

Feeding of the nymphs of nine stonefly species (*Insecta: Plecoptera*) from North Africa (Rif Mountains, Morocco)

Alimentación de nueve especies de plec6pteros (*Insecta: Plecoptera*) en el Norte de frica (Rif, Marruecos)

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SUMMARY

The intestinal contents of the nymphs of 9 species of stoneflies belonging to the families *Perlodidae*, *Perlidae*, *Taeniopterygidae*, *Capniidae* and *Leuctridae* have been studied, analysing the variations in different size categories. Our study provides the first data on feeding in the genera *Hemimelaena* and *Capnioneura*. On the basis of vegetable matter quantities, we found that in the carnivorous species this fraction of the diet diminished in the series *Hemimelaena-Isoperla-Perla*. The dietary habits of the different species belonging to the families *Taeniopterygidae*, *Nemouridae*, *Capniidae* and *Leuctridae* were found to be similar since all of these behave fundamentally as detritivores-herbivores. In almost all these latter species, except *Nemoura lacustris*, we found that over the two size intervals considered, fine organic matter was consumed mainly by the younger nymphs and coarse organic matter mainly by the older ones.

RESUMEN

Se ha estudiado el contenido intestinal de las ninfas de 9 especies de plec6pteros de las familias *Perlodidae*, *Perlidae*, *Taeniopterygidae*, *Capniidae* y *Leuctridae*, analizando la variaci6n en diferentes categoras de tamao. Se aportan los primeros datos sobre la dieta de los generos *Hemimelaena* y *Capnioneura*. Sobre la base de la importancia de la fracci6n vegetal, encontramos que la importancia de dicha fracci6n disminuye en la serie *Hemimelaena-Isoperla-Perla*. La dieta

de las diferentes especies estudiadas de las familias *Taeniopterygidae*, *Nemouridae*, *Capniidae* y *Leuctridae* son similares, ya que todas ellas se comportan fundamentalmente como detritívoras-herbívoras. En todas estas especies, salvo en *Nemoura lacustris*, la materia orgánica particulada fina es consumida principalmente por las ninfas jóvenes, y la materia orgánica particulada gruesa por las ninfas más viejas.

INTRODUCTION

The feeding habits of the nymphs of many stonefly species from North America, Europe and Australia have been well studied (Hynes, 1941; Brinck, 1949; Richardson & Gaufin, 1971; Fuller & Stewart, 1977, 1979; Lavandier, 1979, 1982; Mouthon & Verneaux, 1979; Baekken, 1981; Berthélemy & Lahoud, 1981; Sephton & Hynes, 1983; Jop & Szczytko, 1984; Feminella & Stewart, 1986; etc.). Little is known, however, about the feeding habits of the Palearctic species of other areas, such as southern Europe and North Africa.

The aim of our study therefore was to determine the diet of the nymphs of various species caught in a monthly sampling at several locations in the region of Ketama (Rif Mountains, Morocco) (Sánchez-Ortega & Azzouz, 1998).

MATERIAL AND METHODS

The gut content of nymphs was studied using a transparency technique which has also been used to study feeding in imaginal stages (Tierno de Figueroa *et al.*, 1998; Tierno de Figueroa & Sánchez-Ortega, 2000). We used Hertwigs' liquid, a modification of Hoyer's liquid, which clears the body wall, thus allowing direct examination of the gut content without the need for dissection.

Transparency methods are clearly useless in anatomical or structural studies because the structures disappear in the slides. The same problems arise with feeding studies into fluid-feeding insects. Nevertheless, this method can detect all the components reported in feeding studies using dissection (cf. references in Introduction). Thus it is a useful technique for studying feeding habits amongst aquatic insects that feed on particulate matter (carnivores, detritivores, scrapers, etc.).

The smallest specimens of the families *Taeniopterygidae* (*Brachyptera algirica* and *Brachyptera auberti*), *Nemouridae* (*Nemoura lacustris*), *Capniidae* (*Capnia nigra* and *Capnioneura petitpierreae*), and *Leuctridae* (*Leuctra geniculata*), were prepared on slides with 3-4 drops of Hertwigs' liquid and

were dried in an oven at 60 °C for 24 hours before being examined under a compound microscope (40x). The largest specimens of the families *Perlodidae* (*Hemimelaena flaviventris* and *Isoperla cf. kir*) and *Perlidae* (*Perla marginata*) were placed in vials full of Hertwigs' liquid and then dried in an oven at 60 °C for 24 hours before being mounted on slides.

Of the approximately 500 specimens examined we considered only those which contained some intestinal contents, which amounted to nearly half of the mounted specimens. To analyse the intestinal contents quantitatively we used an estimation method with a micrometric scale as reference to establish the percentage of the different types of food.

We differentiated four fractions: vegetable matter (diatoms, algae and fungus fragments), animal matter (mayflies, chironomids, simuliids and unidentified animal remains), unidentified organic matter (fine-particulate organic matter -FPOM- and coarse organic matter -CPOM-), and mineral matter (sand).

We established 4 size categories for *Perla marginata*, 3 for *Isoperla cf. kir* and *Hemimelaena flaviventris*, and 2 for all the other species. The limits of these intervals were obtained by dividing the range of cephalic capsule width of each species group into regular intervals.

The feeding habits of those species collected at one of the sampling stations with the greatest specific diversity (Cree Achraf, 4 km from Tlata of Ketama, at 1400 m.a.s.l.) together with the different size intervals considered for each species have been compared using Horn's Dietary Overlap Index (1966).

RESULTS

Hemimelaena flaviventris (Navás, 1929) (n=15. Table 1): A high proportion of animal matter appeared in all three size classes, especially in the larger nymphs; chironomids represented a major proportion of the animal fraction and were consumed by almost all the specimens analysed. The smallest nymphs contained the greatest proportion of vegetable matter whilst intermediate nymphs had the smallest fraction. Diatoms constituted an abundant dietary element in almost all the specimens of all three size categories studied. The proportion of organic matter was relatively low compared to the other fractions, although it was present in all the nymphs studied. In the three size classes considered this species behaved fundamentally as a carnivore and the importance of the animal fraction increased with the growth of the nymph.

Isoperla cf. kir Fochetti & Vinçon, 1993 (n=31. Table 2): The animal-matter fraction differed greatly, varying from 22.5% for the smallest specimens to 68.7-73.9% for the two larger ones; Chironomids were the main component

Table I.—Percentages of the different components identified in the gut of *Hemimelaena flaviventris* according to the size categories considered (cc = cephalic capsule; p = % of presence; r = range; m = mean).

Tabla 1.—Porcentajes de los diferentes componentes identificados en el intestino de *Hemimelaena flaviventris* según las categorías de tamaño consideradas (cc = cápsula cefálica; p = % de presencia; r = rango; m = media).

Components	Size c.c.			cc<2mm			2<cc<3mm			cc>3mm		
	p	R	m	p	r	m	p	r	m			
Diatoms	100	10-42	23	88	0-20	8.8	100	5-30	20			
Algal fragments	25	0-20	7.5	55	0-20	7.3	50	0-5	2.5			
Vegetable matter mm			30.5			16.1			22.5			
F.P.O.M.	100	5-20	10.5	100	5-20	10.6	100	5-15	10			
C.P.O.M.	100	5-15	10	100	5-15	13.3	100	2-5	3			
P.O.M.			20.5			23.9			13			
Chironomidae	100	10-50	31.3	88	0-70	46.8	100	10-40	25			
Animal remains	50	0-40	15	88	0-20	10.5	100	25-60	39.5			
Simuliidae	25	0-10	2.8	11	0-10	1.1	—	—	—			
Ephemeroptera	—	—	—	33	0-5	1.6	—	—	—			
Animal matter			49.1			60			64.5			

of the animal fraction, especially in the smallest nymphs; other prey types increased in frequency with the size of the nymph. The vegetable-matter fraction in this species was greatest in the smallest nymphs, diminishing in quantity in the other two size categories and at the same time appearing in a smaller proportion of the specimens. Once more diatoms represented the predominant component of this fraction, both in proportion and frequency. The organic-matter fraction decreased progressively with size but persisted in all the specimens considered. *Isoperla cf. kir* behaved mainly as a herbivorous-detritivorous species in the smallest size category, whilst the intermediate and large nymphs were fundamentally carnivorous.

Perla marginata (Panzer, 1799) (n=27. Table 3): Animal matter was the main food consumed, exceeding 50% of the gut contents and appearing in all specimens. A relatively similar proportion of animal matter was consumed in all the different size categories, though slightly lower in the smaller nymphs. The proportion of vegetable matter decreased over the four size categories. The relatively high value for this fraction in the largest nymphs was due to

Table II.—Percentages of the different components identified in the gut of *Isoperla cf. kir* according to the size categories considered (cc=cephalic capsule; p=% of presence; r=range; m=mean).

Tabla II.—Porcentajes de los diferentes componentes identificados en el intestino de *Isoperla cf. kir* según las categorías de tamaño consideradas (cc= cápsula cefálica; p=% de presencia; r=rango; m=media).

Size c.c.	cc<2mm			2<cc<3mm			cc>3mm		
	P	R	m	p	r	m	p	r	M
Diatoms	100	15-40	23	82	0-10	6.4	75	0-10	3.3
Algal fragments	75	0-30	15	17	0-5	0.4	50	0-10	3.3
Fungus	75	0-5	1.7	17	0-5	0.4	—	—	—
<i>Vegetable matter</i>			39.7			7.2			6.6
F.P.O.M.	100	10-38	15	100	5-25	11.5	100	5-30	10
C.P.O.M.	100	10-40	22.8	29	0-30	10.5	100	5-20	9.5
<i>P.O.M.</i>			37.8			22.0			19.5
Chironomidae	100	5-65	22.5	100	40-75	59	100	5-65	40.2
Animal remains	—	—	—	64	0-25	8.2	87	0-60	30.4
Simuliidae	—	—	—	5	0-5	1.5	25	0-15	3.3
Ephemeroptera	—	—	—	—	—	—	—	—	—
<i>Animal matter</i>			22.5			68.7			73.9

a single specimen (cephalic capsule width = 3.24 mm) containing only diatoms and organic matter. Organic matter comprised 20% to 30% of the gut contents in all four size categories. This species was primarily carnivorous in all the size classes, though at all stages organic matter proved to be abundant (20% to 30% of the gut contents).

Brachyptera algerica Aubert, 1956 (n=22. Table 4): The larger nymphs contained a greater quantity of vegetable matter. Diatoms dominated this fraction in percentage as well as frequency. Organic matter was present in great quantities, exceeding 50% of the gut contents in the two groups of nymphs, although there was a trend towards increased CPOM ingestion at the expense of FPOM concomitant with an increase in specimen size. We found animal remains (or exuviae) in the gut of a mature nymph (cephalic capsule width=1.09 mm). Sand grains also appeared in some of the smallest nymphs, though this mineral fraction represented an insignificant portion of the total ingested matter. Both sizes of this species were detritivorous-herbivorous, though during its development the consumption of organic-matter slightly

Table III.—Percentages of the different components identified in the gut of *Perla marginata* according to the size categories considered (cc=cephalic capsule; p=% of presence; r=range; m=mean).

Tabla III.—Porcentajes de los diferentes componentes identificados en el intestino de *Perla marginata* según las categorías de tamaño consideradas (cc= cápsula cefálica; p=% de presencia; r=rango; m=media).

Components	Size c.c.			cc<1mm			1<cc<2mm			2<cc<3			cc>3mm		
	p	r	m	p	r	m	p	r	m	p	r	m	p	r	m
Diatoms	50	0-10	4	33	0-10	2.5	25	0-10	2.2	60	0-60	13.2			
Algal fragments	40	0-30	10	16	0-5	1	10	0-5	0.4	—	—	—			
<i>Vegetable matter</i>			14			3.5			2.6			13.2			
F.P.O.M.	100	15-40	24	100	10-40	21	100	5-15	10.5	20	0-10	5.4			
C.P.O.M.	20	0-10	2.5	100	5-25	10.6	100	5-20	14.5	100	10-28	15			
<i>P.O.M.</i>			26.5			31.6			25			20.4			
Chironomidae	40	50-80	50	100	10-40	56.2	100	20-70	51.7	100	5-65	45			
Animal remains	100	5-15	9.5	50	0-20	7.5	66	0-60	15.9	60	0-30	19.4			
Simuliidae	—	—	—	—	—	—	22	0-10	1.3	—	—	—			
Ephemeroptera	—	—	—	50	0-5	1.8	44	0-10	3.5	33.3	75641	2			
<i>Animal matter</i>			59.5			65.5			72.4			66.4			

Table IV.—Percentages of the different components identified in the gut of *Brachyptera algerica* according to the size categories considered (cc=cephalic capsule; p=% of presence; r=range; m=mean).

Tabla IV.—Porcentajes de los diferentes componentes identificados en el intestino de *Brachyptera algerica* según las categorías de tamaño consideradas (cc= cápsula cefálica; p=% de presencia; r=rango; m=media).

Components	Size c.c.			cc<1mm			cc>1mm		
	p	r	m	p	r	m	p	r	m
Diatoms	50	0-60	30	76	0-60	30			
Algal fragments	16.6	0-5	2.5	100	2-20	10			
Fungus	—	—	—	—	—	—			
<i>Vegetable matter</i>			32.5			40			
F.P.O.M.	100	9-58	40	100	10-30	25			
C.P.O.M.	100	10-70	27.5	100	25-75	32.5			
<i>P.O.M.</i>			67.5			57.5			
Animal remains	—	—	—	7.1	0-10	2.5			
<i>Animal matter</i>			0			2.5			
Sand	16.6	0-0.1	0.05	—	—	—			
<i>Mineral matter</i>			0.05			0			

diminished whilst the size of the ingested particles tended to increase, complemented by a similar increase in the ingestion of the vegetable fraction.

Brachyptera auberti Consiglio, 1957 (n=24. Table 5): The vegetable fraction constituted the major proportion of the diet in this species, although its consumption decreased slightly in the larger nymphs. The proportion of ingested diatoms, as well as their frequency, increased in larger nymphs. Organic matter represented the greatest fraction of the gut contents in the two groups of specimens (>58%). In contrast to the previous species, the ingestion of organic-matter increased only slightly in larger nymphs. Animal remains also appeared in one nymph (cephalic capsule width=1.48 mm), and some sand grains were found in both size classes of nymphs, although in small proportions. This species is detritivorous-herbivorous in both size categories, although the proportion of organic matter consumed increased slightly in the larger nymphs concomitantly with a decrease in vegetable consumption.

Nemoura lacustris Aubert, 1961 (n=8. Table 6): The larger size class nymphs consumed a greater quantity of vegetable matter than the smaller ones, and the consumption of organic matter decreased with the size of the cephalic capsule. We also found mineral matter, though in minor percentages.

Table V.—Percentages of the different components identified in the gut of *Brachyptera auberti* according to the size categories considered (cc=cephalic capsule; p=% of presence; r=range; m=mean).

Tabla V.—Porcentajes de los diferentes componentes identificados en el intestino de *Brachyptera auberti* según las categorías de tamaño consideradas (cc= cápsula cefálica; p=% de presencia; r=rango; m=media).

Components	Size c.c.	cc<1mm			cc>1mm		
		p	r	m	p	r	m
Diatoms		81	0-40	10	100	5-70	21
Algal fragments		63	0-60	31.9	50	0-50	10
Fungus		—	—	—	—	—	—
<i>Vegetable matter</i>				41.9			31
F.P.O.M.		100	15-50	32	100	5-40	20.2
C.P.O.M.		100	5-40	26	100	37-62	46.6
<i>P.O.M.</i>				58			66.8
Animal remains		—	—	—	12.5	0-10	2.1
<i>Animal matter</i>				0			2.1
Arena		9	0-5	0.04	25	0-0.5	0.1
<i>Mineral matter</i>				0.04			0.1

Table VI.—Percentages of the different components identified in the gut of *Nemoura lacustris* according to the size categories considered (cc=cephalic capsule; p=% of presence; r=range; m=mean).

Tabla VI.—Porcentajes de los diferentes componentes identificados en el intestino de *Nemoura lacustris* según las categorías de tamaño consideradas (cc=cápsula cefálica; p=% de presencia; r=rango; m=media).

Components	Size c.c.		cc<1mm			cc>1mm		
	p	r	m	p	r	m		
Diatoms	—	—	—	100	60-70	65		
Algal fragments	60	0-10	4	50	0-15	7.5		
Fungus	100	1-30	9	—	—	—		
<i>Vegetable matter</i>			13			72.5		
F.P.O.M.	100	50-70	63	50	5-24	14.5		
C.P.O.M.	100	10-30	23.5	100	5-20	12.5		
<i>P.O.M.</i>			86.5			270		
Animal remains	—	—	—	—	—	—		
<i>Animal matter</i>			0			0		
Sand	60	0-2	0.5	50	0-1	0.5		
<i>Mineral matter</i>			0.5			0.5		

Smaller nymphs of this species appear to be detritivorous, and change to becoming more herbivorous as they grow (though this change must be verified by studying a greater number of specimens).

Capnia nigra (Pictet, 1833) (n=30. Table 7): The vegetable and organic matter fractions were similar in both size categories, both in proportion and frequency, although the proportion of organic matter was two- to three-fold greater than vegetable matter. A slightly higher proportion of vegetable matter was found in the larger nymphs, with a slight decrease in organic matter. Once again we found a higher proportion of CPOM in larger nymphs at the expense of FPOM. Sand was also found in minor proportions. In both size intervals, this species was primarily detritivorous, although the exemplars also contained a significant amount of vegetable matter in their diet (approximately 25% to 33% of ingested materials). The contents found in this species are similar to those cited by Hynes (1941) and Brinck (1949), although with marked differences in the proportion of some of these components.

Capnioneura pettipierreae Aubert, 1961 (n=41. Table 8): The composition of the gut contents of this species closely resembled that of *Capnia nigra*, albeit with slightly higher proportions of organic matter and a slightly lower proportion of vegetable matter. The larger nymphs had a slightly higher

Table VII.—Percentages of the different components identified in the gut of *Capnia nigra* according to the size categories considered (cc=cephalic capsule; p=% of presence; r=range; m=mean).

Tabla VII.—Porcentajes de los diferentes componentes identificados en el intestino de *Capnia nigras* según las categorías de tamaño consideradas (cc= cápsula cefálica; p=% de presencia; r=rango; m=media).

Components	Size c.c.			cc<0.55mm			cc>0.55mm		
	p	r	m	p	r	m	p	r	m
Diatoms	50	0-60	25	55	0-60	21			
Algal fragments	—	—	—	11	0-50	9			
Fungus	25	0-1	0.5	38	0-25	0.1			
<i>Vegetable matter</i>			25.5			30.1			
F.P.O.M.	100	20-70	45	100	10-60	32			
C.P.O.M.	100	20-50	29.3	100	30-70	36.4			
<i>P.O.M.</i>			74.3			68.4			
Animal remains	—	—	—	—	—	—			
<i>Animal matter</i>			0			0			
Sand	33	0-1	0.3	66	0-5	1.5			
<i>Mineral matter</i>			0.3			1.5			

proportion of vegetable matter than the smaller nymphs, and a slightly lower proportion of organic matter. We also found inverse proportions of FPOM and CPOM ingested, the smaller nymphs having a greater quantity of FPOM and the larger ones a greater quantity of CPOM. Mineral particles were found in minor quantities in some of the specimens. The species is fundamentally detritivorous in both size categories, although with a considerable vegetable component in the diet (approximately 20-25%).

Leuctra geniculata (Stephens, 1936) (n=9. Table 9): In both size categories this species consumed a great proportion of vegetable matter, while diatoms were absent from the diet. Organic matter constituted the principal dietary component, representing almost 75% of the contents of all the specimens. The larger nymphs contained greater quantities of CPOM than smaller specimens. Given the high proportion of specimens that ingested animal matter, this component appears to be common in the diet of this species, although consumed in low proportions. This species was mainly detritivorous in both size groups, though with a major proportion of vegetable matter (about 30%). These findings concur with Hynes (1941), though in our case we found no diatoms. Organic matter appeared in all the specimens analysed and the proportion animal matter found in our specimens was greater than found in exemplars in England.

Table VIII.—Percentages of the different components identified in the gut of *Capnioneura petitpierreae* according to the size categories considered (cc=cephalic capsule; p=% of presence; r=range; m=mean).

Tabla VIII.—Porcentajes de los diferentes componentes identificados en el intestino de *Capnioneura petitpierreae* según las categorías de tamaño consideradas (cc= cápsula cefálica; p=% de presencia; r=rango; m=media).

Components	cc<0.55mm			cc>0.55mm		
	p	r	m	p	r	m
Diatoms	70	0-70	11.6	28	0-15	3.5
Algal fragments	50	0-20	5.5	100	10-40	17.2
Fungus	62	0-10	2.5	100	0-5	3.4
<i>Vegetable matter</i>			19.6			24.1
F.P.O.M.	100	10-60	46	100	30-80	35.6
C.P.O.M.	100	20-70	34.3	100	5-60	40.3
<i>P.O.M.</i>			80.3			75.9
Animal remains	—	—	—	—	—	—
<i>Animal matter</i>			0			0
Sand	33.3	0-1	0.06	16.6	0-1	0.1
<i>Mineral matter</i>			0.06			0.1

Table IX.—Percentages of the different components identified in the gut of *Leuctra geniculata* according to the size categories considered (cc=cephalic capsule; p=% of presence; r=range; m=mean).

Tabla IX.—Porcentajes de los diferentes componentes identificados en el intestino de *Leuctra geniculata* según las categorías de tamaño consideradas (cc= cápsula cefálica; p=% de presencia; r=rango; m=media).

Components	cc<1mm			cc>1mm		
	p	r	m	p	r	m
Diatoms	—	—	—	—	—	—
Algal fragments	100	20-40	30	100	20-30	27.5
Fungus	33.3	0-1	0.5	60	0-1	0.8
<i>Vegetable matter</i>			30.5			28.3
F.P.O.M.	100	30-56	36	100	30-56	36.6
C.P.O.M.	100	30-50	32.4	100	30-60	40
<i>P.O.M.</i>			68.4			76.6
Animal remains	33.3	0-2	1	60	0-15	6.3
<i>Animal matter</i>			1			6.3
Sand	33.3	0-1	0.1	66.6	0-2	0.7
<i>Mineral matter</i>			0.1			0.7

DISCUSSION

We studied the gut contents of 9 species of Plecoptera, among which previous feeding data was available for *Perla marginata*, *Capnia nigra* and *Leuctra geniculata* alone. Our study provides the first data on feeding in the genera *Hemimelaena* and *Capnioneura*.

On applying the categories traditionally used to classify species on the basis of feeding mechanisms (Cummins, 1973; Merritt & Cummins, 1984; Merritt *et al.*, 1984), we can verify, as indicated by Stewart & Stark (1988), that although each species can be included in a category according to the major fraction comprising the intestinal contents, a species cannot be confined exclusively to one category alone since the presence of different types of food indicate that no single feeding mechanism is involved, and therefore these species maintain the general trend among aquatic insects to be polyphagous and thus lack specialization in food intake (Cummins, 1973).

The two Perlodid species studied, *Hemimelaena flaviventris* (table 1) and *Isoperla cf. kir* (table 2), were found to be primarily predatory, coinciding with the general behaviour described for other species in the same family (Hynes, 1941, Brinck, 1949; Fuller & Stewart, 1977, 1979; Oberndorfer & Stewart, 1977; Lavandier, 1979, 1982; Baekken, 1981; Berthélemy & Lahoud, 1981; Allan, 1982; etc.). Vegetable and organic fractions dominate the diet of the smaller nymphs in both species, although, in larger nymphs these fractions diminished and animal matter increased. This trend coincides with previous descriptions for other species in the same genus (Berthélemy & Lahoud, 1981; Lavandier, 1982), the same family (Schwermer, 1914; Dittmar, 1955; Lavandier, 1979; Baekken, 1981; Allan, 1982; Peckarsky, 1984) and other predatory species (Winterbourn, 1974; Devonport & Winterbourn, 1976; Shepton & Hynes, 1983).

Perla marginata (Table 3), the only species of the family *Perlidae* we have studied, was predacious at all size intervals considered, as described by different authors for the nymphs of this genus (Schoenemund, 1912; Šámal, 1923; Hynes, 1941; Berthélemy & Lahoud, 1981), and in general for the entire family (Hynes, 1941; Brinck, 1949; Chisholm, 1962; Vaught & Stewart, 1974; Fuller & Stewart, 1977, 1979; Mouthon & Verneaux, 1979; Snellen & Stewart, 1979; Berthélemy & Lahoud, 1981). The smaller nymphs were primarily carnivorous, as reported by Berthélemy & Lahoud (1981), which contradicts the observations of other authors for this and other species of the genus *Perla* (Schoenemund, 1912; Šámal, 1923; Schwermer, 1914; Dittmar, 1955).

In these three carnivorous species, especially *Perla marginata* and in the larger nymphs of *Isoperla cf. kir*, the vegetable and organic fractions remained

similarly small throughout the different size intervals. This fact, together with the frequent presence of these components in packages near animal remains, indicates that these materials are not ingested directly but rather come from the intestinal contents of their prey, perhaps complementing the diet of the predator (Yule, 1990). In the different intervals considered for *Hemimelaena flaviventris* and in the small nymphs of *Isoperla cf. kir*, the proportions of organic matter, and especially of the vegetable fraction, remained relatively high and constant, indicating common ingestion of this material by these species during these nymphal stages. Berthélemy & Lahoud (1981), studying carnivorous species in the Pyrenees, reported that vegetable food diminished in the series *Arcynopteryx-Isoperla-Perlodes-Perla-Dinocras*. Our results establish a similar series, following the same arrangement criterion: *Hemimelaena-Isoperla-Perla*.

The most frequent prey consumed by the three predatory species were chironomids. Diptera larvae are generally the most frequent prey for predacious aquatic insects (Minshall & Minshall, 1966; Tarter & Krumholz, 1971; SHeldon, 1972; Stewart *et al.*, 1973; Oberndorfer & Stewart, 1977; Peckarsky, 1984; etc.).

The dietary models found in the different species studied from the families *Taeniopterygidae*, *Nemouridae*, *Capniidae* and *Leuctridae* are similar (tables 4-9), since all of these behaved fundamentally as detritivores-herbivores, although the proportion of vegetal matter was generally higher in the family *Taeniopterygidae* (tables 4 and 5).

In almost all of these species, except in *Nemoura lacustris*, we found that over the two size intervals considered, fine organic matter was consumed mainly by the younger nymphs and coarse organic matter mainly by the older nymphs.

The intestines of most of the detritivorous species contained a low proportion of sand grains. Although these grains can act mechanically in the digestion of vegetable matter (Cummins, 1973), only in some cases did the proportions reach nearly 70%, and therefore the scant sand may represent incidental ingestion with other foods.

A comparison of the feeding habits of the various species using the dietary-overlap coefficient of Horn (Horn, 1966) (Table 10) revealed the following:

—The carnivorous species were clearly separate from the detritivorous-herbivorous ones, given the differences of their feeding regimes. Between these two trophic groups, the highest overlap coefficients were found between the smallest nymphs of *Isoperla cf. kir* and the detritivorous-herbivorous species, especially within the interval corresponding to the larger nymphs in

Table X.—Horn's dietary overlap coefficient for the Plecoptera species captured at sampling station Creek Achraf (4 km from Tlata of Ketama; 1400 a.s.l.) (values greater than 0.60 indicate significant overlap).

Tabla X.—Coeficiente de solapamiento de Horn aplicado a la dieta de las especies de plec6pteros capturados en el Arroyo de Achraf (4 km de Tlata de Ketama; 1400 m.s.n.m.) (Valores mayores de 0.60 indican solapamiento significativo).

cephalic capsule (mm)		L. geniculata		N. lacustris		B. algerica		B. auberti		C. petitpierreae		Isoperla cf. kir			P. marginata			
		<1	>1	<1	>1	<1	>1	<1	>1	<0,55	>0,55	<2	36558	>3	<1	36526	36558	>3
L. geniculata	<1	—	0.98	0.92	0.3	0.67	0.76	0.76	—	0.86	0.7	0.27	0.22	0.11	0.27	0.19	0.24	14
	>1	—	—	0.5	0.29	0.90	0.81	0.77	—	0.76	0.84	0.58	0.21	0.12	0.42	0.36	0.31	19
N. lacustris	<1	—	—	—	0.82	0.65	0.69	0.6	—	0.8	0.76	0.46	0.28	0.19	0.44	0.19	0.24	0.30
	>1	—	—	—	—	0.82	0.76	0.87	—	0.70	0.63	0.64	0.34	0.20	0.28	0.33	0.25	0.28
B. algerica	<1	—	—	—	—	—	0.86	0.80	—	0.80	0.62	0.43	0.77	0.52	0.43	0.27	0.60	0.32
	>1	—	—	—	—	—	—	0.90	—	0.70	0.65	0.78	0.31	0.78	0.32	0.12	0.40	0.24
B. auberti	<1	—	—	—	—	—	—	—	—	0.80	0.82	0.69	0.31	0.17	0.32	0.34	0.27	0.20
C. petitpierreae	<0.55	—	—	—	—	—	—	—	—	—	0.98	0.67	0.24	0.30	0.29	0.24	0.22	0.19
	>0.55	—	—	—	—	—	—	—	—	—	—	0.70	0.30	0.27	0.33	0.26	0.34	0.29
I. cf. kir	<2	—	—	—	—	—	—	—	—	—	—	—	0.66	0.39	0.69	0.78	0.74	0.34
	2-3	—	—	—	—	—	—	—	—	—	—	—	—	0.85	0.73	0.84	0.96	0.52
	>3	—	—	—	—	—	—	—	—	—	—	—	—	—	0.75	0.84	0.67	0.99
P. marginata	<1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.83	0.97	0.92
	1-2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.89	0.84
	2-3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.93
	>3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

these species. These results reinforce the aforementioned predominance of the vegetal organic fractions in the diet of the younger *Isoperla cf. kir* nymphs.

The overlap was also generally large between the different intervals of the two carnivorous species, as well as between the groups of detritivorous-herbivorous species, given the overall similarity in feeding habits. Nevertheless, the overlap between the smaller *Isoperla* nymphs and the other groups considered for the two carnivorous species was somewhat smaller, especially bearing in mind the broader size intervals for the two species, and thus the degree of overlap was comparable to that between the carnivorous and detritivorous-herbivorous species.

In general, therefore, we found no appreciable separation between species sharing similar dietary models, nor between nymphs of different sizes in the same species. As summarized by Stewart & Stark (1988), these results may indicate that factors such as food size, time of feeding, place of feeding, etc. were not taken into account, or else that the quantity of food available in the streams maintaining healthy conditions is not completely exploited by aquatic invertebrates (Sweeny, 1984; Pugsley & Hynes, 1985) or, in other words, that food is not a limiting factor, and, in this case, dietary overlap between niches does not necessarily signify competition between the species studied.

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