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Feeding ecology of *Liocarcinus depurator* (Decapoda: Portunidae) in the Ría de Arousa (Galicia, north-west Spain): effects of habitat, season and life history

Abstract The diet of the portunid crab *Liocarcinus depurator* (L.) in soft-bottom areas of the Ría de Arousa (Galicia, north-west Spain) was studied by analysis of stomach contents, and by comparison of habitats of contrasting abundance, composition and diversity of prey communities. Monthly samples were taken from July 1989 to June 1990 ($N = 3747$) in mussel (*Mytilus galloprovincialis*) raft-culture areas and central channel zones. Ninety-two food items were identified: crustaceans, molluscs, polychaetes, ophiuroids and fishes were the dominant prey. The raft epifauna and the mussels constituted the dominant group of prey in the raft areas and inner channel station (the epifaunal crab *Pisidia longicornis* comprised 30 to 52% of the diet), whereas the benthic macroinfauna was the dominant food component in the mid-outer channel (polychaetes constituted 32% of the diet). In the epifaunal community, diet selection for *P. longicornis* was positive and for amphipods was negative, whereas within the infauna diet selection for bivalves and ophiuroids was positive and for polychaetes negative or neutral. The seasonal importance of *P. longicornis* and *M. galloprovincialis* varied in the diet of *L. depurator* parallel to seasonal activities connected with mussel culture (seeding, thinning, harvesting) that determine the availability of prey from the rafts. Major changes in the composition of the diet related to the life history of *L. depurator* occurred during ontogeny. In the raft zones, consumption of mussels and fishes increased with increasing body size, while the consumption of Natantia, non-decapod crustaceans, gastropods, polychaetes Pectinariidae and plants decreased with increasing crab size. Maximum consumption of *P. longicornis* was by *L. depurator*

individuals of intermediate size (15 to 44 mm carapace width). Stomach fullness (measured as dry weight of food) increased with increasing body size, but with negative allometry. During the late pre-moult and early post-moult periods *L. depurator* did not consume any food; maximum stomach fullness was recorded for the late post-moult and intermoult stages. Female food consumption decreased during egg incubation. Food consumption was greater in autumn and winter than at other seasons; this appears to be related to seasonal changes in reproduction and moulting.

Introduction

Raft culture of the mussel *Mytilus galloprovincialis* has modified the structure of the food webs in the Galician rías (north-west Spain), and specially in the Ría de Arousa (Tenore et al. 1982). Culture ropes constitute a new substratum for the development of an epifaunal and macroalgal community that attains high diversity and biomass (Lapointe et al. 1981; González-Sanjurjo 1982; Román and Pérez 1982; Fernández et al. 1990). However, sediments have been modified by the accumulation of biodeposits, causing a decrease in infaunal diversity and biomass (López-Jamar 1982; Tenore et al. 1982). The production and biomass of the epibenthos is higher in the culture areas than in other rías and other soft-bottom habitats within the Ría de Arousa (Chesney and Iglesias 1979; Iglesias 1981; González-Gurriarán 1982; Olaso 1982; Romero et al. 1982). Decapod crustaceans are one of the dominant epibenthic groups in the Ría de Arousa, and particularly in raft areas (González-Gurriarán 1982; Romero et al. 1982; Tenore et al. 1982), which has given rise to the hypothesis that their distribution and abundance patterns are associated with changes in food availability (González-Gurriarán et al. 1989; Freire et al. 1990; Freire 1993; Freire and González-Gurriarán 1995).

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The crab *Liocarcinus depurator* (L.) (Decapoda: Brachyura: Portunidae) is the most abundant decapod species in raft zones and central channel areas not devoted to aquaculture in the Ría de Arousa, both of which areas are subject to oceanic influences (González-Gurriarán 1982; Fernández et al. 1991). Apart from experimental analyses on the importance of predation by *L. depurator* on soft-bottom infaunal communities (Thrush 1986; Hall et al. 1990a, b), there is little information available on the trophic relationships of this species (qualitative data in Abelló and Cartes 1987 in the north-west Mediterranean, and Hall et al. 1990a in Scotland). Previous studies on *L. depurator* in the Ría de Arousa highlighted the importance of the mussels and associated epifauna from the rafts in the crab's diet (González-Gurriarán et al. 1989), and described its diel pattern of feeding activity (Freire et al. 1991). These studies did not, however, examine spatial, temporal and life-history-related variations in the feeding ecology of this species.

The diet of *Liocarcinus depurator* in the Ría de Arousa was studied by analysis of its stomach contents to identify differences in its diet arising from spatial and seasonal changes and variability related to the various life-history stages. The effect that habitats of contrasting abundance, composition and diversity of prey communities have on the trophic relationships of this species was assessed by comparing the raft culture and central channel areas.

Materials and methods

Study area

Four stations representative of the habitat range of *Liocarcinus depurator* (L.) (González-Gurriarán 1982; Fernández et al. 1991) were selected by sampling a raft polygon and the central channel from the inner and mid–outer areas of the Ría de Arousa (Fig. 1). The inner-raft station (IR) is 10 to 15 m deep, with a mud bottom which is sometimes anoxic (López-Jamar 1982); the outer-raft station (OR) is 20 to 30 m deep, with a sandy-mud bottom. Both central channel areas have mud bottoms; the inner-channel station (IC) is 20 to 30 m deep, the outer-channel station (OC) 60 m deep. The stations in the inner ría experience salinity fluctuations due to the river runoff, while the mid–outer areas are subject to oceanic influence. Material and organisms from the rafts (mussel and associated epifauna, macroalgae, remains of culture ropes, etc.) are deposited on the bottom of the culture areas, providing shelter for the mobile epifauna. The bottoms of the central channel have been modified slightly by deposits from the rafts.

Sampling and laboratory methods

Crabs were sampled with a 4 m beam trawl with a cod-end mesh of 10 mm (González-Gurriarán 1982). Sampling was carried out monthly from July 1989 to June 1990, with the exception of December (inclement weather). Each month, 3 to 5 tows were carried out at each station over a 2 d period (08.00 to 15.00 hrs; a preliminary study in the same areas had indicated that feeding of *Liocarcinus depurator* was continuous throughout the diel cycle, although

stomach fullness was higher at night in the channel station: Freire et al. 1991). After each tow, the samples were fixed in 4% neutralized formalin, and 24 to 48 h later were stored in 70% alcohol.

The following data were recorded for each individual: carapace width (CW, from the tips of the fifth pair of anterolateral spines of the cephalothorax), wet weight (dry weight was estimated using the conversion factor obtained by González-Gurriarán 1982), sex, and, in females, the presence of eggs in the abdomen as well as gonad maturity stage (following the criteria of Abelló 1989a: Stage I, ovaries at rest; Stage II, beginning of maturation; Stage III, mature ovaries actively developing; Stage IV, fully developed ovaries, immediately prior to spawning). The stage of the moult cycle was determined based on the calcification level of the exoskeleton: Stage A, immediate postmoult, very soft exoskeleton (Stage A_1 of Drach and Tchernigovtzeff 1967); Stage B, calcification begins and exoskeleton has a paper-like consistency (A_2–B_2); Stage C, advanced post-moult, whereby exoskeleton is only flexible in the pterigostomial region of the carapace (C_1 and C_2); Stage I, intermoult, with exoskeleton rigid and hard (C_3–C_1); Stage D, premoult, with new exoskeleton almost completely formed beneath the old one (D_2–D_4).

In the stomach contents, the prey were identified to the lowest taxonomic level possible using a stereomicroscope. In cases where more than one food component was present, the relative importance of the different prey was determined by the points-method (Williams 1981), which visually estimates the volume occupied by the food relative to the total stomach volume (taken as the maximum, 100%), and divides the assigned value among the different prey depending on their relative importance. Because of the fragmentation of the prey, it was only possible to determine the number of specimens of each prey per stomach for part of the contents analyzed. Stomach fullness was estimated by means of the dry weight of the food (to the nearest 1 mg) and the points-method.

Data analysis

Stomach fullness was determined from the percentage of stomachs containing food, the percentage of body dry weight index [BDW = (food dry wt ÷ body dry wt) × 100] and the points-index. The importance of the different food components in the diet was recorded as: (1) frequency of appearance, $F_i[= (n_i ÷ N) × 100$, where n_i = number of stomachs containing prey i and N = number of stomachs with food analyzed]; (2) percentage of BDW fullness index corresponding to each prey, $BDW_i[= (\Sigma BDW_{ij} ÷ \Sigma BDW_j)$ × 100, where BDW_{ij} = percentage of body dry weight corresponding to prey i in stomach j, and BDW_j = percentage of body dry weight corresponding to total food for specimen j]; and (3) points-index, $IP_i[= (\Sigma P_{ij} ÷ \Sigma P_j) × 100$, where P_{ij} = value in points of prey i in stomach j, and P_j = total number of points for stomach j]. In cases where stomachs contained more than one prey, BDW_{ij} was estimated from BDW_j and the value in points assigned to each prey. The three indices were tested in preliminary analyses and gave similar estimates of the importance of the different prey in the diet (see present Table 1 and Freire et al. 1991). The results are confined mainly to the BDW index.

An 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, moult stage (B, C and I) and body-size. Log-linear models were 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 relationship between body size and stomach fullness was analyzed by fitting the log-transformed allometric equation by least-squares regression (food dry wt $= a × CW^b$). The differences in stomach fullness [$\log_{10}$(food dry wt + 0.001)] between stations, sexes and moult stages were analyzed by analysis of covariance (ANCOVA).

Fig. 1 Coast of Galicia (north-west Spain). Location of sampling stations (*IR* inner raft; *OR* outer raft; *IC* inner channel; *OC* outer channel) and areas where mussel raft culture is carried out (*shaded areas*) in Ría de Arousa
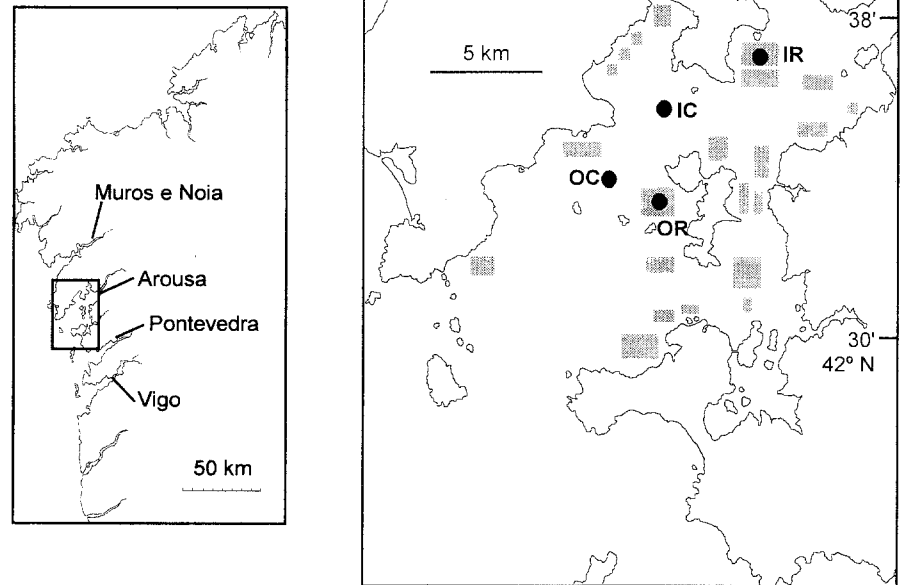
A multivariate test of the influence of life history and stomach fullness on diet composition in the outer-raft station was carried out using partial canonical correspondence-analysis (Ter Braak 1988a, b). The variables for the prey matrix were the dietary components based on their presence or absence in each stomach containing food. The matrix for the crab characteristics or explanatory variables was composed of CW, sex (coded as a nominal variable with three categories: M, males; F, non-ovigerous females; O, ovigerous females) and moult stage (coded as a nominal variable: B, C, I), and stomach fullness (represented by the food dry weight and points-index). For each crab characteristic, canonical axes were extracted that constituted linear combinations of the explanatory variables partialling out the effect of the other life-history variables, that were introduced as covariates. 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 ratio between the eigenvalues of the canonical axes and the first non-canonical axis (obtained after partialling out the effect of all crab characteristics, and thus reflecting the variability in the diet unexplained by these characteristics) indicates the relative importance of each variable in the diet composition.

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: $E = (d - c) \div (d + c)$, where d = proportion of the diet made up of a given prey, and c = importance in number or biomass of the same prey in the field]. Data on prey abundance in the field from Román and Pérez (1982) and López-Jamar (1982) for epifauna and infauna, respectively, and data corresponding to the mid–outer area (epifauna data from a nearby raft area were used for the channel station) and inner zone were used.

Results

Spatial variability in diet composition

Ninety-two food components were recorded in the analysis of the stomach contents of *Liocarcinus depurator*. They were grouped into 25 categories based on importance in the diet, morphology, and biological characteristics (Table 1). At the outer-raft station, from which the greatest number of crabs were analyzed, the diet was composed of 79 prey, whereas stomach contents of crabs from the inner-raft area consisted of 35 components. In the inner and outer channel stations, 14 and 44 types of prey were identified respectively. Crustaceans, molluscs, polychaetes, ophiuroids and fishes constituted most of the diet, while the echinoid *Psammechinus milaris*, the holothurian *Aslia lefevrei*, plants, sponges and other groups were secondary diet components, not exceeding 5% of the total stomach contents.

Habitat was the main factor determining changes in diet composition; 15 of the 23 diet components analyzed differed significantly among stations (Table 2). Dietary diversity was similar for both raft stations, whereas the inner-channel area displayed minimum diversity and the outer-channel area maximum diversity (Fig. 2). Crustaceans dominated the diet at all stations except the outer channel, due mainly to the importance of the anomuran decapod *Pisidia longicornis*, a species abundant in the raft epifauna (González-Sanjurjo 1982; Fernández et al. 1990). There was marked variability among habitats in the consumption of *P. longicornis* which was present at maximum frequency in the diet of *Liocarcinus depurator* from OR and IC. With the exception of *P. longicornis*, crustaceans comprised < 4% BDW of the diet at each station. Predation on the several groups of molluscs varied greatly among habitats, fluctuating between 32% BDW in IR and 11% in IC. Bivalve consumption was greater at the inner-raft station, and the importance of *Mytilus galloprovincialis* in the diet was greater for the raft-culture zones than for the central channel. In contrast, gastropods were more important in the diet in the channel areas. Polychaetes were the most diverse

Table 1 *Liocarcinus depurator*. Composition of diet at various stations (*numbers in parentheses* no. of specimens analyzed/no. containing food) using percentage body dry weight (*BDW*), frequency of appearance (*F*) and points (*IP*) indices (– absent)

Prey	Prey code	Inner raft (409/240)			Outer raft (3008/1367)			Inner channel (75/31)			Outer channel (255/145)		
		BDW	F	IP	BDW	F	IP	BDW	F	IP	BDW	F	IP
Fishes[a]	Fish	6.6	8.8	10.1	1.2	3.4	2.8	–	–	–	4.1	6.9	6.0
Crustaceans													
Natantia	Nata	3.1	2.9	3.8	2.6	3.1	3.5	–	–	–	0.9	2.8	1.9
Brachyura[b]	Brac	2.8	3.3	4.0	2.9	1.9	2.5	0.8	3.2	1.0	1.0	3.4	1.8
Pisidia longicornis	Pisi	30.7	22.1	25.1	51.9	47.1	45.8	52.5	32.3	39.7	14.7	11.0	9.8
Amphipods[c]	Amph	1.3	0.8	0.4	1.8	2.6	1.4	0.4	3.2	0.7	3.4	4.1	3.3
Other crustaceans[d]	Crus	2.3	3.3	1.7	1.1	1.7	0.8	–	–	–	0.8	4.8	2.1
Molluscs													
Mytilus galloprovincialis	Myti	12.5	22.1	18.8	8.9	18.5	16.0	2.1	3.2	6.8	2.5	2.1	1.9
Other bivalves[e]	Biva	10.5	12.5	11.9	2.0	5.5	2.6	3.2	16.1	5.5	6.1	9.0	8.2
Gastropods[f]	Gast	7.2	2.9	3.0	1.3	3.4	2.1	5.6	6.5	8.9	6.7	16.6	7.8
Egg cases of *Nassa* spp.	Nass	2.2	3.3	2.9	0.5	1.4	0.6	–	–	–	0.6	0.7	0.2
Echinoderms													
Ophiuroids[g]	Ophi	–	–	–	9.1	6.6	5.0	23.4	32.3	16.1	5.4	4.1	4.8
Psammechinus miliaris	Psam	–	–	–	1.3	1.2	0.9	–	–	–	–	–	–
Aslia lefevrei	Asli	3.2	2.5	2.9	2.2	1.9	1.2	–	–	–	1.5	1.4	0.9
Polychaetes													
Nereidae[h]	Nere	–	–	–	0.6	1.1	0.8	–	–	–	0.9	1.4	2.2
Lumbrineridae[i]	Lumb	–	–	–	0.7	0.9	0.8	–	–	–	4.8	4.8	6.5
Cirratulidae[j]	Cirr	0.1	0.4	0.3	0.8	0.7	0.5	–	–	–	4.2	6.2	3.9
Polynoidae[k]	Poly	–	–	–	0.9	2.4	2.1	–	–	–	–	–	–
Nephthydae[l]	Neph	0.3	0.4	0.2	0.4	0.4	0.5	0.6	3.2	1.4	9.6	6.2	7.3
Leanira yhleni	Lean	–	–	–	0.2	0.3	0.3	0.8	3.2	5.5	10.8	7.6	12.0
Pectinariidae	Pect	3.7	3.3	2.7	0.2	0.9	0.5	1.2	3.2	3.4	–	–	–
Other polychaetes[m]	Polc	1.5	2.5	2.8	3.5	4.8	3.8	6.7	6.5	4.8	3.4	6.2	6.2
Plants[n]	Plan	1.1	3.8	1.3	1.7	2.7	1.3	–	–	–	6.1	2.1	2.8
Sponges	Spon	0.0	0.8	0.2	0.1	1.0	0.5	–	–	–	2.0	0.7	0.8
Other animal prey[o]	Othe	0.1	1.3	0.6	0.0	0.2	0.1	–	–	–	1.0	3.4	2.3
Unidentified animal remains	Unid	10.9	15.0	7.1	4.2	6.5	3.5	2.8	16.1	6.2	9.4	11.0	7.2

[a] Gobiidae (*Gobius* spp., *G. niger*, *Lesueurigobius friesii*, *Pomatoschistus* spp.), *Trisopterus* spp.

[b] *Liocarcinus depurator*, Portunidae unidentified, *Inachus dorsettensis*, *Atelecyclus* spp., *Pilumnus hirtellus*

[c] *Jassa falcata*, Gammaridea unidentified, *Caprella aequilibra*, *Pthisica marina*

[d] Cumaceans, harpacticoid copepods, *Nebalia bipes*, ostracods

[e] *Musculus* spp., Cardiacea, *Abra alba*, Pectinidae, *Nucula* spp., Veneridae, *Thyasira flexuosa*

[f] Trochiidae, *Aplysia* spp.

[g] *Amphiura* spp., *Amphiura chiajei*

[h] *Nereis* spp.

[i] *Lumbrinereis* spp. *Lumbrinereis impatients*

[j] *Audouinia tentaculata*, *Chaetozone setosa*

[k] *Harmothoe* spp.

[l] *Nephthys* spp.

[m] Ampharetidae (*Ampharete acutifrons*), Capitellidae, Glyceridae (*Glycera convoluta*), Hesionidae (*Gyptis capensis*), Maldanidae (*Euclimene oerstedii*), Stemaspidae (*Stemaspis scutata*), Sygalionidae unidentified

[n] Diatoms, *Ulva* spp., *Enteromorpha* spp., *Cladophora* spp., Laminariales, Ectocarpales, *Scitosiphon* spp., *Polysiphonia* spp., *Callithamnium* spp., *Zostera nana*

[o] Chitons (*Lepidochitona cancellata*), cephalopods, crinoids (*Antedon bifida*), foraminiferans, sipunculids, ascidians

group of prey, and all prey items displayed significant differences among habitats with the exception of the Nereidae. Polychaetes constituted the dominant dietary component in the outer-channel station (34% BDW); at the other stations they made up < 10% of the diet. The Pectinariidae were the only polychaetes that was consumed to a greater extent in the inner-raft area; the rest of the prey items were more abundant in the diet of *L. depurator* from the outer channel (Cir-

ratulidae, *Leanira yhleni*) or from both channel stations (Lumbrineridae, Nephthydae).

Number of prey items and specimens per stomach

Prey diversity per stomach was low, with an average of 1.22 different dietary components (81% of stomachs contained only one prey, 17% contained two,

Table 2 *Liocarcinus depurator.* Analysis of consumption of prey using log-linear models fitted to contingency tables. Model design is prey (2) x station (4) x size (9) x sex (3) x moult stage (3) (number of levels in parentheses). Statistical significance of the χ^2 statistic for partial association between factors is shown (effects with $P < 0.05$ are underlined); fourth-order interactions have been omitted as they displayed non-significant effects in all cases ($P > 0.05$) (*prey codes* as in Table 1)

Prey code	Effect of prey x									
	stn × size	stn × sex	stn × moult	sex × size	sex × moult	size × moult	stn	size	sex	moult
Fish	0.994	0.750	0.996	0.650	1.000	0.986	_0.000_	_0.000_	0.123	0.005
Nata	1.000	0.699	0.905	0.820	0.970	_0.033_	0.594	_0.027_	0.479	0.140
Brac	0.962	0.974	0.711	0.967	0.958	0.938	0.457	0.211	0.187	0.637
Pisi	0.453	_0.004_	0.084	0.380	_0.003_	0.070	_0.000_	_0.000_	_0.026_	_0.038_
Amph	0.519	_0.011_	0.094	0.095	0.825	0.939	0.166	_0.004_	0.745	0.218
Crus	0.881	0.133	0.646	0.929	0.575	0.928	_0.048_	_0.025_	0.863	0.874
Myti	0.761	0.814	_0.011_	0.688	0.469	0.094	_0.000_	_0.000_	_0.000_	0.576
Biva	0.497	0.954	0.281	0.814	0.126	0.155	_0.001_	0.068	0.769	0.219
Gast	0.644	0.956	0.572	0.746	0.927	0.996	_0.000_	0.130	0.753	_0.011_
Nass	0.994	1.000	0.999	0.474	0.246	0.223	0.123	0.098	0.311	0.977
Ophi	0.826	0.465	_0.040_	0.453	0.607	_0.001_	_0.000_	0.166	0.631	0.157
Psam	1.000	1.000	1.000	0.800	0.755	0.918	_0.033_	0.353	0.957	0.565
Asli	0.985	0.751	0.631	0.056	0.675	0.134	0.455	0.172	_0.027_	_0.003_
Nere	1.000	0.626	1.000	0.996	0.791	1.000	0.192	0.080	0.251	0.407
Lumb	0.999	0.416	0.998	0.947	0.914	0.993	_0.001_	0.476	0.351	0.185
Cirr	1.000	0.902	0.989	1.000	0.989	0.926	_0.000_	0.115	0.062	0.946
Poly	1.000	1.000	1.000	0.973	0.633	0.883	_0.001_	0.305	_0.025_	0.961
Neph	1.000	0.765	0.579	1.000	0.860	0.983	_0.000_	0.226	0.191	0.535
Lean	0.938	0.716	1.000	1.000	0.655	1.000	_0.000_	0.251	0.922	0.306
Pect	0.999	1.000	0.717	0.364	0.321	0.962	_0.001_	_0.020_	_0.041_	_0.024_
Polc	0.296	0.639	0.460	0.782	0.455	_0.043_	0.243	0.482	0.100	0.547
Plan	0.985	0.346	0.963	1.000	0.669	0.283	0.198	_0.002_	0.383	0.191
Spon	0.999	0.742	1.000	0.999	0.933	1.000	0.907	0.081	0.654	0.947
(*df*)	(27)	(6)	(6)	(18)	(4)	(18)	(3)	(9)	(2)	(2)

Table 3 *Liocarcinus depurator.* Importance in diet (BDW index) of prey with significant differences in frequency of occurrence in stomach contents between sexes (log-linear models, $P < 0.05$; see Table 2). Data presented separately for each station (*numbers in parentheses* no. of specimens analyzed/no. containing food; *ovig* ovigerous)

Prey	Inner raft			Outer raft			Outer channel		
	Males	Females		Males	Females		Males	Females	
		non-ovig	ovig		non-ovig	ovig		non-ovig	ovig
	(215/125)	(167/103)	(27/12)	(1423/656)	(1055/491)	(530/220)	(142/71)	(84/58)	(29/16)
Pisidia longicornis	31.3	31.6	7.5	48.1	53.5	61.7	29.2	2.6	–
Mytilus galloprovincialis	16.5	7.8	9.6	11.9	6.0	11.2	–	0.6	32.3
Aslia lefevrei	4.9	–	21.4	0.9	3.5	1.1	3.3	–	–
Polynoidae	–	–	–	1.7	0.2	0.4	–	–	–
Pectinariidae	1.4	6.7	–	–	0.2	0.7	–	–	–

2% contained three, and only 0.3% contained four different dietary items). The number of prey items per stomach did not differ significantly among stations, body size-classes, moult stages or sexes (log-linear model $P > 0.05$). The percentage of stomachs in which it was possible to determine the number of specimens ranged between 12 and 95% for echinoids and cirratulids, respectively, and the average for the different prey items was 60%. The number of prey specimens per stomach was low; for all prey items, $> 90\%$ of the stomachs contained only one specimen, and in most cases this percentage attained 100%. The maximum number of specimens per stomach for most prey was two, and only *Pisidia longicornis*, bivalves, and gastropods were occasionally present in greater numbers.

Changes in composition of diet as function of life history

Data for body size, sex, moult stage and season of the year is available only for the raft and outer-channel

Fig. 2 *Liocarcinus depurator.*
Dietary diversity (index
$H' \pm 95\%$ confidence interval)
at Sampling Stations IR (inner
raft), OR (outer raft), IC (inner
channel) and OC (outer
channel), as a function of sex (*M*
males; *F* non-ovigerous females;
O ovigerous females), Moult
Stages B, C and I (see "Materials
and methods – Sampling and
laboratory methods" for
description of moult stages),
body-size classes and monthly
evolution throughout yearly
cycle at Station OR, and
seasonal evolution at IR and OC
(in the case of IR and OC, dots
are located at mid-point of
months corresponding to each
season). Data correspond to
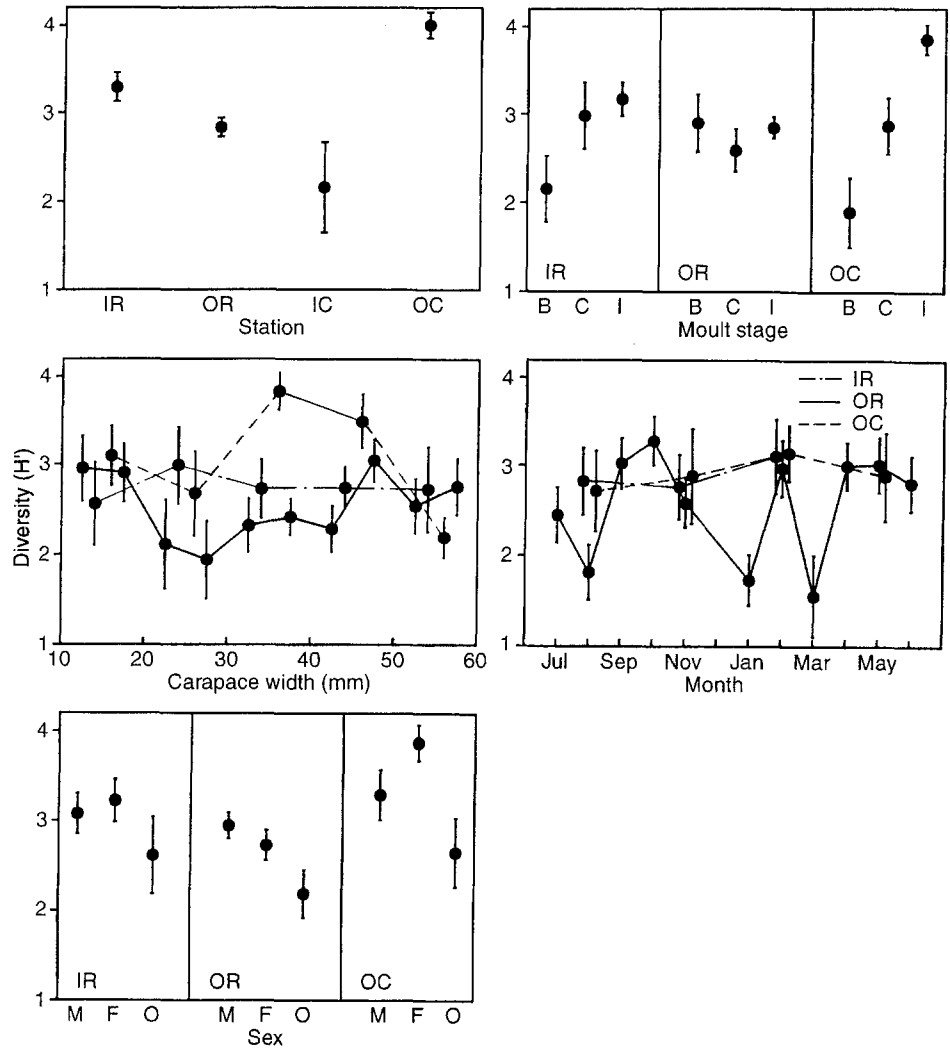body dry weight (BDW) index of
diet composition

Table 4 *Liocarcinus depurator.* Importance in diet (BDW index) of prey with significant differences in frequency of occurrence in stomach contents among moult stages (log-linear models, $P < 0.05$; see Table 2). Data presented separately for each station (*numbers in parentheses* no. of specimens analyzed/no. with food; Moult Stages B, C and *I* are described in "Materials and methods – Sampling and laboratory methods")

Prey	Inner raft			Outer raft			Outer channel		
	B (14/11)	C (25/19)	I (384/210)	B (144/81)	C (378/247)	I (2324/1029)	B (11/6)	C (23/15)	I (213/121)
Fishes	–	3.8	7.5	–	0.8	1.4	–	–	4.9
Pisidia longicomis	24.2	15.3	34.1	43.0	55.5	51.8	5.0	9.2	15.9
Gastropods	–	27.2	3.7	–	0.5	1.5	–	–	8.0
Aslia lefevrei	35.6	–	1.9	4.7	2.1	1.9	–	–	1.8
Pectinariidae	14.2	3.9	3.0	–	0.2	0.1	–	–	–

stations, since a too small number of specimens was analyzed for the inner-channel station. Males and non-ovigerous females displayed a similar dietary diversity of diet, and a higher diversity than ovigerous females

(Fig. 2). Significant differences between the sexes were detected in five dietary components (Table 2, $P < 0.05$) although only two prey items were quantitatively important in the diet (Table 3). *Pisidia longicornis* was
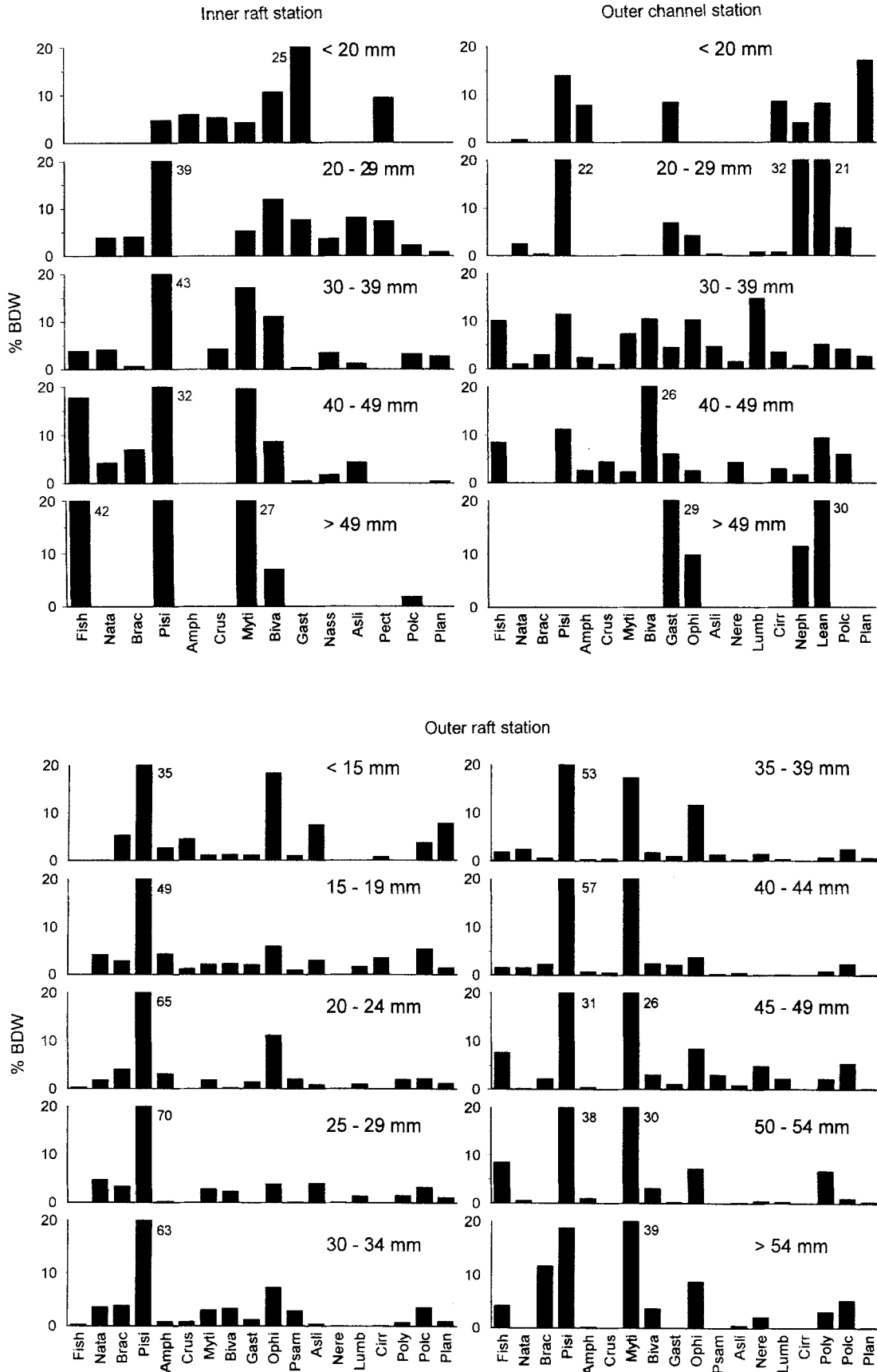
Fig. 3 *Liocarcinus depurator*. Diet composition (BDW index) as a function of body-size (carapace width in mm) at Stations IR, OR and OC (*Prey codes* as in Table 1)

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more important for females in the outer-raft area, whereas in the channel station it was more important in the diet of males. In the raft areas, the consumption of *Mytilus galloprovincialis* was greater for males than for females.

Changes due to moult cycle were of low quantitative importance in diet composition, except at the inner-raft station (Tables 2 and 4), while dietary diversity increased gradually throughout the moult cycle at Stations IR and OC (Fig. 2). During the initial post-moult phase (Stage B), there was an increase in the consumption of *Aslia lefevrei* and Pectinariidae at Station IR; the consumption of gastropods increased in the advanced post-moult period (Stage C), while in the

intermoult phase (Stage I) the diet was dominated by *Pisidia longicornis* and predation on fishes increased. Dietary patterns were similar at the other stations, but differences in prey consumption between moult stages were smaller there than for the inner-channel crabs.

Major ontogenetic changes were observed in the composition of the diet, particularly for the raft areas (Fig. 3). Differences between body-size classes affected the presence of several prey items (Table 2), especially fishes, crustaceans, *Mytilus galloprovincialis* and plants. At the inner-raft station, fishes and *M. galloprovincialis* appeared mainly in crabs of > 30 mm CW. *Pisidia longicornis* showed the same pattern, increasing in importance in the diet of specimens of > 20 mm CW.
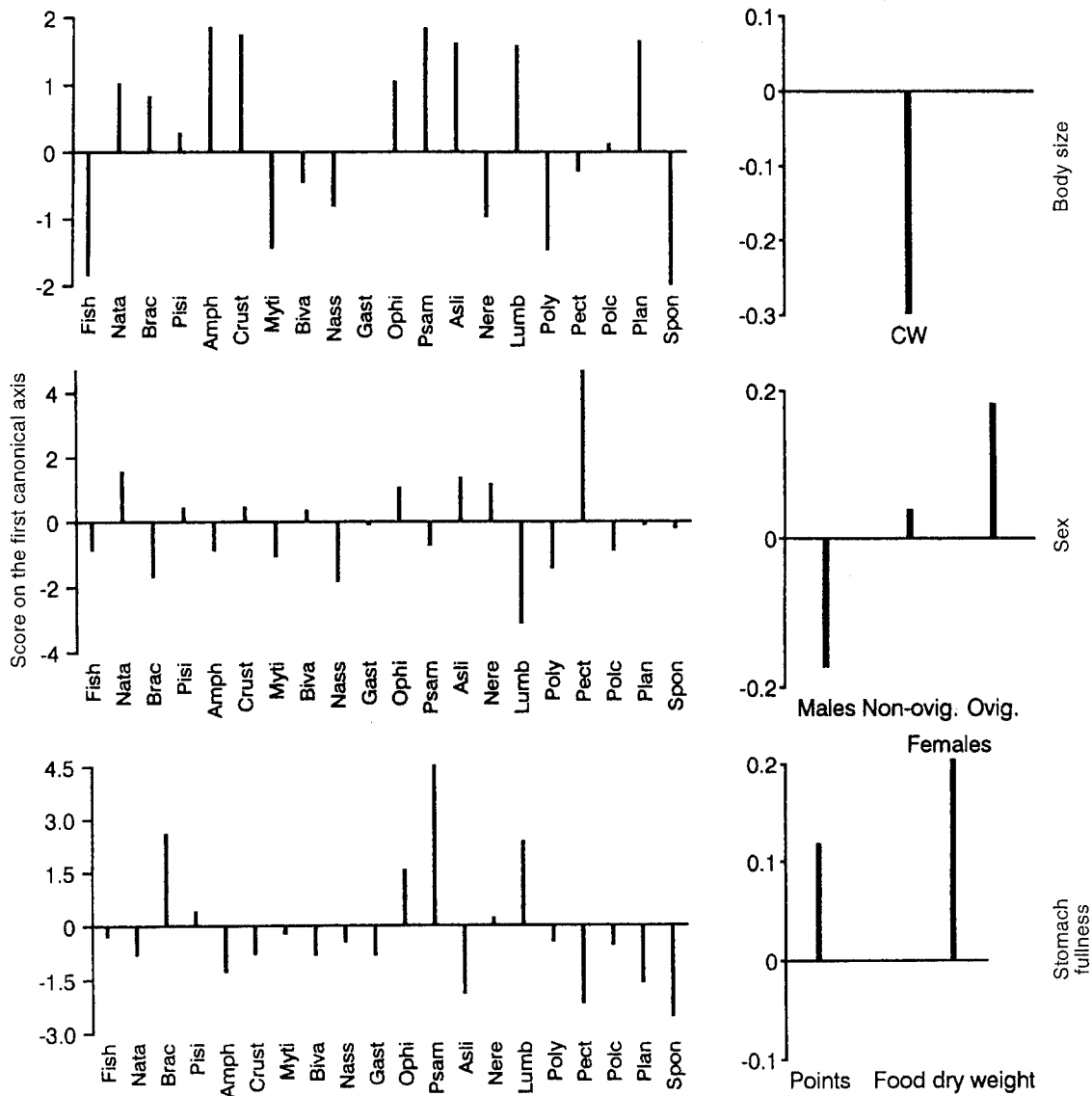

Fig. 4 *Liocarcinus depurator*. Ordination of prey (*prey codes* as in Table 1) and crab attributes on first axis extracted from partial canonical correspondence-analyses testing effect of different life-history variables (body size, sex, moult stage) and stomach fullness (food dry weight and points-index) on diet composition in outer raft area. In each analysis, effect of other life-history variables was partialled out, introducing them as covariates. Results of analysis for moult cycle are not presented, as this factor showed no significant effect (Monte-Carlo test: $P > 0.1$, $P = 0.01$ for the other factors) (*CW* carapace width)

Non-decapod crustaceans appeared mainly in crabs of < 20 mm CW, and gastropods and Pectinariidae were only important in the diet of individuals of < 30 mm CW. In both raft areas, fishes and *M. galloprovincialis* appeared mainly in crabs of > 35 mm CW. *P. longicornis* reached maximum importance in the diet of intermediate-sized crabs (between 15 and 44 mm CW). Non-decapod crustaceans appeared mainly in specimens of < 25 mm CW; the consumption of plants in the outer area was also important only in crabs of < 15 mm, and gastropods and Pectinariidae in the inner area were important in the diet of individuals of < 30 mm. Unlike crabs from the raft areas, those at the outer-channel station showed no pattern of diet change linked to growth, due mainly to the fact that most of the individuals analyzed were from a narrow size range (20 to 49 mm CW). Dietary diversity at the outer-raft station was minimum in crabs of intermediate size (20 to 45 mm CW) due to the dominance of *P. longicornis* in the diet. In contrast, ontogenetic variability at the other stations was lower, and maximum diversity was recorded for intermediate size-classes (Fig. 2).

The partial canonical correspondence analyses (Fig. 4) indicated that diet composition of crabs at the outer-raft station was determined mainly by crab body-size and to a lesser extent, by sex (ratio between eigenvalues of canonical and first non-canonical axes = 0.116 and 0.062, respectively), although both factors were significant (Monte-Carlo test, $P = 0.01$). Moult stage had no significant effect on diet composition ($P = 0.14$). Stomach fullness (defined by food dry weight and points index) had a significant effect on the presence of different prey in the stomach contents ($P = 0.01$; ratio of eigenvalues = 0.072), although it

mainly affected prey of small quantitative importance to the diet.

Seasonal changes in composition of diet

In the diet of crabs from the outer-raft station, peaks in importance of the dominant prey varied seasonally (Fig. 5). *Pisidia longicornis* was present in highest volume from November to March (up to 77% BDW), with a second peak in July and August. *Mytilus galloprovincialis* made up between 11 and 20% BDW between April and August, with a second peak in January and February, whereas in other months it constituted < 10% BDW. Of the infaunal prey, ophiuroids were less important in the diet only during winter, while polychaetes were present in maximum abundance in the diet in spring and autumn. Other prey were important in the diet for periods of only 1 or 2 mo (fishes in May, Natantia in February and May, Brachyura in February, non-decapod crustaceans and plants in September and October). Because of the small sample size for Stations IR and OC and the seasonal catch variability, the monthly data have been grouped by season. At the inner-raft station, *P. longicornis* and *M. galloprovincialis* were the dominant prey in summer. However, the mussel was absent from the diet in autumn, the diet at this time being composed chiefly of *P. longicornis, Aslia lefevrei* and Pectinariidae. In winter, *P. longicornis* diminished in importance, and gastropods constituted the dominant prey. In the outer-channel station, the polychaetes were the dominant prey item of the stomach contents in summer and in winter, while in autumn the most abundant food component was *P. longicornis*,

Fig. 5 *Liocarcinus depurator.* Seasonal changes in diet composition (BDW index) at Sations IR, OR and OC. For IR and OC stations, monthly data were grouped seasonally (diet of spring in IR is not presented because only small number of individuals containing food were analyzed; $N = 6$)
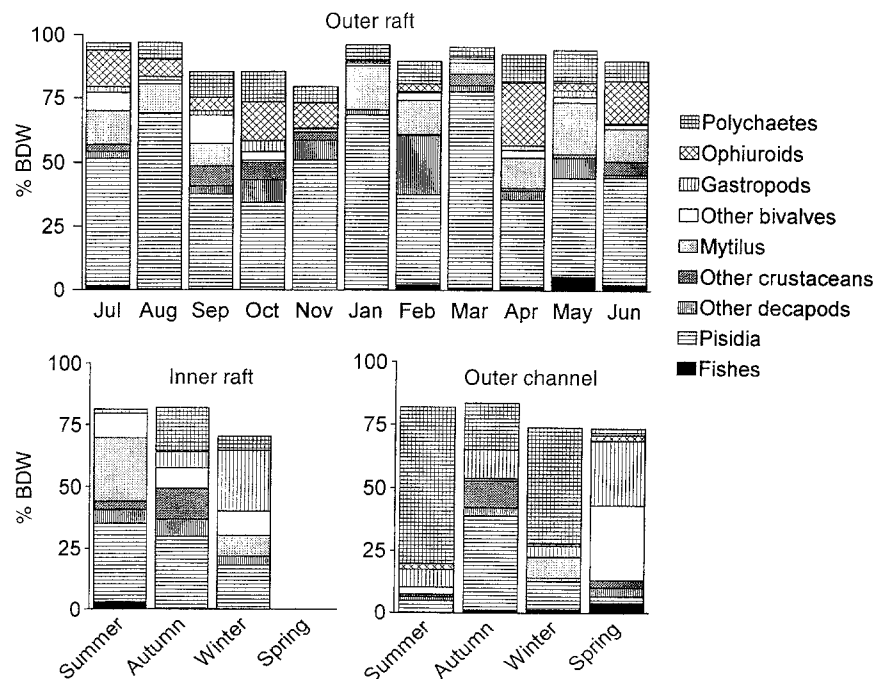
although gastropods, *Leanira yhleni*, and amphipods were also important. In spring, there was a major change due to the almost total disappearance of polychaetes from the diet, which was then composed mainly of bivalves and gastropods. No major seasonal trends were observed in diet diversity, except for low values in August, January and March for crabs of the outer-raft station (Fig. 2) due to the increase in the importance of *P. longicornis* in their diet.

Relationship between predator and prey size

Fragmentation of the prey consumed prevented estimation of their body size from the stomach contents, except for five dietary components. Only *Pisidia longicornis* (size estimated from abdomen width) showed a significant positive correlation with predator size ($N = 64, r = 0.41, P < 0.01$; abdomen width $= 0.116 \times CW^{0.792}$). Nereidae (size estimated from jaw length; $N = 6$), Trochiidae and other gastropods (operculum diameter; $N = 8$ and 6, respectively) and *Mytilus galloprovincialis* (maximum thickness of shell fragments; $N = 12$), displayed a non-significant positive correlation (log-transformed data, $P > 0.05$).

Stomach fullness

The individuals of *Liocarcinus depurator* analyzed had a mean stomach fullness of 5.8 mg dry weight, 0.288% BDW and 24.6% based on the points index. The relationship between body size and food dry weight was significant ($P < 0.05$) when only specimens with > 0 fullness were analyzed, except for the inner-channel station, although the explained variance was low (Table 5). The slope was always < 1, except for ovigerous females. The negative allometry of fullness was reflected in the drop in the BDW index with increasing body size (Fig. 6), although there

was an increase in food dry weight (from an average of 1.23 mg for crabs of < 15 mm CW to 7.18 mg for those > 50 mm CW). There were significant differences in stomach fullness (food dry weight) between stations, sexes, moult stages (B, C and I) and monthly samples (ANCOVA, $P < 0.05$; covariate effect, crab size: $P > 0.1$), although in both comparisons between sexes and seasons the variability disappears when individuals with empty stomachs are omitted ($P > 0.1$; $P < 0.05$ for stations and moult stages; covariate effect: $P < 0.05$). Fifty two percent of the specimens analyzed had no food in their stomachs, fluctuating between 55% in the outer raft station and 43% in the inner raft area and outer channel. During the breeding cycle, ovigerous females exhibited decreased food consumption compared to non-ovigerous females and males (Fig. 6). There were no significant differences in stomach fullness between females of different gonad maturity stages (ANCOVA, $P > 0.05$), and the highest fullness level of females with resting gonads was due to the inclusion of small-sized immature crabs (covariate effect: $P < 0.05$). During the moult cycle, important changes in the food-consumption rate were detected. During Moult Periods D and A (late pre-moult and early post-moult) fullness was minimal, and 92% of the crabs had no food in their stomachs. Fullness increased during the postmoult stage, and reached a maximum at Stage C; decreasing again during moult Stage I. Stomach fullness was highest from October to January and lowest in spring and summer.

Prey selection and predation on infauna and raft epifauna

Prey were grouped according to habitat and life style (Fig. 7). The raft epifauna and the mussels were the dominant prey of *Liocarcinus depurator* at the raft stations and the inner channel ($> 50\%$BDW), with the

Table 5 *Liocarcinus depurator*. Parameters of allometric equation log food dry weight $= \log a + b \times CW$ (carapace width) fitted for each station, sex and moult stage and for specimens having maximum fullness (points index $= 100$). Coefficient of determination (r^2), significance level (P) and number of specimens analyzed (N) are shown. Equations fitted using data from crabs with food in their stomachs

Parameter	Log a (SE)	b (SE)	r^2	P	(N)
Station					
inner raft	− 3.497 (0.320)	0.932 (0.206)	0.084	0.000	(227)
outer raft	− 3.194 (0.101)	0.742 (0.066)	0.087	0.000	(1323)
inner channel	− 0.819 (1.137)	− 0.738 (0.714)	0.034	0.310	(31)
outer channel	− 2.835 (0.342)	0.503 (0.222)	0.037	0.025	(137)
Sex					
males	− 3.088 (0.127)	0.673 (0.081)	0.077	0.000	(832)
non-ovigerous females	− 3.248 (0.145)	0.792 (0.019)	0.091	0.000	(645)
ovigerous females	− 4.683 (0.649)	1.689 (0.419)	0.064	0.000	(241)
Moult stage					
B	− 3.303 (0.382)	0.854 (0.253)	0.104	0.001	(100)
C	− 3.455 (0.232)	0.999 (0.151)	0.136	0.000	(279)
I	− 3.076 (0.100)	0.648 (0.065)	0.069	0.000	(1328)
Maximum fullness					
(points index $= 100$)	− 3.925 (0.137)	1.499 (0.089)	0.464	0.000	(327)

Fig. 6 *Liocarcinus depurator.* Stomach fullness (mean ± 95% confidence interval of BDW index) at Stations IR, OR and OC as a function of sex, stage of gonad development in females, moult stage, body size, and monthly evolution throughout yearly cycle [Moult stages (*A, B, C, I, D*) are described in "Materials and methods – Sampling and laboratory methods"]
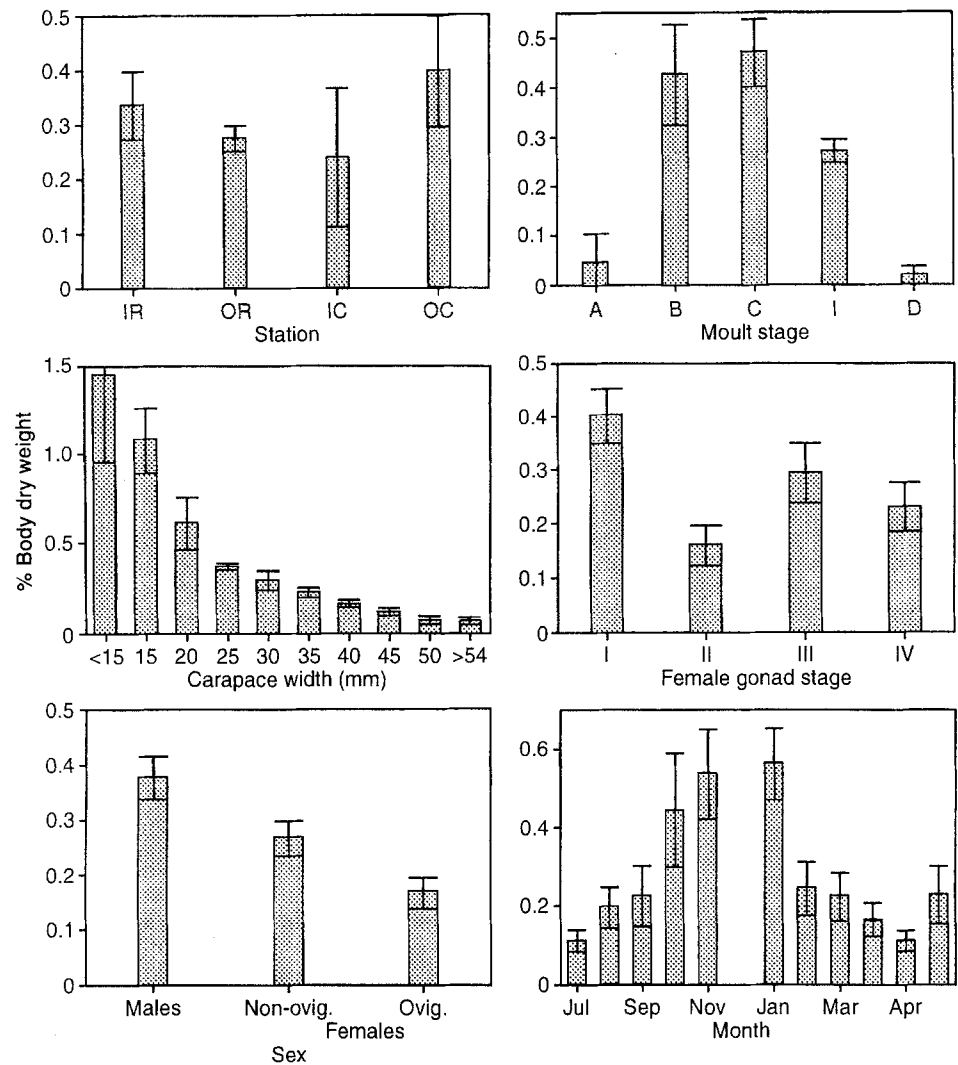
importance of the epifauna decreasing considerably in the outer channel. Consumption of benthic macroinfauna was opposite to that of the epifauna, being more important at stations with no raft culture (36 and 46% in IC and OC, respectively). In the culture areas, the macrofauna comprised ≃ 20% of the diet. Of the benthic megafauna, sessile and slow-moving prey (holothurians and echinoids) as well as mobile prey (fishes and decapods) were more important at the raft stations, with a greater consumption of mobile megafauna at all stations.

The pattern of prey selection was similar for both raft stations, although there were substantial differences in the outer area between channel and raft areas (Fig. 8). For the epifauna, the Ivlev index revealed positive values for *Pisidia longicornis* in raft areas, whereas in the channel the importance of this species in the crab's diet reflected its abundance in the epifauna. Amphipods constituted the other dominant group of the culture epifauna, but were negatively selected for in the raft zones.
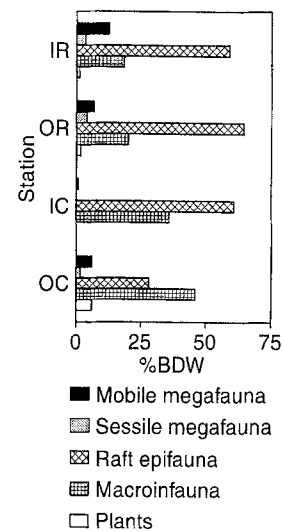

Fig. 7 *Liocarcinus depurator.* Diet composition at Stations IR, OR, IC and OC. Prey are grouped in terms of habitat, biological characteristics and mobility

Fig. 8 *Liocarcinus depurator.*
Ivlev index of prey selection in
inner- and outer-raft stations
and outer-channel station.
Selection indices were obtained
independently for that part of
diet corresponding to epifauna
and infauna in terms of
importance in crab stomach
contents of different prey and
their density or biomass in
infauna (data from López-Jamar
1982) and epifauna (data from
Román and Pérez 1982)
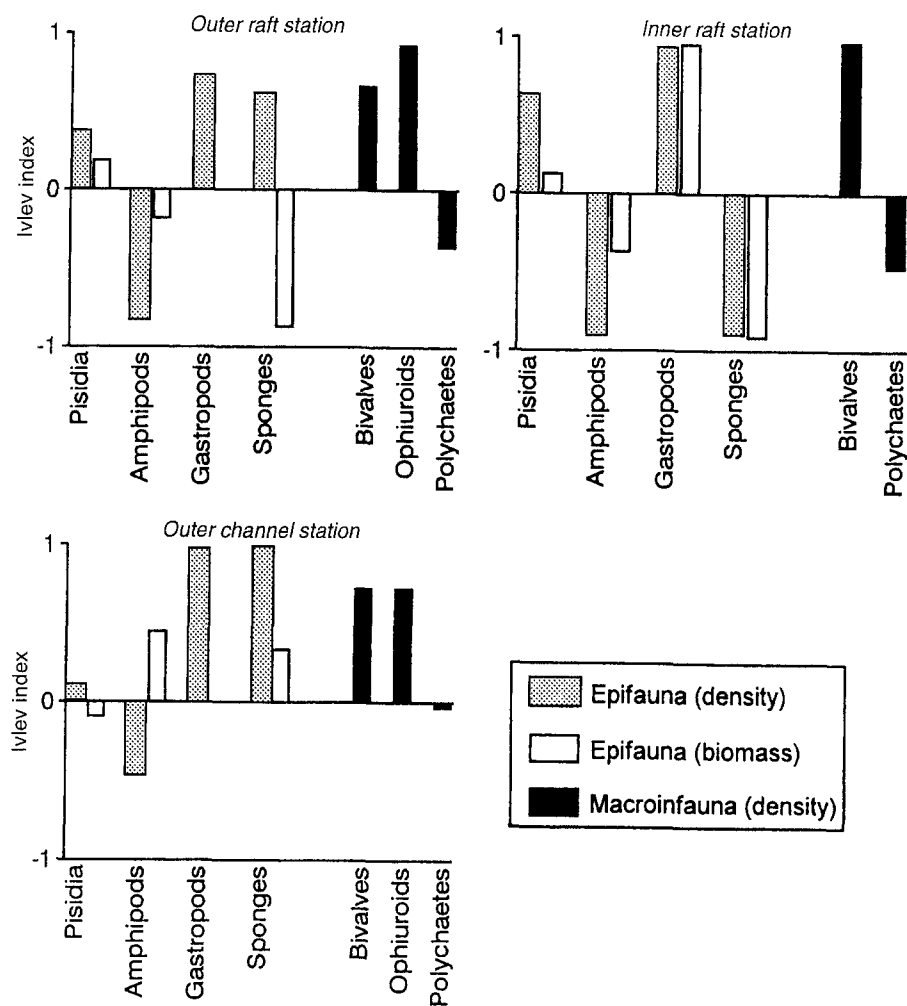
Gastropods and sponges were of little importance in the diet, but were of some importance in the epifaunal community. Gastropods were positively selected for at all stations, while selection for the sponges was more variable. Among the benthic macroinfauna, ophiuroids were important in the diet as well as in the field only in the mid–outer area, whereas both polychaetes and the bivalves were the dominant groups in both zones. A positive selection was observed for bivalves and ophiuroids in both raft areas. With reference to predation on polychaetes, there was negative selection, with similar values at both raft stations. At the channel station, *Liocarcinus depurator* showed a similar selection pattern of infaunal prey to that at the other sampling stations, although the polychaetes (which made a major contribution to the diet at this station) had an index value very close to 0.

Discussion

The diets of portunid crabs are dominated by macroinvertebrates (molluscs and crustaceans) which are sessile or possess little mobility (Hill 1976, 1979; Paul 1981; Williams 1981, 1982; Laughlin 1982; Wear and Haddon 1987; Ropes 1988; Abelló 1989b; Edgar 1990; Hines et al. 1990; Hsueh et al. 1992; Freire and González-Gurriarán 1995), and reflect the structure of their prey communities. Prey selection in the Ría de Arousa by *Liocarcinus depurator* and other portunids depends to some extent on the abundance of available food items, but selection does take place on different scales (community, taxonomic and morphological groups, and species) (Freire 1993; Freire and González-Gurriarán 1995; present paper). Both *L. depurator* and *Necora puber* prey mainly on the decapod *Pisidia longicornis*, although bivalves, the dominant prey of other portunids (Williams 1981, 1982; Laughlin 1982; Wear and Haddon 1987; Ropes 1988; Hines et al. 1990), are highly abundant in the area. This selection is associated with the design of the chelipeds of both species that display biomechanical characteristics especially suitable for predation on mobile prey (Freire et al. 1996). Spatial variability in prey availability is the most important factor affecting changes in the dietary composition of various portunid species (Paul 1981; Williams 1982; Alexander 1986; Wear and Haddon 1987;

Edgar 1990; Freire et al. 1990; Freire and González-Gurriarán 1995). Spatial differences in the diet of *L. depurator* are related to the differences between raft and channel habitats in abundance and structure of the different communities of potential prey.

The limited information provided by previous studies on the diet of *Liocarcinus depurator* (Abelló and Cartes 1987; Hall et al. 1990a) indicates that this species undergoes major changes in its feeding habits that are related to life history and habitat. On the north-west Mediterranean shelf (between 50 and 300 m), this species preys on decapods (mainly Natantia) and teleost fishes, and to a lesser extent on cephalopods and polychaetes (Abelló and Cartes 1987). In contrast, on the Scottish coast (< 10 m depth) algae, polychaetes and brachyuran crabs appear most frequently in its gut contents. In the Ría de Arousa, there is great spatial variability in the composition of its diet; in the deeper channel areas, *Pisidia longicornis*, molluscs, ophiuroids and polychaetes are the dominant prey, while in the raft zones the major food components are *P. longicornis* and bivalves (particularly *Mytilus galloprovincialis*).

The dominant food items in the diet of *Liocarcinus depurator* in the Ría de Arousa are the raft epifauna, macroinfauna and megafauna. In the central channel areas which support no aquaculture, the macroinfauna constitutes the dominant prey group. On the other hand, in the raft areas, the epifaunal prey are more important, the epifaunal organisms reach high densities on the culture ropes (González-Sanjurjo 1982; Román and Pérez 1982; Fernández et al. 1990). The dominant prey, *Pisidia longicornis*, is present at maximum density in the mid-outer zone of the ría, where it achieves greatest importance in the diet of *L. depurator* becoming less abundant on the culture ropes (and hence in the diet) in the inner area. Decapods are able to feed on prey living on the culture ropes when the mussels and their epifauna fall off as a result of weather conditions or human activity (seeding, thinning-out and harvesting the mussel: Pérez and Román 1979). On occasion the ropes may touch the bottom at low tide, and the portunid crabs then have direct access to the culture ropes over the anchoring points or by their own swimming ability (Hartnoll 1971). The small importance of the infauna in the diet at the raft stations compared to areas where no cultures are present may be attributable to the decrease in abundance and biomass observed in the Ría de Arousa compared to other rías; and also to a similar decrease within this ría between raft areas and non-culture zones (López-Jamar 1982; Tenore et al. 1982; López-Jamar and Mejuto 1986). The megafauna are present in higher densities and in higher biomass in the raft areas (Chesney and Iglesias 1979; Iglesias 1981; González-Gurriarán 1982; Olaso 1982; Romero et al. 1982), but risk of predation by *L. depurator* is low due to the mobility and large body size of the megafauna, and its contribution to this crab's diet is lower than that of the raft epifauna and infauna. Moreover,

the contribution of food from the rafts appears to cause a change in the diel patterns of food consumption by *L. depurator*, resulting in no significant diel differences in stomach fullness in the raft zones, but greater stomach fullness at night in the central channel (Freire et al. 1991).

Similar patterns of prey selection have been recorded for portunids and demersal fishes in the Ría de Arousa (López-Jamar et al. 1984; Freire 1993; Freire and González-Gurriarán 1995; present paper), despite the problems associated with prey-selection estimates due to the selectivity of the different sampling methods used for infauna and epifauna, to predator mobility that could give them access to areas other than the habitat sampled (especially in the case of fishes), and to the fact that diet and prey studies have not always been carried out simultaneously. In the present study, selection was positive for *Pisidia longicornis* and negative for amphipods within the epifauna, and positive for bivales and ophiuroids and negative or zero for polychaetes within the benthic infauna. For each taxonomic group, the specific composition of prey in the diet of *Liocarcinus depurator* may be quite different from that in its habitat as in the case of polychaetes, in which the dominant species within the infauna either did not appear in the crabs' diet or did so only occasionally [e.g. *Spiochaetopterus costarum, Sternaspis scutata* and *Tharyx* spp. (*Leanira yhleni* is the only abundant macrofaunal species that constitutes an important part of the diet of *Liocarcinus depurator* in the outer channel: López-Jamar 1982; López-Jamar and Mejuto 1986)].

The seasonal changes in the diet of *Liocarcinus depurator* in the Mediterranean have been associated with temporal variation in the availability of its prey, especially of fishes and cephalopods (Abelló and Cartes 1987). Similarly, in the Ría de Arousa, the temporal variation observed in the predation of this crab on *Pisidia longicornis* and *Mytilus galloprovincialis* at the outer-raft station appears to be linked to the seasonal cycle of the activities connected with mussel culture. Culturing activities on the rafts (thinning-out and harvesting), that cause the mussel to become detached, and thus make it readily available to *L. depurator*, are more frequent in winter and summer (Pérez and Román 1979); this coincides with the maximum importance of *M. galloprovincialis* in the gut contents of this crab. Temporal changes in the epifaunal community occur both as result of the seasonality of the environment and because of species succession after the mussel seed is placed in the sea or after thinning-out. Ropes bearing organisms at varying stages of culture and epifaunal succession are present throughout the year (Mariño et al. 1982; Pérez-Camacho et al. 1991), which means that the availability of various epifaunal groups does not undergo any major fluctuations throughout the year. Hines et al. (1990) demonstrated that temporal changes in the diet of the portunid *Callinectes sapidus* were associated with changes in prey availablity arising

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from prey depletion by epibenthic predators. In the case of *L. depurator*, none of the caging experiments carried out by Thrush (1986) and Hall et al. (1990a, b) detected any important effect of predation on the regulation of the abundance and structure of the infaunal macrobenthos on shallow soft bottoms of the northwest Atlantic, albeit this species was one of the dominant epibenthic predators. Temporal changes in prey availability would arise from external causes and not from predation, although the variability in the food-consumption rates and diet composition between the different life-history stages observed in the present study would be difficult to detect during short-term caging experiments.

Like other portunid species, both in the Ría de Arousa (Freire 1993; Freire and González-Gurriarán 1995) and in other geographical areas (Paul 1981; Laughlin 1982; Choy 1986; Stoner and Buchanan 1990; Hsueh et al. 1992; Norman and Jones 1992), growth is the biotic factor which determines the most important changes in the diet of *Liocarcinus depurator*. In general, there was an ontogenetic increase in the importance of prey with hard exoskeletons, although all sizes of *L. depurator* consume prey with a great diversity of morphological and biomechanical characteristics, in contrast to other portunid species (*Necora puber* or *L. arcuatus*) which occupy the same habitats, due to the greater biomechanical versatility in the structure of the chelipeds of the former (Freire et al. 1996). Both the findings of Abelló and Cartes (1987) and the results of the present paper indicate that differences between the diet of males and females are of secondary importance compared to differences arising from ontogenetic changes. However, there is no data available on ontogenetic changes and changes during the moult cycle in the diet of *L. depurator* from other geographical zones. Although moulting is a key event in the life history of the decapods, in the case of *L. depurator* it is not related to major changes in diet composition. However, both this study and that of Abelló and Cartes discovered that great variations do exist in the food consumption throughout the moult cycle. In general, decapods do not consume food during the pre-ecdysis and post-ecdysis stages, and stomach fullness is maximum in the initial post-moult stages (Abelló and Cartes 1987; O'Halloran and O'Dor 1988; Norman and Jones 1992; Freire 1993; Freire and González-Gurriarán 1995).

The variability in various aspects of the feeding ecology of decapod crustaceans and demersal fishes in the Ría de Arousa that belong to higher trophic levels (López-Jamar et al. 1984; Freire 1993) reflects ecosystem changes induced by environmental factors or by human activity. The changes observed in the diet of *Liocarcinus depurator* reflect differences in the abundance and community structure of different trophic groups in raft-culture zones and channel areas. Raft mussel-culture is an extensive aquaculture

process that affects most of the Ría de Arousa and which has caused a series of alterations to the ecosystem (Tenore et al. 1982). These are reflected to a great extent in the trophic relationships of the megabenthos. The raft zones offer a wider availability of food because of the increased biomass of potential prey in the culture areas. Moreover, the bottoms of the culture polygons are extremely heterogenous, creating numerous shelters and microhabitats for megabenthic organisms. For these reasons, the population dynamics of *L. depurator* in the Ría de Arousa is linked to the raft-culture areas, with increased density, biomass and growth rate in the raft areas compared to other habitats (Fernández et al. 1991).

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