

Angling baits and invasive crayfish as important trophic subsidies for a large cyprinid fish

Tea Bašić · J. Robert Britton · Michelle C. Jackson ·
Peter Reading · Jonathan Grey

Abstract Invasive species and anthropogenic sources of allochthonous trophic subsidies can have substantial ecological consequences for freshwater ecosystems, including modifying the diet of consumers and altering food web structure. Here, the diet of an omnivorous cyprinid fish, European barbel *Barbus barbus*, was assessed in relation to the presence of invasive signal crayfish *Pacifastacus leniusculus* and pelletized fish-meal in four rivers in England. Pellets are often used in large quantities by river anglers and thus could provide an important trophic subsidy, not only to the fish but also indirectly via *P. leniusculus*. Carbon and nitrogen stable isotopes were used to estimate the proportion of diet assimilated from natural sources and from *P. leniusculus* and pellets by *B. barbus* of lengths between 420 and 800 mm. Pellets generally made a large contribution to the overall biomass of *B. barbus* (up to 59 % of population diet) and in the two rivers where they were present, *P. leniusculus* were also an important resource (up to 30 % of population diet). The proportion derived from macro-invertebrates (excluding *P. leniusculus*) was substantially lower. Stable isotope mixing models further demonstrated considerable intraspecific variability in *B. barbus* diet within the rivers, with pellets comprising up to 79 % of the biomass of individual *B. barbus* in rivers where *P. leniusculus* was absent. Where present, *P. leniusculus* effectively replaced and thus reduced the contribution of pellets to individual fish diet. Thus, isotopic evidence from three of the four rivers indicates that *B. barbus* populations are heavily reliant ([50 %] upon angler-introduced baits that act as an important allochthonous subsidy and will also prey upon invasive *P. leniusculus* where they are present.

Keywords Allochthonous · Barbel · Fishmeal · Signal crayfish · Stable isotopes

T. Bašić · J. R. Britton (✉) · M. C. Jackson
Faculty of Science and Technology, Centre for Conservation
Ecology and Environmental Sciences, Bournemouth University,
Poole, Dorset BH12 5BB, UK
e-mail: rbritton@bournemouth.ac.uk

M. C. Jackson
Department of Zoology and Entomology, Centre for Invasion
Biology, University of Pretoria, Pretoria, Gauteng, South Africa

P. Reading
Barbel Society, 1 Larchwood, Castlegate, Scotforth,
Lancaster LA1 4QG, UK

J. Grey
School of Biological and Chemical Sciences, Queen Mary
University of London, London, UK

Introduction

Environmental disturbances caused by human activities, such as deforestation, invasive species and over-exploitation of fisheries, are impacting upon food web structure and ecosystem functioning (Petchey et al. 1999; Harmon et al. 2009). These disturbances alter the supply of resources and, therefore, often cause changes in the diet of resident species (Harmon et al. 2009). Evidence suggests that food webs in freshwater ecosystems shift under the influence of invasion and fishery activities through inputs of novel resources (Vander Zanden et al. 1999; Britton et al. 2010; Jackson et al. 2012). Fishery activities associated with angling and aquaculture can magnify the input of allochthonous resources to freshwater ecosystems via the introduction of energy rich foods, such as pelletized fish-meal, and introductions of invasive species; both of which

can supplement the diet of native species (Grey et al. 2004; Jackson et al. 2013). Whilst inputs of allochthonous resources enhance the in situ productivity of freshwater systems and increase food web stability (Jones et al. 1998; Jefferies 2000), when inputs become excessive, the food web is often modified across numerous trophic levels through alterations of food web connectivity and bottom-up or top-down control (Jefferies 2000; Marczak et al. 2007). This can lead to shifts in the diet composition of consumers as they become increasingly reliant on the allochthonous resource as a trophic subsidy (Marcarelli et al. 2011; Sato and Watanabe 2013).

Trophic subsidies that originate from fishery activities can provide recipient aquatic communities with alternative food resources that are energy rich and highly nutritious (Grey et al. 2004; Arlinghaus and Niesar 2005; Fernandez-Jover et al. 2011a, b), such as pelletized fishmeal that are usually high in protein (from fishmeal) and lipid (from fish oil) (Naylor et al. 2000). Whilst it was recently estimated that the global annual production of fishmeal pellets was 3.7 million tonnes (Tacon and Metian 2008), only a small proportion of this production is used directly as bait for recreational angling. Nevertheless, pellets are increasingly being used by freshwater anglers in Europe as both an attractant and hook-bait to target fish of the Cyprinidae family, such as common carp *Cyprinus carpio* and European barbel *Barbus barbus* (Jackson et al. 2013). Moreover, the quantities used can be substantial, with the amount of bait used annually per angler in Germany estimated at 7.3 kg (Arlinghaus and Niesar 2005). Given that these pellets were originally designed for feeding carnivorous fish in aquaculture to maximise their growth through the input of an energy rich resource that is relatively easy to assimilate (Naylor et al. 2000), then this at least partially explains their effective use within freshwater angling for a range of omnivorous and carnivorous species.

Aquatic ecosystems are also vulnerable to species invasions, especially those that are already disturbed through human activities (MacDougall and Turkington 2005). These invasive species, when present in sufficient abundance, can act as novel autochthonous resources for native species, resulting in shifts in food web structure (Coulas et al. 1998; Vander Zanden et al. 1999; Ellis et al. 2011). Moreover, invasive species often create novel trophic pathways, acting as both consumers and resources with, for example, invasive crayfish consuming both plant and animal material (Jackson et al. 2014) and providing an abundant food resource for many taxa (e.g. Beja 1996; Correia 2001; Tablado et al. 2010). In many European countries, invasive crayfish species have been widely introduced, with the signal crayfish (*Pacifastacus leniusculus*) usually being the most abundant (Kouba et al. 2014), including in the UK (Jackson and Grey 2013).

Consequently, the aim of this study was to assess how angling baits and invasive crayfish influenced the diet of freshwater fish in riverine environments, using *B. barbus* as the model species. They were studied in four English rivers in which they are the main target species for the majority of the anglers practising catch-and-release; of these rivers, invasive *P. leniusculus* had well-established populations in two but were absent from the other two. As Grey et al. (2004) established that the predominantly marine-derived material of pellets makes them isotopically distinct in freshwater food webs, the specific objective was to assess the relative dietary contribution of fishmeal pellets and *P. leniusculus* to *B. barbus* compared to that from native and naturally available species. *B. barbus* is indigenous in some English rivers but non-indigenous in others and is popular with many anglers due to its sporting qualities and relative ease of capture (Britton and Pegg 2011). An omnivore that is occasionally piscivorous (Kottelat and Freyhof 2007), it is regularly fished for using relatively large quantities of fishmeal pellets (often >1 kg per angler per day; J. R. Britton personal observation).

Materials and methods

The four study rivers were the Rivers Teme (52°19.40'N; 2°28.50'W), Hampshire Avon (50°54.38'N; 1°47.30'W), Kennet (51°25.32'N; 1°05.11'W) and Lee (51°48.40'N; 0°14.29'W). On all of these rivers, angling was permitted throughout the coarse angling open season (between June 16 and March 14), with the majority of angling activity focused between June and September. *P. leniusculus* was present in the Kennet and Lee, but not the Teme and Hampshire Avon. We used the stable isotope analysis of fish scales as a non-destructive method to assess the diet of *B. barbus* in preference to using muscle tissue or gut contents analysis (GCA) because the sampling sites were all recreational fisheries that practised catch-and-release angling. Stable isotope analysis reveals food web structure and trophic linkages through the naturally occurring ratios of $^{15}\text{N}:^{14}\text{N}$ and $^{13}\text{C}:^{12}\text{C}$ (Grey 2006). The carbon ratios reflect the consumer diet with typical enrichment of 0–1 ‰, whereas nitrogen ratios show greater enrichment of 2–4 ‰ from resource to consumer (i.e. indicate trophic position) (Post 2002; McCutchan et al. 2003).

Samples of *B. barbus* were captured from each river during August and September 2012 by angling. Following capture, each fish was measured (fork length, nearest 5 mm) and between 3 and 5 scales were removed from between the base of the dorsal fin and the lateral line. These were transferred to paper envelopes and rapidly dried to maintain their condition. At the same time, samples of the angler bait were taken for subsequent analyses. To obtain

Table 1 Sample size, fork length range, mean fork length (\pm SD) and mean stable isotope values (\pm SD) of *B. barbus* at each site

Site	River	<i>n</i>	Length range (mm)	Mean length (mm)	Mean $\delta^{13}\text{C}$ (‰)	Mean $\delta^{15}\text{N}$ (‰)
1	Avon	19	590–800	680 \pm 71	–27.28 \pm 1.33	11.51 \pm 1.27
2	Teme	9	470–650	556 \pm 72	–25.52 \pm 2.02	11.81 \pm 0.96
3	Kennet	9	550–710	631 \pm 56	–25.02 \pm 2.33	11.34 \pm 0.92
4	Lee	9	420–600	534 \pm 55	–27.23 \pm 1.45	18.16 \pm 1.46

samples of the putative food resources of *B. barbus* from each river, kick-sampling was used in September 2012 to provide representative samples of the macro-invertebrate communities. In all rivers, this also provided samples of small fishes, primarily 3-spined stickleback *Gasterosteus aculeatus*, minnow *Phoxinus phoxinus* and bullhead *Cottus gobio* (subsequently referred to as ‘small fishes’). In the Rivers Kennet and Lee, kick-sampling was also used to sample *P. leniusculus*.

For stable isotope analysis, replicate samples of the putative food resources of *B. barbus* were used ($n = 3$ –10 per resource). Given the size (>400 mm; Table 1) and likely age (>10 years; Britton et al. 2012) of all of the *B. barbus* in the samples, only material from the very outer portions of scales were used in analyses, i.e. material outside of the last annulus that was produced through growth in 2012 rather than earlier in life (Hutchinson and Trueman 2006). Prior to analysis, all samples were ground using an agate pestle and mortar and 0.5 mg was weighed into 6×4 mm tin cups using an ultra-microbalance (UM \times 2 Automated-S, Mettler Toledo). Carbon and nitrogen isotopic analysis was carried out at Queen Mary, University of London, using an elemental analyser (Flash EA, 1112 series, Thermo-Finnigan) coupled to a continuous flow isotope ratio mass spectrometer (Finnigan MAT DeltaPlus, Thermo-Finnigan). Ratios of $^{13}\text{C}:^{12}\text{C}$ and $^{15}\text{N}:^{14}\text{N}$ are expressed in per mille (‰) using the delta notation (δ). Secondary standards (sucrose for carbon; ammonium sulphate for nitrogen) with known relation to international standards (Pee Dee Belemnite for carbon; nitrogen in air for nitrogen) were used as reference materials. Cyclohexanone-2, 4-dinitrophenylhydrazone or urea was used as an internal standard and repeat analyses resulted in typical precision of <0.1 ‰ for carbon and <0.3 ‰ for nitrogen.

Prior to the data analysis, the stable isotope data from the *B. barbus* scales were converted to values for dorsal muscle as muscle stable isotope values reflect that of the diet of individual fish most closely (Pinnegar and Polunin 1999; Grey et al. 2009). Consequently, samples of scales and dorsal muscle from 20 *B. barbus* of 150–250 mm that were available from an unconnected and completed study (Pegg and Britton 2011) and that had been raised on a

standardised diet of consistent isotopic composition were analysed and the offset between scale and muscle determined via subtraction. Material only on the scale edge was used in the analyses (as per the fish used in the main study) and provided muscle values of -1.8 ± 0.49 ‰ for $\delta^{13}\text{C}$, and $+0.6 \pm 0.35$ ‰ for $\delta^{15}\text{N}$ relative to scale values. We tested fish length against $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in each river using linear regression to identify any ontogenetic influences. Bayesian mixing models were then used to determine the relative contribution of each resource to the diet of each *B. barbus* population and individual. The individual analysis was used to assess individual variation in diet choice. Models were run using the SIAR package in the R computing programme (Parnell et al. 2010; R Core Development Team 2013). As excessive putative food resources can cause the model to underperform, the data for resources with similar isotope values were combined a priori, whilst respecting the taxon and functional affiliation of the individual species (Phillips et al. 2005). Accordingly, the resources were pooled into the following groups at each site where available: fish pellets, small fish, Arthropoda (*Gammarus pulex*, Hydropsychidae, Simuliidae spp. and Ephemeroptera spp. that were present in all the rivers) and *P. leniusculus*. To correct for isotopic fractionation between resources and consumers, 3.4 ‰ (± 0.98 ‰) was used for $\delta^{15}\text{N}$ and 0.39 ‰ (± 1.3 ‰) for $\delta^{13}\text{C}$ (Post 2002).

Anecdotal evidence from anglers encountered during the study revealed concerns over *P. leniusculus* consuming angler baits, particularly pellets. To test for this, a further mixing model was run substituting *P. leniusculus* as the consumer, and inserting values for pellets, small fish, leaf litter and arthropods as resources. The fractionation factors used were as already described for *B. barbus*.

Results

The lengths of the *B. barbus* captured from the rivers spanned 420–800 mm (Table 1). There was considerable variability in the $\delta^{13}\text{C}$ of individual *B. barbus* in the rivers, with this less apparent for $\delta^{15}\text{N}$ (Fig. 1). Small fishes and *P. leniusculus* tended to be very similar in $\delta^{13}\text{C}$ with *P. leniusculus* ^{15}N -depleted by 1–2 ‰, whilst values for

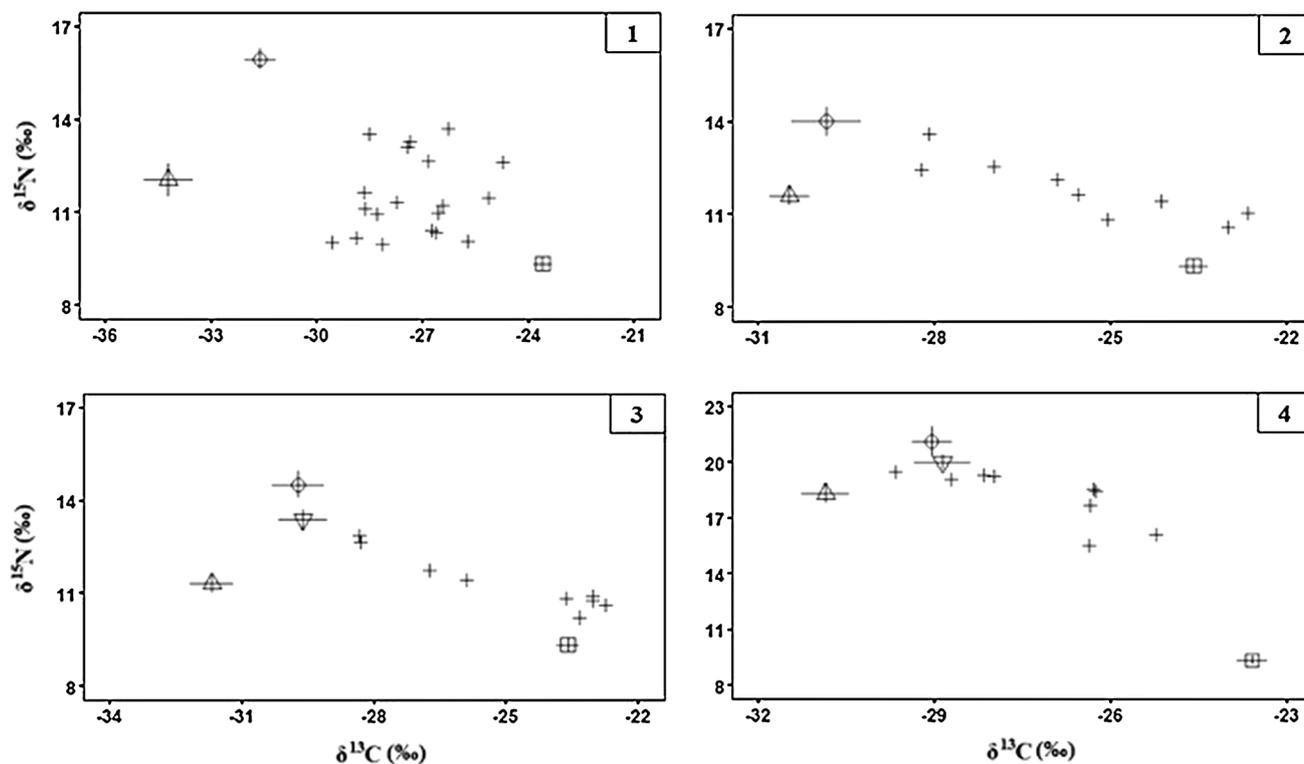


Fig. 1 Stable isotope bi-plots for each site, showing individual *Barbus barbus* muscle isotope values (pluses) and mean (\pm SE) values of potential food sources (corrected for isotopic fractionation); pellet (square), small fish (circle), crayfish (triangle point down), Arthropoda (triangle point up). Note the different scales on the axes. The number in the right hand top corner of each plot denotes the river (cf. Table 1)

fishmeal pellets were clearly isotopically distinct compared to any other resource (Fig. 1). The influence of fish length on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was not significant in all rivers ($\delta^{13}\text{C}$: Teme $R^2 = 0.50$, $F_{1,8} = 2.31$, $P = 0.17$; Kennet $R^2 = 0.01$, $F_{1,7} = 0.01$, $P = 0.94$; Lee $R^2 = 0.03$, $F_{1,8} = 3.84$, $P = 0.09$; Avon $R^2 = 0.05$, $F_{1,17} = 0.82$, $P = 0.38$; $\delta^{15}\text{N}$: Teme $R^2 = 0.10$, $F_{1,8} = 0.77$, $P = 0.54$; Kennet $R^2 = 0.01$, $F_{1,7} = 0.05$, $P = 0.81$; Lee $R^2 = 0.35$, $F_{1,8} = 4.38$, $P = 0.07$; Avon $R^2 = 0.20$, $F_{1,17} = 4.15$, $P = 0.06$).

Fishmeal pellets generally made a substantial contribution to the overall biomass of *B. barbus* (mean value range 23–59 %) and was the most important resource in the Hampshire Avon and Kennet (Fig. 2). Where *P. leniusculus* was present (Lee and Kennet), it was also an important resource in *B. barbus* diet (mean values: 30 and 20 %; Fig. 2). The dietary contribution of the other food resources varied between rivers, with Arthropoda generally representing the least important food source (Fig. 2).

Data from individual *B. barbus* per river also suggested that in the rivers where *P. leniusculus* was absent, there were relatively high proportions of pellets in diet, ranging from 35 to 72 % in the Avon and 20–79 % in the Teme (Table 2). Where *P. leniusculus* was present, the contribution of pellets was more varied between rivers, ranging from 22 to 77 % in

the Kennet, and 8–41 % in the Lee (Table 2). In the Lee, pellets contributed < 30 % to the diet of most fish (seven of nine fish) and *P. leniusculus* was an additional important resource, contributing 22–31 %. The proportion of pellets in the diet of *B. barbus* varied considerably between individuals in the Rivers Teme and Kennet (as indicated by high standard deviations; Table 2), suggesting a degree of individual specialisation. In contrast, the proportion of crayfish in the diet of *B. barbus* (when available) varied little between individuals (as indicated by low standard deviations; Table 2). Small fish were also important resources in all four rivers, contributing up to 50 % to fish diet especially in the absence of crayfish (Table 2).

The mixing model run with crayfish as the consumer revealed that, contrary to anecdotal reports, the pellets were of relatively low dietary importance to *P. leniusculus*, with a mean contribution of 6 % in the Kennet and 12 % in the Lee.

Discussion

The fish analysed from the four *B. barbus* populations were strongly reliant on introduced fishmeal pellets as a food

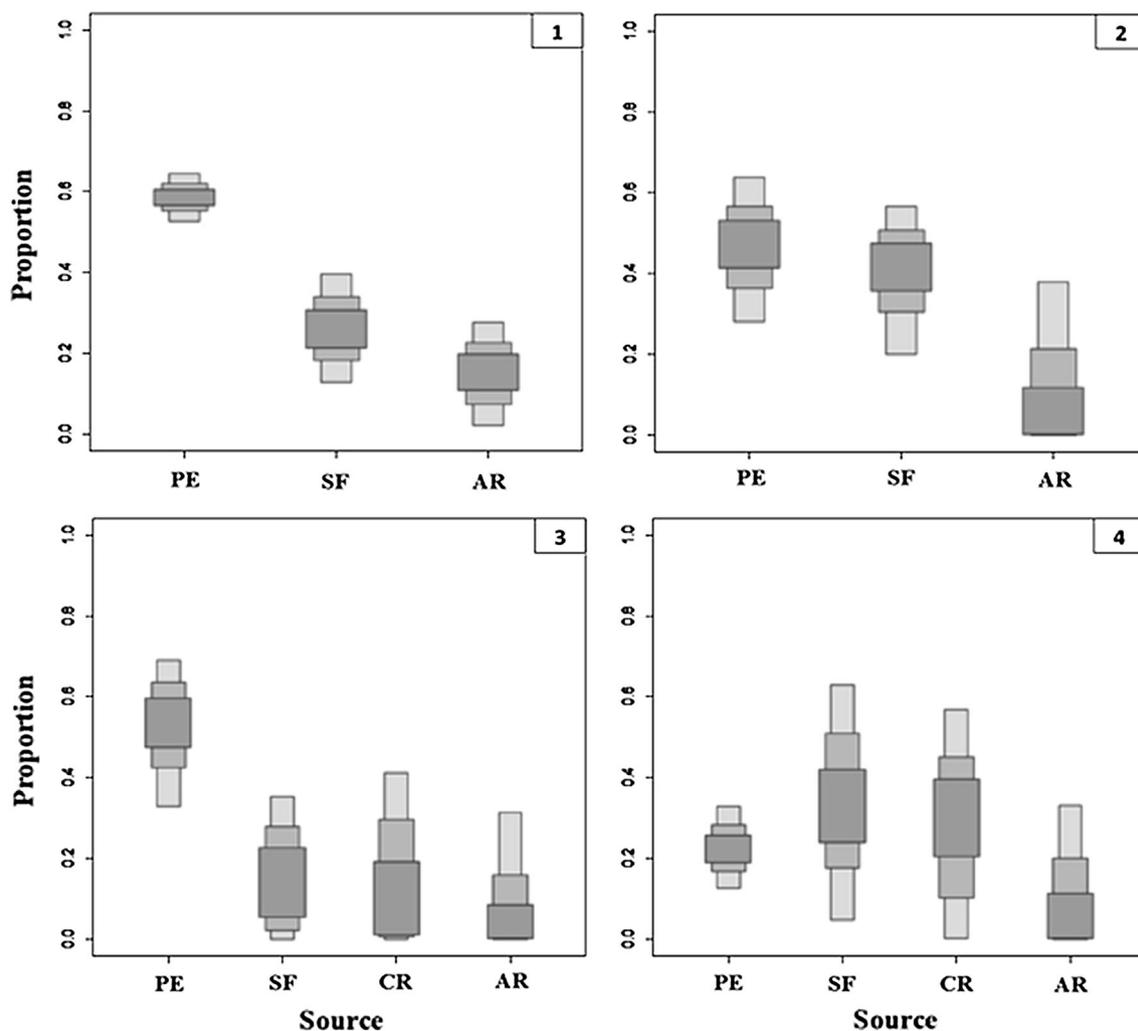


Fig. 2 Boxplots for each site, showing estimated contribution of different carbon sources (*PE* pellet, *SF* small fish, *AR* Arthropoda, *CR* crayfish) to the diet of *Barbus barbus*; dark grey box represents the 50 % of the data, posterior light grey box 75 % of the data and the outer light grey box 95 % of the data. The number in the right hand top corner of each plot denotes the river (cf. Table 1)

resource. In the Rivers Kennet, Teme and Hampshire Avon, analyses from individual fish revealed that pellets comprised up to 79 % of assimilated resources. The River Lee differed in that the highest contribution of pellets to the diet of an individual fish was estimated at 41 %. Here, other items in the diet, especially invasive *P. leniusculus* and small fish, were important dietary resources. Perhaps surprisingly, the models estimated that Arthropods were the least important of the natural dietary resources included in the models.

Although the study was based on single collections of material sampled towards the start of autumn 2012, the use of stable isotope analysis provided a temporally integrated assessment of *B. barbus* diet that reflected their assimilated food items in the preceding months (Grey 2006). The influence of pellets on barbel diet might have decreased had samples been taken following the winter period, given

that angling activities tend to be focused in summer on the study rivers. However, *B. barbus* growth rates, movement and activities peak in summer and almost cease when winter temperatures fall to close to the species' thermal limit (4 °C; Baras 1995a, b). Consequently, their food intake and muscle turnover would be likely to be very low in winter, emphasising that sampling following the summer was the optimal period for the study (Perga and Gerdeaux 2005). For similar reasons, it is likely our estimates of the contribution of crayfish to *B. barbus* biomass is also near to the annual maximum, as crayfish are less active over winter and hence probably less available as a prey resource. Ideally, including control rivers where pellets were not used would have made our study more robust, allowing us to identify the isotopic niche of *B. barbus* without such an allochthonous resource; this, however, represents a major challenge in many English rivers given that *B. barbus* is

Table 2 Intra-population variation in estimated diet of *B. barbus* at each site, indicating minimal, maximal and mean (\pm SD) contribution of each source, and where crayfish are exclusively *P. leniusculus*

Site	River	Source	Min (%)	Max (%)	Mean (%)
1	Avon	Pellet	34.6	71.6	52.0 \pm 10.3
		Small fish	11.5	43.6	23.9 \pm 10.8
		Arthropoda	12.1	44.4	24.1 \pm 9.3
2	Teme	Pellet	20.0	79.5	50.5 \pm 21.4
		Small fish	11.9	49.8	29.1 \pm 13.0
		Arthropoda	8.1	33.1	20.4 \pm 8.8
3	Kennet	Pellet	21.7	77.2	55.8 \pm 23.5
		Small fish	8.1	30.3	16.0 \pm 9.1
		Crayfish	8.7	27.6	16.3 \pm 8.0
		Arthropoda	6.1	21.1	12.0 \pm 6.4
4	Lee	Pellet	7.9	40.6	22.2 \pm 12.2
		Small fish	20.4	32.8	29.0 \pm 4.7
		Crayfish	21.9	30.9	28.8 \pm 3.2
		Arthropoda	12.2	30.2	20.1 \pm 6.1

a highly attractive target species for anglers and the use of pellets is now ubiquitous.

Fishmeal pellets used by anglers were thus an important allochthonous trophic subsidy for these *B. barbus* populations. There are, however, few studies that have dealt with how subsidies such as these are incorporated into food webs and what their relative importance is at the population and community level. Notwithstanding, Grey et al. (2004) revealed that in Esthwaite Water, England, approximately 65 % of *Daphnia* spp. and over 80 % of roach *Rutilus rutilus* body carbon was ultimately derived from pellet material originating from an in situ fish farm. Other studies on the fate of pelletized feeds from aquaculture have shown their integration into the food web of the surrounding environment (Fernandez-Jover et al. 2011a, b; Deme'trio et al. 2012). Jackson et al. (2013) revealed that the growth, density and fitness of the invasive fish, *Pseudorasbora parva*, was enhanced in pond mesocosms that received trophic subsidies in the form of small fishmeal pellets, with this often being an indirect mechanism as the elevated nutrient concentrations that occurred as a result of pellet introduction had the effect of increasing rates of algal standing stocks. Whilst the quantity of fishmeal pellets that were introduced into each river was not quantified, for comparative purposes it has been estimated that recreational anglers in Germany introduced a total of 24,000 tonnes of angling bait into freshwater fisheries in 2004 (Arlinghaus and Niesar 2005). This was not only believed to represent a significant trophic subsidy for the fish, but also elevated nutrient concentrations in the water and subsequently impacting adversely on water chemistry

(Niesar et al. 2004; Arlinghaus and Niesar 2005; Lewin et al. 2006).

Invasive crayfish have been shown to have numerous negative effects on local fish communities through predation on small benthic fish and eggs (Guan and Wiles 1997; Thomas and Taylor 2013), competition for food and shelter (Guan and Wiles 1997; Bobeldyk and Lamberti 2010), and alteration of habitat by burrowing activities (Guan and Wiles 1997).

Other studies on invasive crayfish have highlighted their importance as a food resource for many predatory fish (Blake and Hart 1995; Garvey et al. 2003; Hein et al. 2006; Nyström et al. 2006; Jackson et al. 2012), which could potentially help in controlling the invasive crayfish abundance (Hein et al. 2006; Nyström et al. 2006). Our results indicate that invasive crayfish represent an important food source for adult *B. barbus*, even in the presence of an abundant allochthonous food resource such as fishmeal pellets. Although it was estimated that both the crayfish and pellets were important dietary resources, it was not determined whether their presence in *B. barbus* diet provided any benefits to the fish or indeed the wider population, such as in improved condition and increased somatic growth rates and fitness. However, fish-meal pellets are manufactured to be highly nutritious compared with many other food resources and, in other studies, have resulted in enhanced fish growth rates (Naylor et al. 2000; Jackson et al. 2013) and so it can be speculated that similar advantages might have been provided to *B. barbus* here. When the mixing models were being developed, it was apparent that the presence of *P. leniusculus* and 'small fish' in analyses tended to reduce the model performance due to their isotopic similarity. However, even with the small fish in the analyses, it was evident that *P. leniusculus* was an important food source in fish diet, as suggested by Nyström et al. (2006), who showed their high contribution to fish diet in streams and lakes in Sweden.

Classical dietary studies have reported that *B. barbus* is omnivorous, eating benthic invertebrates (Cherghou et al. 2002; Piria et al. 2005; Corse et al. 2010) and small fish (Kottelat and Freyhof 2007), with algae also present in their diet (Cherghou et al. 2002; Piria et al. 2005). Our stable isotope data revealed a different story with little evidence that benthic macro-invertebrates (excluding *P. leniusculus*) were as important to diet when compared to fishmeal pellets and *P. leniusculus*. It may be that the majority of fish which were sampled by angling for this study were 'conditioned' to feeding upon high quality angling baits simply by the sheer volume of bait introduced and thus favoured those over other more natural diets. Nevertheless, our results tend to support Cherghou et al. (2002) who observed high dietary plasticity in *B. barbus* populations depending on the available prey items. In the Rivers Teme and Kennet there

was also high intraspecific variability in the use of fishmeal pellets, with certain individuals clearly specializing on pellets as a principal food source. This plasticity could play an important role in different environments with diverse population dynamics, where resources might vary in their quantity and quality, enabling individual *B. barbatus* to shift diet according to prey availability. In addition, the barbel used in the study were all relatively large and had smaller individuals been available for analysis, particularly those < 100 mm, then it is likely that much higher proportions of macro-invertebrates would have been estimated in their diets due to their more limited gape-size. Irrespective, the outputs here indicated that the diet of *B. barbatus* in rivers that are exploited by angling can be heavily reliant on their introduced baits, and invasive crayfish, that act as an important allochthonous trophic subsidies.

Acknowledgments We thank the Barbel Society for their support in the completion of the work.

References

- Arlinghaus R, Niesar N (2005) Nutrient digestibility of angling baits for carp, *Cyprinus carpio*, with implications for groundbait formulation and eutrophication control. *Fish Man Ecol* 12:91–97
- Baras E (1995a) Seasonal activities of *Barbus barbatus* L.: effect of temperature on time-budgeting. *J Fish Biol* 46:816–828
- Baras E (1995b) Thermal related variations of seasonal and daily spawning periodicity in *Barbus barbatus*. *J Fish Biol* 46:915–917
- Beja PR (1996) An analysis of otter *Lutra lutra* predation on introduced American crayfish *Procambarus clarkii* in Iberian streams. *J Appl Ecol* 33:1156–1170
- Blake MA, Hart PJB (1995) The vulnerability of juvenile signal crayfish to perch and eel predation. *Freshw Biol* 33:233–244
- Bobeldyk AM, Lamberti GA (2010) Stream food web responses to a large omnivorous invader, *Orconectes rusticus* (Decapoda, Cambaridae). *Crustaceana* 83:641–657. doi:10.1163/001121610X49103
- Britton JR, Pegg J (2011) Ecology of European Barbel *Barbus barbatus*: implications for river, fishery, and conservation management. *Rev Fish Sci* 19:321–330. doi:10.1080/10641262.2011.599886
- Britton JR, Davies GD, Harrod C (2010) Trophic interactions and consequent impacts of the invasive fish *Pseudorasbora parva* in a native aquatic foodweb: a field investigation in the UK. *Biol Invasions* 12:1533–1542. doi:10.1007/s10530-009-9566-5
- Britton JR, Pegg J, Davies GD (2012) Spatial variation in the somatic growth of European barbel *Barbus barbatus*: a UK perspective. *Ecol Freshw Fish* 22:21–29
- Cherghou S, Khodari M, Yaâkoubi F, Benabid M, Badri A (2002) Contribution to study a barbel (*Barbus barbatus callensis* Valenciennes, 1842) diet in Moroccan Medium-Atlas stream: oued Boufekrane. *Revue des Sci de l'Eau* 15:153–163
- Correia AM (2001) Seasonal and interspecific evaluation of predation by mammals and bird on the introduced red swamp crayfish *Procambarus clarkii* (Crustacea, Cambaridae) in a freshwater marsh (Portugal). *J Zool* 255:533–541
- Corse E, Costedoat C, Chappaz R, Pech N, Martin JF, Gilles A (2010) A PCR-based method for diet analysis in freshwater organisms using 18S rDNA barcoding on faeces. *Mol Ecol Res* 10:96–108. doi:10.1111/j.1755-0998.2009.02795.x
- Coulas RA, Macisaac HJ, Dunlop W (1998) Selective predation on an introduced zooplankton (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedii*) in Harp Lake, Ontario. *Freshw Biol* 40:343–355
- Demétrio JA, Gomes LC, Latini JD, Agostinho AA (2012) Influence of net cage farming on the diet of associated wild fish in a Neotropical reservoir. *Aquaculture* 330–333:172–178. doi:10.1016/j.aquaculture.2011.11.026
- Ellis BK, Stanford JA, Goodman D, Stafford CP, Gustafson DL, Beauchamp DA, Chess DW, Craft JA, Deleray MA, Hansen BS (2011) Long-term effects of a trophic cascade in a large lake ecosystem. *Proc Natl Acad Sci USA* 108:1070–1075
- Fernandez-Jover D, Arechavala-Lopez P, Martinez-Rubio L, Tocher DR, Bayle-Sempere JT, Lopez-Jimenez JA, Martinez-Lopez FJ, Sanchez-Jerez P (2011a) Monitoring the influence of marine aquaculture on wild fish communities: benefits and limitations of fatty acid profiles. *Aquac Environ Interact* 2:39–47. doi:10.3354/aei00029
- Fernandez-Jover D, Martinez-Rubio L, Sanchez-Jerez P, Bayle-Sempere JT, Lopez Jimenez JA, Martínez Lopez FJ, Bjørn PA, Uglem I, Dempster T (2011b) Waste feed from coastal fish farms: a trophic subsidy with compositional side-effects for wild gadoids. *Estuar Coast Shelf S* 91:559–568. doi:10.1016/j.ecss.2010.12.009
- Garvey JE, Rettig JE, Stein RA, Lodge DM, Klosiewski SP (2003) Scale-dependent associations among fish Predation, littoral habitat, and distributions of crayfish species. *Ecology* 84:3339–3348
- Grey J (2006) The use of stable isotope analyses in freshwater ecology: current awareness. *Pol J Ecol* 54:563–584
- Grey J, Waldron S, Hutchinson R (2004) The utility of carbon and nitrogen isotope analyses to trace contributions from fish farms to the receiving communities of freshwater lakes: a pilot study in Esthwaite Water, UK. *Hydrobiologia* 524:253–262
- Grey J, Graham CT, Britton JR, Harrod C (2009) Stable isotope analysis of archived roach (*Rutilus rutilus*) scales for retrospective study of shallow lake responses to nutrient reduction. *Freshw Biol* 54:1663–1670. doi:10.1111/j.1365-2427.2009.02215.x
- Guan RZ, Wiles PR (1997) Ecological impact of introduced crayfish on benthic fishes in a British lowland river. *Conserv Biol* 11:641–647
- Harmon JP, Ives AR, Moran NA (2009) Species response to environmental change: impacts of food web interactions and evolution. *Science* 323:1347–1350. doi:10.1126/science.1167396
- Hein CL, Roth BM, Ives AR, Vander Zanden MJ (2006) Fish predation and trapping for rusty crayfish (*Orconectes rusticus*) control: a whole-lake experiment. *Can J Fish Aquat Sci* 63:383–393. doi:10.1139/F05-229
- Hutchinson JJ, Trueman CN (2006) Stable isotope analyses of collagen in fish scales: limitations set by scale architecture. *J Fish Biol* 69:1874–1880. doi:10.1111/j.1095-8649.2006.01234.x
- Jackson MC, Grey J (2013) Accelerating rates of freshwater invasions in the catchment of the River Thames. *Biol Invasions* 15:945–951. doi:10.1007/s10530-012-0343-5
- Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J (2012) Population-level metrics of trophic structure based on stable isotopes and their application to invasion ecology. *PLoS ONE* 7:e31757. doi:10.1371/journal.pone.0031757
- Jackson MC, Allen R, Pegg J, Britton JR (2013) Do trophic subsidies affect the outcome of introductions of a non-native freshwater fish? *Freshw Biol* 58:2144–2153. doi:10.1111/fwb.12197

- Jackson MC, Jones T, Milligan M, Sheath D, Taylor J, Ellis A, England J, Grey J (2014) Niche differentiation among invasive crayfish and their impacts on ecosystem structure and functioning. *Freshw Biol* 59:1123–1135. doi:10.1111/fwb.12333
- Jefferies RL (2000) Allochthonous inputs: integrating population changes and food-web dynamics. *Trend Ecol Evol* 15:19–22
- Jones RI, Grey J, Sleep D, Quarmby C (1998) An assessment, using stable isotopes, of the importance of allochthonous organic carbon sources to the pelagic food web in loch ness. *Proc R Soc Lond B* 265:105–110. doi:10.1098/rspb.1998.0270
- Kottelat M, Freyhof J (2007) Handbook of European freshwater fishes. Kottelat, Cornol
- Kouba A, Petrusek A, Kozák P (2014) Continental-wide distribution of crayfish species in Europe: update and maps. *Knowl Manag Aquat Ecosyst* 413:05
- Lewin WC, Arlinghaus R, Mehner T (2006) Documented and potential biological impacts of recreational fishing: insights for management and conservation. *Rev Fish Sci* 14:305–367. doi:10.1080/10641260600886455
- MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55
- Marcarelli AM, Baxter CV, Mineau MM, Hall RO (2011) Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* 92:1215–1225
- Marczak LB, Richardson JS, Thompson RM (2007) Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148
- McCutchan JH, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102:378–390. doi:10.1034/j.1600-0706.2003.12098.x
- Naylor RL, Goldburg RJ, Primavera JH, Kautsky N, Beveridge MCM, Clay J, Folke C, Lubchenco J, Mooney H, Troell M (2000) Effect of aquaculture on world fish supplies. *Nature* 405:1017–1024. doi:10.1038/35016500
- Niesar M, Arlinghaus R, Rennert B, Mehner T (2004) Coupling insights from a carp, *Cyprinus carpio*, angler survey with feeding experiments to evaluate composition, quality and phosphorus input of groundbait in coarse fishing. *Fish Man Ecol* 11:225–235
- Nyström P, Stenroth P, Holmqvist N, Berglund O, Larsson P, Granéli W (2006) Crayfish in lakes and streams: individual and population responses to predation, productivity and substratum availability. *Freshw Biol* 51:2096–2113. doi:10.1111/j.1365-2427.2006.01641.x
- Parnell AC, Inger R, Bearhop S, Jackson AL (2010) Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5(3):e9672. doi:10.1371/journal.pone.0009672
- Pegg J, Britton JR (2011) Effects of inter- and intra-specific competition on the growth rates of juvenile European barbel *Barbus barbus* used in the stock enhancement of UK fisheries. *Fish Res* 112:8–12. doi:10.1016/j.fishres.2011.08.003
- Perga ME, Gerdeaux D (2005) Are fish what they eat all year round? *Oecologia* 144:598–606
- Petchey OL, McPhearson PT, Casey TM, Morin PJ (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72. doi:10.1038/47023
- Phillips DL, Newsome SD, Gregg JW (2005) Combining sources in stable isotope mixing models: alternative methods. *Oecologia* 144:520–527. doi:10.1007/s00442-004-1816-8
- Pinnegar JK, Polunin NVC (1999) Differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fish tissues: implications for the study of trophic interactions. *Func Ecol* 13:225–231
- Piria M, Treer T, Aničić I, Safner R, Odak T (2005) The natural diet of five cyprinid fish species. *Agric Conspec Sci* 70:21–28
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/>
- Sato T, Watanabe K (2013) Do stage-specific functional responses of consumers dampen the effects of subsidies on trophic cascades in streams? *J Anim Ecol*. doi:10.1111/1365-2656.12192
- Tablado Z, Tella JL, Sánchez-Zapata JA, Hiraldo F (2010) The paradox of the long-term positive effects of a North American crayfish on a European community of predators. *Conserv Biol* 24:1230–1238
- Tacon AGJ, Metian M (2008) Global overview on the use of fish meal and fish oil in industrially compounded aquafeeds: trends and future prospects. *Aquaculture* 285:146–158. doi:10.1016/j.aquaculture.2008.08.015
- Thomas CL, Taylor CA (2013) Scavenger or predator? Examining a potential predator–prey relationship between crayfish and benthic fish in stream food webs. *Freshw Sci* 32:1309–1317. doi:10.1899/12-169.1
- Vander Zanden MJ, Rasmussen JB, Casselman JM (1999) Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401:464–467