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Dietary analysis of the marine Amphipoda (Crustacea: Peracarida) from the Iberian Peninsula

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ABSTRACT

The gut contents of 2982 specimens of 33 amphipod families, 71 genera and 149 species were examined, representing a high percentage of amphipod diversity in the Iberian Peninsula. Material was collected mainly from sediments, algae and hydroids along the whole coast of the Iberian Peninsula from 1989 to 2011. Although detritus was the dominant food item in the majority of amphipods, gammarideans also included carnivorous (mainly feeding on crustaceans) and herbivorous species (feeding on macroalgal tissues). Our study revealed that general assignment of a type of diet for a whole family is not always adequate. Some families showed a consistent pattern in most of the studied species (Corophiidae, Pontoporeiidae = detritivorous; Oedicerotidae, Phoxocephalidae, Stenothoidae = carnivorous; Ampithoidae = primarily herbivorous on macroalgae), but others included species with totally different feeding strategies. In general terms, detritivorous families were characterized by a stronger mandibular molar, while in carnivorous taxa this feature was less developed or reduced. The percentage of macroalgae in the digestive contents was associated in most cases with a reduction or loss of the mandibular palp. It seems that high trophic diversity in amphipods is a generalized trait along different ecosystems in all latitudes, and could be related to the ecological success of this group in marine benthic communities.

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1. Introduction

Understanding the dietary habits of benthic invertebrates is pivotal to the studies of food webs and energy flows in marine ecosystems, but basic information on the feeding ecology of most taxa is still lacking nowadays (Legeżyńska et al., 2012).

Amphipods are the most diverse group of crustaceans with respect to life styles, trophic types, habitats and sizes (De Broyer and Jazdzewski, 1996) and constitute one of the dominant groups of marine rocky habitats and soft bottoms (de-la-Ossa-Carretero et al., 2011). Their high abundance, species richness and wide distribution suggest that amphipods indeed play major roles in the ecology of these habitats (Conlan, 1994). They are an important link between primary and secondary production and higher trophic levels such as fishes, birds and mammals (see Legeżyńska et al., 2012). In studies of marine food webs, amphipods are often grouped into a single trophic guild based on the assumption that they are functionally redundant, but this assumption has been challenged

due to contrary evidence provided by feeding assays and gut content analysis (Farlin et al., 2010). As consumers, benthic amphipods are known to have versatile feeding strategies (Carrasco and Arcos, 1984; Sarvala and Uitto, 1991). Amphipods inhabit a variety of marine environments and, in consequence, they show a high diversity of feeding habits; they can feed on debris, detritus, bacteria, aquatic fungi, living animals, carrion and dead plant fragments (Conradi and Cervera, 1995). They also constitute an important food source for a large variety of marine predators (see Vázquez-Luis et al., 2013), hence playing a key role in energy flow through food webs. Furthermore, amphipods have often been included in ecotoxicological tests and proposed as good bioindicators of the quality of marine habitats (Bat, 2005; Conradi et al., 1997; de-la-Ossa-Carretero et al., 2012; Guerra-García and García-Gómez, 2001) and they can also be an interesting potential resource in aquaculture (Baeza-Rojano et al., 2010).

In spite of the importance of amphipods in marine ecosystems, little is actually known about the feeding habits of these crustaceans, and the diversity of amphipod feeding behaviors in the wild remains an important gap in our knowledge of benthic ecosystems (Farlin et al., 2010). The ecofunctional and trophodynamic roles of epibenthic amphipods are still poorly known (Mancinelli and Rossi, 2002); moreover, trophic roles and functional types have been studied in fewer than about 10%

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of amphipod species, with very few quantitative approaches so far (Dauby et al., 2001). Traditionally, amphipod feeding preferences have been assessed using in situ and laboratory observations, feeding experiments, gut-content analysis and studies of the functional morphology of feeding appendages (Legeżyńska et al., 2012). Knowledge of amphipod feeding ecology has recently expanded thanks to the use of biomarkers such as lipids and fatty acids (FAs) and stable isotopes (Mancinelli, 2012). In fact, in marine food web studies, stable isotopes of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) are widely used to estimate organisms' trophic levels and carbon sources, respectively (Søreide and Nygård, 2012). The utility of these methods lies in the fact that, in contrast to gut content examination, which provides insight into short-term preferences, they provide dietary information integrated over periods of weeks to months (Legeżyńska et al., 2012). However, the isotope studies require fresh material preventing the use of specimens already fixed in ethanol or formalin, and also depend on the abundance of available material (especially if the species are small) to have enough amounts for chemical analysis. On the other hand, traditional studies dealing with the direct observation of digestive contents are very scarce, probably due to the difficult task of removing the digestive tract by dissection.

Recently, a method used by entomologists for studying the digestive contents of insects (e.g. Tierno de Figueroa et al., 2006) was successfully essayed for caprellids (Guerra-García and Tierno de Figueroa, 2009). This study concluded that caprellids feed mainly on detritus based on the examination of 742 specimens of 31 genera and 62 species from all around the world. This pattern has recently been supported by C and N isotope analysis (Jeong et al., 2012). After this, several additional studies using this methodology have been published to explore variations in the diet of tropical caprellids (Alarcón-Ortega et al., 2012), to describe the diet of amphipods (caprellideans and gammarideans) from soft bottoms submarine caves (Navarro-Barranco et al., 2013) and to assess if the feeding habits of amphipods associated with coastal seaweeds could be affected by the spread of invasive algae (Vázquez-Luis et al., 2013). Although the knowledge of amphipod feeding habits has increased during the last few years, a comprehensive study of gammaridean trophic diversity is still lacking. There is information available for some species (Torrecilla-Roca and Guerra-García, 2012; Vázquez-Luis et al., 2013), including a recent review on the studies based on stable isotope data (Mancinelli, 2012), but a comprehensive dietary analysis is necessary. In fact, several authors have pointed out that information on the species-specific trophic ecology of amphipods is needed to better understand their potential role in the trophic dynamics and carbon flow of marine ecosystems (Jeong et al., 2012). Consequently, the main objective of the present study is to characterize the diet of amphipods from the Iberian Peninsula, including both Mediterranean and Atlantic species.

2. Material and methods

We examined 2982 specimens from 33 families, distributed in 71 genera and 149 species (Table 1), representing a high percentage of amphipod diversity in the Iberian Peninsula. Material was collected mainly from sediments, algae and hydroids along the whole coast of the Iberian Peninsula from 1989 to 2011. Although most sampling efforts were conducted in the Strait of Gibraltar area and the Galician coasts, material collected along the whole coasts of Spain and Portugal was included. The Iberian Peninsula is a very interesting geographical zone since it is the confluence of several biogeographic areas and is located between two different water masses: the Atlantic Ocean and the Mediterranean Sea. We have also included, especially for caprellids, samples collected from Ceuta, located in North Africa at the Strait of Gibraltar, and Alborán Island located in south-eastern Spain. All the material was collected between 0 and 40 m deep by snorkeling, scuba diving and van Veen grabs or corers. The whole list of analyzed material is included in Appendix 1 (see supplementary data). The number of specimens observed for each species depended on the availability of material, but

we tried, whenever possible, to study at least 10–20 specimens of each species. Data of those species with a very low number of specimens examined should be taken with caution. Families, genera and species' names are in accordance with the World Register of Marine Species – WoRMS (<http://www.marinespecies.org/aphia.php?p=search>).

Animals were fixed in 4% formalin or 70% ethanol depending on the samples and all material was preserved in 70% ethanol. For the diet study, individuals were analyzed following the methodology proposed by Bello and Cabrera (1999) with slight variations. This method has been used to study the gut contents of different arthropod groups and other animals, both aquatic and terrestrial forms and both ethanol and formalin preserved samples, revealing that it is a very appropriate method for gut content analysis (e.g. López-Rodríguez et al., 2009; Tierno de Figueroa et al., 2006). Recently, this method has been successfully used in amphipods (Alarcón-Ortega et al., 2012; Guerra-García and Tierno de Figueroa, 2009; Navarro-Barranco et al., 2013; Torrecilla-Roca and Guerra-García, 2012; Vázquez-Luis et al., 2013). Specimens of each species were introduced in vials with Hertwig's liquid (consisting of 270 g of chloral hydrate, 19 ml of chloridric acid 1 N, 150 ml of distilled water and 60 ml of glycerin) and heated in an oven at 65 °C for 2 to 24 h depending on the cuticle thickness of the specimens. After this, they were mounted on slides for study under the microscope. The percentage of absolute gut content (at 40× or 100×), as the total area occupied by the content in the whole digestive tract, and relative gut content (at 100× or 400×), as the area occupied for each component within the total gut content, were estimated using a microscope equipped with an ocular micrometer. Mean and standard error of the mean were calculated.

3. Results

Gut contents of the studied amphipod species included detritus, metazoan preys (crustaceans, polychaetes, oligochaetes, kinorhynch and hydroids), macroalgae, microalgae (e.g. diatoms), dinoflagellates and foraminifers (Table 1). The dominant component was detritus, followed by crustaceans (mainly copepods), which were the dominant prey of carnivorous species, and macroalgal tissues, which were characteristic of herbivorous amphipods. Dinoflagellates were found in caprellideans but not in gammarideans, foraminifers were rarely represented and were found mainly in the family Maeridae. There were oligochaetes and kinorhynch occasionally. The average area occupied by content in the whole digestive tract ranged from 6.0% in *Caprella andreae* to 93.6% in *Ampelisca spinipes*. In general terms, detritivorous species had a higher area occupied by content in the digestive tract than carnivorous species. Furthermore, empty guts predominated in carnivorous species. For example, we examined 49 individuals of *Metaphoxus fultoni* and 42 of *Stenothoe tergestina*, and only 5 and 15 specimens respectively had digestive contents. For some species, such as *Amphilochus brunneus*, *Colomastix pusilla*, *Cressa cristata*, *Cressa mediterranea*, *Peltocoxa gibbosa*, *Jassa occia* and *Pereionotus testudo*, all specimens examined had empty guts so diet for these amphipods could not be characterized.

When diet was characterized at family level, detritus was also the main component of most of them, apart from Leucothoidae, Stenothoidae, Phoxocephalidae, Oedicerotidae, Liljeborgidae and Pontogeneiidae, in which prey was the dominant item (Fig. 1). Some important families showed a very consistent pattern for all species included (see Table 1), such as Corophiidae or Pontoporeiidae, which can be considered detritivorous families. The 7 species that were studied of the Oedicerotidae family, the 8 species of Phoxocephalidae and the 3 species of Stenothoidae were clearly carnivorous. Most members of the family Ampithoidae were herbivorous, so we could assign herbivory to this family. However, many families included species with different feeding habits, such as Amphilochidae, with carnivorous species (*Amphilochus neapolitanus* and *Amphilochus spencebatei*), detritivorous (*Gitana sarsi*) or omnivorous (*Amphilochus picadurus*).

Table 1 (continued)

	Hab	N/n	%Abs	%Det	%Cru	%Pol	%Oii	%Kin	%Hyd	%MAlg	%µalg	%Din	%For
Calliopiidae													
<i>Apherusa alacris</i>	Sed	15/15	66.7 (6.9)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Apherusa bispinosa</i>	Alg	22/21	44.7 (5.7)	96.2 (3.8)	3.8 (3.8)	–	–	–	–	–	–	–	–
<i>Apherusa jurinei</i>	Alg	19/19	54.7 (4.5)	88.4 (5.8)	2.6 (2.6)	1.1 (1.1)	–	–	–	5.3 (5.3)	2.6 (1.7)	–	–
Colomastigidae													
<i>Colomastix pusilla</i>	Alg	1/0	–	–	–	–	–	–	–	–	–	–	–
Corophiidae													
<i>Apocorophium acutum</i>	Alg	22/16	49.4 (5.8)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Corophium multisetosum</i>	Sed	19/17	46.8 (6.0)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Leptocheirus hirsutimanus</i>	Sed	25/17	43.5 (8.3)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Leptocheirus pectinatus</i>	Sed	23/22	83.9 (5.0)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Medicorophium annulatum</i>	Sed	25/23	51.5 (5.1)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Medicorophium longisetosum</i>	Sed	14/12	58.8 (6.5)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Medicorophium runcicorne</i>	Sed	15/12	51.7 (4.6)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Monocorophium acherusicum</i>	Sed	24/18	50.6 (5.0)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Monocorophium insidiosum</i>	Sed	24/23	64.6 (4.5)	100 (0)	–	–	–	–	–	–	–	–	–
Cressidae													
<i>Cressa cristata</i>	Alg	1/0	–	–	–	–	–	–	–	–	–	–	–
<i>Cressa mediterranea</i>	Alg	8/0	–	–	–	–	–	–	–	–	–	–	–
Cyproideidae													
<i>Peltocoxa gibbosa</i>	Alg	1/0	–	–	–	–	–	–	–	–	–	–	–
<i>Peltocoxa marioni</i>	Alg	2/1	5 (–)	80 (–)	–	–	–	–	20 (–)	–	–	–	–
Cheirocratidae													
<i>Cheirocratus intermedius</i>	Sed	12/12	84.6 (3.5)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Cheirocratus sundevalli</i>	Sed	9/9	72.2 (8.1)	100 (0)	–	–	–	–	–	–	–	–	–
Dexaminidae													
<i>Dexamine spiniventris</i>	Alg	12/6	25.8 (9.5)	92.5 (5.1)	–	–	–	–	–	7.5 (5.1)	–	–	–
<i>Dexamine spinosa</i>	Alg	23/14	44.6 (9.5)	54.3 (13.1)	–	–	–	–	–	45.7 (13.1)	–	–	–
<i>Guerneia coalita</i>	Alg	17/6	32.5 (8.1)	33.3 (21.1)	41.7 (20.1)	–	25.0 (17.1)	–	–	–	–	–	–
<i>Tritaeta gibbosa</i>	Alg	20/14	23.2 (5.9)	100 (0)	–	–	–	–	–	–	–	–	–
Hyalidae													
<i>Apophyle prevostii</i>	Alg	17/6	40.0 (8.9)	76.7 (16.7)	5.0 (5.0)	6.7 (6.7)	–	–	–	11.7 (11.7)	–	–	–
<i>Hyale perieri</i>	Alg	286/233	50.9 (4.3)	7.6 (2.9)	14.7 (5.4)	–	–	–	–	62.1 (5.6)	4.0 (0.7)	10.6 (1.4)	–
<i>Hyale pontica</i>	Alg	40/3	66.7 (8.8)	56.7 (29.6)	–	–	–	–	–	43.3 (29.6)	–	–	–
<i>Hyale schmidtii</i>	Alg	33/31	53.8 (5.3)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Hyale spinidactyla</i>	Alg	20/12	53.3 (5.1)	48.9 (13.3)	50.8 (13.3)	–	–	–	–	–	0.3 (0.3)	–	–
<i>Hyale stebbingi</i>	Alg	26/17	59.1 (8.2)	46.1 (12.0)	6.3 (6.3)	–	–	–	–	47.2 (12.1)	0.4 (0.3)	–	–
Iphimediidae													
<i>Iphimedia minuta</i>	Alg	9/7	33.6 (7.8)	97.1 (2.9)	–	–	–	–	–	–	2.9 (2.9)	–	–
Ischyroceridae													
<i>Erichthonius punctatus</i>	Alg, Sed	35/27	45.0 (5.3)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Ischyrocerus inexpectatus</i>	Alg	9/7	64.3 (6.5)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Jassa cadetta</i>	Alg	50/35	53.3 (4.7)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Jassa ocia</i>	Alg	2/0	–	–	–	–	–	–	–	–	–	–	–
<i>Jassa pusilla</i>	Alg	4/4	60.0 (10.8)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Parajassa pelagica</i>	Alg	53/49	63.9 (3.0)	88.3 (2.8)	11.1 (2.7)	–	–	–	–	0.6 (0.6)	–	–	–
<i>Siphonocetes kroyeranus</i>	Sed	55/47	33.5 (3.5)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Siphonocetes sabatieri</i>	Sed	70/60	41.7 (4.0)	100 (0)	–	–	–	–	–	–	–	–	–
Leucothoidae													
<i>Leucothoe incisa</i>	Sed	33/15	52.0 (6.9)	86.7 (6.4)	9.3 (5.6)	4.0 (4.0)	–	–	–	–	–	–	–
<i>Leucothoe liljeborgi</i>	Sed	2/2	60.0 (10.0)	40.0 (10.0)	60.0 (10.0)	–	–	–	–	–	–	–	–
<i>Leucothoe oboa</i>	Sed	3/2	40.0 (30.0)	55.0 (45.0)	45.0 (45.0)	–	–	–	–	–	–	–	–
<i>Leucothoe spinicarpa</i>	Alg	13/10	46.5 (5.8)	15.0 (10.7)	85.0 (10.7)	–	–	–	–	–	–	–	–
Liljeborgiidae													
<i>Liljeborgia dellavallei</i>	Alg	2/1	30.0 (–)	30.0 (–)	70.0 (–)	–	–	–	–	–	–	–	–
Lysianassidae													
<i>Hippomedon denticulatus</i>	Sed	8/8	76.3 (9.9)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Hippomedon massiliensis</i>	Sed	30/17	69.4 (6.0)	58.2 (9.9)	41.5 (9.9)	–	–	–	–	–	0.3 (0.3)	–	–

(continued on next page)

Table 1 (continued)

	Hab	N/n	%Abs	%Det	%Cru	%Pol	%Oii	%Kin	%Hyd	%MAlg	%µalg	%Din	%For
Pontogeneiidae													
<i>Eusiroides dellavallei</i>	Alg	12/7	57.9 (8.9)	14.3 (14.3)	85.7 (14.3)	–	–	–	–	–	–	–	–
Pontoporeiidae													
<i>Bathyporeia borgi</i>	Sed	6/6	29.2 (6.9)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Bathyporeia elegans</i>	Sed	17/16	50.9 (7.1)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Bathyporeia guilliamsoniana</i>	Sed	14/13	46.5 (8.7)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Bathyporeia lindstromi</i>	Sed	3/2	12.5 (2.5)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Bathyporeia pilosa</i>	Sed	20/20	46.3 (5.7)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Bathyporeia tenuipes</i>	Sed	14/14	32.1 (7.3)	100 (0)	–	–	–	–	–	–	–	–	–
Stenothoidae													
<i>Stenothoe dollfusi</i>	Alg	10/4	15.0 (5.0)	25.0 (25.0)	75.0 (25.0)	–	–	–	–	–	–	–	–
<i>Stenothoe monoculoides</i>	Alg	38/21	25.7 (3.9)	61.0 (8.9)	39.0 (8.9)	–	–	–	–	–	–	–	–
<i>Stenothoe tergestina</i>	Alg	42/15	14.7 (1.7)	60.7 (12.0)	39.3 (12.0)	–	–	–	–	–	–	–	–
Talitridae													
<i>Talitrus saltator</i>	Sed	8/8	55.0 (9.4)	60.0 (10.9)	–	–	–	–	–	40.0 (10.9)	–	–	–
Urothoidae													
<i>Urothoe elegans</i>	Sed	26/21	21.0 (2.5)	73.3 (5.4)	25.3 (5.6)	–	–	–	–	–	1.4 (1.0)	–	–
<i>Urothoe grimaldii</i>	Sed	12/11	27.3 (5.3)	85.5 (9.7)	14.5 (9.7)	–	–	–	–	–	–	–	–
<i>Urothoe hesperiae</i>	Sed	25/20	30.5 (3.3)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Urothoe intermedia</i>	Sed	8/6	30.8 (4.9)	100 (0)	–	–	–	–	–	–	–	–	–
<i>Urothoe pulchella</i>	Sed	11/10	38.0 (6.3)	100 (0)	–	–	–	–	–	–	–	–	–

Although half of the studied species of the family Hyalidae were clearly herbivorous (*Hyale perieri*, *Hyale pontica* and *Hyale stebbingi*), *Hyale schmidti* was undoubtedly detritivorous, *Hyale spinidactyla* carnivorous and *Aphoyale prevostii* omnivorous (Table 1).

In general terms, the families feeding on detritus were characterized by a stronger mandibular molar, while in carnivorous species there seems to be a trend towards a reduction of this structure. The percentage of macroalgae in the digestive contents was associated in most cases to a reduction or loss of mandibular palp (Fig. 1).

4. Discussion

4.1. The importance of detritus in amphipod diet

The trophic diversity of amphipod species measured in the present study indicates that they use different food resources within their microhabitats. This suggests that they play species-specific functional roles as mediators in trophic pathways from producers to higher-level consumers of the marine ecosystems they inhabit.

Although amphipods form a trophic continuum from primary herbivores to carnivores (Legeżyńska et al., 2012), this comprehensive work reveals that detritus is the main food item in the majority of species. The importance of detritus in benthic communities has often been reported in the literature. More energy and materials flow through detritus food webs than through grazer food webs in most freshwater, estuarine and marine ecosystems, and many animals can use detritus directly because it is highly nutritious after a short period of microbial colonization (Mann, 1998). The data obtained herein for amphipods of the Iberian Peninsula (gammarideans and caprellideans) support the previous observations obtained for worldwide caprellids (Guerra-García and Tierno de Figueroa, 2009).

The percentage of species feeding on metazoan prey was higher than that of species feeding on macroalgae. Animal matter is more easily assimilated than vegetal matter. In fact, marine plants are little used by animals that graze directly on them because they can have a relatively high content of indigestible fibers and low nitrogen content (Mann, 1998). Thus, our study shows that even in species with high contents of macroalgae in their digestive tracts, detritus was the main

gut component (Fig. 1). Howard (1982) reported that the inclusion of epibenthic gammaridean amphipods in a laboratory microcosm containing eelgrass, substantially reduced the load of attached epiphytes and settled detritus on eelgrass leaves, when compared to a microcosm without amphipods. Duffy and Hay (2000), based on mesocosm experiments, reported that grazing amphipods, which are ubiquitous in marine vegetation but poorly understood ecologically, may have strong impacts and play important roles in the organization of benthic communities, particularly where predation pressure is low. In addition to their abundance and rates of consumption, the way in which mesograzers consume plants is of great importance for predicting their effects on plant fitness (Poore, 1994). Several experimental studies of mainly herbivorous amphipods have compared feeding impacts of amphipods on the plant (and invertebrate) communities of which they are a part and often found quite different impacts (Best and Stachowicz, 2012; Duffy, 1990; Duffy and Harvilick, 2001).

The method used in the present study let us clearly differentiate the presence of detritus from other types of items such as crustaceans, microalgae and macroalgae. However, detritus feeders can display relatively different diets depending on the vegetal or animal origin of the organic matter. In this sense, isotopic values for amphipods associated with leaf litter of the seagrass *Posidonia oceanica* showed a certain degree of trophic diversity, with a major contribution of algal material in *Gammarella fucicola* (micro and macro-epiphytes or drift macro-algae) and a more important contribution of *P. oceanica* carbon in *Gammarus aequicauda* (Lepoint et al., 2006).

The paucity of microalgae found in the digestive tracts is surprising, due to the fact that many amphipod have been reported to feed heavily on microalgae, both in natural habitats (Costa, 1960; Saunders, 1966) or under culture in laboratory (see e.g. Baeza-Rojano et al., 2011). We could think that the method used in the present study might underestimate the amount of microalgae; however, when the amphipod has ingested microalgae, these microalgae can be clearly distinguished in the gut, so the method seems to be reliable to detect them when they are present. Therefore, we do not think that active microalgae-feeders are being seriously under-represented by gut content data. Furthermore, we must take into account that detritus, when it has vegetal origin, can contain abundant rests of microalgae.

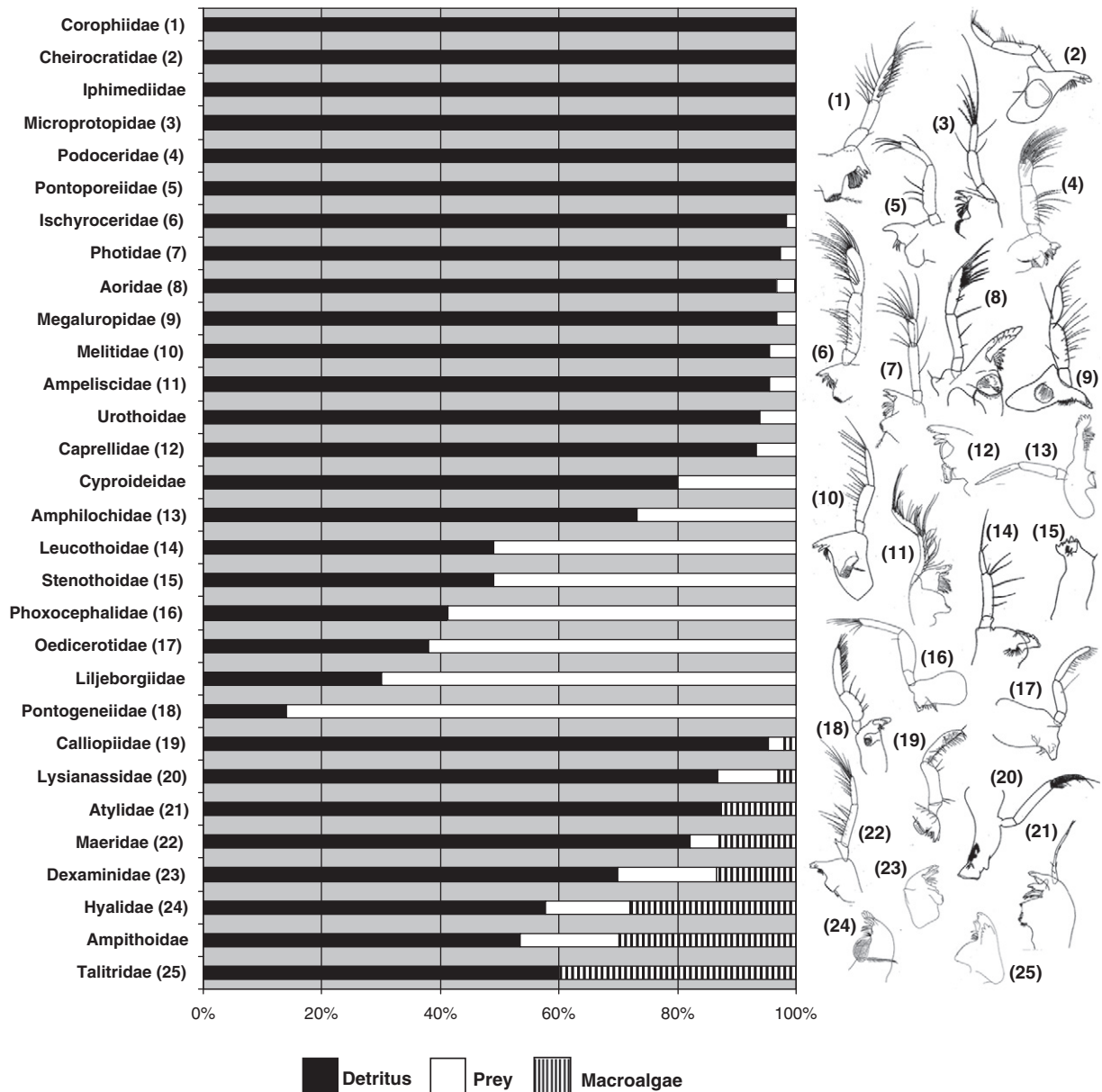


Fig. 1. Percentage of the three dominant food items in the diet of the studied amphipod families. The values were obtained as the mean of the different species studied of each family. Representative mandibles of different families are also included. Figures redrawn from Ruffo (1982–1998).

4.2. Diet diversity at family and species level

Several ecological studies focused on amphipod trophic aspects usually allocate the species to trophic groups according to previous literature (see for example Conradi and Cervera, 1995; Dauvin, 1984; de-la-Ossa-Carretero et al., 2012; Enequist, 1949; Hily, 1984; Lastra et al., 1991; Lewis, 1992; Procaccini and Scipione, 1991; Sánchez-Mata et al., 1993; Scipione, 1989; Sparla et al., 1993). Although in general terms, there is agreement between our results and assumptions in literature data, many of the assignments are to some degree conjectural, so direct gut examination in the present study is desirable in order to verify precisely the feeding behavior of most species (Conradi and Cervera, 1995).

The results obtained for the caprellideans of the Iberian Peninsula are in agreement with the general pattern for the group reported in a worldwide study conducted by Guerra-García and Tierno de Figueroa (2009), with detritus as the dominant food item.

Regarding gammarideans, data from the literature are dispersed or incomplete, with isolated information for some species and/or families. Our study reveals that general assignment of a type of diet for a whole family is not always adequate. Some families such as Corophiidae, Oedicerotidae, Leucothoidae and Pontoporeiidae, showed a consistent pattern in all the studied species, but others included species with totally different feeding strategies (Table 1). For Ampeliscidae, our results agree with the data of Lincoln (1979) and Enequist (1949), the latter based on aquarium experiments, which confirm that they are mainly detritus-feeders. In spite of the fact that Amphilochoidea are traditionally considered as detritivores/herbivores (De Broyer et al., 2012), our results indicate a wider trophic diversity including also carnivorous species such as *Amphilochochus neapolitanus*. Many of the species included in the families Ampithoidae, Hyalidae and Atylidae are clearly herbivorous, coinciding with data recorded by Conradi and Cervera (1995) and Vázquez-Luis et al. (2013). Greze (1968) studied the feeding habits of

the amphipod *Dexamine spinosa* and found that its diet consists primarily of seaweeds, similarly to the results obtained for this species in the present study. Vázquez-Luis et al. (2013) also found an herbivorous diet for *Dexamine spiniventris*, while in our study this species showed clear preference for detritus. Dixon and Moore (1997) conducted a comparative study on the tubes and feeding behavior of eight corophioid species, among them several included in the present study such as *Lembos websteri*, *Aora spinicornis* and *Erichthonius punctatus*. *Leptocheirus hirsutimanus* is considered a deposit or suspension feeder (Eleftheriou and Basford, 1989) and *Cheirocratus sundevallei* is considered a deposit feeder by Enequist (1949). Our observations for these two species are in total agreement. Although we found that *L. websteri* is mainly detritivorous, Shillaker and Moore (1987) described an omnivore diet based mainly on detritus, macroalgal fragments, naviculoid diatoms, and occasionally arthropods. Sainte-Marie (1986) studied the gut contents of several lysianassid amphipods in a shallow cold-water bay and found great diversity in their diets including large carrion, crustaceans, polychaetes and detritus. The present study supports these previous observations. In the literature, the family Oedicerotidae is surprisingly homogeneous in regard to feeding habits, being considered as detritus feeders by some authors (Enequist, 1949). However, our results dealing with this family are totally different, including only carnivorous species, in agreement with the results of other authors (e.g. Farlin et al., 2010; Yu and Suh, 2002). Enequist (1949) reported that *Harpinia antennaria* and *Harpinia crenulata* are subsurface deposit feeders, and pointed out that males, after reaching maturity, probably ingest no food and soon die. However, Oakden (1984) indicated that phoxocephalids are predators/omnivorous, consuming a variety of meiofaunal prey as well as detritus. Oliver et al. (1982) concluded that this group acts as a key taxon in soft bottom communities, playing an important functional role as predators. Other studies using stable isotope analysis also showed the carnivorous behavior of *Harpinia* species (Fanelli et al., 2009). Our research shows that Phoxocephalidae mainly includes carnivorous species. Dekker (1989) reported that *Bathyporeia* spp. and *Urothoe elegans* are deposit feeders. A diet based on detritus is also found for Pontoporeiidae and Urothoidea in the present study.

4.3. Problems in establishing trophic or functional feeding groups

Different trophic classifications have been used in the literature, often mixing type of food consumed and feeding strategies. We can classify amphipods according to their method of collecting food, such as filter feeders (provided with numerous setose appendices, antennae and gnathopods, adapted to filter by creating a filtration current), grazers (amphipods which scrape the substrate surface to either consume the film of microorganisms – diatoms, bacteria, ciliates – or directly the vegetal substrate), predators (usually attached to a sessile substrate feeding on small prey, larvae, copepods, annelids, nematodes), scavengers (deep-sea forms provided with a very sensitive and efficient system to locate corpses and eat carrion), and symbionts (Bellan-Santini, 1998). Additionally, some authors consider macro versus microphages based on food size (Bellan-Santini, 1998; Zimmerman et al., 1979). If we just take into consideration the food contents of the guts, regardless of the method used for collection and the food size, we can distinguish carnivorous, herbivorous, detritivorous and omnivorous species. Even the assignment of a species into one of these four categories based on the dietary analysis can be a difficult task. Herbivorous species also ingest detritus, which is probably attached to the macroalgal tissues. Detritivorous species can also accidentally feed on small preys, such as copepods. Therefore, the limits between omnivorous and the remaining categories are often difficult to establish based on the percentages of each item, and different authors can assume different criteria. For example, Guerra-García and Tierno de Figueroa (2009) considered caprellids as globally detritivorous since detritus was clearly the dominant food item in the digestive tracts of the majority of species. Navarro-Barranco et al. (2013) assigned feeding groups to the studied species in marine

cave habitats, only considering species with 100% detritus in the digestive tract as detritivores, and as carnivores those with more than 50% prey. If we consider the term omnivorous for species feeding on different trophic resources, such as prey, detritus or algae (without establishing percentage limits of each food item), most of the studied amphipod species should be classified as omnivorous, including the species with more than 95% detritus (such as *Pedoculina garciagomezi*, *Ampelisca diadema*, *Ampithoe helleri*, *Lembos websteri*, *Atylus falcatus*, *Socarnes filicornis*, *Maera grossimana*, *Maerella tenuimana*, *Melita palmata*, *Gammaropsis maculata*, *Gammaropsis ostroumowi* and *Gammaropsis palmata*). Obviously, for many authors, a detritus percentage higher than 95% could be considered as evidence to assign the species as detritivorous instead of omnivorous. In this sense, Minshall (1988) noted that distinctions between feeding groups remain arbitrary because the majority of macroinvertebrates are 'opportunistic generalists' or 'selective omnivores' (see references in Macneil et al., 1997).

4.4. Digestive contents and mandible morphology

Myers and Lowry (2003), based on an analysis of 104 genera and 156 species of corophiidean amphipods, presented a phylogeny and higher-level classification for the suborder Corophiidea Leach, 1814. Their phylogeny divided the corophiideans into two infraorders, the Corophiida and the Caprellida, based on the hypothesis of evolution of different feeding strategies. According to these authors, members of Corophiida are derived from bottom-feeding detritivores, whereas members of Caprellida are derived from ancestors that fed on material suspended in the water column. Further details and discussions about the amphipod phylogenetic relationships can be found in Lowry and Myers (2013). Guerra-García and Tierno de Figueroa (2009) conducted a dietary analysis of caprellids, based on the examination of 743 specimens of 31 genera and 62 species. These authors suggested that it would be possible that not all members of the Caprellidae derived from filter-feeding ancestors, and that a different line of caprellids lacking molar process and having six-articulate pereopods 3 and 4 derived from a carnivorous ancestor that used these pereopods to manipulate prey.

Although there have been some attempts to relate feeding mechanisms to mouthpart morphology (Caine, 1977; Coleman, 1989), the correlation between the latter and the feeding habits of amphipods is still poorly understood (Conradi and Cervera, 1995). In general, a relation between feeding mode, preferred food and mouthpart morphology is shown for several feeding-specialists among amphipods (Mayer et al., 2008). Traditionally, feeding mechanisms of caprellids have been considered a function of mouthpart morphology (Caine, 1974, 1977). However, Guerra-García and Tierno de Figueroa (2009) only found a clear correlation between the absence of the molar and a predatory strategy, and they reported that the presence/absence of the mandibular palp was not related to the digestive contents. For the gammarideans, Watling (1993) conducted a detailed study on functional morphology of the mandible and proposed two independent pathways leading to carnivory; one involving a shortening of the incisor process with subsequent reduction of the molar, and the other a lengthening of the incisor process before molar loss. In the present study the absence of molars in amphipods is also related to a carnivorous diet. Mayer et al. (2008) summarized that the incisors and the lacinia mobilis of amphipods specialized in feeding on animal tissue are broadened to sharp cutting edges, molars are non-triturative, and setae are reduced in number and size. The present study also shows that a reduction or absence of mandibular palp is observed in herbivorous gammaridean species. The absence of the mandibular palp in gammaridean species adapted to feeding on macrophytes has also been pointed out by other authors (Mayer et al., 2008). In this sense, no relationship was detected in the worldwide study of caprellids by Guerra-García and Tierno de Figueroa (2009) due to a lack of herbivorous species.

4.5. Latitudinal diversity of feeding strategies

The present study reveals a great diversity of digestive contents in amphipods from the Iberian Peninsula, a typical temperate region. Legeżyńska et al. (2012) also found highly diverse feeding strategies among Arctic amphipods, and Dauby et al. (2001) interpreted high trophic diversity of amphipods in the Weddell Sea as a function of species diversity related to the long evolutionary history of the Antarctic, abundance of accessible micro-habitats and variability of food sources. In general, high trophic diversity appears to be a general feature of amphipod communities and one of the most important factors responsible for the dispersal success of these crustaceans (Legeżyńska et al., 2012). Future research is necessary to compare data obtained from the Iberian Peninsula with other areas of the world and properly address global patterns of feeding habits.

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Appendix 1. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.seares.2013.08.006>.

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