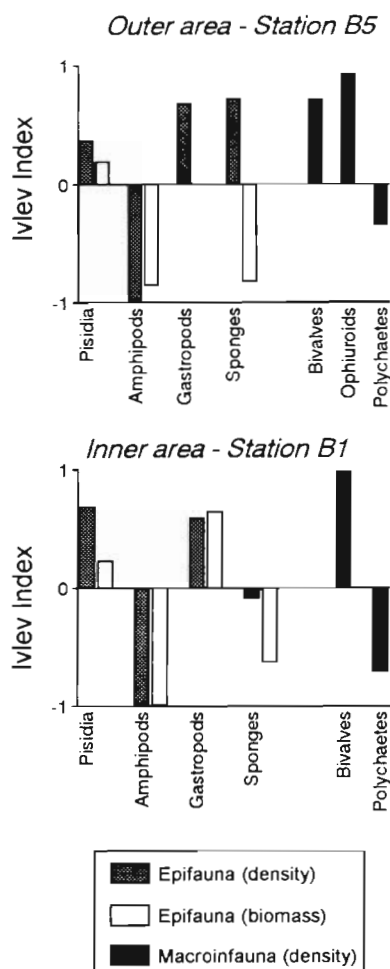


Fig. 8. *Necora puber*. Ivlev index of prey selection at Stns B1 (inner ría area) and B5 (outer area). Selection indices are calculated independently for the part of the diet corresponding to epifauna and infauna in terms of importance in the stomach contents of the different prey and their density or biomass in infauna (data from López-Jamar 1982) and epifauna (data from Román & Pérez 1982)

constituted only between 2 and 7% of the diet at the different stations, while meiofauna did not constitute part of the diet in any of the areas studied. Within the benthic megafauna, 2 groups of prey can be distinguished in terms of mobility: sessile or with little mobility (holothuroids and echinoids) and mobile species (fishes and decapods). The consumption of megafauna was greater at Stns B6 and B1 (36 and 18% respectively) than at Stn B5 (15%) following a pattern opposite to that of the epifauna of the culture.

Prey selection patterns were analyzed using data from Román & Pérez (1982) and López-Jamar (1982) for epifauna and infauna respectively, relating to the mid-outer areas (Stn B5) and the inner zone (Stn B1) in the Ría de Arousa. Annual mean density and biomass

were obtained from epifaunal samples taken from the ropes used for thinning out and seeding by Román & Pérez (1982) and the 4 dominant groups in the diet or in the epifaunal community were analyzed (*Pisidia longicornis*, amphipods, gastropods and sponges). Data from López-Jamar (1982) on density of infauna allowed us to analyze the selection of polychaetes, bivalves (except mussel) and ophiuroids, which are the most important components of the benthic macroinfauna in the Ría de Arousa. In general, prey selection patterns were similar in the inner and outer zones (Fig. 8). Among the epifauna, the Ivlev index presented positive values for *P. longicornis* at both stations, especially using density data. The other dominant group within the epifauna is the amphipods, which were selected negatively. Gastropods and sponges are unimportant taxa in the diet, but they are somewhat important in the epifaunal community, especially in density in the case of the gastropods and biomass in the sponges. The gastropods had positive values of the Ivlev index; however, the selection pattern that sponges followed was much more variable. Within the groups of benthic macroinfauna analyzed, the ophiuroids were important, both in the diet and field, only in the mid-outer zone, whereas the polychaetes as well as the bivalves were the dominant groups in both areas. *Necora puber* had a positive selection for bivalves and ophiuroids and negative for polychaetes both at Stns B1 and B5.

DISCUSSION

Necora puber has a generalist diet which is determined in the first place by the structure of the prey community and secondly, by the selection of available prey. In general, portunid crabs have unspecialized diets that reflect the taxonomic composition and structure of the potential prey communities, mainly macroinvertebrates (molluscs and crustaceans) sessile or with little mobility (Hill 1976, 1979, Paul 1981, Williams 1981, Laughlin 1982, Wear & Haddon 1987, Ropes 1988, Abelló 1989, Edgar 1990, Haefner 1990, Hines et al. 1990, Stoner & Buchanan 1990, Hsueh et al. 1992). The spatial variability in the availability of prey has been identified as the primary cause of the changes in the trophic relationships of decapod crustaceans (Paul 1981, Alexander 1986, Wear & Haddon 1987, González-Gurriarán et al. 1989, Edgar 1990, Freire et al. 1990). The habitats sampled in the Ría de Arousa show differences in the abundance and structure of the benthic communities (González-Sanjurjo 1982, López-Jamar 1982, Román & Pérez 1982), which is the reason that the spatial changes are the most important factor in the variability of diet composition in *N. puber*. The

distribution of *Pisidia longicornis* in the ría (González-Sanjurjo 1982, Román & Pérez 1982, Fernández et al. 1990), with maximum densities in the mid-outer zones (Stn B5) and the sharp drops in the inner area (Stn B1), determines spatial changes in its importance in the diet of *N. puber*.

Studies carried out on the feeding of *Necora puber* in the south of England (Norman & Jones 1992) and Wales (Choy 1986) analyzed populations located in rocky inter- and subtidal zones, whereas our research concentrates on soft bottom habitats located in the mussel culture areas. In the rocky zones, the diet is dominated by brown seaweeds, crustaceans (Brachyura and barnacles), bivalves and gastropods. The major differences that were observed between the diet on the coasts of Galicia and in the British Isles appear to be linked more to differences in prey availability between habitats than to geographical changes. In keeping with this, Norman & Jones (1992) suggest that there are major changes in the diet with depth, which implies that the velvet swimming crab decreases its consumption of seaweeds and tends to feed more on benthic invertebrates with increasing depth. In the mussel culture areas, *N. puber* preys chiefly on the raft epifauna and megafauna, with plants and macrofauna providing a secondary source of food. Although herbivory is more widespread among the family Majidae (Wolcott & O'Connor 1992), enzymes specific to the digestion of reserve carbohydrates found in different groups of seaweeds have also been detected in portunid species such as *Callinectes sapidus* (McClintock et al. 1991) and *N. puber* (Norman & Jones 1990). In spite of this, both Choy (1986) and Norman & Jones (1992) suggest that the importance of the seaweeds in the diet of *N. puber* is due to their abundance in the area studied, although *N. puber* prefers animal prey. Similarly, *C. sapidus* feeds mainly on invertebrates and fishes (Hines et al. 1990) even though it is capable of producing carbohydrases.

Several studies on the diet of decapods highlight ontogenetic changes as the most important biotic factor in diet variability. During growth, crabs increase the consumption of fishes and decapods (especially Brachyura) and sharply reduce the predation on non-decapod crustaceans and plants (Paul 1981, Stevens et al. 1982, Stoner & Buchanan 1990, Hsueh et al. 1992). In the Ría de Arousa the ontogenetic evolution in the diet of *Necora puber* is similar to that described for other species of Brachyura. We observed an increase in the consumption of fishes, Brachyura and molluscs (especially mussels) with size, whereas *Pisidia longicornis* and non-decapod crustaceans follow the opposite trend. In general, an increase in the predator's body size means that the prey size will increase, with the predator feeding more on prey having hard exo-

skeletons in relation to the ontogenetic changes in the biomechanical characteristics of the chelipeds and mechanisms for the selection of the prey (ap Rheinallt & Hughes 1985, ap Rheinallt 1986, Freire unpubl. data).

Decapods do not generally show any significant differences in diet composition between the sexes (Wear & Haddon 1987, Haefner 1990, Hsueh et al. 1992). *Necora puber* only exhibits slight differences in diet between males and females, and they may be attributed to the greater body size of the males, as the changes linked to growth are similar to the differences observed between males and females. Norman & Jones (1992) report that sexual differences in the diet are due only to the breeding cycle, during which time ovigerous females reduce their predation activity. In the Ría de Arousa, female stomach fullness decreases during the breeding cycle and in advanced stages of gonad development.

The intermoult cycle brings about drastic changes in the feeding activity of the Brachyura. They cease their intake of food in the immediate pre- and post-ecdysis stages, and increase stomach repletion in the recent postmoult stages (Abelló & Cartes 1987, O'Halloran & O'Dor 1988, Abelló 1989, Norman & Jones 1992). This study reports on the changes in the consumption of different prey that *Necora puber* undergoes during the intermoult cycle, and highlights the increased consumption of *Pisidia longicornis*, fishes and plants in the early post-ecdysis stages (the consumption of fishes in the early postmoult stage may correspond to necrophagous activity). These changes are determined chiefly by the decreased capacity for predation during the early postmoult stages, which causes a greater consumption of plants and sedentary prey, and by the calcium required to form the new carapace that may be supplied by the different skeletal structures of the prey organisms (Abelló & Cartes 1987).

The epifauna are the dominant prey in the stomach contents of the portunids in the raft areas of the Ría de Arousa, making up very high percentages of the food consumed (reaching over 80% in the case of *Necora puber*) (González-Gurriarán et al. 1989, Freire et al. 1990, Freire 1993). These results correspond to the high biomass that these organisms reach on the 3-dimensional support consisting of the culture ropes (González-Sanjurjo 1982, Román & Pérez 1982, Fernández et al. 1990). The mussel and epifauna that detach from the ropes as a result of weather conditions or human activity carried out on the raft (Pérez & Román 1979) facilitate the availability of these prey for the epibenthos. In addition, the portunids have direct access to the culture ropes because the crabs are able to swim (Hartnoll 1971), because they can gain access by means of the anchoring points, and also because the

ropes occasionally touch the bottom at low tides. The fact that the infauna is of little importance in the diet of *N. puber* in the raft stations may be attributed to the decrease in abundance and biomass that is observed both in the Ría de Arousa, compared to other rías, and within this ría, in the raft zones, as compared to areas that are not devoted to culture (López-Jamar 1982, Tenore et al. 1982, López-Jamar & Mejuto 1986). However, the megafauna has higher densities and biomass in the raft areas (demersal fishes and echinoderms as well as decapod crustaceans) (Chesney & Iglesias 1979, Iglesias 1981, González-Gurriarán 1982, Olaso 1982, Romero et al. 1982). In spite of its abundance, *N. puber* has a limited ability to prey on this group of organisms, as its mobility and size make it difficult for this crab to capture and handle these prey (ap Rheinallt & Hughes 1985, ap Rheinallt 1986). According to this, although the megafauna are an important part of the diet, it does not come close to the levels reached by the more accessible, and probably more abundant, epifaunal prey in the culture polygons.

The prey selection patterns seen in *Necora puber* are similar to those observed in other portunid species (Freire 1993) and demersal fishes (López-Jamar et al. 1984) in the mussel culture areas of the Ría de Arousa. Within the epifauna there is a positive selection on the species having the greatest biomass in the community, *Pisidia longicornis*, and negative for the amphipods, which also reach high densities (González-Sanjurjo 1982, Román & Pérez 1982). Of the infauna, the polychaetes, which are dominant in density and biomass (López-Jamar 1982, Tenore et al. 1982, López-Jamar & Mejuto 1986), are of proportionally small importance in the diet. Both the ophiuroids and bivalves, which are less abundant groups within the benthic macrofauna, are selected positively.

The temporal changes in the epifaunal community are determined by both environmental seasonality and the succession that is established after the mussel seed is placed in the sea or after thinning out (which means that the associated epifauna is eliminated). Since these processes have a strong temporal variability (Pérez-Camacho et al. 1991), ropes in different stages of culture exist throughout the year, which makes the seasonal pattern more complex. For this reason, the diet and availability of the different groups of epifauna do not undergo major seasonal fluctuations.

Mussel culture on rafts brings about different changes in the ecosystem which directly affect the benthic megafauna. On the one hand, the bottoms of the culture areas are structurally complex, giving rise to shelters and microhabitats for the megabenthic organisms. Food is also more widely available, due to the appearance of new prey communities such as the epifauna or the cultured mussel itself. These are the

factors which cause the population dynamics of the decapods in the Ría de Arousa to be linked to the raft areas (González-Gurriarán 1982, 1985a, b, Romero et al. 1982, Fernández et al. 1991, Freire et al. 1991). There is an increase in density and biomass, growth rates and the secondary production of different species and of the community as a whole in the raft areas, as compared to other habitats. Also, species such as *Necora puber* carry out seasonal migrations towards the culture areas (González-Gurriarán 1981, 1985a, b). In contrast, demersal fishes are more mobile than the decapods, which is why it has been suggested that they have different feeding and habitat selection strategies, even though they feed on the raft epifauna. The teleost species which are dominant in the Ría de Arousa do not show differences in abundance between habitats (Chesney & Iglesias 1979, Iglesias 1981) since they have access to the raft polygons for feeding from other areas (López-Jamar et al. 1984).

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Amino acid and related compound composition in two symbiotic mytilid species from hydrothermal vents

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ABSTRACT: Two species of deep-sea mussels belonging to the genus *Bathymodiolus* were collected from 5 vent fields distributed over 2 basins of a hydrothermal system in the South Pacific. Free and bound primary amino compounds were analysed in gills and mantles using OPA-HPLC. The method allowed the detection of 32 amino acids and related compounds (AARCs). An undetermined free chemical was found at high levels (up to 30% of the total free AARCs) in vent mussel tissues. This amino compound is presumed to be an end-product from specific metabolism occurring in vent mussels. Except for this unknown compound, comparison of the biochemical composition between vent and littoral mussels revealed that the general nitrogenous requirement as well as the endogenous metabolic pathways of the main amino acids seem to be similar for the 2 mussel types. Ultrastructural observations indicated that these deep mussels harbour bacteria in their gills. Indices of high metabolic rates found in these organs appear to be related to the presence of endobacterial. It seems that symbionts could provide a preponderant fraction of essential amino acids to their host. In particular, free thiotaurine displayed high concentrations (up to 13% of the total free AARCs). This sulphur-containing compound could be involved in a specific metabolism related to toxic forms of sulphur. Variations of the AARC composition between the 2 vent mussel species do not appear to be species related but appear to be due to environmental constraints. As shown by stress indices, deterioration of the physiological condition in these mussels is directly linked to the quantity and/or the quality of the hydrothermal vent emissions.

KEY WORDS: Amino acids and related compounds · Symbiotic mussels · Sulphur-oxidizing bacteria · Hydrothermal vent · Physiological index

INTRODUCTION

The bivalves Mytilidae have a world-wide distribution with a great majority of species occurring intertidally in littoral and shallow sublittoral ecosystems (Russell-Hunter 1983, Koehn 1991). This family, like most other marine invertebrates, depends for its food supplies on the phytoplanktonic primary production that constitutes the base of the general marine food-web (Jørgensen 1990). Until recently, mussels were considered to be exclusively sedentary, filter-feeding organisms living on plankton and organic detritus (Bayne 1976, Allen 1983), free bacteria (Priour 1981, Birkbeck & McHenery 1982) or dissolved organic solutes (Stephens 1972, Melaouah 1990). Discovery of

a new fauna associated with deep hydrothermal vents has shown that at least 1 genus, *Bathymodiolus*, can use another nutritional strategy (Fiala-Médioni et al. 1986a, Fiala-Médioni & Le Pennec 1987, Fiala-Médioni 1988). Species of this genus were found associated with deep, active tectonic areas in the Atlantic and Pacific (Fiala-Médioni 1988). These environments, which often correspond to the aphotic zone, are depleted of photosynthetic carbon but are full of energy-rich chemicals and sometimes highly toxic substances like hydrogen sulphide (H₂S) or heavy metals (Childress & Fisher 1992). All of the *Bathymodiolus* species critically examined to date harbour autotrophic prokaryotes in their gill cells. These bacteria appear to be able to use sulphur or methane to power carbon fix-