FOOD WEB STRUCTURE AND RESOURCE USE BY FISH IN THE UPPER PART OF THE VLTAVA RIVER, CZECH REPUBLIC

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ABSTRACT

Understanding trophic niche structure is essential for describing the organization and functioning of fish communities in river ecosystems. Stable isotope analysis of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) was used to characterize trophic niches and food web structure of eight species of fish inhabiting the upper reaches of the Vltava river (Czech Republic). Eight species were analysed together with six categories of food resources. The isotopic composition of muscle tissue and basal food resources was measured using a Delta V mass spectrometer, and trophic metrics were calculated using Stable Isotope Bayesian Ellipses in R (SIBER) and MixSIAR models. Results revealed distinct isotopic separation among species, indicating variation in resource use and trophic position. The highest $\delta^{15}N$ enrichment and thus the highest trophic position within the community were recorded for dace *Leuciscus leuciscus*, which is likely to be because it mainly feeds on terrestrial invertebrates. In contrast, nase, *Chondrostoma nasus* occupied the lowest trophic level and was the most enriched in $\delta^{13}C$, due to feeding on periphyton and sediment-associated organic matter. Chub (*Squalius cephalus*), roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*) occupy broad isotopic niches. Species with more specific habitat requirements, such as barbel (*Barbus barbus*) and bullhead (*Cottus gobio*), had narrower trophic niches, reflecting their feeding specialization on aquatic invertebrates. This study highlights the value of stable isotopes for understanding community trophic structure and supports their use in riverine ecosystem management and river community ecology.

Keywords: $\delta^{13}C$; $\delta^{15}N$; freshwater fish; food web; MixSIAR; SIBER; stable isotopes; trophic niche; Vltava river

Introduction

Understanding the trophic niches of fish is fundamental to describing river community ecology. The position of trophic niches within isotopic niche space and their overall arrangement within fish assemblages are essential for elucidating patterns of productivity and energy flow in river ecosystems. Stable isotope analysis provides an effective way of quantifying trophic niches, as it integrates long-term foraging behaviour and dietary sources of fish. Traditionally, Gut Content Analysis (GCA) was used to assess fish diets; however, this approach primarily reflects short-term feeding activity and is limited in its ability to characterize community-wide trophic structure or long-term interspecific trophic relationships. Here, carbon (C) and nitrogen (N) stable isotopes were used to construct the detailed food web in the upper part of the Vltava river. Eight species of fish were analysed, quantifying both the size and spatial position of their isotopic niche space. Trophic variability is influenced by environmental conditions, anthropogenic effects and availability of food resources (Van Valen 1965; Grant et al. 1976; Horka et al. 2023). By incorporating food resources into the analysis, a more precise characterization of individual species' positions within the riverine food web was achieved. The aim was to describe the structure of the food web of the fish community in the upper part of the Vltava river. Stable isotope analysis of $\delta^{15}N$ and $\delta^{13}C$ was used to assess the trophic positions of individual species, as well as the size and spatial arrangement of their trophic niches within isotopic space, reflecting the positions of their respective food sources. The isotopic ratio $\delta^{15}N$ provides valuable information about the trophic position of consumers (Fry 2006). The stepwise enrichment of $\delta^{15}N$ along the food chain serves as an important tool for estimating the trophic levels of organisms and for identifying their positions within a food web (Wada et al. 1991; Post 2002). In contrast, the carbon isotope ratio $\delta^{13}C$ is commonly used to identify the sources of organic matter for consumers. It reflects the contribution of different food resources and can indicate habitat use and the extent of resource assimilation (deNiro and Epstein 1978; Newsome et al. 2007; Baeta et al. 2017). The diversity and arrangement of trophic niches determine how energy flows through food webs and how fish affect the transfer of nutrients between trophic levels. Understanding trophic niches thus helps to reveal the functional role of species in maintaining riverine ecosystem stability and resilience.

Material and Methods

Samples of white dorsal muscle tissue, obtained from 93 specimens of 8 species of fish and of their prey (basal food resources), were analysed. Samples of fish were collected by electric fishing, with an output voltage of 300–600 V (50 Hz) powered by a Honda engine and a LENA generator (Bednář, Czech Republic). Fish were

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caught by electrofishing using a two-pass depletion method to ensure representative estimates of fish abundance at each site. Sampling site was located at the upper part of the Vltava river (near Borsov, 48°53′47.6″N 14°23′38.2″E) in June 2019. It was surrounded by naturally heterogenous habitats and characterized by a combination of shallow fast-flowing reaches with aquatic vegetation interspersed with deeper and slower flowing sections. Samples were kept frozen until laboratory processing at the Centre for Stable Isotope Research of Charles University, Prague, Czech Republic. Muscle samples were dried and homogenised using a ball mill (MM400, Retsch, Germany) and then ±0.50 mg of a sample was placed in a tin capsule. The resources were divided into six categories: terrestrial invertebrates, aquatic invertebrates, terrestrial plants, aquatic plants, periphyton and sediment. Total carbon and nitrogen content as well as their isotope ratios were measured using a Delta V mass spectrometer coupled to a Conflo IV and elemental analyser Flash 2000 (all instrumentation by Thermo Fisher Scientific, Bremen, Germany). The carbon and nitrogen isotope ratios are expressed in delta notations as follows: $\delta X = (R_{sample}/R_{standard} - 1) \times 1000$, where X stands for ^{13}C or ^{15}N, respectively, and R is the carbon or nitrogen isotope ratio ($R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$). Repeated measurements of a series of international standards (IAEA-CH3, IAEA-CH6, IAEA-600, IAEA-N1, IAEA-N2, IAEA-NO3) were used to normalise the measured isotope ratios to the Vienna Pee Dee Belemnite (VPDB) and the atmospheric N_2 scales (Coplen 1996). In addition, a glycine standard was measured after every 10th sample to provide calibration for elemental composition and a quality control for isotopic measurement. Analytical precision was within 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$.

All statistical analyses were conducted using R 4.0.5 (R Core Team 2021). Isotopic niche area of species, and trophic position of species in the community were evaluated using stable isotopes $\delta^{13}C$ and $\delta^{15}N$ (Laymann et al. 2007; Jackson et al. 2011). Bayesian ellipse analyses were used *via* the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011). Stable isotope metrics of the fish assemblage were evaluated and presented using three approaches: (i) Trophic niche areas (SEA – *Standard Ellipse Area*, SEAc – *corrected Standard Ellipse Area*, TA – *Total Area*), showing isotopic niche width and overlap among species, (ii) trophic positions derived from $\delta^{15}N$ values indicating relative trophic levels, and (iii) MixSIAR model outputs estimating percentage contributions of fish diets, showing isotopic positions of each species relative to food sources (Phillips et al. 2014). Values of Standard Ellipse Area (SEA, ‰^{2}), sample-size corrected ellipse area (SEAc, ‰^{2}), and Total Area of the convex hull (TA, ‰^{2}) were evaluated for each species of fish (Table 1). SEA represents the core isotopic niche area encompassing approximately 40% of the data and provides an estimate of trophic niche width. SEAc adjusts for small sample sizes, allowing for more robust comparisons among species with different *n*. TA is the total extent of the isotopic space occupied by a species and reflects the overall dietary variability within the population. Large SEAc and TA values indicate broad trophic niches and high dietary variability within the population. Mean (± SD) $\delta^{15}N$ values of individual species describe differences in trophic level within the fish assemblage. Posterior probability distributions from the Bayesian mixing model (MixSIAR, Stock et al. 2018) were used to show estimated percentage contributions of the diet of each species of fish. The model incorporated six resource categories: terrestrial invertebrates, aquatic invertebrates, terrestrial plants, aquatic plants, periphyton and sediment. Species-specific isotope values are plotted in isotopic $\delta^{13}C$-$\delta^{15}N$ bi-space alongside modelled mean source signatures.

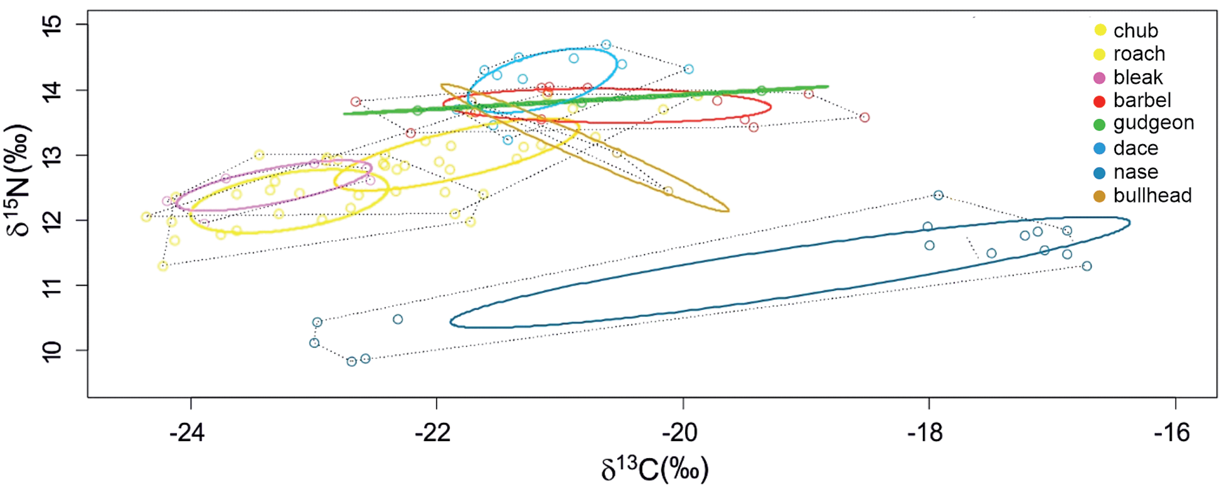

Fig. 1 Isotopic niche ellipses (SEAc) of fish in the upper Vltava river. Biplot of $\delta^{13}C$ and $\delta^{15}N$ stable isotope values (‰) showing corrected standard ellipses (SEAc) for eight species of fish inhabiting the upper Vltava river. Ellipses represent the core isotopic niche area and indicate trophic niche width and overlap between species.

Table 1 Isotopic niche metrics (SEAc and TA) of fish in the upper Vltava river. Values of Standard Ellipse Area (SEA), corrected Standard Ellipse Area (SEAc, ‰^{2}) and Total Area (TA, ‰^{2}) are shown for each species, which are the core isotopic niche and total isotopic niche breadth, respectively.

Fish species (*latin name*)	**SEA (‰²)**	**SEAc (‰²)**	**TA (‰²)**
European chub (*Squalius cephalus*)	1.041	1.103	2.924
Roach (*Rutilus rutilus*)	1.093	1.146	3.528
Bleak (*Alburnus alburnus*)	0.545	0.682	0.724
Barbel (*Barbus barbus*)	0.994	1.084	2.149
Gudgeon (*Gobio gobio*)	0.058	0.116	0.032
Dace (*Leuciscus leuciscus*)	0.718	0.797	1.429
Nase (*Chondrostoma nasus*)	3.020	3.253	6.257
European bullhead (*Cottus gobio*)	0.352	0.704	0.194

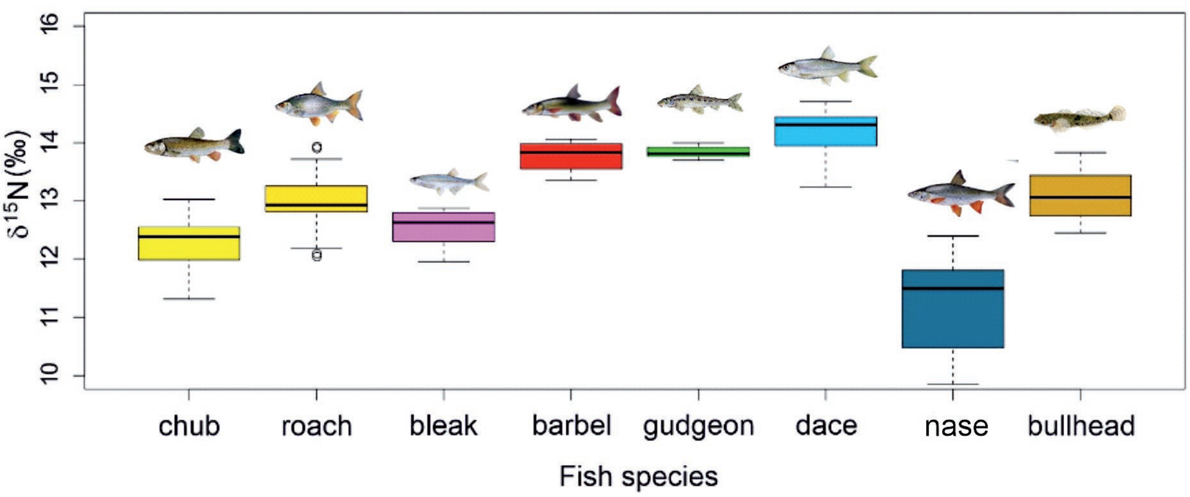

Fig. 2 Trophic positions of fish in the Vltava river based on δ^{15}N values. Mean (± SD) δ^{15}N values of individual species illustrate differences in trophic level within the fish assemblage.

Results

A total of 93 individuals of eight species of fish were analysed in order to evaluate trophic structure and resource use of the fish community in the upper part of the Vltava river. Chub, roach and nase had the largest SEA, SEAc and TA values, the narrowest trophic niches were recorded for gudgeon and bullhead (Fig. 1, Table 1). Nase was at the lowest trophic level and compared to other species was also the most enriched one in carbon isotope δ^{13}C (Fig. 1). Species such as chub, roach and bleak occupied higher trophic positions, while gudgeon and barbel were at slightly lower trophic levels. In the highest trophic position was dace (*Leuciscus leuciscus*), which had the highest enrichment in the nitrogen isotope δ^{15}N (Fig. 2). The most pronounced niche overlap was recorded between bleak and chub (46%). The trophic niche of roach (SEAc = 1.146, $p < 0.05$) overlapped with chub (11%), bleak (6%), bullhead (13%), and, to a small extent, barbel (2%). The niche of nase (SEAc = 3.253, $p < 0.05$) was significantly larger than those of chub, roach, bleak, and did not overlap with any other species (Fig. 1). Values of SEA, SEAc, and TA for the fish species at this site are presented in Table 1.

Discussion

Using isotopic values δ^{15}N and δ^{13}C, the extent of the niche breadth of individual species and their placement along the overall isotopic mixing axis was determined. The trophic niche size was determined using SEAc, as this measure provides accurate estimates even when only a small number of individuals are included in the analysis (Jackson et al. 2011; Philips et al. 2014). In the upper part of the Vltava river, eurytopic and omnivorous species such as chub (*Squalius cephalus*), roach (*Rutilus rutilus*) and bleak (*Alburnus alburnus*) had the largest SEA and SEAc values, indicating broad trophic niches and use of many resources. Also, the most pronounced niche overlap was recorded between bleak and chub (46%). Chub is a typically omnivorous species inhabiting a wide range

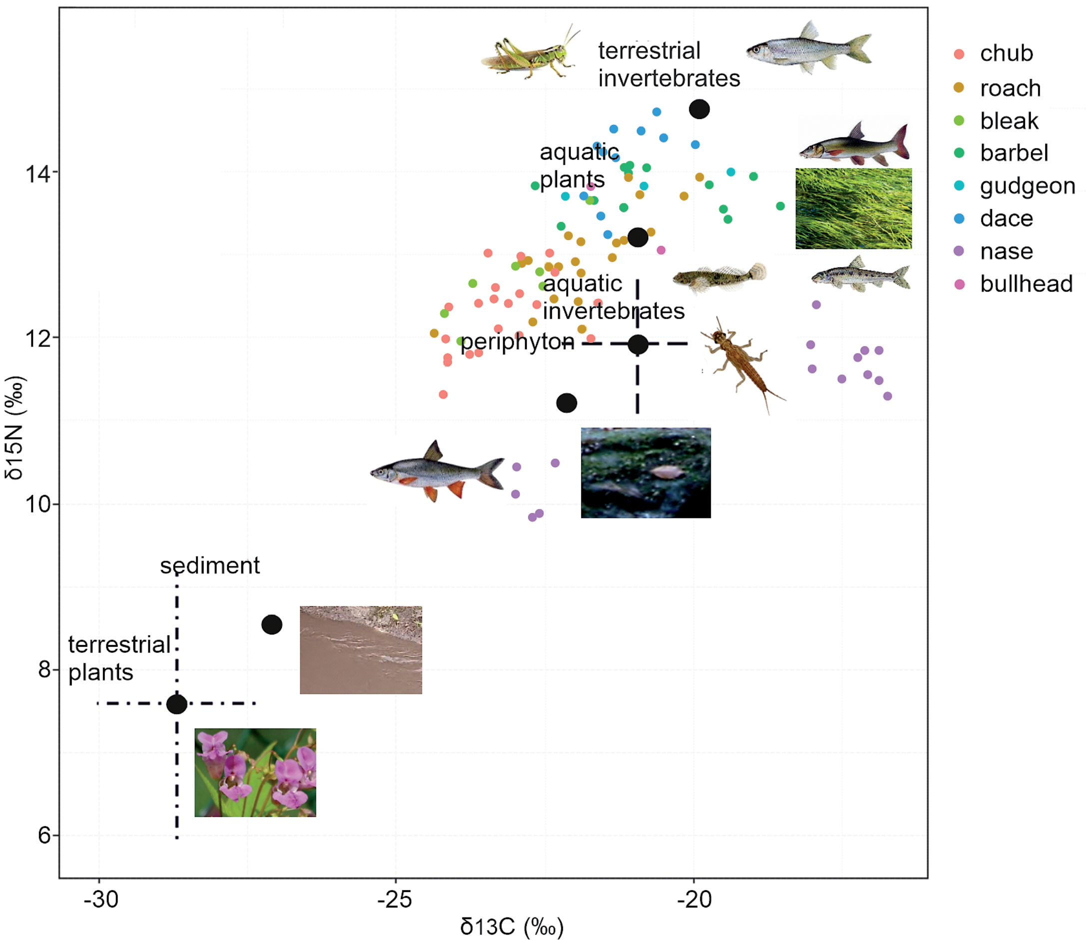

Fig. 3 MixSIAR model estimates of resource contributions to fish diets in the upper Vltava river. Posterior probability distributions based on the Bayesian mixing model (MixSIAR) show estimated percentage contributions of resources to the diet of each species. Species-specific isotope values ($\delta^{13}C$, $\delta^{15}N$) are plotted in isotopic space alongside modelled mean source signatures.

of habitats. In adulthood, it may even consume small fish, but its diet is primarily composed of insects, and it also feeds on plant material collected throughout the water column (Allouche et al. 1999). Chub occupies an intermediate position in the food web, with $\delta^{15}N$ values around 12 ‰ and wide trophic niche space. Chub is often described in the literature as a rheophilic species (Aarts et al. 2003; Capra et al. 2018). However, it may be considered a eurytopic species with a very broad habitat and dietary requirements. Chub occupied a broader niche than the other species, indicating a high degree of dietary plasticity. Roach is a typical generalist (Svanbäck et al. 2008; Hayden et al. 2014; Nahon et al. 2020), utilizing a wide range of food including detritus (Persson 1983), zooplankton, macrophytes and benthic invertebrates (Persson and Hansson 1999). Its niche may expand with increasing eutrophication of an aquatic environment (Olin et al. 2002). According to Hayden et al. (2014), the main components of roach diet are aquatic snails and chironomid larvae. In this study, the trophic niche of roach was slightly higher than that of chub and bleak, possibly reflecting higher proportion of aquatic plants in its diet. $\delta^{15}N$ values ranged from 12–14‰, confirming its feeding generalisation.

Bleak is shoal-forming, visually orientated pelagic fish considered an obligate zoophage (Kottelat and Freyhof 2007; Horka and Vlachova 2024). They occupy a key trophic role as plankton consumers and are essential prey of predators (e.g., asp *Leuciscus aspius*, Linnaeus 1758) in river ecosystems (Krpo-Cetkovic et al. 2010). Their diet primarily consists of plankton, larvae and adult aquatic invertebrates, as well as of terrestrial insects that fall into the water or fly above the surface, which the fish can capture by leaping (Haberlehner 1988; Chappaz et al., 1998). These prey items provide a high caloric and protein content (Giller and Malmqvist 2000). The trophic position of bleak ranged from 12–13‰ $\delta^{15}N$, and was comparable to that of chub, indicating that aquatic invertebrates, and periphyton was the main dietary source. Bleak, chub, and roach which are exhibiting the widest trophic niches are also among the most widely distributed in the Elbe river basin (Horky et al. 2013). This implies that an omnivorous feeding strategy may enhance population development, since effective assimilation of food resources is critical to population dynamics.

In contrast, species with more specific habitat requirements, such as barbel (*Barbus barbus*) and bullhead (*Cottus gobio*), had smaller SEA and TA values, reflecting narrower isotopic niches and diets dominated by aquatic invertebrates. At the study site, gudgeon and barbel occupied higher trophic positions, with gudgeon having the smallest trophic niche. This may be explained by their diet, which consists mainly of insect larvae and benthic invertebrates (Hanel and Lusk 2005; Nunn et al. 2012). The trophic level of gudgeon, as indicated by $\delta^{15}N$, ranged between 13–14 ‰. The high trophic position of gudgeon and barbel can be attributed to two main factors. First, it may reflect the relatively high trophic level of its prey, such as insect larvae and benthic invertebrates. Second, its trophic position may be influenced by benthic feeding, where nitrogen in the food sources is enriched due to decomposition in detrital-pathway occurring at the sediment-water interface (Steffan et al. 2017). A slightly lower trophic niche was occupied by European bullhead, reflecting its benthophagous diet. According to Hyslop (1982), bullhead primarily consume algae and aquatic insect larvae, including chironomids, simuliids, Trichoptera and Ephemeroptera.

Dace (*Leuciscus leuciscus*) occupied the highest trophic position within the assemblage, which indicates high percentage of terrestrial prey, such as insects in its diet (Weatherley 1987). This is also consistent with its placement along the overall isotopic mixing axis. Nase (*Chondrostoma nasus*) had a wide but distinct niche, separate from other species, consistent with its specialized feeding on periphyton and sediment-associated organic matter (Reckendorfer et al. 2001). This fish feeds primarily by scraping periphyton from the streambed. These periphyton layers contain not only plant material, but also animal components, including various insect larvae, chironomids and other invertebrates. At the site studied, its $\delta^{15}N$ values were 10–12 ‰. Compared to all other species, nase occupied a lower trophic position. This lower trophic position could be influenced by the absence of animal components in the periphyton scraped from stones. In addition, two relatively distinct groups were recorded in the diet of nase, which may indicate that fishery managers introduce two distinct size classes of fish during regular stocking (Horky et al. 2013; Lyach 2021), resulting in the variation in its diet, or that the isotopic signatures reflect the feed they received in fish farms. Its low trophic position suggests that its unique feeding strategy may reduce competition with other species, and to provide a competitive advantage of this species in the assemblage.

In anthropogenically affected rivers, fish with low environmental requirements are supposed to have an advantage over more specialised species. Such features include, for example, limited migration and habitat requirements, unspecialised breeding strategies and flexible use of food resources (Musil et al. 2012; Horky et al. 2013). In European rivers, several species belong to the eurytopic ecological group, often exhibiting omnivorous feeding habits. It is suggested that these species benefit from omnivory, in contrast to more specialized rheophilic fish species, particularly in ecosystems affected by nutrient loading (Horka et al. 2023). In this study, chub, roach and bleak had the widest trophic niches, confirming their omnivorous feeding strategies. In addition, nase occupied a niche in a low trophic position largely separated from other fish, which may indicate reduced competition and a potential competitive advantage over co-occurring species. Knowledge of trophic niches is essential for effective management of freshwater ecosystems and for the restoration of habitats (Fráguas et al. 2025). The arrangement and position of the trophic niches of individual species provides critical insights into community food web structure and resource use, and can be especially valuable in managing biodiversity conservation for eutrophic ecosystems (Di Prinzio et al. 2024; Luo et al. 2025). Future research should employ a more detailed categorization of food resources together with Bayesian mixing models to improve our understanding of resource use and trophic differentiation among fish in freshwater ecosystems exposed to different types and intensities of anthropogenic pressures.

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