Feeding of an Iberian Stream Cyprinid Assemblage: Seasonality of Resource Use in a Highly Variable Environment

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# Feeding of an Iberian stream cyprinid assemblage: seasonality of resource use in a highly variable environment

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**Abstract.** Food resource use by seven cyprinids from an Iberian stream was analysed over 9 months. Differences in food resource use were found both between species and within species between seasons. Plant material was a more important food for carp, nase, goldfish and barbel than for gudgeon, roach and chub, irrespective of the season. Chironomid larvae were the staple animal food for the former five species throughout the year. Roach and chub, especially the latter, displayed large seasonal variations in prey use, with chironomid larvae only being important during autumn. Ephemerellid nymphs and ephemeropteran imagos dominated the animal diet of chub during spring and summer, respectively. Dipteran adults and Formicidae were the most important prey for roach during spring and summer, with other common prey being ephemerellid nymphs and hydropsychid larvae. Food resource overlap among the three dominant species (roach, barbel and chub) displayed a large seasonal variation. High overlaps were observed during autumn when these species used the same resources. During summer overlaps were much lower with each species specialising on different prey. The remaining less abundant species had large diet overlaps amongst themselves and with barbel, over all seasons. It is suggested that morphological constraints, habitat partitioning and temporal changes in food resource limitation may be involved in producing these patterns of food resource use.

**Key words:** Cyprinids – Iberian stream – Feeding ecology – Resource partitioning – Seasonal variability

Competition for resources between coexisting species has long been considered a major factor regulating the organisation of freshwater fish communities (Larkin 1956; Zaret and Rand 1971; Schoener 1974). However, renewed discussion in the past few years has emphasised the role of abiotic factors, such as physical harshness and physical disturbance, as determinants of stream fish communities structure (Grossman et al. 1982, 1985). The relative importance of abiotic versus biological processes in regulating community structure appears to change dramatically between communities along environmental gradients (Schlosser 1987). Biotic interactions are considered to play a major role in regulating community attributes in stable environments (Moyle and Vondracek 1985; Ross et al. 1985), whereas environmental variability is advanced as a factor decreasing the importance of biological interactions and preventing the formation of persistent, repeatable fish communities (Grossman et al. 1982, 1985). In unstable streams mortality associated with the occurrence of physical extremes, such as floods and droughts, acts to prevent resource limitation or competitive exclusion (Grossman et al. 1990), thus community structure is suggested to be mainly determined through differential reproductive success and recolonisation rates (Schlosser 1982, 1985).

Streams in the southern Iberian Peninsula may provide useful test systems to assess the influence of biological processes and frequent physical disturbances on the structure and dynamics of fish communities. These streams have a highly seasonal flow and are generally exposed to a broad range of discharge conditions, including both large winter floods and severe summer droughts. Furthermore, fish assemblages include both endemic and introduced species (Almaça 1983), which are likely to differ in their ability to cope with such variability.

As a preliminary insight into the structuring of stream fish communities in southern Iberia, this study examines the patterns of food resource use within the cyprinid assemblage of a lowland system. Although studies of resource partitioning are limited in their ability to demonstrate the mechanisms creating observed relationships, they provide the requisite background for generating testable hypotheses concerning the roles of equilibrium or non-equilibrium factors in community control (Ross 1986). Feeding relationships were examined because trophic separation is an important means of resource partitioning in stream fish communities (Ross 1986). Cyprinids were chosen for analysis because they

are the predominant component of the freshwater fish fauna throughout the Iberian Peninsula (Almaça 1971).

Specifically, the following objectives were addressed: (i) to identify the food resources potentially important to cyprinids; (ii) to identify interspecific and seasonal changes in diet composition, diet breadth and diet overlap; (iii) to examine the evidence from (i) and (ii) for resource partitioning and feeding niche shifts among cyprinids; and (iv) to relate patterns of variation in resource use to probable processes of community organisation.

## Material and Methods

### Study area

The study was conducted in the River Sorraia catchment, Portugal. The Sorraia drains an alluvial plain with a mean altitude of 200 m, discharging into the upper zone of the Tagus estuary. Three main tributaries flow into the Sorraia (the Sor, Divor and Raia). Average annual rainfall is low, 600–800 mm, with 75% falling from October to March. During summer, particularly in drought years, the tributaries partially dry up, becoming a succession of unconnected pools. In the Sorraia water flows continuously.

Seven cyprinids are common inhabitants of the Sorraia catchment (Magalhães 1990). The most abundant species are Iberian roach "*Rutilus alburnoides* complex" (Steindachner 1866), Iberian barbel *Barbus bocagei* Steindachner 1865, and Iberian chub *Leuciscus pyrenaicus* Gunther 1868. Other common but much less abundant cyprinids are Iberian nase *Chondrostoma polylepis*, Steindachner 1865, gudgeon *Gobio gobio* (L.), goldfish *Carassius auratus* (L.) and carp *Cyprinus carpio* L. Gudgeon was introduced to Portuguese inland waters in recent years whereas the introduction of goldfish and carp seems to be very old (Almaça 1983). Iberian arched-mouth nase *Chondrostoma lusitanicum* Collares-Pereira 1980 and Iberian long-snouted barbel *Barbus comiza* Steindachner 1865 were not included in this study owing to their extreme rarity in the Sorraia catchment.

### Diet analysis

Fish sampling was conducted three times during 1988: early spring (April), the beginning of fish spawning season and seasonal plant

**Table 1.** Numbers and size ranges (standard length) of fish used in diet analysis

| Species | Code | Gut contents | | | | | |
|---|---|---|---|---|---|---|---|
| | | Spring | | Summer | | Autumn | |
| | | Number | Size range (mm) | Number | Size range (mm) | Number | Size range (mm) |
| *Barbus bocagei* | BAR | 67 | 51–233 | 53 | 56–237 | 51 | 53–217 |
| *Carassius auratus* | CAR | 28 | 54–120 | 13 | 50–124 | 26 | 46–118 |
| *Chondrostoma polylepis* | CHP | 27 | 70–168 | 9 | 70–162 | 10 | 72–160 |
| *Cyprinus carpio* | CYP | 13 | 63–240 | 23 | 59–233 | 11 | 64–220 |
| *Gobio gobio* | GOB | 18 | 46– 84 | 13 | 50– 86 | 10 | 48– 83 |
| *Leuciscus pyrenaicus* | LEU | 39 | 44–162 | 43 | 50–170 | 26 | 44–157 |
| *Rutilus alburnoides* | RUT | 12 | 64– 90 | 32 | 60– 87 | 12 | 56– 80 |

**Table 2.** Percentage occurrence of plant material (in brackets) and percent number of the main animal prey categories in the diet of each cyprinid, over all study sites and seasons

| Prey numbers | BAR 16225 | CAR 1886 | CHO 302 | CYP 4188 | GOB 2718 | LEU 1830 | RUT 583 |
|---|---|---|---|---|---|---|---|
| Plant material | (60.2) | (68.7) | (71.7) | (76.6) | (14.6) | (41.7) | (32.1) |
| Ostracoda | 0.1 | 0.8 | 2.0 | 1.3 | 0.2 | 0.0 | 0.0 |
| Mollusca | 0.6 | 0.2 | 0.0 | 0.8 | 0.4 | 2.8 | 0.0 |
| Baetidae-nymphs | 2.4 | 1.1 | 2.6 | 1.3 | 7.1 | 1.8 | 4.5 |
| Caenidae-nymphs | 4.0 | 3.0 | 2.6 | 8.0 | 0.3 | 0.4 | 2.2 |
| Ephemerellidae-nymphs | 1.5 | 1.6 | 2.0 | 0.1 | 3.8 | 9.7 | 8.7 |
| Ephemeroptera-imagos | 0.5 | 0.6 | 0.0 | 0.4 | 0.8 | 64.7 | 6.0 |
| Odonata | 0.2 | 0.1 | 0.0 | 0.1 | 0.1 | 0.1 | 0.5 |
| Corixidae | 0.6 | 0.2 | 0.0 | 0.3 | 0.1 | 1.0 | 0.8 |
| Naucoridae | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 |
| Ceratopogonidae-larvae | 0.1 | 0.2 | 0.0 | 0.8 | 0.2 | 0.2 | 0.2 |
| Simuliidae-larvae | 4.0 | 0.3 | 4.0 | 0.4 | 12.4 | 0.2 | 6.4 |
| Chironomidae-larvae | 81.8 | 87.3 | 79.5 | 76.9 | 71.0 | 5.9 | 19.7 |
| Diptera-nymphs | 0.4 | 1.7 | 0.7 | 2.2 | 0.8 | 0.1 | 5.2 |
| Diptera-adults | 0.1 | 0.1 | 0.0 | 0.0 | 0.1 | 0.4 | 12.7 |
| Dytiscidae-larvae | 0.1 | 0.1 | 0.0 | 0.8 | 0.0 | 0.1 | 0.3 |
| Coleoptera-adults | 0.1 | 0.5 | 0.0 | 0.2 | 0.2 | 1.0 | 1.8 |
| Hydropsychidae-larvae | 2.7 | 0.1 | 2.0 | 0.1 | 2.3 | 2.5 | 8.4 |
| Formicidae | 0.2 | 0.2 | 2.0 | 0.7 | 0.0 | 7.3 | 20.9 |
| Other prey | 0.6 | 1.9 | 2.6 | 5.6 | 0.2 | 1.6 | 1.7 |

Only prey categories accounting at least once for more than 1% of total numbers, for at least one species, are listed. Fish codes as in Table 1

growth; summer (August), the period of maximum drought; and autumn (November), the beginning of the wet season. No sampling was conducted during floods (winter) because the high water level prevented efficient sampling. Six study sites, each 60–70 m long, were selected to represent the range of habitats in the Sorraia catchment [see Magalhães (1993) for details]. Fish were captured by electrofishing (350 V, 3–4 A, d.c.), counted and measured for total length. Whenever available, 15 individuals of each species, representing the entire size range of fish in the collection, were retained for analysis. These fish were either placed in an ice bath or injected with a 10% formalin solution and deep frozen within 3 h.

In the laboratory, fish were measured for standard length and their guts were removed and carefully unfolded. The entire gut contents were examined. Presence of seeds, vascular plant parts and algae were recorded. Animal prey remains were identified to the lowest readily recognisable taxon (usually family) by comparison to a reference collection and counted. Percentage occurrence of plant material and numeric percentage of animal prey for each species during each sampling date, over all sampling sites, were calculated. Empty guts were omitted in calculating percentage occurrence and numeric percentage was based on total number of prey in a sample (Hyslop 1980).

### Data analysis

Detrended correspondence analysis (DCA) was used to find the best simultaneous representation of the matrix of animal prey numbers (with animal prey categories as columns and species/seasons as rows) underlying resource gradients in the dietary data. This ordination technique, designed specifically for discrete data, is very effective for dietary data analysis, producing a small number of interpretable resource axes (Graham and Vrijenhoek 1988). DCA involves the derivation of new axes that maximally account for the structure of the points in a multi-dimensional space, making possible the reduction of dimensionality (Gauch 1982). These new axes maximise the correspondence between row and column categories, so that species/seasons with similar diets are positioned close to each other as are the prey categories eaten by similar sets of species/ seasons. A measure of the importance of each ordination axis is given by the corresponding eigenvalue; eigenvalues of DCA all lie between 0 and 1 and only the axis with the largest eigenvalues displays the biologically relevant information (Ter Braak 1987a).

DCA was carried out using the CANOCO computer program (Ter Braak 1987b), with the option for detrending by second-order polynomials.

Animal prey breadth and animal prey-use overlap were calculated by the Shannon-Wiener and the Schoener formulae, respectively (Wallace 1981).

## Results

Altogether the contents of 536 guts were analysed (Table 1). Cyprinids consumed a broad spectrum of food categories, although a smaller subset composed the main forage base (Table 2). Plant material was consumed by all species, occurring most frequently in the diets of carp, nase, goldfish and barbel (>60%) and being much less common in the diet of gudgeon (<15%). Chironomid larvae were the staple animal food for the latter five
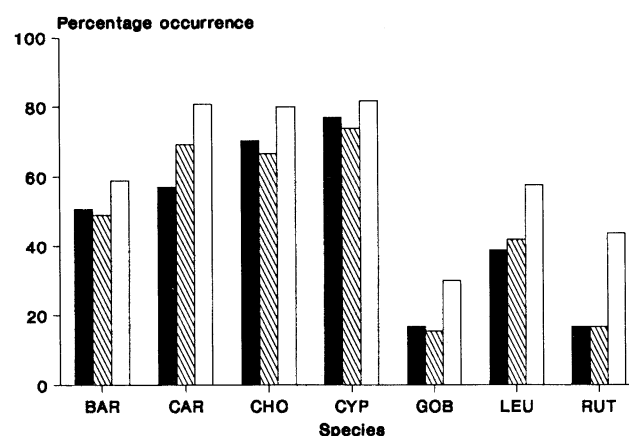


**Fig. 1.** Seasonal variation of the percentage occurrence of plant material in the diets of cyprinids, over all study sites. Fish codes as in Table 1. *Black bars,* spring; *shaded bars,* summer; *open bars,* autumn
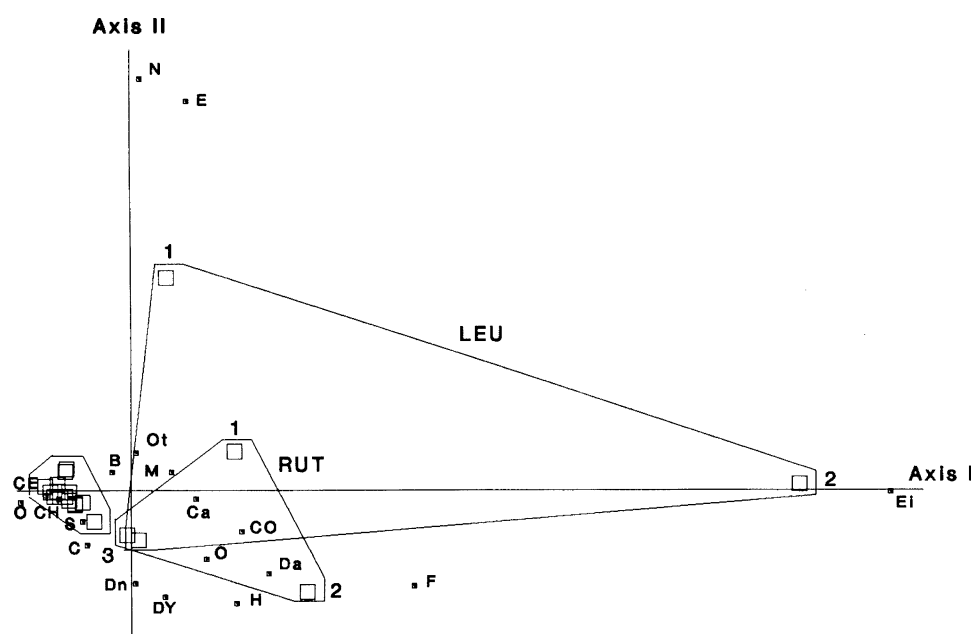


**Fig. 2.** Plot of the first two axes obtained from the detrended correspondence analysis. Chub (LEU), roach (RUT), and remaining species are delimited by minimum polygons. Prey categories are represented by *black squares:* $O$=Ostracods; $M$=Molluscs; $B$=Baetidae nymphs; $C$=Caenidae nymphs; $E$=Ephemerellidae nymphs; $Ei$=Ephemeropteran imagos; $OD$=Odonata; $CO$=Corixidae; $N$=Naucoridae; $CE$=Ceratopogonidae larvae; $S$=Simuliidae larvae; $CH$=Chironomidae larvae; $DN$=Dipteran nymphs; $Da$=Dipteran adults; $D$=Dytiscidae; $Ca$=Coleopteran adults; $H$=Hydropsychidae larvae; $F$=Formicidae; $OT$=Other prey. $1$=Spring; $2$=summer; $3$=autumn

species accounting for more than 70% of total prey numbers recorded. The dominant animal prey in the overall diet of chub were ephemeropteran imagos (65%). The diet of the roach contrasted with those of all the other species, with a much more even distribution of animal prey categories, the most important of which were Formicidae (21.6%), chironomid larvae (19.7%) and dipteran adults (12.7%).

The consumption of plant material increased during autumn, although the overall pattern among species remained the same throughout the year (Fig. 1). Seasonal variations in animal prey use were also found (Appendix, 1–3). Chironomid larvae dominated the animal diet of barbel, carp, nase and goldfish in all seasons, but to a lesser extent during autumn (48.6–80.4% versus 69.7–93.8%). Conversely, during autumn chironomid larvae increased in the diets of roach (37.1%) and chub (28.2%). Other common prey in the diets of roach and chub this season were simuliid larvae (12.1%) and dipteran nymphs (15.1%), respectively. Ephemerellid nymphs were consumed during spring mostly by roach (23.2%) and chub (55.3%), being the prevalent prey for the latter species. Ephemeropteran imagos (82.3%) dominated the animal diet of chub during summer. Prey of terrestrial origin (dipteran adults and Formicidae) were mostly found in the diet of the roach during all seasons, but especially during spring and summer (16.3–16.4% versus 10.8%). During this season there was also an increase in the proportions of Formicidae and hydropsychid larvae in the diets of chub (8.8%) and roach (24.3%), respectively.

For the DCA only animal prey categories accounting at least once for more than 1% of total numbers, for at least one cyprinid species, were used (Appendix 1–3). The representation of the data matrix achieved by the first two axes generated by the DCA is presented in Fig. 2. The eigenvalues of axis I and axis II were 0.66 and 0.34, respectively. The ordination of species/seasons along both axes was mostly related to the consumption of seasonal prey. Chub/summer and its major prey (ephemeropteran imagos) had high scores on axis I whereas, irrespective of the season, barbel, carp, goldfish, gudgeon, nase and their regular prey, (dipteran larvae) had low scores. Chub/spring and their main prey (ephemerellid nymphs) had high scores on axis II whereas roach/summer and their main prey (Formicidae, dipteran adults and hydropsichid larvae) had the lowest scores. On the subsequent axis of the ordination (eigen values <0.10) there were no consistent trends on the positions of the species/seasons and prey categories, so they are not presented here. In an attempt to enlarge the remainder of the diagram (to avoid compression of the ordination space) a second DCA was performed without displaying roach and chub diets. Results of this analysis were qualitatively similar to those for the previous DCA and did not convey any further information.

From the results of DCA it is clear that (i) chub displayed a much larger seasonal variation in prey use than any other species; (ii) roach was the species most closely resembling chub in prey use but during spring and summer these species fed upon different prey, which were rarely used by the remaining species; (iii) irrespective of
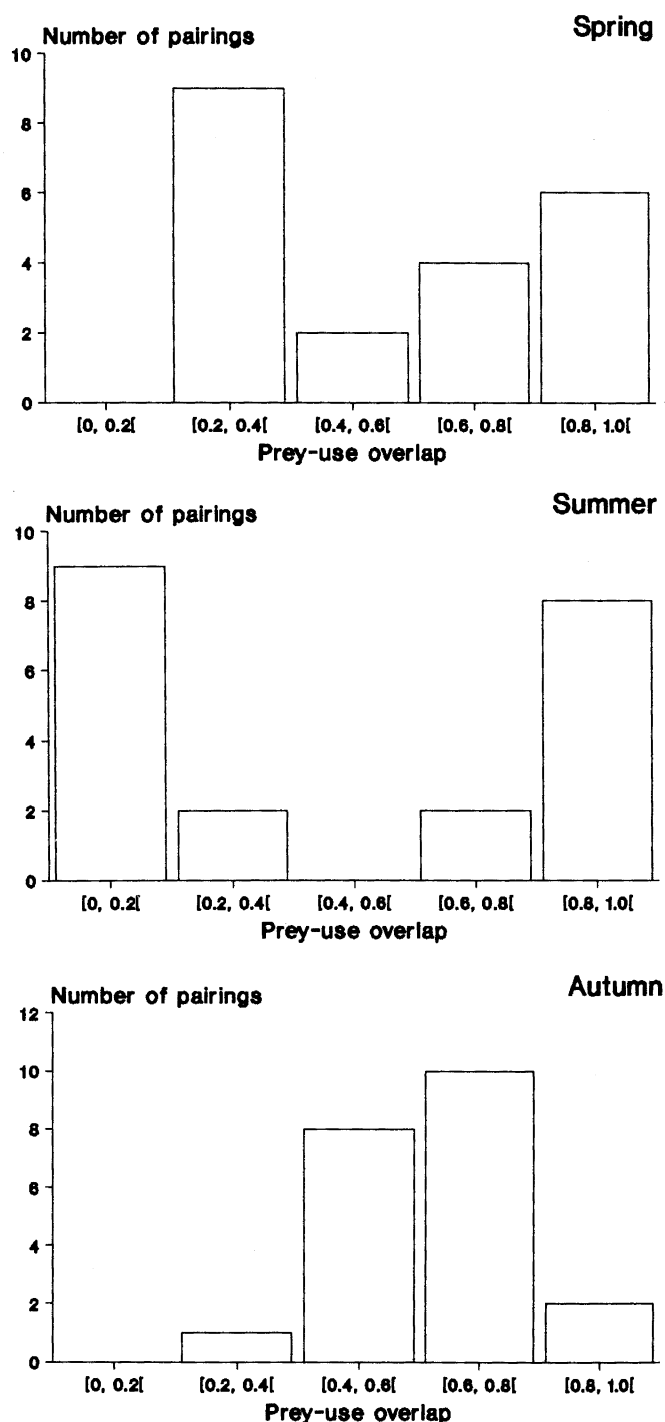


**Fig. 3.** Frequency histograms for prey-use overlaps among cyprinids during each season

the season, barbel, carp, goldfish, gudgeon and nase showed only slight differences in prey use; and (iv) differences in prey use among all cyprinids were much less important in autumn.

Animal prey breadth for roach, carp and gudgeon displayed a much less seasonal variation than it did for the remaining species (Table 3). The latter presented a trend towards narrower prey breadths in summer and more generalised feeding in autumn. Roach and chub presented the largest prey breadth in all seasons.

**Table 3.** Variation of animal prey breadth across seasons. Fish codes as in Table 1

|        | BAR   | CAR   | CHP   | CYP   | GOB   | LEU   | RUT   |
|--------|-------|-------|-------|-------|-------|-------|-------|
| Spring | 0.789 | 0.794 | 0.956 | 0.801 | 0.972 | 1.621 | 2.094 |
| Summer | 0.352 | 0.540 | 0.374 | 0.734 | 0.970 | 0.761 | 1.995 |
| Autumn | 1.659 | 1.071 | 1.107 | 0.807 | 0.993 | 2.263 | 2.206 |

Animal prey overlap displayed a large seasonal variation (Appendix 4–6). No pairs with overlaps less than 0.20 were observed in spring and autumn whereas in summer 9 pairs out of 21 showed overlaps less than 0.20 (Fig. 3). These latter pairs involved either roach or chub and each of the other species, but overlap between roach and chub had also a low value (0.25). In autumn, overlaps equal to or exceeding 0.80 were obtained only for 2 pairs (goldfish × carp; goldfish × gudgeon) whereas 6 and 8 overlapping pairs were found in spring and summer, respectively. These high overlaps were always obtained between barbel, carp, goldfish, gudgeon and nase. In autumn, of the 21 pairs, 18 pairs displayed overlaps between 0.40 and 0.80.

## Discussion

The results of this study indicate that cyprinids do show differences in food resource use. Carp, nase, goldfish and barbel were the primary consumers of plant material whereas gudgeon, roach and chub used plants to a much lesser extent. The former five species preyed mainly upon chironomid larvae throughout the year. Conversely roach and chub, especially the latter, displayed a large seasonal variation in prey use, relying on chironomid larvae only during autumn. Roach used terrestrial insects (e.g. Formicidae, dipteran adults) to a much greater extent than did any other species. More detailed accounts of barbel and chub feeding ecology are presented elsewhere (Magalhães 1992, 1993).

Two primary factors are probably involved in producing overall feeding differences among cyprinids. First, diets may be shaped by morphologically based feeding limitations. Barbel, nase, goldfish and carp have long guts and allometric growth of the gut, whereas gudgeon, roach and chub have short guts and an isometric growth of the gut (Magalhães 1990). As elongation of the gut is likely to result in more efficient processing of plant diets (Hofer 1991), the former species may find plant material much more profitable than the latter, so that it is worth including in their diets. In addition, barbel, gudgeon and nase have mouths in an inferior position, which may constrain their use of terrestrial insects, which are found primarily on the stream surface (Garman 1991). Conversely, roach have a mouth in a superior position, which may allow them to feed on terrestrial insects much more effectively than any other species. Second, differences in food resource use may be related to differences in space use. According to Grossman et al. (1987) chub, carp, barbel and gudgeon are most likely to occur in the upper water column, in the mid-water column, in the lower water column and close to the substrate, respectively. Among these species, chub preyed heavily on ephemeropteran larvae and imagos which are often found in drift (Waters 1972) whereas all the remaining species preyed mainly on chironomid larvae which are mostly associated with the substrate (Pinder 1986).

The degree of food resource overlap among the three dominant species displayed a large seasonal variation. Roach, barbel and chub used the same food resources during autumn (plant material and chironomid larvae) but during spring, and specially during summer, overlap in resource utilisation between all species was much lower. In fact a marked drop in food-resource overlap occurred from spring to summer owing to (i) the increased specialisation on chironomidae larv by barbel; (ii) the intake of temporarily abundant prey (ephemeropteran imagos) by chub; and (iii) the switching from aquatic to terrestrial (Formicidae and dipteran adults) prey feeding by roach. Reductions in diet overlap among co-occurring species during summer, although less marked, have also been reported for other Iberian freshwater fish assemblages (Granado-Lorencio and Garcia-Novo 1986; Rodriguez-Jimenez 1987).

These seasonal trends in resource use by fish are probably related to fluctuations in the abundance and diversity of aquatic invertebrates. The aquatic invertebrate groups of greatest importance for fish (e.g. Ephemeroptera, Chironomidae, Simuliidae, Hydropsychidae) all present aerial adult stages. In Iberian streams, as in most temperate streams (Mason and Macdonald 1982), emergence occurs from late spring through early autumn (Montanez and Lobon-Cervia 1986; Puig et al. 1986; Graça et al. 1989), thus presumably leading to a progressive decrease in prey availability throughout this period. Moreover, prey availability is most likely further decreased, owing to the increase in fish metabolic demands with increasing temperature (Persson 1983), and because during summer drought fish often become confined to shrinking pools of high fish density (Sostoa and Lobon-Cervia 1989; personal unpublished observations). In autumn prey availability is probably at its lowest.

Fish seemed to react to food resource scarcity through specialisation during summer on "exclusive", temporarily abundant prey (e.g. ephemeropteran imagines and terrestrial insects), resulting in increased resource partitioning within the fish assemblage, followed in the autumn by a shift to alternative, less profitable but superabundant and easily accessible food (plant material). Enhanced diet segregation and shifts to underutilised food during periods of food depression are commonly reported in fish literature (e.g. Persson 1983; Schmitt and Holbrook 1986; Persson 1987; Prejs and Prejs 1987).

Seasonal variation in resource availability has been considered to reinforce the importance of competition in the structuring of natural communities: in seasonally heterogeneous environments ecological crunches may occur as predictable events, each year, during the season when resources are in shorter supply (Dubowy 1988;

Persson and Johansson 1992). During such "lean" seasons of resource limitation, foraging optimisation strategies that maximise resource partitioning and/or shifts to alternative less profitable food will be favoured, whereas during "fat" seasons species may have high overlap in food resources (Dubowy 1988; Persson and Johansson 1992). Seasonal variation in food resource use by cyprinids fish may thus be promoted to avoid competition for food during periods of reduced prey availability; competition for food would be potentially intense during summer/autumn and null or weak during spring, when resources are not limited (or at least are more abundant). This hypothesis is tentative and warrants further research.

Other cyprinids than roach, barbel and chub were both much rarer and had a narrower diet breadth. They used the same resources over all seasons (plant material and chironomid larvae) and presented a great degree of diet overlap among them and with barbel. Lack of diet segregation among these species may partly be due to the high taxonomic level of chironomid identification used

in this study; the use of broad food categories often inflates overlap values (Greene and Jaksic 1983). Further studies, with larger samples, are needed to sort out accurately the patterns of food resource use by these species.

The results of the present study suggest that food resource use by cyprinids is a dynamic process. To understand whether or not seasonal and interspecific changes in feeding are determined by resource limitation and interspecific interactions more information is needed on food availability and on the demographic effects of such changes. Further laboratory and long-term field studies are essential to assess what factors are involved in the structuring of Iberian stream fish communities, in ecological time.

**Appendix 1.** Percent number of the main animal prey categories in the diet of each cyprinid during spring

| Prey category | BAR | CAR | CHO | CYP | GOB | LEU | RUT |
|---|---|---|---|---|---|---|---|
| Ostracoda | 0.1 | 0.8 | 0.0 | 3.0 | 0.0 | 0.0 | 0.0 |
| Mollusca | 2.7 | 0.1 | 0.0 | 0.6 | 0.0 | 2.8 | 0.0 |
| Baetidae – nymphs | 2.2 | 0.6 | 3.8 | 0.0 | 7.8 | 7.5 | 3.2 |
| Caenidae – nymphs | 1.0 | 1.6 | 8.9 | 5.7 | 0.1 | 1.6 | 0.4 |
| Ephemerellidae nymphs | 5.4 | 2.1 | 0.0 | 0.4 | 6.4 | 55.3 | 23.2 |
| Ephemeroptera imagos | 0.1 | 0.4 | 0.0 | 2.4 | 0.1 | 0.9 | 10.0 |
| Odonata | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.6 | 0.4 |
| Corixidae | 0.1 | 0.3 | 0.0 | 0.0 | 0.1 | 0.3 | 1.4 |
| Naucoridae | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.2 | 0.0 |
| Ceratopogonidae larvae | 0.1 | 0.3 | 0.0 | 2.4 | 0.1 | 0.0 | 0.4 |
| Simuliidae – larvae | 1.7 | 0.1 | 0.0 | 1.0 | 14.9 | 0.9 | 7.3 |
| Chironomidae larvae | 83.4 | 90.3 | 74.7 | 75.0 | 69.7 | 16.4 | 24.5 |
| Diptera – nymphs | 0.4 | 1.7 | 0.0 | 4.3 | 0.4 | 0.0 | 3.2 |
| Diptera – adults | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 1.2 | 16.4 |
| Dytiscidae – larvae | 0.1 | 0.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Coleoptera – adults | 0.3 | 0.3 | 0.0 | 0.4 | 0.1 | 2.2 | 1.4 |
| Hydropsychidae larvae | 1.4 | 0.0 | 3.8 | 0.2 | 0.2 | 1.9 | 4.1 |
| Formicidae | 0.2 | 0.0 | 3.8 | 2.0 | 0.0 | 1.9 | 3.2 |
| Other prey | 0.6 | 0.4 | 5.0 | 2.6 | 0.1 | 5.3 | 0.9 |

Fish codes: BAR, *Barbus bocagei*; CAR, *Carassius auratus*; CHP, *Chondrostoma polylepis*; CYP, *Cyprinus carpio*; GOB, *Gobio gobio*; LEU, *Leuciscus pyrenaicus*; RUT, *Rutilus alburnoides*

**Appendix 2.** Percent number of the main animal prey categories in the diet of each cyprinid during summer

| Prey category | BAR | CAR | CHO | CYP | GOB | LEU | RUT |
|---|---|---|---|---|---|---|---|
| Ostracoda | 0.0 | 0.5 | 2.4 | 0.0 | 0.0 | 0.0 | 0.0 |
| Mollusca | 0.5 | 0.5 | 0.0 | 0.9 | 1.2 | 1.3 | 0.0 |
| Baetidae – nymphs | 0.5 | 4.3 | 0.0 | 0.9 | 5.5 | 0.4 | 4.9 |
| Caenidae – nymphs | 1.5 | 5.4 | 0.0 | 8.6 | 0.3 | 0.1 | 4.9 |
| Ephemerellidae nymphs | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.1 | 0.0 |
| Ephemeroptera imagos | 0.9 | 1.7 | 0.0 | 0.3 | 0.2 | 82.3 | 9.8 |
| Odonata | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 1.6 |
| Corixidae | 0.2 | 0.0 | 0.0 | 0.5 | 0.0 | 1.2 | 0.0 |
| Ceratopogonidae larvae | 0.2 | 0.0 | 0.0 | 0.3 | 0.2 | 0.0 | 0.0 |
| Simuliidae larvae | 0.2 | 0.0 | 0.0 | 0.3 | 9.3 | 0.1 | 1.6 |
| Chironomidae larvae | 93.8 | 82.7 | 90.3 | 83.6 | 75.2 | 0.6 | 4.9 |
| Diptera – nymphs | 0.3 | 0.5 | 0.0 | 2.0 | 1.6 | 0.1 | 4.9 |
| Diptera – adults | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 16.3 |
| Dytiscidae – larvae | 0.1 | 0.5 | 0.0 | 0.9 | 0.0 | 0.0 | 1.6 |
| Coleoptera – adults | 0.7 | 1.1 | 0.0 | 0.2 | 0.2 | 0.3 | 3.2 |
| Hydropsychidae larvae | 0.6 | 0.0 | 0.0 | 0.0. | 5.6 | 2.6 | 24.3 |
| Formicidae | 0.2 | 0.0 | 0.0 | 0.4 | 0.0 | 8.8 | 17.9 |
| Other prey | 0.2 | 2.8 | 7.3 | 0.9 | 0.6 | 2.0 | 4.1 |

**Appendix 3.** Percent number of the main animal prey categories in the diet of each cyprinid during autumn

| Prey category | BAR | CAR | CHP | CYP | GOB | LEU | RUT |
|---|---|---|---|---|---|---|---|
| Ostracoda | 0.0 | 1.2 | 5.7 | 9.6 | 1.1 | 0.0 | 0.0 |
| Mollusca | 0.1 | 0.0 | 0.0 | 0.2 | 0.0 | 10.1 | 0.0 |
| Baetidae – nymphs | 8.4 | 1.7 | 0.0 | 0.5 | 10.1 | 2.5 | 8.8 |
| Caenidae – nymphs | 14.3 | 10.0 | 0.0 | 4.6 | 1.1 | 10.1 | 4.1 |
| Ephemeroptera imagos | 0.0 | 1.2 | 0.0 | 0.0 | 0.0 | 1.0 | 0.7 |
| Odonata | 0.6 | 0.0 | 0.0 | 0.2 | 0.0 | 2.5 | 0.0 |
| Corixidae | 2.4 | 0.0 | 0.0 | 0.0 | 0.0 | 3.0 | 1.4 |
| Ceratopogonidae larvae | 0.1 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 |
| Simuliidae larvae | 18.2 | 2.1 | 17.1 | 0.2 | 8.4 | 8.0 | 12.1 |
| Chironomidae larvae | 48.6 | 74.6 | 63.0 | 80.4 | 73.1 | 28.2 | 37.1 |
| Diptera – nymphs | 0.9 | 3.0 | 2.8 | 0.0 | 0.6 | 15.1 | 10.8 |
| Diptera – adults | 0.2 | 0.4 | 0.0 | 0.0 | 0.0 | 5.0 | 10.8 |
| Dytiscidae – larvae | 0.1 | 0.0 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 |
| Coleoptera – adults | 0.1 | 1.2 | 0.0 | 0.0 | 0.6 | 1.5 | 3.4 |
| Hydropsychidae larvae | 4.5 | 0.4 | 0.0 | 0.0 | 4.4 | 5.5 | 6.8 |
| Formicidae | 0.5 | 1.7 | 0.0 | 1.1 | 0.0 | 3.0 | 2.0 |
| Other prey | 1.0 | 2.5 | 11.4 | 1.5 | 0.6 | 4.5 | 2.0 |

**Appendix 4.** Prey-use overlap between species pairs during spring

| Species | CAR | CHP | CYP | GOB | LEU | RUT |
|---|---|---|---|---|---|---|
| BAR | 0.89 | 0.80 | 0.80 | 0.80 | 0.31 | 0.31 |
| CAR | | 0.77 | 0.81 | 0.74 | 0.22 | 0.31 |
| CHP | | | 0.85 | 0.74 | 0.31 | 0.36 |
| CYP | | | | 0.77 | 0.26 | 0.36 |
| GOB | | | | | 0.32 | 0.42 |
| LEU | | | | | | 0.53 |

**Appendix 5.** Prey-use overlap between species pairs during summer

| Species | CAR | CHP | CYP | GOB | LEU | RUT |
|---|---|---|---|---|---|---|
| BAR | 0.87 | 0.91 | 0.88 | 0.78 | 0.04 | 0.10 |
| CAR | | 0.85 | 0.92 | 0.82 | 0.06 | 0.20 |
| CHP | | | 0.84 | 0.76 | 0.02 | 0.09 |
| CYP | | | | 0.80 | 0.05 | 0.16 |
| GOB | | | | | 0.06 | 0.20 |
| LEU | | | | | | 0.25 |

**Appendix 6.** Prey use overlap between species pairs during autumn

| Species | CAR | CHP | CYP | GOB | LEU | RUT |
|---|---|---|---|---|---|---|
| BAR | 0.59 | 0.62 | 0.50 | 0.66 | 0.60 | 0.72 |
| CAR | | 0.72 | 0.84 | 0.81 | 0.52 | 0.54 |
| CHP | | | 0.70 | 0.74 | 0.24 | 0.54 |
| CYP | | | | 0.77 | 0.44 | 0.44 |
| GOB | | | | | 0.46 | 0.62 |
| LEU | | | | | | 0.72 |

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