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Ontogenetic Dietary Shifts in a Predatory Freshwater Fish Species: The Brown Trout as an Example of a Dynamic Fish Species

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Additional information is available at the end of the chapter

1. Introduction

The brown trout (*Salmo trutta*) is a species of Eurasian origin, but at has become naturalized in many other parts of the world. It has an outstanding socio-economic importance, both in commercial and sport fisheries, and it is frequently used as tourist attraction [1,2]. The case of brown trout is a clear example of a 'dynamic' fish species, as its diet and feeding behaviour can vary greatly among individuals, age classes, seasons and rivers. The composition of brown trout diet is strongly influenced by environmental and biotic factors. For example, water temperature plays an important role, as it influences food intake and the activity of fishes [3], but also the emergence and activity of aquatic insects or other potential prey items. Also water flow rate can be extremely important for drifting feeders such as brown trout, as they regulate food availability. The are many abiotic factors that influence feeding behaviour, but in general, biotic factors such as the locomotor ability of fishes, accessibility, abundance and antipredator behaviour of prey are thought to be the most important factors in the determination of the diet and feeding strategies in fishes. Usually not all the available prey is consumed by the predator, a feature that allows biologists to distinguish between trophic base and trophic niche (Figure 1). The trophic base consists of all potential prey items that the brown trout is able to consume and it is determined by the feeding habits of the fish, the size of the mouth and the anatomical characteristics of its digestive tract. However, the trophic niche is the variety of organisms that are really consumed by the predator, which depends on different factors that play an important role when choosing criteria prey items as, for example, prey abundance, including site-specific

prey accessibility, prey size, energetic selection criteria and prey preference. In this context, the trophic niche for brown trout is very flexible and is usually broader in adults than juveniles.
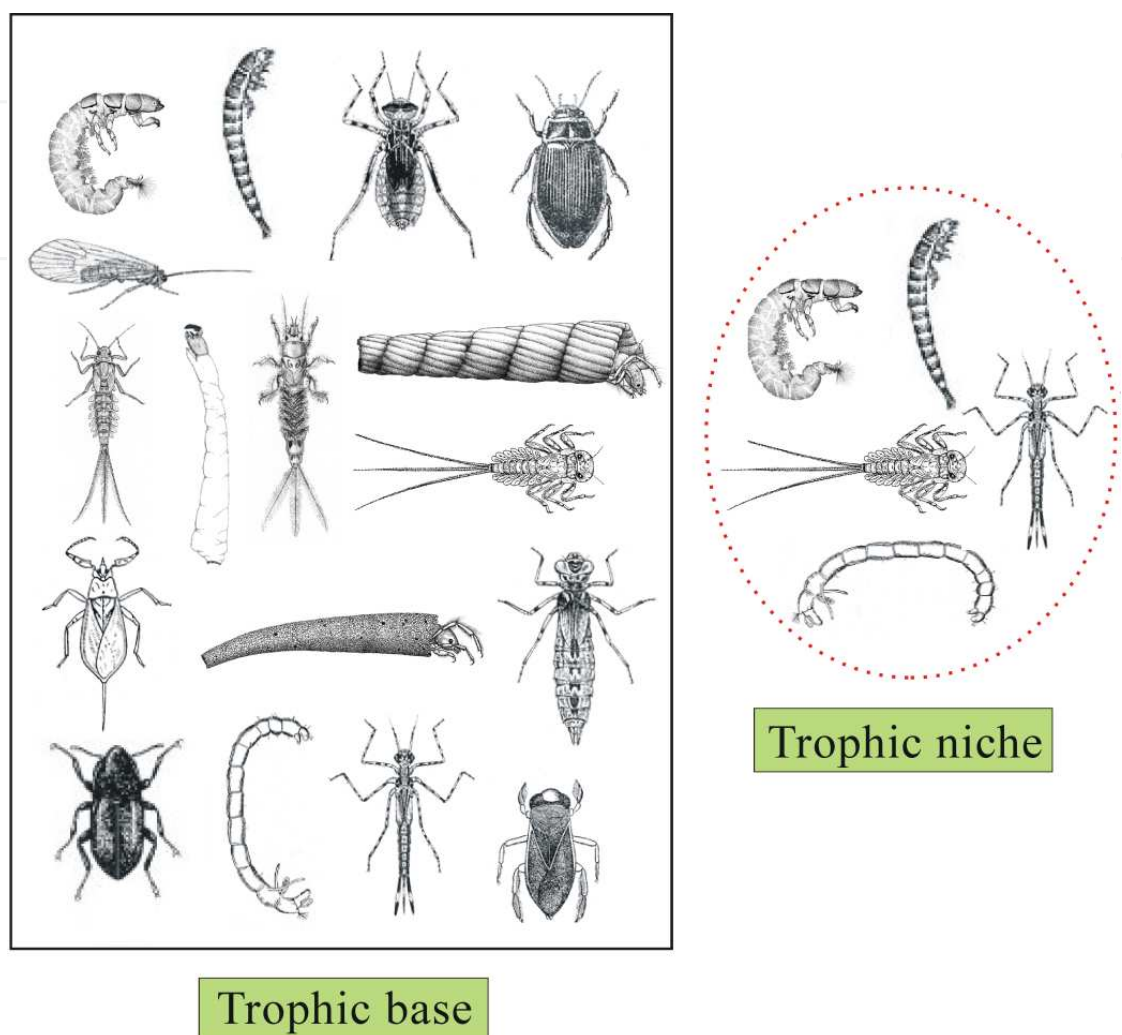

Figure 1. Graphical example of the trophic base and niche for brown trout.

A knowledge of the foraging ecology of fishes is fundamental to understanding the processes that function at the individual, population and community levels since the factors that influence the acquisition and assimilation of food can have significant consequences for the condition, growth, survival and recruitment of fishes [4]. In this context, the development of effective conservation programmes requires a clear understanding of fish ecological require‐ments, so the knowledge of its feeding habits is essential to achieve this objective. For example, the knowledge on how food is shared among individuals of the same population is critical for understanding its functioning. Hence, conclusions of field studies on feeding could help wildlife managers to take measures to preserve fish populations, especially for threatened and exploited species. In this chapter we will briefly discuss the variables that are involved in the feeding behaviour of brown trout as an example of a predatory freshwater fish species.

2. Methodology and types of analysis employed in feeding and ontogenetic dietary shifts studies

The majority of researchers have conducted feeding studies in feral fish populations based on diet descriptions of the stomach contents, using occurrence, numerical, gravimetric and volumetric methods. The main disadvantage of feeding studies is that fish are systematically killed in order to study their stomach contents. However, due to the decline of many natural fish populations, the studies that use non-lethal methods are now more frequent. Different techniques have been used to collect stomach contents without harming the fish such as gastric lavage, emetics or forceps [5-7]. The effectiveness of the gastric lavage is not related to the size of the trouts, but rather to the prey's own morphological characteristics, the degree of repletion of the stomach and the extent of digestion of the food [8]. The effectiveness of this method is inversely related to the degree of repletion [8].

2.1. Prey selection analysis

Prey selection is an important part of fish feeding ecology. In order to study prey selection of fishes, several indices have been employed, such as the Savage index [9] and Ivlev's selectivity index [10]. The Savage index varies from zero (maximum negative selection) to infinity (maximum positive selection), whereas possible values of Ivlev's selectivity index range from –1 to +1, with negative values indicating rejection or inaccessibility of the prey, zero indicating random feeding, and positive values indicating active selection. Moreover, several researchers have demonstrated that studies based on food selection provide insight into factors involved in prey choice of brown trout [e.g. 11-13].

2.2. Stomach content analysis

In the early 80s Hyslop reviewed the methods used to study the feeding behaviour of fishes and their application to stomach content analyses [14]. Hyslop pointed out the difficulties in the application of these methods and, where appropriate, proposed alternative approaches. Food overlap between age classes can be assessed with Schoener's overlap index [15]. The overlap index has a minimum of 0 (no prey overlap), and a maximum of 1 (all prey items in equal proportions), and diet overlap is usually considered significant when value of the index exceeds 60% [16]. A chi-square ($\chi 2$) test can be used to test for significant differences in the diet composition between age classes [e.g. 17].

2.3. Graphical methods

Graphical methods proposed by Costello [18] and Tokeshi [19] were used to illustrate the relative importance of prey species and to assess the feeding strategy of fish species. Amundsen and collaborators designed an alternative method of Costello graphical method, by plotting prey abundance (Ai) (y - axis) against the frequency of occurrence in diet (Fi) (x - axis) for each prey species. Information on prey importance, feeding strategy and niche breadth can be

obtained by examining the distribution of points along the diagonals and axes of the graph [20] (Figure 5 and Section 4.1).

2.4. Niche breadth indexes

Marshall and Elliott compared univariate and multivariate numerical and graphical techniques for determining inter- and intraspecific feeding relationships in estuarine fish [21] and on the basis of this study, different indices have been employed by ichthyologists to study niche breadth and diet specialisation. Generally, the Shannon diversity index was combined with the Levin's index to assess niche breadth [21] and the evenness index was used to evaluate diet specialisation, these being indices employed to study feeding habits in brown trout populations [22,23]. However, stable isotope analysis is a potentially powerful method of measuring trophic niche width, particularly when combined with conventional approaches [24]. For this reason, over the past two decades this methodology has been employed to study the trophic interactions and dietary niche in different fish species, and it has been recently used to study ontogeny and dietary specialization in brown trout [25,26].

2.5. Multivariate approaches

Recently prey trait analysis has been proposed as a functional approach to understand mechanisms involved in predator–prey relationships [27,28]. Despite the disadvantages of this methodology [29 and references therein], it has been used in order to get a deeper insight into the mechanisms that regulate diet composition and feeding habits of fishes, providing extremely valuable ecological information and complementing traditional diet analysis [23,29,30]. For the application of prey trait analysis, researchers have to use the same trait database and trait analyses as de Crespin de Billy [27]. To evaluate the potential vulnerability of invertebrates to fish predation, de Crespin de Billy and Usseglio-Polatera created a total of 71 different categories for 17 invertebrate traits [(1) macrohabitat, (2) current velocity, (3) substratum, (4) flow exposure, (5) mobility/attachment to substratum, (6) tendency to drift in the water column, (7) tendency to drift at the water surface, (8) trajectory on the bottom substratum or in the drift, (9) movement frequency, (10) diel drift behaviour, (11) agility, (12) aggregation tendency, (13) potential size, (14) concealment, (15) body shape (including cases/tubes), (16) body flexibility (including cases/tubes) and (17) morphological defences] [28]. The information of this trait database is structured using a 'fuzzy coding' procedure; thus, a score is assigned to each taxon describing its affinity for each category of each trait, with '0' indicating 'no affinity' to '5' indicating 'high affinity'. The taxonomic resolution (order, family and genus) use in the classification process corresponds to the lowest possible level of determination of taxa in fish gut contents. When identification to genus is not possible or in the case of missing information for a certain genus, the value assign for a trait is that of the family level, using the average profile of all other genus of the same family. Additionally, all the taxa and their assigned scores for each category can be found in previous works [27,28]. Prey trait analysis should be carried out with the software R (version 2.11.1), its ADE4 library for the analysis in R is free and downloadable at http://cran.es.r-projet.org/. Finally, the analysis of prey traits has provided ichthyologists with important clues for understanding the ontogenetic dietary shifts

in freshwater fish species. As shown in sections 4 and 5, it is an important tool to disentangle the food resource partitioning among both sympatric age classes and fish species.

3. Diet composition of newly emerged brown trout fry

In brown trout populations there is strong evidence for a critical period with high mortality in the first few weeks after fry emergence [3]. Furthermore, the most critical stage for population regulation in the whole life cycle is the density-dependent mortality of young trout in the first few weeks of the life cycle soon after the young fish start to feed [3 and references therein]. Thus, first feeding of newly emerged fry is very important for brown trout survival in this phase of the life cycle, and in newborns of brown trout first feeding can occur even prior to emergence [13,31,32]. In this sense, the feeding behaviour of newly emerged brown trout fry has been studied in both laboratory conditions and in natural spawning areas. Results of those studies show that feeding in recently emerged fry can be initiated before complete yolk exhaustion [13,31,32]. Zimmerman and Mosegaard observed that alevins of brown trout began feeding in experimental conditions when yolk constituted approximately 40% of the total alevin dry weight [31]. Other researchers have indicated that brown trout fry under natural conditions start feeding when having almost 30% of yolk sac remaining compared to the presumed original size of the yolk sac at hatching [32], while in a recent study no food particles have been found in the stomachs of fry having >10% of the yolk sac remaining [13].

The optimal foraging theory (OFT) explains adaptation via natural selection through quantitative models, which led to a better understanding of foraging behaviour. Hence, OFT predicts that predators should select prey that maximise the energetic gains available in relation to the energetic costs of capturing, ingesting and digesting the prey [33,34]. In this context, Many researchers have found that chironomid larvae and baetid nymphs seem to be the most important food items for newborns in different geographical areas [e.g. 13,32,35]. These are probably the most accessible invertebrates living in the gravel interstices on nesting grounds at the moment of emergence, providing over 80% of the energetic input [13]. However, although chironomid larvae and baetid nymphs seem to be the most important food items for newborns, newly emerged brown trout fry can show differences in the selection of these prey items. Although Baetidae is abundant in the benthos, this taxon is negatively selected according to Ivlev's selectivity index, whereas Chironomidae remains positively selected (Figure 2), demonstrating that abundance of prey items in the benthos is not the only factor explaining the complex mechanism that operates in the food selection during this phase of the ontogeny. Thus, prey size may affect the prey ingestion in early fish larvae, and much literature focuses on the relationship between prey size and mouth size as the primary factor of prey selection [e.g. 36]; but in general, other factors apart from size, such as locomotor skills of fish or accessibility and antipredator behaviour of prey items play an important role in feeding behaviour. These hypotheses that could explain the absence of some items in the stomachs in spite of their abundance in the benthos [13].
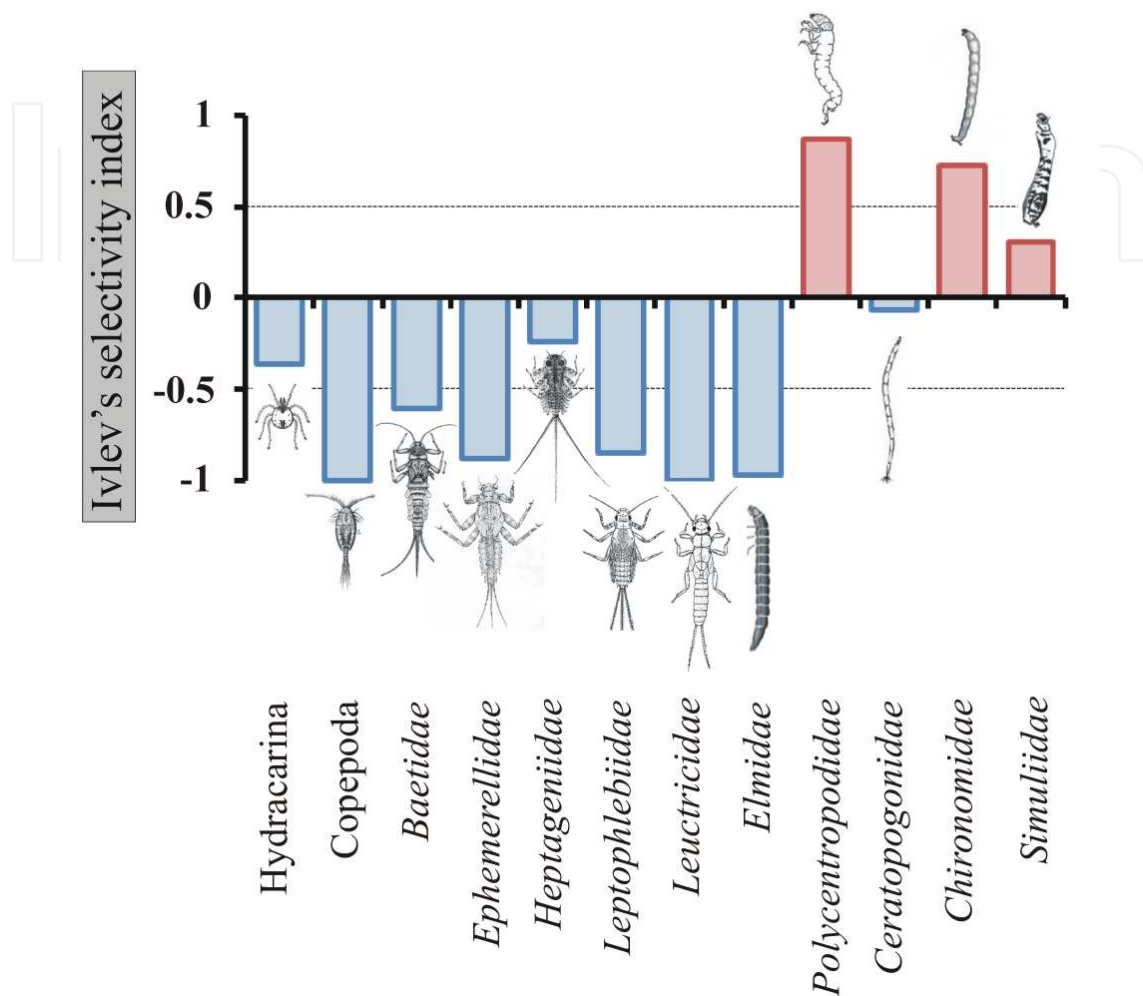
Figure 2. Prey selectivity according to Ivlev's selectivity index of newly emerged brown trout fry in the River Iso (NW Spain) (modified from [13]).

The feeding diversity of juvenile fishes is generally greater than during the larval period, and there is often an increase in the importance of species-specific dietary traits [4]. However, recent studies have demonstrated that at the moment of complete yolk absorption, the fry shows a dramatic shift in niche breadth, which might be related to the improvement of swimming and handling ability of fry for capturing and ingesting both aquatic invertebrates and aerial imagoes [13].

A common practice in many countries associated with river restoration is the rehabilitation of spawning sites with different techniques [37], but recently different authors have emphasized the importance of the complete recolonization of spawning grounds by benthic macroinvertebrates, including first instars, in order to assure the presence of the required amount of prey for the feeding of young fry after restoration works [13]. Hence, at the moment of hatching, a

certain density of small prey should be present in the gravel, as searching for food is limited to the nest area and fry forage on available prey [13].

4. Diet changes with age: Food resource partitioning and change in piscivorous behaviour

In Salmonid populations, dominant fishes may exclude less aggressive individuals, limiting their access to resources within patches. For example, dominant Atlantic salmon *Salmo salar* Linnaeus, 1758 may exclude subordinates from high-quality patches by intimidation or direct aggression [38,39]. However, subordinate fish may gain access to food by using high-quality patches when dominants are absent [40] or may be constrained to foraging in marginal areas [41]. When brown trout and Atlantic salmon co-occurred, trout has been observed to be dominant over salmon, holding feeding stations by swimming actively in the central regions of food patches, whereas salmon occupied the margins, generally remaining stationary on the stream bed [41]. Moreover, in habitats in which food is patchily distributed in time and space, fishes can benefit by moving between patches [42,43], with subordinate animals moving little in comparison with dominant fishes [39].

During their life history brown trout undergo ontogenetic habitat shifts [44 and references therein] due to changes in habitat selection operating at multiple spatial scales [44]. These shifts during fish life stage transitions may be accompanied by a marked reduction in intra-specific competition in the fish population, facilitating the partitioning of resources [e.g. 45,46]. Moreover, dietary analyses usually show high values of diet overlap among age classes, but the differences in the use of feeding habitat and behavioural feeding habits are important adaptive features that may reduce the intra-specific competition in the population [23]. Thus, although the diet comparison among age classes can show a remarkable similarity in their prey utilization patterns, sometimes the high overlap values may not indicate competition, since fishes can adopt different strategies to overcome competence, i.e. resource partitioning among age classes can occur at five different levels: (1) diet composition; (2) prey selection; (3) prey size; (4) habitat utilization for feeding; and (5) niche breadth. Also stomach fullness can vary among age classes as shown in section 4.6.

4.1. Changes in diet composition with age

In brown trout, as in many other fish species, there is normally a change in the diet composition during the life of the fish. Thus, juveniles mainly consume prey items linked to the bottom of the river, many of them interstitial, i.e. living among grains of sand or gravel. Opposite, terrestrial invertebrates and fishes are important resources for large trouts. The contribution of these food items to fish diets increases with predator size or age because larger fish can feed on a wider range of preys as shown in Figures 3 and 4. Within a population, the percentage of the most important prey items change with age. In one study of a river in Italy the percentage of plecopteran nymphs in the diet tended to increase with the individual's age [17]. In another study, *Baetis* spp. dominated in all age classes in different proportions, whereas the percentage

of caddisflies with cases, (*Allogamus* sp.) and mayflies (*Ecdyonurus* spp.) tended to increase with age [23]. Thus, as shown in Table 1, each age class consumes significantly different prey items, Chironomidae being the most frequently consumed prey item in age 0+ and age 3+ (44.41% and 29.84% respectively) and aerial imagoes of Ephemeroptera in age 1+ and age 2+ (77.49% and 49.08% respectively).

Regarding the changes in the proportion of terrestrial invertebrates consumed by trouts during the ontogeny, previous studies have demonstrated that aquatic invertebrates dominated the diet in all age classes [23,47], but it seems clear that terrestrial invertebrates were more frequently consumed by older trout [17,23,48], terrestrial organisms being important prey during warmer seasons in salmonids [49,50].
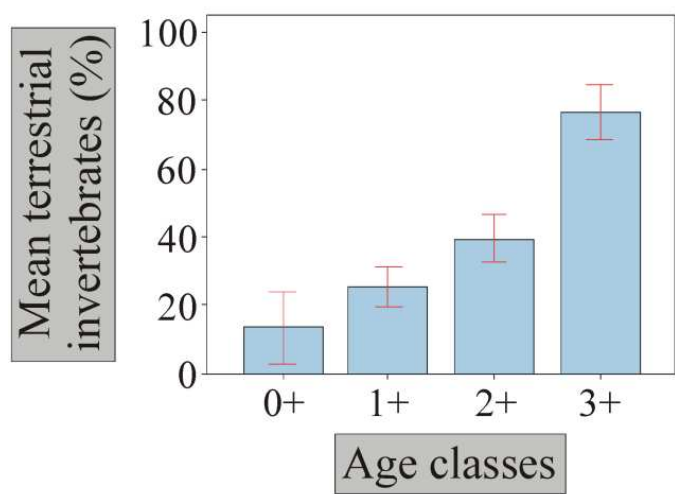

Figure 3. Percentage of terrestrial invertebrates (in terms of relative abundance) consumed by each age class of *Salmo trutta* in the River Anllóns (NW Spain) during summer. Error bars represent 95% confidence intervals.
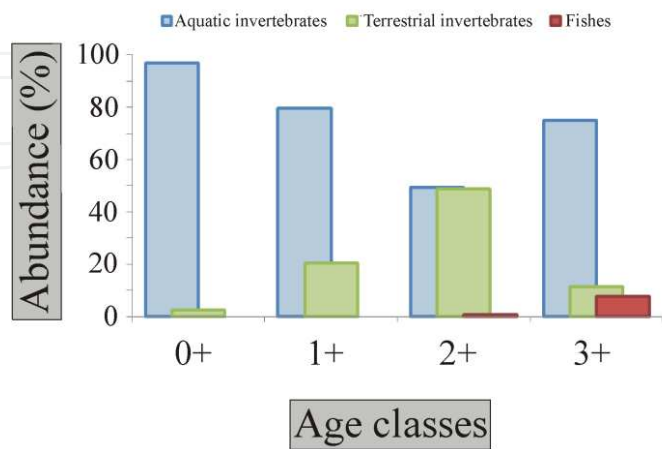

Figure 4. Diet composition consumed by each age class of *Salmo trutta* in the River Lengüelle (NW Spain) during summer.

| | Age 0+ | | | Age 1+ | | | Age 2+ | | | Age 3+ | | |
| | Diet | Ivlev | | Diet | Ivlev | | Diet | Ivlev | | Diet | Ivlev | |
	(%)	Benthos	Drift	(%)	Benthos	Drift	(%)	Benthos	Drift	(%)	Benthos	Drift
Aquatic invertebrates												
Oligochaeta gen. sp.	0.14	-0.68	1	0	-1	—	0	-1	—	0	-1	—
Ancylidae	2.07	0.04	1	0.15	-0.85	1	0	-1	—	0	-1	—
Hydrobiidae	2.48	0.90	0.82	2.11	0.88	0.79	0.92	0.74	0.58	4.84	0.95	0.90
Lymnaeidae	1.66	-0.18	-0.01	1.96	-0.10	0.07	20.64	0.79	0.85	29.03	0.85	0.89
Sphaeriidae	0	-1	—	0.53	0.59	1	1.38	0.82	1	0	-1	—
Hydracarina gen. sp.	0.41	0.64	-0.61	0.23	0.43	-0.76	0	-1	-1	0	-1	-1
Ostracoda gen. sp.	0.55	1	1	0.23	1	1	0	—	—	0	—	—
Baetidae	1.93	0.49	-0.06	0.15	-0.63	-0.87	8.72	0.86	0.60	0	-1	-1
Caenidae	5.10	0.94	0.50	0.60	0.59	-0.48	0.46	0.49	-0.57	0	-1	-1
Ephemerellidae	0	-1	-1	0.23	-0.77	-0.86	2.29	0.14	-0.12	0	-1	-1
Ephemeridae	0	—	—	0.08	1	1	0	—	—	0	—	—
Leuctridae	0.55	0.85	1	0.08	0.25	1	0.46	0.82	1	0	-1	—
Aeshnidae	0	—	—	0.08	1	1	0	—	—	0	—	—
Calopterygidae	6.07	1	1	3.78	0.45	0.17	8.72	0.72	0.53	0	-1	-1
Coenagrionidae	0.28	0.61	1	0	-1	—	0	-1	—	0	-1	—
Gomphidae	0.14	-0.13	1	0	-1	—	0	-1	—	0	-1	—
Aphelocheiridae	0.41	-0.27	-0.28	0.08	-0.81	-0.81	0	-1	-1	0.81	0.05	0.05
Gerridae	0.14	1	-0.28	0	—	-1	0	—	-1	0.81	1	0.54
Sialidae	0.14	1	1	0.23	1	1	0	—	—	0	—	—
Dytiscidae	0	—	—	0	—	—	0.46	1	1	0	—	—
Elmidae	0.41	-0.58	-0.56	0.15	-0.83	-0.81	0.46	-0.55	-0.52	0	-1	-1
Brachycentridae	0	-1	—	0.08	-0.64	1	0	-1	—	0	-1	—
Hydropsychidae	2.76	-0.61	0.17	0.45	-0.92	-0.62	0.92	-0.85	-0.36	0.81	-0.87	-0.41
Leptoceridae	0.28	1	1	0	—	—	0	—	—	0	—	—
Limnephilidae	0.55	0.92	1	0.45	0.91	1	0.46	0.91	1	0.81	0.95	1
Philopotamidae	0.14	0.51	1	0	-1	—	0	-1	—	0	-1	—
Polycentropodidae	0	-1	—	0.30	0.25	1	0	-1	—	0	-1	—
Rhyacophilidae	0	-1	—	0	-1	—	0.46	0.49	1	0	-1	—
Sericostomatidae	0.14	1	1	0.15	1	1	0.46	1	1	0	—	—
Chironomidae	44.41	0.31	0.18	4.08	-0.71	-0.76	1.83	-0.86	-0.89	29.84	0.12	-0.01
Simuliidae	15.17	-0.51	-0.18	1.89	-0.92	-0.84	0.92	-0.96	-0.92	12.90	-0.56	-0.26
Tipulidae	0	-1	—	0.08	0.54	1	0	-1	—	0	-1	—
Terrestrial invertebrates												
Ephemeroptera gen. sp.	12.14	—	1	77.49	—	1	49.08	—	1	2.42	—	1
Trichoptera gen. sp.	0.14	—	-0.28	0.45	—	0.30	0	—	-1	0	—	-1
Chironomidae	0.69	—	-0.93	2.04	—	-0.82	0	—	-1	13.71	—	-0.20
Simuliidae	0.69	—	1	0.68	—	1	0	—	—	2.42	—	1

| | Age 0+ | | | Age 1+ | | | Age 2+ | | | Age 3+ | | |
| | Diet (%) | Ivlev | | Diet (%) | Ivlev | | Diet (%) | Ivlev | | Diet (%) | Ivlev | |
		Benthos	Drift		Benthos	Drift		Benthos	Drift		Benthos	Drift
Arachnida gen. sp.	0	—	—	0.08	—	—	0	—	—	0	—	—
Acanthosomatidae	0	—	—	0.08	—	1	0.46	—	1	0	—	—
Psyllidae	0	—	—	0.15	—	1	0	—	—	0	—	—
Chloropidae	0.14	—	-0.28	0	—	-1	0	—	-1	0	—	-1
Diptera gen. sp.	0	—	-1	0.08	—	-1	0	—	-1	0	—	-1
Syrphidae	0	—	-1	0	—	-1	0	—	-1	0	—	-1
Xylomyidae	0	—	—	0.15	—	1	0	—	—	0	—	—
Cynipidae	0	—	-1	0	—	-1	0	—	-1	0.81	—	0.25
Formicidae	0	—	-1	0	—	-1	0	—	-1	0.81	—	0.54
Carabidae	0	—	—	0.08	—	1	0	—	—	0	—	—
Chrysomelidae	0.28	—	-0.28	0	—	-1	0	—	-1	0	—	-1
Coleoptera gen. sp.	0	—	—	0	—	—	0.46	—	1	0	—	—
Other prey items												
Pseudochondrostoma duriense	0	—	—	0.45	—	—	0.46	—	—	0	—	—
Eggs	0	—	—	0.15	—	1	0	—	—	0	—	—

Table 1. Diet composition and prey selection according to Ivlev's selectivity index in each age class of *Salmo trutta* in the River Furelos (NW Spain) during summer.

The maximum and mean prey size eaten generally increases with size in predatory fish species [51]. Piscivorous behaviour is most frequent in large brown trout, and studies show that it occurs in older individuals with a size of 20–30 cm. Trout in smaller size classes have rarely/ never been recorded eating other fish [23,26,52,53]. In contrast, Sánchez-Hernández and collaborators have recorded piscivorous behaviour in an age-0 trout (the individual found was 8.5 cm in fork length) [29]. This behaviour could be related with the hypothesis of Mittelbach and Persson, who stated that fish species that had larger mouth gapes became piscivorous at younger ages and at smaller sizes [51], and demonstrating that mouth gape is not a limitation to use fishes by small trouts [29]. One possible advantage for small trout in diversifying into eating fish is a reduction in competition with other individuals in the same size classes.

The feeding strategy among age classes may be illustrated with graphical methods, such as the modified Costello graphical method [20] based on the relative importance of prey species. Figure 5, shows plots of prey abundance (A_i) against frequency of occurrence of prey in the diet (F_i) for three different age classes. The plots show feeding strategy differs between age classes, varying in degrees of specialization and generalization on different prey types. For all age classes, *Baetis* spp. were the most important prey, always being eaten by more than eighty-five percent of the individuals ($F_i = 87.5\%$ in age-1+ to 100% in age-2+) and represented a high contribution in specific abundance ($A_i = 23.93\%$ in age-1+ to 68.95% in age-0+). However, the majority of the prey items presented low values for both F_i and A_i (lower left quadrant) for all

age classes (Figure 5), displaying evidence of a generalist strategy for these prey (e.g. *Chimarra marginata*, Simuliidae (adult), Chironomidae (adult) and *Ophiogomphus* sp.).
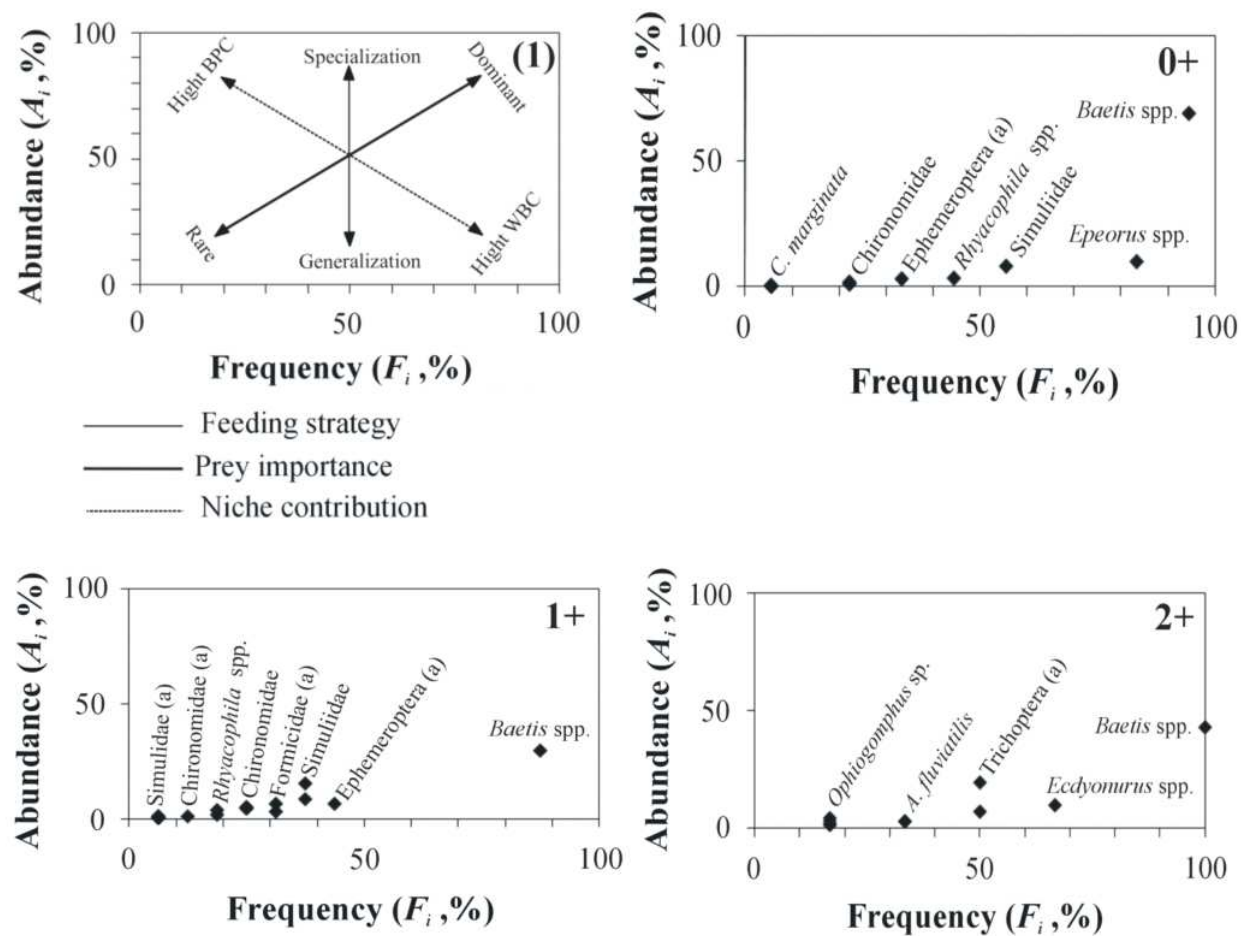

Figure 5. Feeding strategy diagram. (1) Explanatory diagram of the modified Costello method according to Amundsen and collaborators [20]. Data are presented for each age class.

Finally, although in some occasions the diet comparison among age classes can show a remarkable similarity in their prey utilization patterns, sometimes the high overlap values may not indicate competition, since the differences in the behavioural feeding habits are important adaptive features that may reduce the intra-specific competition in the population [23]. Previously, the differences in the behavioural feeding habits among age classes had been studied using prey trait analysis [23], obtaining important advances to disentangle food resource partitioning among cohorts. Details and information needed for the elaboration of prey trait analysis can be found in the introduction section and bibliography [27-29]. Thus, in the reference [23] 'diel drift behaviour' trait showed that age-2+ is clearly separated from the other age classes. Age-2+ tended to feed on prey with no tendency in diel drift behaviour as shown by the presence of *Ancylus fluviatilis*, Gerridae, Coleoptera and Formicidae in their stomachs. On the contrary, age-0+ preferred to feed on prey with nocturnal diel drift behaviour tendency due to the presence of Philopotamidae (*C. marginata*). Age-0+ showed a wider

distribution of values in the fuzzy principal component analysis (FPCA) of the 'trajectory' trait; age-0+ tended to feed on prey with oscillatory and by random trajectory (Lumbriculidae, Simuliidae and Chironomidae), whereas age-2+ tended to feed on prey with lineal trajectory due to the presence of Gerridae [23]. On the other hand, no clear differences have been found in the traits 'tendency to drift in the water column' and 'tendency to drift at the water surface' for prey among age classes [23], however as shown in Figure 6 (fuzzy principal component analysis calculated with the values reported in Table 1), age-3+ is clearly separated from the other age classes, showing that the differences ability to feed at different depths of the water column is possible among cohorts.
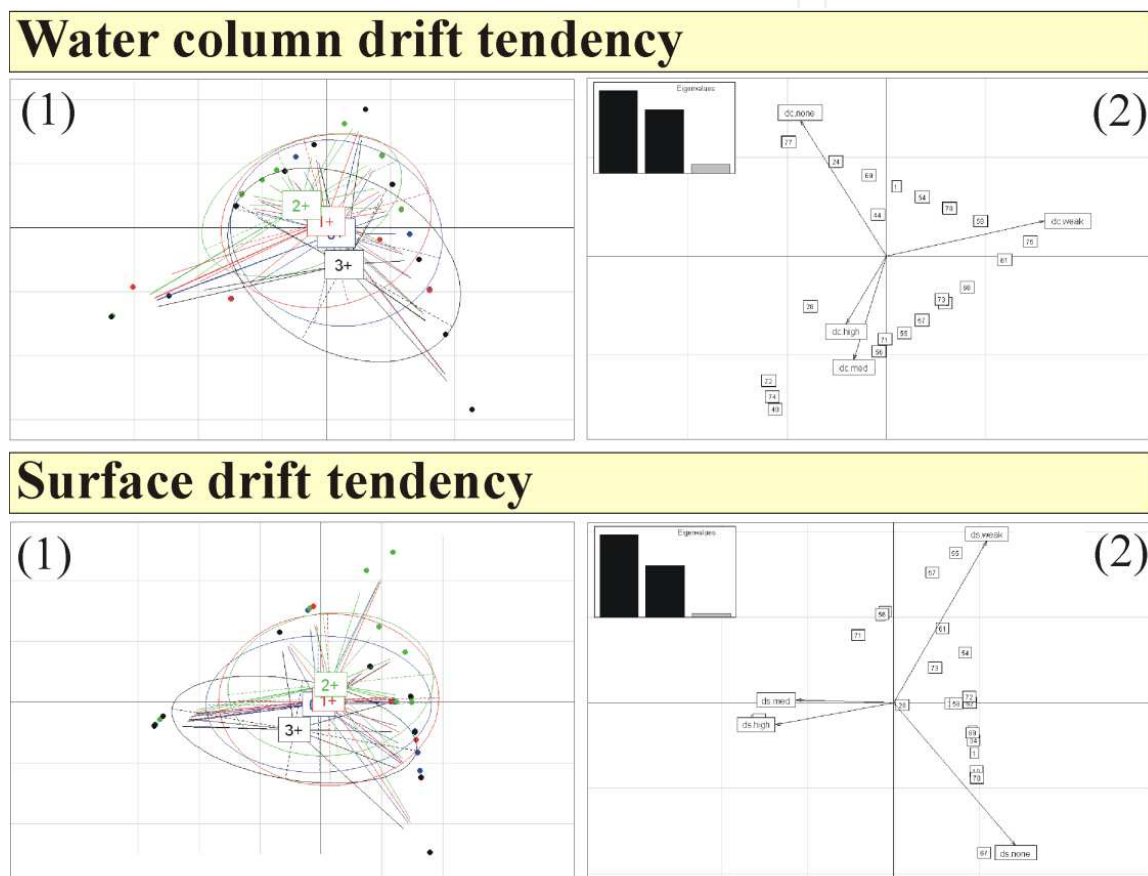
Figure 6. Biplot of gut contents obtained from a fuzzy principal component analysis (FPCA) based on behavioural feeding habits of the four age classes. (1) Similarity results among age classes according to the gut contents of Table 1. Data are presented for each age class. 0+: age-0+, 1+: age-1+, 2+: age-2+ and 3+: age-3+. Ellipses envelop weighted average of prey taxa positions consumed by age classes: Labels (0+, 1+, 2+ and 3+) indicate the gravity centre of the ellipses (2) Factorial correspondence analysis between both traits and prey items and their spatial distribution with histogram of eigenvalues. Details needed for the elaboration of these graphics can be found in the introduction section and bibliography [27-29].

4.2. Changes in prey selection with age

Prey abundance should be an important factor involved in prey choice. However, fishes do not always consume the most abundant taxa available in the environment [13,29,54]. The total

abundance and biomass of invertebrates drifting during the day describe the potential prey available to juvenile brown trout better than abundance and biomass of benthic invertebrates do [55]. Different authors have shown that active choice guided by energetic optimization criteria appeared to be of limited importance in determining the size composition of prey eaten by trouts [11]. These authors also stated that the operating mechanisms of prey-size selection are probably not independent of the characteristics of the size-frequency distribution of the available prey. Moreover, in brown trout spatial and temporal variations in prey selection are possible, due to the preference for the different prey items related to the site-specific prey accessibility [12]. As shown in section 3, the size-frequency distribution of potential prey items in the benthos was different to that of prey in the stomachs of newly emerged brown trout [13], a result that agrees with observations made in other fish species [e.g. 54] and observations made in age-0+ individuals of *S. trutta* during the autumn [29]. In spite of the high abundance of Elmidae in the benthos, this prey item was negatively selected [29]. The rejection of the elmid beetle may be due to their low energetic value, as they have an intense sclerotisation, but it may also be due to their bad taste [56-58]. Hence, other factors, besides prey abundance, including site-specific prey accessibility, prey size, energetic selection criteria and prey preference of fishes, play an important role in the feeding behaviour of freshwater fishes [54].

Fochetti and collaborators found a high preference for species of Trichoptera by trout younger than 3+, a preference for plecopteran species by those older than three years, and a general negative avoidance for species of Ephemeroptera by all age classes [17]. As shown in Table 1, prey selection is clearly different among age classes and important prey items such as Chironomidae in age 0+ and age 3+ and aerial imagoes of Ephemeroptera in age-1+ and age-2+ are positively selected in the benthos and drift respectively. Overall, as different researchers have demonstrated, the mechanisms involved in prey selection among age classes in the same population are complex and may be related at different levels: (1) prey selection in fishes is related to prey characteristics, such as size, locomotor skills, accessibility or anti-predator behaviour, (2) prey selection in fishes is related to fish characteristics, like prior experience, locomotor skills, stomach fullness, mouth gape, sensory capabilities and fish size and (3) prey selection in fishes is related to physical habitat characteristics, as flow patterns and structural complexity of habitat [12,13,34,54].

4.3. Changes in prey size with age

Ontogenetic dietary shifts may also occur at the level of prey size [23,54]. Steingrímsson and Gíslason showed a consistent, but moderate, shift towards larger prey with increased body size in brown trout [59]. Several researchers have found that mean prey size increases as predator size increases [e.g. 23,48,54,60]. The size-frequency distributions of the available terrestrial prey were always greatly dominated (75–90%) by the two smallest size classes (1–2 and 2–3 mm long), prey over 4 mm long being extremely scarce, while size distributions of aquatic prey were less skewed [11]. Thus, in general it is correct to state that trout fed mainly on prey within 1–4 mm size range [11,48], with 2–3 mm prey being the most commonly consumed [48]. On the contrary, Rincón and Lobón-Cerviá showed that organisms 1–2 mm long were generally the most numerous [11]. By age classes the average prey size consumption

is different with higher values in age-2+ (8.4 mm ± 1.62) than age-0+ (4.2 mm ± 0.25) and age-1+ (5.9 mm ± 0.51), but there are no significant differences between age-0+ and age-1+ [23]. Figure 7 illustrates the age-related variation in prey size, showing that mean prey size tends to increase with age.

In conclusion, prey-size selection is probably dependent on the characteristics of the size-frequency distribution of the available prey [11], and the size-related differences in the diet of trout can be related to gape-limitations, increasing mean prey size and maximum prey-size with trout size [48].
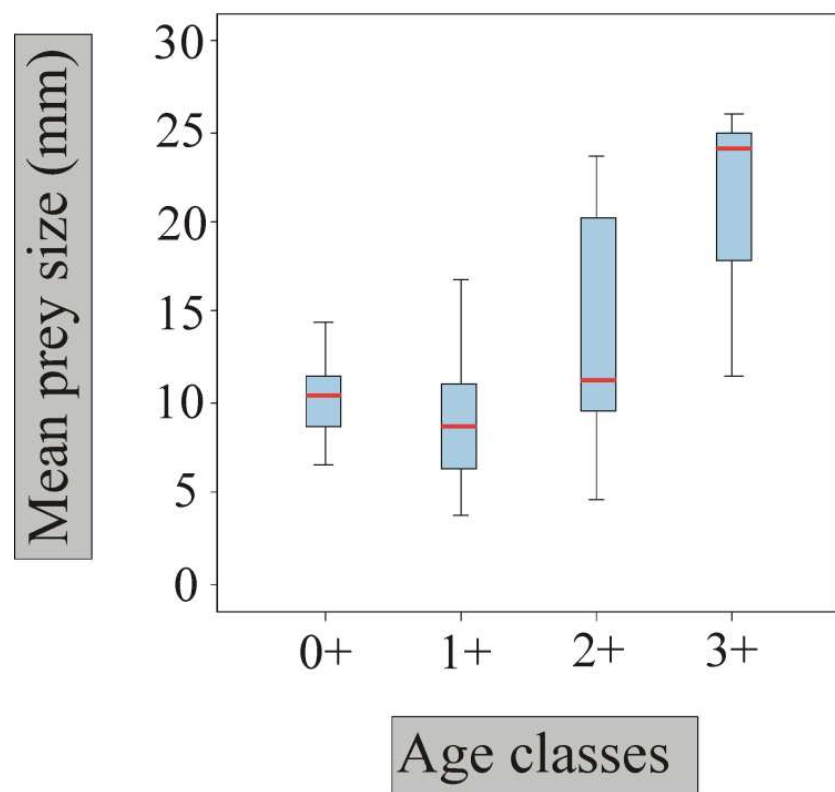
Figure 7. Box plots of the age-related variation in prey size of *Salmo trutta* in the River Furelos (NW Spain) during summer. The solid line within each box represents the median, the bottom and top borders indicate the 25th and 75th percentiles, the notches represent the 95% confidence intervals.

4.4. Changes in the habitat used for feeding with age

In fishes, patches used for feeding and refuges are normally different, as shown by several researchers [61-63], due to brown trout being a habitat generalist. Also, patterns in habitat selection have been shown to be driven by physical and environmental factors operating at multiple spatial scales [44].

Many organisms exhibit ontogenetic shifts in their diet and habitat use, which often exert a large influence on the structure and expected dynamics of food webs and ecological commun-

ities [64]. Special attention has been given to ontogenetic shift in habitat preference in brown trout populations [e.g. 44,65-67]. It is well-known that in brown trout populations habitat use changes during ontogeny, preferring deeper and slower flowing water as they increased in size [e.g. 44,65].

Habitat patches used by brown trout can be monitored by radio telemetry [e.g. 68] and although these studies have shown that brown trout feed on young white suckers *Catostomus commersonii* (Lacepède, 1803) at night in shallow habitats, little information was obtained about the habitat used for feeding. Also, microhabitat use of freshwater fishes has been studied by snorkel observations in previous studies [e.g. 69]. This methodology could be used to study feeding habitat requirements of fish species. However, there are still gaps to be filled before snorkel surveys can be fully adopted in fish diet studies. In fact, one of the main disadvantages of this approach is the need for good visibility. This has been one of the main handicaps because, although brown trout normally yields a bimodal (crepuscular) pattern of activity with a major peak at dawn and a lower one around dusk [70], brown trout can also feed at night [71]. Another limiting factor for the application of snorkel surveys to study feeding habitat requirements is related to the physical characteristic of the river such as current, depth or turbidity. It is well-known that different macroinvertebrates have different preferences for habitats [72] and so prey trait analysis has been proposed as a functional approach to understand mechanisms involved in predator-prey relationships [27-29]. Consequently it may be useful for understanding inter-species interactions and the mechanisms that determine food partitioning between them [29,30]. Nowadays, they have been recently used to provide interesting results about differences in feeding habitat requirements among age classes in brown trout [23], for example, young of the year (0+) tend to capture prey living in moderate current velocities, whereas other age classes (1+ and 2+) tend to feed on prey living in fast current velocities [23].

A previous study on habitat choice in a littoral zone of Lake Tesse (Norway) showed that small trout had a strong association with the bottom and larger trout occurred more frequently higher up in the water column, and suggested that this difference in vertical distribution was also reflected in food choice [73]. In streams, competition among fish species may also be reduced by vertical segregation [e.g. 41,69,74]. In spite that terrestrial invertebrates, as component of the diet, are more important in adults than juveniles of brown trout [23], these same authors found that the ability to feed at different depths of the water is similar among age classes. Nevertheless, it is possible that different age classes of fish may become vertically segregated by concentrating on different prey types living in different parts of the water column as shown in section 4.1. Hence, additional studies are needed in order to clarify whether vertical segregation among cohorts is related to the ability to feed at different depths of the water column.

Finally differences in the use of feeding habitat are important adaptive features that may reduce the intra-specific competition in the population. In this context, fuzzy principal component analysis (FPCA) has shown that age-0+ tended to feed on prey living in moderate current velocities, although overlap was higher between age-1+ and age-2+, preferring to feed on prey living in fast current velocities [23]. Moreover, these researchers have found that age-0+ showed a higher spectrum of prey, which revealed a greater ability to prey on different

macrohabitats, whereas age-1+ and age-2+ preferred to feed on epibenthic prey living in erosional macrohabitats. In our case with the values reported in Table 1 and as shown in Figure 8, 'current velocity' trait shows no clear differences for prey of the four age classes. On the contrary, 'macrohabitat' trait shows that age-1+ has the most ample spectrum for this trait, tending to feed on epibenthic prey living in erosional macrohabitats, whereas age-3+ tends to feed on prey items available in the water column (Figure 8).
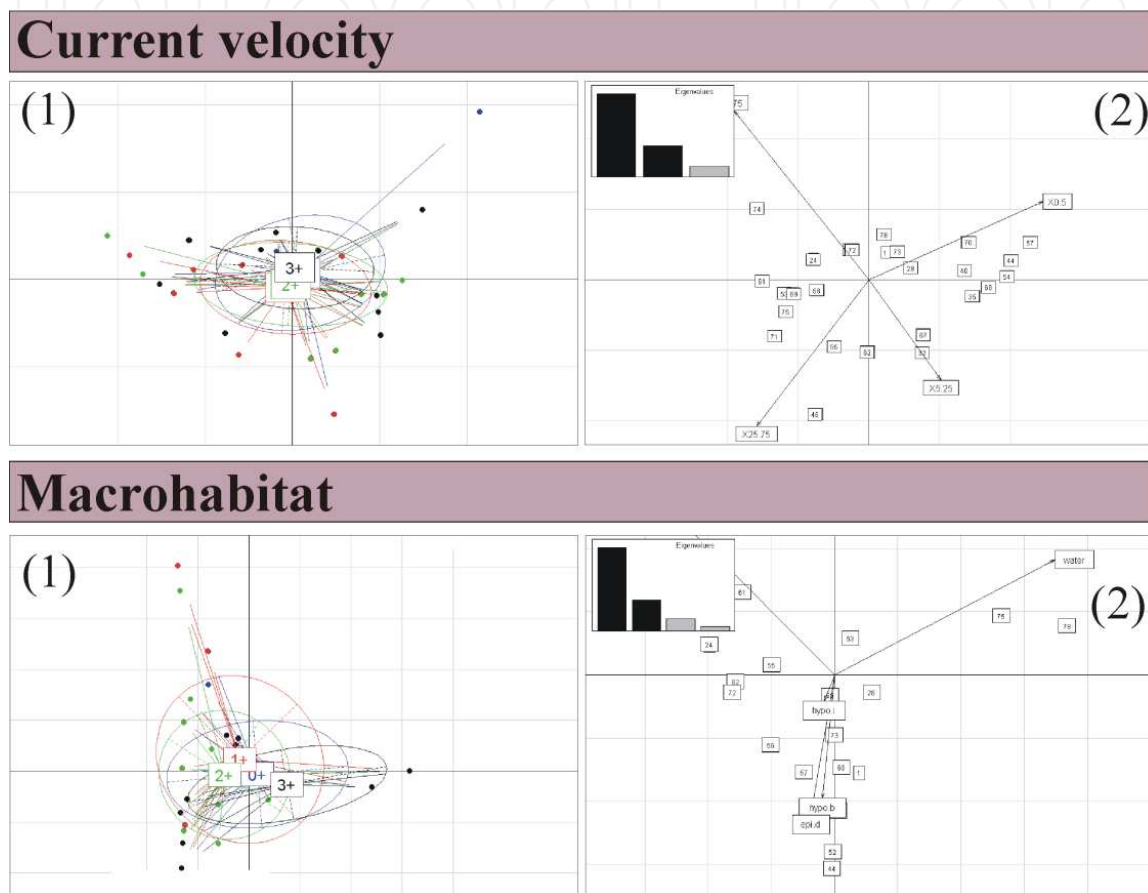
Figure 8. Biplot of gut contents obtained from a fuzzy principal component analysis (FPCA) based on preferential habitat utilization for feeding of the four age classes. (1) Similarity results among age classes according to the gut contents of Table 1. Data are presented for each age class. 0+: age-0+, 1+: age-1+, 2+: age-2+ and 3+: age-3+. Ellipses envelop weighted average of prey taxa positions consumed by age classes: Labels (0+, 1+, 2+ and 3+) indicate the gravity centre of the ellipses. (2) Factorial correspondence analysis between both traits and prey items and their spatial distribution with histogram of eigenvalues. Details needed for the elaboration of these graphics can be found in the introduction section and bibliography [27-29].

4.5. Changes in the niche breadth with age

Deady and Fives showed that niche breadth decreases with fish length in corkwing wrasse, *Symphodus (Crenilabrus) melops* (Linnaeus, 1758), indicating an increase in dietary specialization with increasing length [75]. Magalhães found dietary shifts throughout the ontogeny in an endemic cyprinid of the Iberian Peninsula (*Squalius pyrenaicus* (Günther, 1868)), including

shifts from soft-bodied to hard-shelled prey and decreased animal prey breadth [76]. In contrast, several other researchers have found that niche breadth increases with body size [e.g. 23,77]. Oscoz and collaborators found that larger fish have a higher number of potential prey items available and a wider niche breadth, as indicated by their higher trophic diversity index values [77]. As mentioned in section 3, analysis of diet changes on newly emerged brown trout fry suggests a dramatic shift in niche breadth at the moment of complete yolk absorption, which might be related to the improvement the fry's swimming and handling ability in capturing and ingesting prey [13]. In a recent study on brown trout populations, it has been demonstrated that niche breadth, measured as Levin's index, increases with fish length in *Salmo trutta*. However, no differences were found in the Shannon diversity and evenness indices of prey eaten among age classes [23].

As can be seen in Figure 9; the number of different prey types consumed by S. trutta increases during ontogeny. Age-0+ shows the smallest prey spectrum, whereas in age-1+ a significant increase in the prey types consumed by juveniles is observed. However, no significant differences in the dietary niche among ages-1+, 2+ and 3+ are observed in Figure 9. Hence, although no clear results have been observed in the variation of the diversity indices of prey among age classes [23], it could be argued that there is a tendency to increase dietary niche with increasing length or age, at least when the niche breadth of juveniles (0+), subadults (1+) and adults (≥2+) is compared.
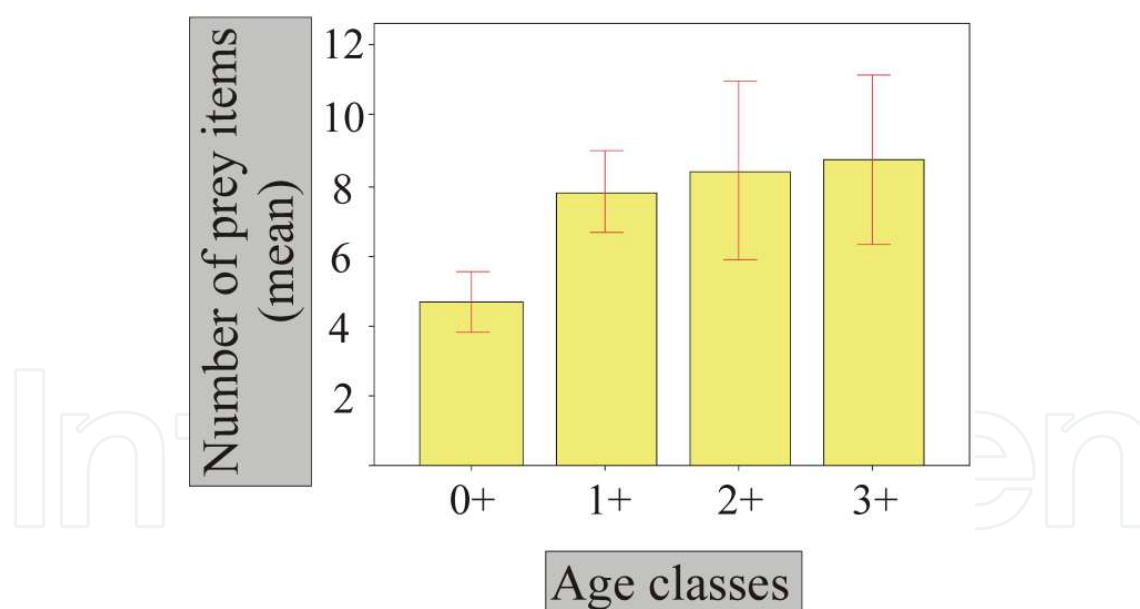

Figure 9. Age-related variation in the number of different prey types consumed by *Salmo trutta* in the River Lengüelle (NW Spain) during summer. Error bars represent the 95% confidence intervals.

4.6. Changes in the fullness index with age

Several researchers have found in different fish species that the stomach fullness index (defined as the weight of the stomach contents (in grams) divided by the weight of the predator (in

grams) and multiplied by 100) varies during ontogeny [78,79]. In salmonids the results are contradictory: in brook charr *Salvelinus fontinalis* (Mitchill, 1814) no differences have been found in the stomach fullness [80], whilst other researchers have demonstrated that the stomach fullness of brown trout varies among size classes [47]. Brown trout between the size of 40 mm and 320 mm fed more intensively, whilst the intensity declined above 320 mm length [47]. In the River Furelos (NW Spain), we have found that stomach fullness during the summer is different among age classes (Kruskal-Wallis test; $p < 0.001$), being higher in age-0+ (9% ± 0.64) than age-1+ (1.1% ± 0.14), age-2+ (1% ± 0.25) and age-3+ (1.1% ± 0.24) (all Mann–Whitney U test, $p < 0.001$) but no differences have been found between ages-1+, 2+ and 3+ (all Mann–Whitney U test, $p > 0.05$). Moreover, stomach fullness decreases with fish size ($r = -0.72$; $p < 0.001$) (unpublished data). Hence, stomach fullness can vary among age classes; however additional studies are needed in order to clarify whether stomach fullness varies during ontogeny in brown trout.

5. Competion for food between brown trout and other sympatric fish species

Trophic interactions between species are important factors structuring animal communities. Brown trout are top-consumers in freshwater habitats and play an important role as carriers of energy from lower to higher trophic levels (i.e. predators). Many freshwater fish species tend to occupy a specific type of habitat but there are lots of exceptions. For example, spatial niche overlap is considerable where Atlantic salmon and brown trout co-occur, although young Atlantic salmon tend to occupy faster flowing and shallower habitats [e.g. 74]. Moreover, when both fish species co-occur, the habitat used by Atlantic salmon is restricted through interspecific competition by the more aggressive brown trout, indicating an interactive segregation between fish species [e.g. 41,74]. Indeed, it is well known that brown trout is a territorial drift feeder [3,81], and several authors have reported the behavioural dominance of trout over cyprinids in streams [82-84].

The competitive coexistence between species occupying similar niches may be facilitated by a generalisation of niche width as predicted by the optimal foraging theory (OFT), rather than the specialised niche width predicted by the classic niche theory as a response to interspecific competition [85]. However, studies on food partitioning in fish communities have obtained contradictory results. Whereas several authors have found differences in diet composition among sympatric fish species [e.g. 86,87], other researchers concluded that the same food resource can be shared by several species [29,30,85]. In these cases, the differences in behavioural feeding habits, handling efficiency and feeding habitat utilization are important adaptive features that may reduce the inter-specific competition in the fish community and permit the partitioning of food that allows coexistence [29,30]. Thus, sympatric fish species can adopt different strategies to overcome competion and food resource partitioning can occur at different levels.
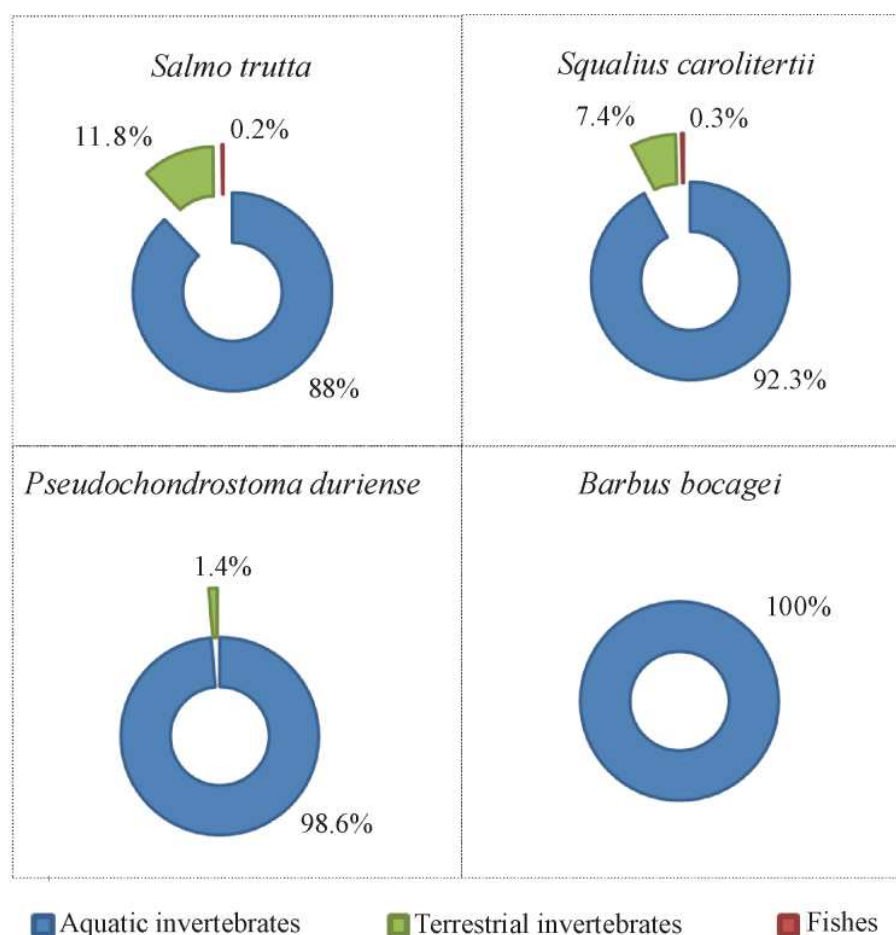
Figure 10. Diet composition consumed by each fish species in the Tormes River (Central Spain) during summer.

Firstly, the use of microhabitats is often different between species, due to segregation of microhabitats, an important factor in reducing the effects of competition for food [69,88,89]. For example, *Barbus bocagei* Steindachner, 1865 occupied deeper habitats and selected lower positions in the water column than *Pseudochondrostoma polylepis* (Steindachner, 1865), and *Squalius pyrenaicus* (Günther, 1868), *P. polylepis* occupied microhabitats with greater velocities than the other two species and *S. pyrenaicus* selected shallower habitats than the other two species [69]. In another study, *S. trutta* showed wider diversity in the habitat used for feeding than *Squalius carolitertii* (Doadrio, 1988), *Pseudochondrostoma duriense* (Coelho, 1985) and *B. bocagei* [30]. Hence, differences were found among species in their ability to feed at different depths of the water column [29,30] as shown in snorkelling studies into microhabitat use in fish [69].

Secondly, different species may specialise in different resources. For example, many cyprinid fish sympatric with trout feed on a significant amount of detritus and plant material not used by trout, leading to reduced inter-specific competition [29,30]. Moreover, resource partitioning may also occur at the level of prey size [29,30,90], although it is not clear whether this size selective strategy is adopted to reduce interspecific competition or it is the result of foraging

behaviour and/or morphological constraints such as gape size [29,91]. Also, terrestrial prey are present primarily on the stream surface and although tend to be absent from the diets of benthic feeders such as *B. bocagei* (Figure 10), terrestrial inputs may constitute an important food resource for freshwater fish species and especially for brown trout. Thus, the utilization of allochthonous food resources such as terrestrial invertebrates by fishes may reduce competition facilitating the partitioning of resources [30].

Thirdly, diel segregation is possible among fish species, and this may also lead to reduced interspecific competition between fish [29,92,93]. According to macroinvertebrate trait analyses, sticklebacks (*Gasterosteus aculeatus* Linnaeus, 1758) and *P. duriense* show a slight preference for prey that drift during the day, whilst age-0 *S. trutta* seem to prefer to feed at dusk, whereas *Achondrostoma arcasii* (Steindachner, 1866) differs from the other three species due to its preference to feed on prey on organisms with weak or no tendency to drift [29]. However, the "diel drift behaviour" of macroinvertebrate prey of brown trout and three sympatric cyprinids is similar [30]. Hence, the differences in the diel feeding behaviour among sympatric fish species might only be adopted in highly competitive communities, where food is a more limiting resource.

6. Conclusion

To summarize, the present study supports the hypothesis differences in the feeding habits and habitat utilization of different age classes of trout could reduce competition for food, by allowing food resource partitioning. Hence, age-related diet shifts occur at five different levels: (1) diet composition changes with fish age; (2) prey selection varies with fish age, probably due to prey-size selection which is in turn dependent on the size-frequency distribution of the available prey; (3) mean prey size increases with fish size and age; (4) habitat utilization for feeding may be different among age classes; (5) niche breadth tends to increase with age and fish size. Finally, also the stomach fullness can vary among age classes. However, additional studies are needed in order to clarify whether stomach fullness varies during the ontogeny in brown trout.

Acknowledgements

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