DIET VARIATIONS OF *EPHEMERELLA IGNITA* (PODA) (EPHEMEROPTERA: EPHEMERELLIDAE) IN RELATION TO THE DEVELOPMENTAL STAGE

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The life cycle and diet of *Ephemerella ignita* (PODA) were studied in a Northern Spanish stream. In the area of study *E. ignita* is an univoltine species with one generation that emerges in spring and summer. Nymphs can be found in the stream for nine months. This mayfly acts as a detritivore throughout its development, and the increase in the proportions of other types of food it ingests is only detected in the last nymphal stages.

INTRODUCTION

Most of the studies that deal with the stream macroinvertebrate communities from a functional point of view assume the trophic categories described by MERRITT & CUMMINS (1984) for the insects of North America. However, it is recognised that fluvial macroinvertebrates ingest a wide variety of food types (e.g. CUMMINS & KLUG, 1979; LAMBERTI & MOORE, 1984; PALMER *et al.*, 1993) and their diet may change depending on larval developmental stage and on the availability of food in their environment (e.g. FULLER & MACKAY, 1980). Up to now, only MALO (1993) and PUIG (1993) have reported data on the diet of invertebrates in the fluvial benthos of Spain.

Ephemerella ignita (PODA) is a very common species in European rivers (e.g. LAVANDIER & CAPBLANC, 1975; BOURNAUD *et al.*, 1987; HEFTI & TOMKA, 1990; WRIGHT, 1992) broadly spread along the Iberian Peninsula (e.g. ALBA-TERCEDOR, 1983; PUIG *et al.*, 1984; HERRANZ & GONZÁLEZ DEL TÁNAGO, 1985; IMBERT & POZO, 1989; BARGOS *et al.*, 1990; SOLER & PUIG, 1993; ZAMORA-MUÑOZ *et al.*, 1993). Its biological cycle has been the aim of different studies (MAITLAND, 1965; MACAN, 1979; WELTON *et al.*, 1982; ROSILLON, 1986; ALBA-TERCEDOR, 1990) and several authors have recently focused on the study of its food habits (ROSILLON, 1988; MALO, 1993). Nevertheless, there are few studies about how diet varies throughout the development of this species.

In the Agüera stream basin (Northern Spain), we are carrying out research on the life cycles and diet of fluvial macroinvertebrates. In this context, the aim of the present study is to determine the life cycle and diet changes in relation to the larval development stage of *E. ignita*, one of the most abundant mayflies in the middle-low reaches of the Agüera stream.

STUDY AREA, MATERIAL AND METHODS

The Agüera stream in Northern Spain (UTM coordinates are 30 T VN 7883 for its source and 30 T VP 7403 for its mouth) lies in a basin with an area of 144 km^2 that is moderately populated (20 inhabitants/km^2). The main economic activity is farming. The basic geological composition of the basin is siliceous with the exception of a calcareous central strip (Fig. 1). The study has been carried out at a site in a middle-low

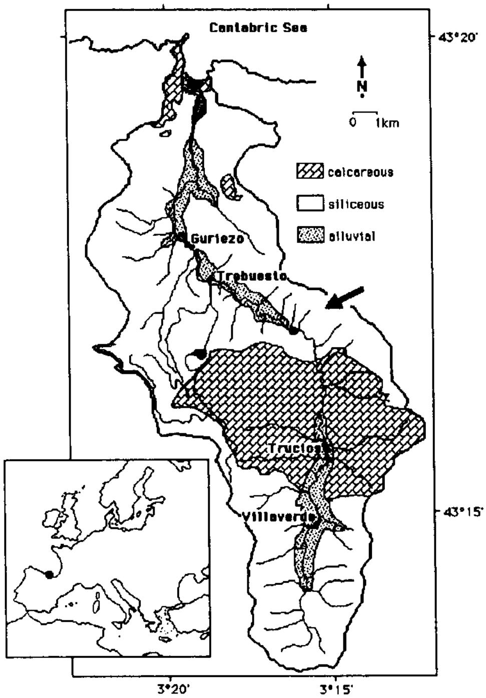

Fig. 1. Study area: geological characteristics and sampling site.

reach of the Agüera stream (order 3) with a slight slope (0.86%), about 10 m of average width and a flow that varies from 73 to 10,000 l/s (ELÓSEGUI, 1992). The stream bed is made up of pebbles and big stones in a typical lotic structure. The surrounding vegetation is mainly eucalyptus plantations, with trees (mainly alders) along the banks. Throughout the study period, water temperature varied from 6.5 to 20.3 °C and the oxygen concentration from 9.8 to 16.5 mg/l, (saturation percentage between 100 and 140%). Moderate values of conductivity were registered (from 192 to 289 µS/cm) and pH varied from 7.3 to 9.07.

Samples of macroinvertebrates were collected monthly, from November 1992 to December 1993, with a Surber net of 250 µm mesh size. These samples were fixed with 5% formaldehyde in the field. Once in the laboratory, the organisms were sorted and kept in 70% ethanol.

The life cycle of *E. ignita* was analysed from the frequency distribution histogram (0.1 mm intervals) of the head width of 825 individuals.

For diet analysis, 129 nymphs were dissected, their guts extracted and the contents put in Hoyer liquid before observation under a microscope. The area covered by the content extracted from each organism was measured by means of a grided eyepiece at 32X. Additionally, 10% of this surface was analysed at 400X. As a result, it was possible to distinguish six types of food: remains of vascular plants, animal remains, diatoms, filamentous algae, detritus (where all the remains of unidentified origin were included) and fungi. The percentage of area covered by each food type was estimated. Individuals of *E. ignita* were classified into four size classes based on their head width: class I, between 0.15 and 0.54 mm (31 individuals dissected); class II, between 0.55 and 0.94 mm (36 individuals dissected); class III, between 0.95 and 1.34 mm (45 individuals dissected); and class IV, between 1.35 and 1.85 mm (17 individuals dissected). One way analysis of variance (ANOVA) was performed with the diet data arc sin transformed for normality (ZAR, 1984).

RESULTS

E. ignita seems to be an univoltine species in our study area (Fig. 2). The first nymphs appear in November and grow quickly all winter long till they reach their final developmental stage in spring and early in summer, when presumably the emergence of adults occurs. In spring, when the maximum abundance was observed (641 individuals/m^2) (Fig. 3), we found also the higher variety of developmental stages (Fig. 2). Nymphs were absent from samples taken during August, September and October.

Dietary analysis shows that detritus is the major component of *E. ignita* gut content in all life stages (Fig. 4). However, as the animals grow to maturity, the proportion of other components such as plant and animal remains, diatoms and filamentous algae, acquire importance. Isolated presence of fungi has also been observed.

Among the different types of food considered for this analysis, significant differences can be noticed only in the proportion of detritus found in the gut contents through the development of this species ($p<0.0001$; C.IV = C.III < C.II < C.I). The smallest nymphs (class I) ingest a higher amount of unidentified remains (nearly 100%) (Fig. 4a). Other components of the diet make up a greater fraction as individuals become larger. In spring, the biggest individuals

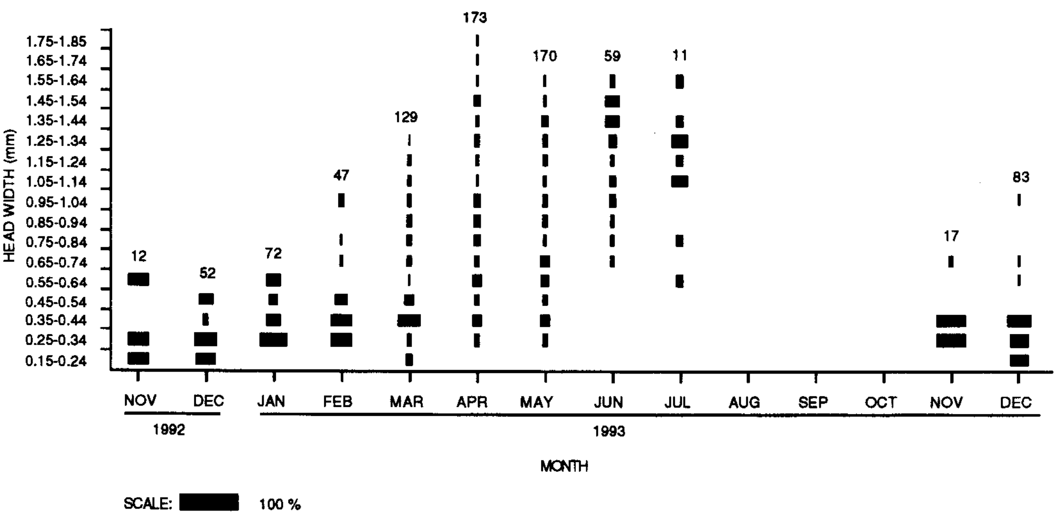

Fig. 2. Life cycle of *Ephemerella ignita*, during the study period (November 92-December 93). The number of collected nymphs each month is indicated.

(class III and IV) have a diet that includes vegetal and animal remains (Figs 4c, 4d).

DISCUSSION

The life cycle of *Ephemerella ignita* in different European rivers (MAITLAN, 1965; MACAN, 1979; CLIFFORD, 1982; WELTON *et al.*, 1982; ROSILLON, 1986; ALBA-TERCEDOR, 1990) has been described as univoltine with adult emergence occurring in the summer. The life cycle of *E. ignita* is similar in our area, although the precise timing of nymphal development differs from that outlined by other authors. According to our data, the first nymphs appear in November, develop in winter and emerge in spring and summer, whereas in higher latitudes than ours smaller nymphs

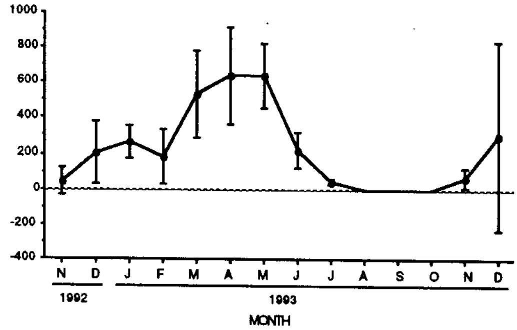

Fig. 3. Abundance of *Ephemerella ignita* (number indiv/m²) during the study period (November 92-December 93).

occur later in time. In Scotland, MAITLAND (1965) found that nymphs from this species started appearing in spring, growing very quickly and emerging as adults in summer, and

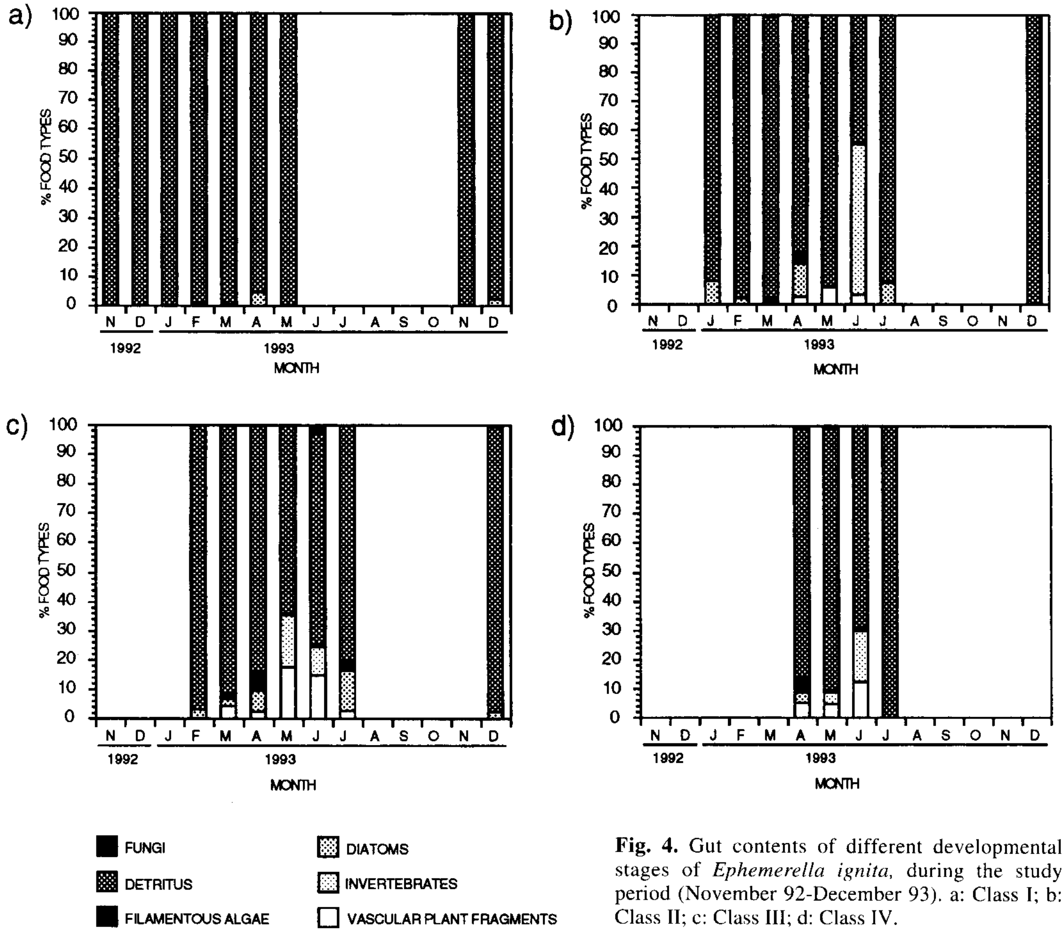

Fig. 4. Gut contents of different developmental stages of *Ephemerella ignita*, during the study period (November 92-December 93). a: Class I; b: Class II; c: Class III; d: Class IV.

HEFTI & TOMKA (1990) in the Swiss Alps found a short cycle, where eclosion, growth and emergence of *E. ignita* took place at the end of spring and summer. In Spain, ALBA-TERCEDOR (1990) found that nymphs first appeared in February in rivers of Sierra Nevada (Southern Spain). Although these southern rivers are situated at a lower latitude than ours, they are characteristic of high mountains streams where temperatures are much lower, a factor that determines the eclosion time as well as nymphal development. Our results are similar to those of WELTON *et al.* (1982), who found that, under a controlled temperature from 8 to 14°C, young nymphs appeared near the end of October. ROSILLON (1986), in Belgium, noticed the presence of small specimen of *E. ignita* since February, and hypothesized that a second generation may originate in the autumn, as the result of an early eclosion of some of the eggs, but whose nymphs are unable to survive to cold temperatures in winter. In our study the first nymphs appear in autumn, but they continue developing during winter, probably favoured by moderate temperatures (12.49 ± 4.02) along the middle-low stretch of the Agüera stream, reaching their adult stage in spring and summer. We see no evidence of a second generation from our data. The absence of nymphs of this species during the collections in August, September and October is likely due to the fact that after being laid, the eggs may have a long period of incubation, as some authors have stated (e.g. MAITLAND, 1965; MACAN, 1979). Increasing the egg eclosion period of *E. ignita* (WELTON *et al.*, 1982) would result in a presence of small nymphs until April and May. Undoubtedly, water temperature plays an important role in the life cycle of *E. ignita* as is the case of most insects (e.g. CUMMINS & KLUG, 1979; SWEENEY, 1984; SWEENEY & VANNOTE, 1986; BRITTAIN, 1983; WEBB & MERRITT, 1987; SÖDERSTROM, 1988). MACAN (1979), maintains that the plasticity that *E. ignita* presents during its life cycle in relation to temperature allows it a wide distribution. Furthermore, this plasticity could contribute to finding nymphs at any time throughout the year.

Our results confirm the essentially detritivorous nature of this species pointed out by ELLIOTT *et al.* (1988) and by MERRITT & CUMMINS (1984) for other species belonging to this genus. This nutritional habit seems to be extensive to mayflies according to SIVARAMAKRISHNAN & VENKATARAMAN (1987). However, ROSILLON (1988) noticed that, under experimental conditions, *E. ignita* prefers to feed on diatoms. MALO (1993) reports a highly variable composition of the diet, diatoms representing up to 67%.

Dietary changes occurring in the final stages of nymphal growth could be related with the requirement for higher quality nutrition during the last stages of larval development (ANDERSON & CUMMINS, 1979; CUMMINS & KLUG, 1979; LAMBERTI & MOORE, 1984). On the other hand, changes observed in the gut content may simply reflect that larger animals can ingest larger particles. This could account for the observed increase in the proportion of both animal and plant material in the guts in final instar nymphs.

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