



Trophic Plasticity of the Highly Invasive Topmouth Gudgeon (*Pseudorasbora parva*) Inferred From Stable Isotope Analysis

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A wide trophic niche and high trophic plasticity are often invoked to explain the successful establishment of many aquatic invaders, but there is little information regarding the diet of most invasive fish in European waters. We combined stomach content and stable isotope analysis (SIA) of ^{13}C and ^{15}N to examine the trophic niche of the highly invasive topmouth gudgeon (*Pseudorasbora parva*) in three contrasting ponds and a reservoir in South Wales. Marked differences in diet and trophic position were found among neighboring systems only a few kilometers apart. The most diverse diet was found in ponds with the fewest number of inter-specific competitors, and resulted in topmouth gudgeon having the highest condition factor, the widest variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and the highest carbon content, typical of generalist feeders. In contrast, topmouth gudgeon that coexisted with other cyprinids, were much more likely to have an empty stomach and relied almost exclusively on plant seeds, resulting in fish having a poor condition factor and low trophic position. Comparisons with other trophic studies indicate that variation in isotope values among neighboring sites can exceed variation across continents, making it difficult to predict the diet or trophic impacts of the invasive topmouth gudgeon. Given the importance of obtaining reliable data on trophic position for risk assessment, our study shows that the use of SIA could be used to prioritize control and eradication measures that take into account trophic plasticity.

Keywords: aquatic invasive species, diet breadth, generalist feeder, foraging, stomach content analysis, isotopes

INTRODUCTION

The topmouth gudgeon (TMG, *Pseudorasbora parva*) is a highly invasive fish native of Asia that has become one of the worst aquatic invaders in Europe due its potential impact on native biodiversity (Pinder et al., 2005; Britton et al., 2007). TMG possesses many ecological traits that make it a successful invader, including short generation time, high fecundity, and substantial phenotypic plasticity (Gozlan et al., 2010). The species can also grow rapidly (Ye et al., 2006; Adrović and Skenderović, 2007; Kapusta et al., 2008) and mature fast (Pinder et al., 2005), especially when living at high density (Britton et al., 2007, 2008).

During the first few years of the invasion, TMG populations appear to be composed mainly of young-of-the-year, up to 50 mm in total length, although the species can reach up to 120 mm (Ye et al., 2006; Adrović and Skenderović, 2007; Kapusta et al., 2008). The species displays substantial variation in the timing of spawning, depending on water temperature (Yan and Chen, 2009). Its diet can be wide and, although previous studies had described it as mostly omnivorous (Weber, 1984; Xie et al., 2001), it can also adopt a strict planktivorous diet in some cases (Priyadarshana et al., 2001; Asaeda et al., 2007). Depending on prey availability, TMG can feed on chironomid larvae (Wolfram-Wais et al., 1999), but also on the eggs and larvae of other fish, which may pose a threat to native species (Stein and Herl, 1986; Xie et al., 2000). The preferred prey size appears to be size dependent, as observed in a comparative pond study where the smaller size class (20–25 mm) fed exclusively on cladoceran zooplankton, the bigger size classes (35–60 mm) fed mainly on chironomid larvae, and the intermediate size classes fed on a mixture of the two preys (Declerck et al., 2002). The diet of topmouth gudgeon can also change seasonally, shifting from chironomid larvae in spring and summer to ostracods in winter (Xie et al., 2000). Where introduced, topmouth gudgeon has been found to compete for food with native species in Great Britain (Britton et al., 2010), Belgium (Declerck et al., 2002), and Poland (Witkowski, 2002) which can lead to depressed growth rates, reduced reproduction outputs and shifts in the trophic position of native fish (Britton et al., 2010). When other invasive species are present, the topmouth gudgeon's plasticity in food selection allows it to shift its trophic niche and co-exist with other invaders (Jackson and Britton, 2014).

TMG can negatively impact native fish through competition for food and space, resulting in depressed growth rates (and also in production), and also a shift in trophic levels (Britton et al., 2010). Another relevant threat posed by TMG is its ability to carry non-native pathogens such as the intracellular parasite *Sphaerothecum destruens* that can become lethal for salmonids (Gozlan et al., 2005; Andreou et al., 2011). For these reasons, it is feared that the spread of TMG could result not just in a significant loss of native river biodiversity, but also on substantial economic losses caused by damage to sport fisheries and salmon farming alike (Gozlan et al., 2005).

TMG was first recorded in Great Britain in 1996, in a pond in Southern England (Domaniewski and Wheeler, 1996). It is thought that the first introduction may have occurred a decade earlier, in the mid 1980's, when TMG originating from Germany were delivered to an ornamental aquaculture facility in Hampshire, and subsequently became established in Lake Tadburn (Gozlan et al., 2002). Within few years, TMG had spread rapidly and has now been reported in 32 locations across England and Wales, most of which are lentic systems, and 10 of which are connected to major catchments (Britton et al., 2007, 2010). Recent eDNA data show that more sites are infested than previously thought (Robinson et al., 2019), probably because traditional sampling techniques do not detect the species at low densities (Britton et al., 2011). Due to its speed of colonization, and the potential for major ecological and economic impacts, TMG has been classified as highly impactful by the UK Technical

Advisory Group on the Water Framework Directive (Panov et al., 2009) and is the subject of costly eradication programs (Robinson et al., 2019).

Stable isotope analysis (SIA) can be used to study food webs (Vander Zanden et al., 1999), based on the fact that the ratios of heavy to light isotopes in animal tissues are often affected by diet (DeNiro and Epstein, 1978, 1981). Carbon and nitrogen isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) are the ones most commonly used in freshwater biology, as they are related to the sources of primary productivity ($\delta^{13}\text{C}$) and to trophic level ($\delta^{15}\text{N}$). As trophic markers, SIA can be used at different ecological levels, to study variation among individuals, species, and also among communities (Whitledge and Rabeni, 1997; Newsome et al., 2009). They can be used to examine trophic position (Roth et al., 2006; Chérel et al., 2008), animal migrations (Chérel et al., 2007; McClellan et al., 2010), impacts of invasive species (Vander Zanden et al., 1999; Nilsson et al., 2012), trophic subsidies (Izquierdo-Gomez et al., 2015), and the contribution of allochthonous vs. autochthonous food resources in aquatic ecosystems (Solomon et al., 2011; Venarsky et al., 2014).

Here we employed SIA of nitrogen and carbon, complemented with analysis of stomach contents, to investigate variation in the trophic ecology of topmouth gudgeon in four contrasting freshwater habitats in South Wales. Our aims were twofold: (1) to describe the trophic niche of this highly invasive species to gain a better understanding of the potential for interference competition with native fish, and (2) to assess the value of SIA for monitoring diet plasticity of a rapidly expanding invasive species in different colonized habitats.

MATERIALS AND METHODS

Origin of Samples

We analyzed 118 topmouth gudgeon originating from four contrasting water bodies in South Wales (**Figure 1** and **Table 1**) that differed greatly in size, use, and fish community composition: two small decorative ponds with few or no fish species other than eel (Turbine Pond, TUR, $n = 27$; Dyfatty pond, DYE, $n = 29$), a eutrophic pond used for recreational fishing regularly stocked with eight species of coarse fish (Sylen Lake, SYL, $n = 30$), and a larger, cooler reservoir used for water supply and stocked with salmonids (Upper Lliedi Reservoir, LLI, $n = 32$). Sylen Lake, Turbine pond, and Dyfatty pond were fished between November 2012 and February 2013 while the Upper Lliedi Reservoir (LLI) was fished in June 2018 as no fish could be caught during the winter of 2017/2108. Specimens were kept frozen until analysis. We obtained biometry data (total length, weight, condition factor) and stable isotope data ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N) for the four ponds, and stomach contents for three of them (no stomach data was available for LLI).

Biometry Data

We took paired measurements of total length and weight of TMG from one site (LLI) before (fresh) and after they had been frozen to derive a regression equation to estimate fresh body size from

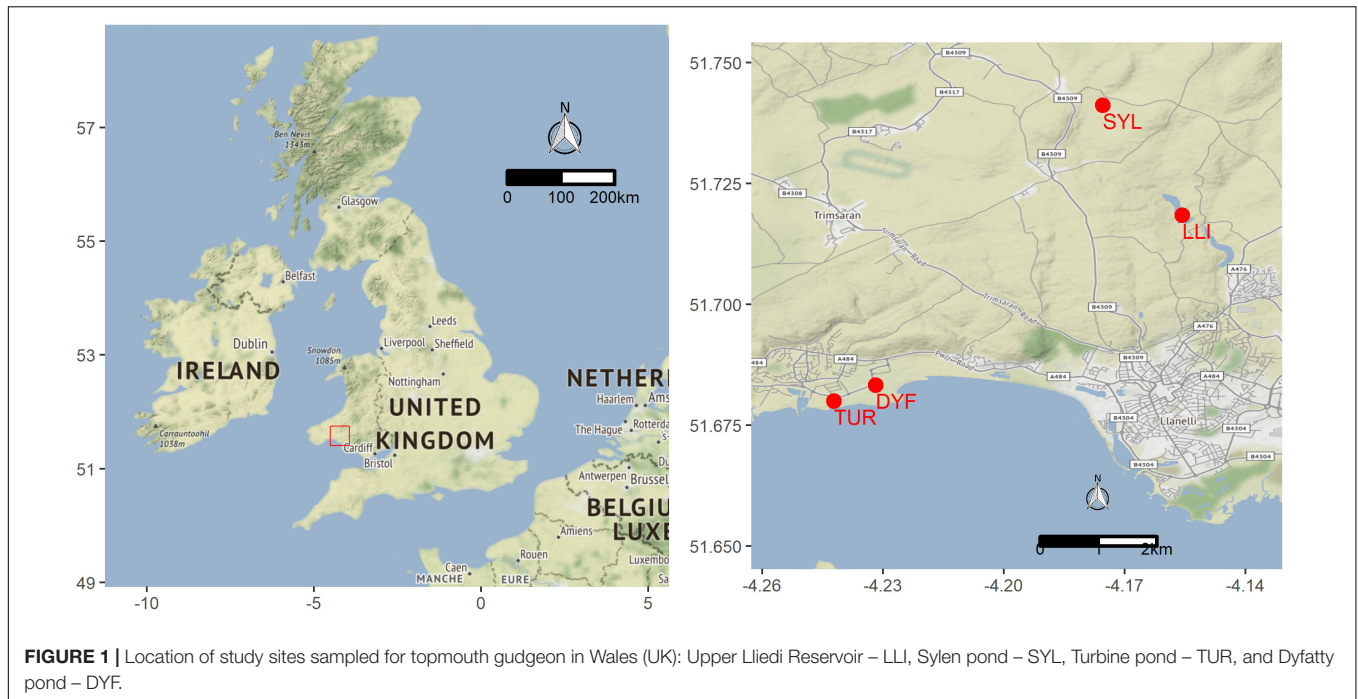


FIGURE 1 | Location of study sites sampled for topmouth gudgeon in Wales (UK): Upper Lliedi Reservoir – LLI, Sylen pond – SYL, Turbine pond – TUR, and Dyfatty pond – DYF.

TABLE 1 | Characteristics of the four study sites examined for trophic position of topmouth gudgeon (*Pseudorasbora parva*) in South Wales.

Site	UK National Grid Map Reference (SN)	Area (km ²)	Alt (m)	Sampling period	No. TMG sampled	Use	Other fish present	1st TMG record
Upper Lliedi (LLI)	5109 0459	0.130	86	June 2018	32	Public water reservoir Recreational angling	Brown trout (<i>Salmo trutta</i>) Rainbow trout (<i>Oncorhynchus mykiss</i>) Others	Unknown
Sylen (SYL)	49914 07018	0.016	144	November 2012	30	Recreational angling	Carp (<i>Cyprinus carpio</i>) Tench (<i>Tinca tinca</i>) Bream (<i>Abramis brama</i>) Roach (<i>Rutilus rutilus</i>) Chub (<i>Squalius cephalus</i>) Rudd (<i>Scardinius erythrophthalmus</i>) Goldfish (<i>Carassius auratus</i>)	2005
Turbine (TUR)	45021 00334	0.011	7	February 2013	27	Decorative pond	Eel (<i>Anguilla anguilla</i>)	2001
Dyfatty (DYF)	45829 00627	0.004	4	February 2013	29	Decorative pond	Eel (<i>Anguilla anguilla</i>) Perch (<i>Perca fluviatilis</i>) Rudd (<i>Scardinius erythrophthalmus</i>) Roach (<i>Rutilus rutilus</i>)	2001

frozen specimens collected from the other three populations. The regression equations were:

$$\text{Length}_{(fresh)} = 1.025013 \times \text{Length}_{(frozen)}^{0.99633324}$$

$$R^2 = 0.9744, P < 0.001$$

$$\text{Weight}_{(fresh)} = 1.029898 \times \text{Weight}_{(frozen)}^{1.01114309}$$

$$R^2 = 0.9979, P < 0.001$$

We calculated Fulton’s condition factor (K) from total length (TL) and weight (WT) measurements [$K = (WT * 100) / TL^3$] to derive an index of body condition (Bolger and Connolly, 1989).

Stomach Content Analysis

For stomach content analysis, frozen samples were slowly thawed and then transferred to 30, 50, and 70% ethanol solutions. We analyzed stomach contents of fish in three ponds (TUR, DYF,

SYL) with a stereo microscope (Nikon SMZ1270) at 12.7× (0.63–8×) magnification. The vast majority of prey consisted of zooplankton (67%) that we classified at family level. Insect parts (1%), seeds (24.1%) and plant material were also present, but these could not be identified. We counted every food item and measured the size (longest axis) of a subsample of food items to obtain an average size for each prey category.

Stable Isotope Analyses

We obtained 1–2 mg of white muscle from the caudal part of the fish, above the lateral line, and freeze dried the samples for 24 h before analysis. Analyses of %C, %N, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ were conducted by Isotope Ratio Mass Spectrometry (EA-IRMS) at Iso-Analytical Ltd (Marshfield Bank, Crewe CW2 8UY, United Kingdom) using a Europa Scientific 20–20 IRMS Elemental Analyzer, samples being combusted at 1,000°C in the presence of oxygen using IA-R068 as reference material (soy protein, $\delta^{13}\text{C}_{\text{V-PDB}} = -25.22\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 0.99\text{‰}$). The following standards were run as quality controls: IA-R068, IA-R038 (L-alanine, $\delta^{13}\text{C}_{\text{V-PDB}} = -24.99\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = -0.65\text{‰}$), IA-R069 (tuna protein, $\delta^{13}\text{C}_{\text{V-PDB}} = -18.88\text{‰}$, $\delta^{15}\text{N}_{\text{AIR}} = 11.60\text{‰}$) and a mixture of IAEA-C7 (oxalic acid, $\delta^{13}\text{C}_{\text{V-PDB}} = -14.48\text{‰}$) and IA-R046 (ammonium sulfate, $\delta^{15}\text{N}_{\text{AIR}} = 22.04\text{‰}$) was run as quality control samples during analysis and were calibrated against inter-laboratory standards distributed by the International Atomic Energy Agency, Vienna. Repeatability of isotope values in samples analyzed in duplicate (20%) was high (Cohen's weighted kappa coefficient: $\delta^{13}\text{C} = 0.99$; $\delta^{15}\text{N} = 0.98$; C:N = 0.94) indicating that SIA results were precise. Duplicates were then averaged before numerical analysis. The carbon to nitrogen ratio (C:N) ranged between 3.13 and 3.81, but was significantly below 3.5 (U95CI = 3.35), so lipid correction normalization was not deemed necessary (Post et al., 2007). In total we analyzed 118 specimens for SIA (DYF, $n = 29$; LLI, $n = 32$; SYL, $n = 30$; TUR, $n = 27$).

Statistical Analysis

We used R 3.3 (R Core Team, 2017) for analyses. We transformed % carbon and % nitrogen content with the arcsine transformation to make the data suitable for linear model analysis. We analyzed nitrogen and carbon content %, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N ratio as function of fish size, condition factor and pond (location), and used the *dredge* and *anova* functions in the MuMIn R package for model selection. We calculated the Shannon diversity index (H) to estimate the taxonomical diversity of the food items present in fish stomachs. Quadratic weights were applied to give greatest emphasis to large differences between scores. GLM binary logistic regression was used to model the occurrence of an empty stomach (yes or no) as a function of fish size, condition factor and pond type. We performed an analysis of similarities (ANOSIM) with the *vegan* R package (Oksanen et al., 2013) to test for differences in diet composition among locations, merging together the less frequent food classes (unidentified, insect parts and *Cyclops*). Differences in the Shannon index of diversity (H) were assessed by bootstrapping (1,000 permutations) to obtain means and 95 confidence intervals (Gardener, 2014), we then used the Hutcheson t -test to compare the diversity among sites

(Hutcheson, 1970). Trophic breadth for each pond was calculated using Levin's measure of niche breadth (Krebs, 1999):

$$B = \frac{Y^2}{\sum N_j^2}$$

where, B = Levin's measure of niche breadth.

N_j = Number of individuals using prey $_j$.

$Y = \sum N_j$ = Total number of individuals sampled.

Ethics Statement

This study was reviewed and approved by Swansea University, College of Science Ethics Committee, Permit Student Project 210519/1544.

RESULTS

Variation in Body Size and Condition Factor

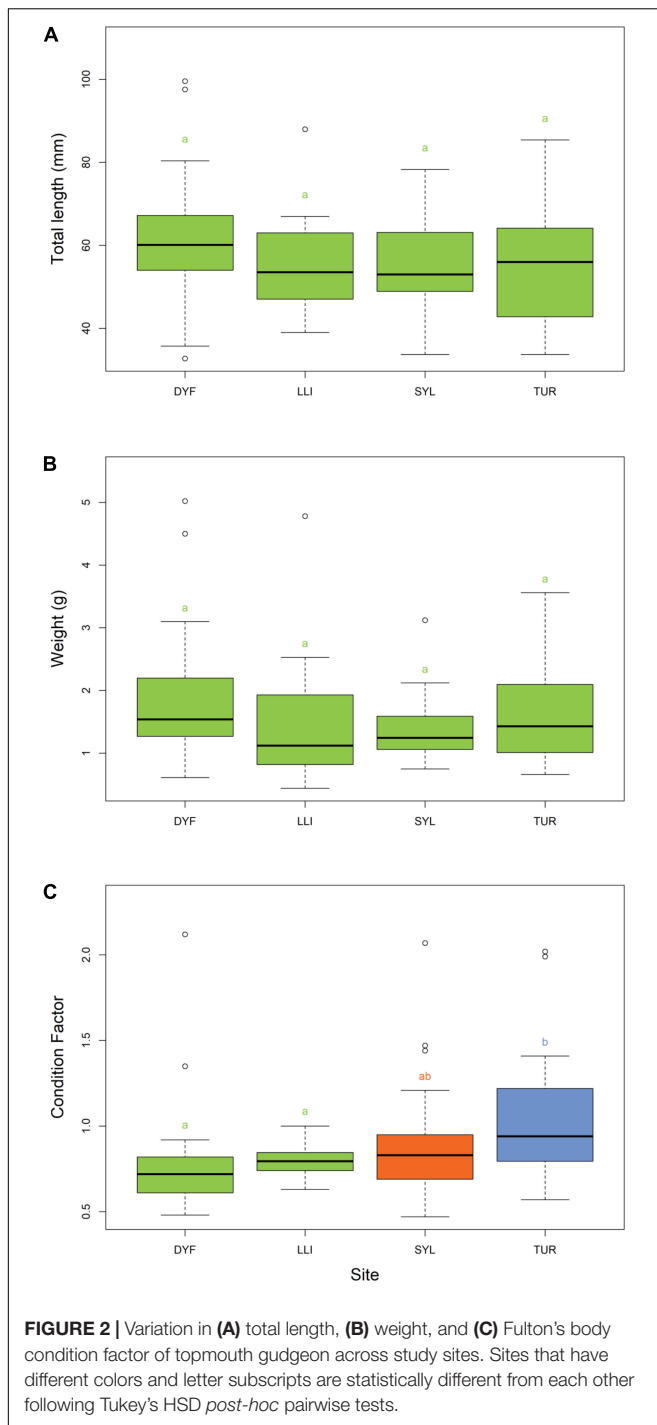
The body size (total length) of topmouth gudgeon varied from 33 to 100 mm, and the calculated wet weight from 0.44 to 5.02 g. There were no significant differences between ponds in the length or weight after Tukey's HSD correction (**Figures 2A,B**) but there was a significant difference in condition factor [$F_{(3,114)} = 5.05$, $P = 0.003$; **Figure 2C**] with fish in Turbine Pond having a better condition than those in Dyfatty pond ($P = 0.006$) or the Upper Liedi Reservoir ($P = 0.003$).

Diet Analysis

The proportion of fish with an empty stomach differed significantly among sites (GLM binary logistic regression: deviance = 22.09, $P < 0.001$), but was unrelated to body size (deviance = 2.57, $P = 0.417$), or condition factor (deviance = 0.14, $P = 0.70$). The pond with the greatest incidence of empty stomachs was DYF (21/25 or 84%), followed by SYL (19/29 or 65.5%), while TUR had the lowest incidence (6/27 or 22.2%). Tukey multiple comparisons at 95% family wise confidence level show that the incidence of empty stomachs was significantly lower at TUR than at DYF ($P < 0.001$) or SYL ($P < 0.005$), while no significant difference was observed between DYF and SYL ($P = 0.237$).

The majority of stomach contents (756 food items or 67% of the total) was composed of zooplankton, including *Daphniidae* (268 specimens or 23.8%), *Bosminidae* (136 specimens or 12%), *Chydoridae* (348 specimens or 30.9%), and *Cyclopidae* (4 specimens or 0.3%). The remaining was composed of plant seeds (272 items or 24.1%), unidentified insect parts (12 items or 1%), and unidentified organic and plant material (88 items or 7.8%; **Figure 3**). Mean prey size varied considerably, being largest in insect parts (2.14 mm), followed by *Cyclopidae* (1.51 mm), *Daphniidae* (1.28 mm), *Bosminidae* (0.67 mm), plant seeds (0.62 mm), and *Chydoridae* (0.48 mm).

Analysis of similarities (ANOSIM) indicated that the diet of TMG differed markedly among sites ($R = 0.28$, $P = 0.005$), and this was reflected in different prey diversity estimates.



Thus, the diet of fish at DYF had a much lower prey diversity (mean bootstrapping estimate $H = 0.148$, 95CI = 0.089–0.218) than those at TUR ($H = 1.270$, 95CI = 1.223–1.317) or SYL ($H = 1.244$, 95CI = 1.173–1.318). Pairwise Hutcheson t -test comparisons indicated that there were statistical differences between TUR and DYF ($P < 0.001$) and between SYL and DYF ($P < 0.001$), but not between TUR and SYL ($P = 0.392$).

Differences in diet were reflected in measures of diet breadth (Table 2). Thus, while fish at TUR and SYL had, similarly, wide diets (bootstrapping estimates B , TUR = 3.286, 95CI = 1.666–5.005; SYL = 3.270, 95CI = 1.611–4.998), the diet breadth at DYF was much narrower ($B = 1.522$, CI = 1.058–2.000), consistent with greater diet specialization, but also with lack of prey choice.

Stable Isotope Analysis

The carbon content in the muscle of topmouth gudgeon ranged between 41 and 60% among individuals, and differed significantly among ponds (Figure 4A, $F_{(3,113)} = 11.54$, $P < 0.001$), being lowest in the LLI reservoir and highest in the eutrophic SYL pond (*post-hoc* pairwise HSD, SYL-LLI, $P < 0.001$; TUR-LLI, $P < 0.001$). Carbon content did not depend on body length ($t = -0.385$, $P = 0.701$), condition factor ($t = -0.035$, $P = 0.972$) or the presence of food items in the stomach ($t = -0.69$, $P = 0.490$). The nitrogen content varied from 12 to 18% among individuals, and as with %C, it also varied significantly among ponds (Figure 4B, $F_{(3,113)} = 6.77$, $P < 0.001$), but did not depend on body length ($t = 0.51$, $P = 0.610$), condition factor ($t = 0.31$, $P = 0.754$), or presence of food items in the stomach ($t = -1.51$, $P = 0.133$). Nitrogen content was lowest in the reservoir and highest in the eutrophic angling pond (*post-hoc* pairwise HSD, SYL-LLI $P < 0.001$; SYL-DYF $P = 0.004$).

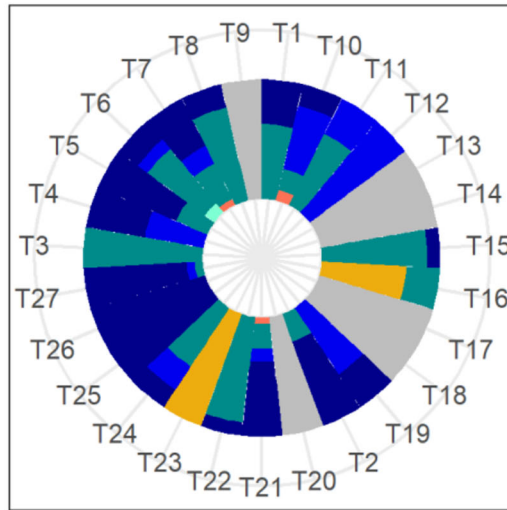
C:N ratios (a measure of lipid reserves) varied between 3.13 and 3.81 among individuals, but were unaffected by body length ($t = -1.22$, $P = 0.224$), condition factor ($t = 0.2$, $P = 0.835$), or presence of food items in the stomach ($t = -0.96$, $P = 0.335$). They varied significantly among sites (Figure 4C, $F_{(3,113)} = 4.15$, $P = 0.007$), being highest in one of the small ornamental ponds, and lowest in the reservoir (DYF-LLI, $P = 0.016$).

$\delta^{13}\text{C}$ varied markedly among individuals (range = -30.95‰ to -16.43‰) and differed significantly among all sites (Figure 5; $F_{(3,113)} = 24.77$, $P < 0.001$), being highest in the small ornamental ponds and lowest in the eutrophic angling pond (pairwise comparisons, LLI-DYF, $P < 0.001$; TUR-DYF, $P < 0.001$; SYL-LLI, $P < 0.001$; TUR-SYL, $P < 0.001$). $\delta^{13}\text{C}$ was unaffected by body length ($t = -0.09$, $P = 0.927$) or condition factor ($t = -1.14$, $P = 0.909$), but increased (i.e., it was more enriched) among fish that had food in their stomach ($t = 2.90$, $P = 0.004$).

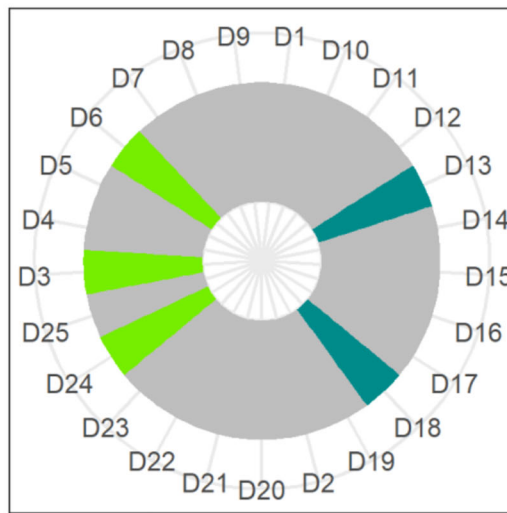
$\delta^{15}\text{N}$ varied from 5.17 to 15.10‰ among individuals, and also varied significantly among all sites (Figure 5; $F_{(3,113)} = 574.27$, $P < 0.001$), all ponds being significantly different from each other ($P < 0.001$), being highest in the reservoir and lowest in the small ornamental ponds. As for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ was unaffected by body length ($t = -0.567$, $P = 0.572$) or condition factor ($t = -0.156$, $P = 0.876$), but increased (i.e., it became more enriched) among fish that had food in their stomach ($t = -3.23$, $P = 0.001$).

Examination of the isotopic $\delta^{13}\text{C}$ vs. $\delta^{15}\text{N}$ plot (Figure 5) indicate a substantial trophic discrimination among study sites, particularly with respect to $\delta^{15}\text{N}$, with the large, deep reservoir (LLI) being nitrogen enriched and the small ornamental pond (DYF) being nitrogen depleted compared to the other sites.

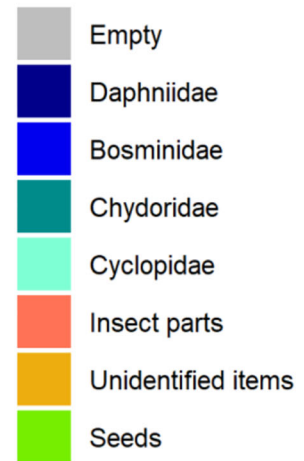
TUR
H=1.267



DYF
H=0.129



Prey Category



SYL
H=1.226

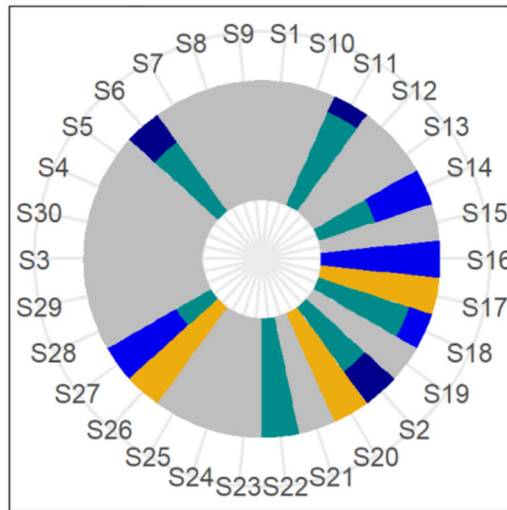
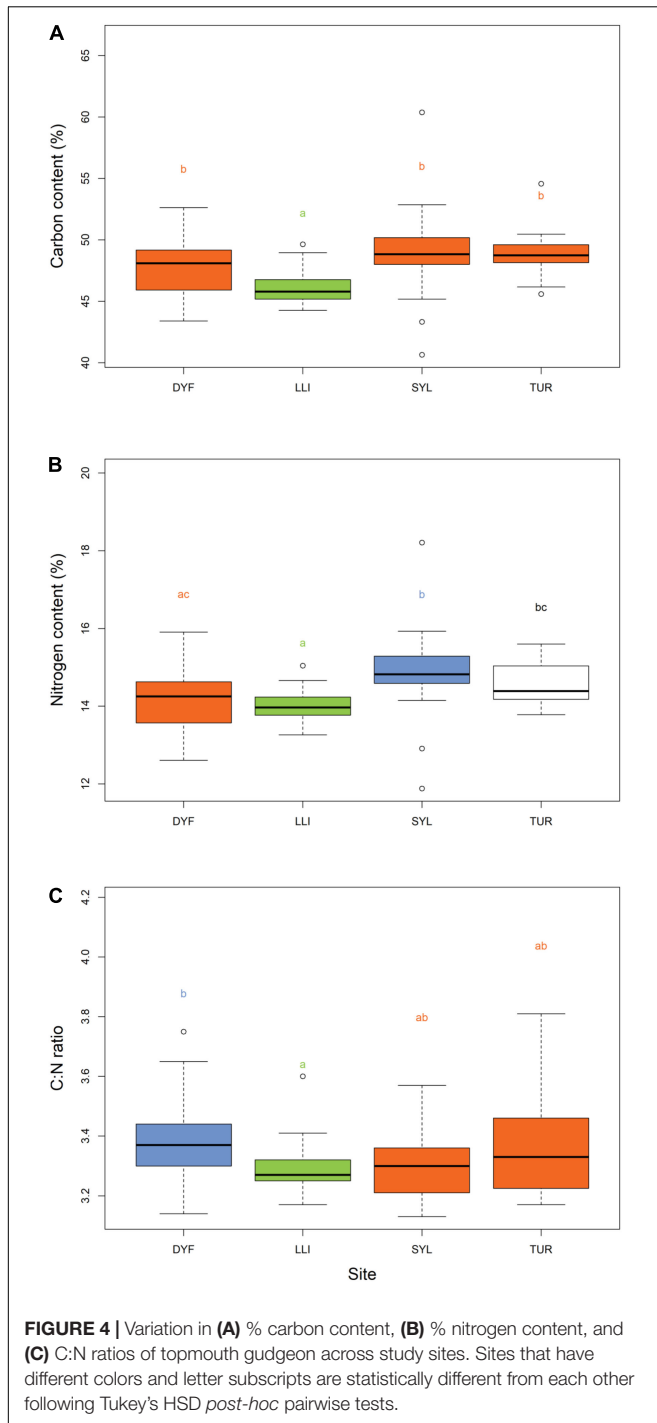


FIGURE 3 | Individual variation in the diet of topmouth gudgeon (% items) across study sites showing Shannon diversity index (*H*). Each numbered sector represents one fish.

TABLE 2 | Diet of topmouth gudgeon based on stomach content analysis (% number).

Site	<i>Daphniidae</i>	<i>Bosminidae</i>	<i>Chydoridae</i>	<i>Cyclopidae</i>	Insect parts	Unidentified items	Seeds	No. prey items	Percentage empty stomach (%)	Levins's B (niche breadth)	Lower CI	Upper CI
Turbine TUR	0.38	0.16	0.39	0.01	0.02	0.04	0.00	664	22.2	3.07	1.666	5.005
Sylen SYL	0.09	0.15	0.43	0.00	0.00	0.33	0.00	184	65.5	3.07	1.611	4.998
Dyffatty DYF	0.00	0.00	0.03	0.00	0.00	0.00	0.97	280	84.0	1.06	1.058	2.000



DISCUSSION

Our study sheds light on the topmouth gudgeon's trophic plasticity and shows that its diet varies markedly among sites, even between neighboring ponds only a few kilometers away from each other. We acknowledge that differences in the timing of sampling must have introduced some unwanted variation in our study, but marked differences in stomach contents, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and condition factor were also found between sites DYF and TUR which were sampled at the same time in February. Thus, season alone cannot explain our results. Isotopic turnover in TMG is not known, but data on other cyprinids indicate that isotopic equilibrium may take several months in muscle tissue. Half-life muscle turnover rate for $\delta^{15}\text{N}$ was 84 days for barbel *Barbus barbus* (Busst and Britton, 2018) and 68 days for grass carp *Ctenopharyngodon idellus* (Xia et al., 2013); equilibrium in barbel was not reached even after 125 days, with 95% turnover taken 371 days (Busst and Britton, 2018). This indicates that SIA signals, unlike stomach contents, are relatively stable over time. Furthermore, as muscle isotopic turnover is mostly influenced by body growth (Busst and Britton, 2018), we would not expect substantial changes in isotopic signatures during the colder parts of the year, when three of our four ponds were sampled. Isotopic signatures of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ showed little seasonal variation in the muscle of whitefish in Lake Geneva during autumn and winter, and only reflected the food consumed during spring and summer (Perga and Gerdeaux, 2005).

Trophic plasticity, i.e., the ability to switch diets, is expected to facilitate establishment success among invasive species (Schröder and Garcia de Leaniz, 2011; Pettitt-Wade et al., 2015), and may have allowed the topmouth gudgeon to colonize different environments, exploit novel food resources, and outcompete many native fish species (Záhorská et al., 2009, 2010). However, trophic plasticity also carries costs (Shea and Chesson, 2002). Trophic shifts are common in response to changes in habitat and food availability (Werner and Hall, 1977), but can also represent a strategy to avoid potential trophic competition (Jackson et al., 2012). In our study, topmouth gudgeon with a mean size of 57 mm were feeding on relatively small food items, most of which were within the 0.7–1.3 mm size range, and hence less than 2% of their body size. The consumption of small zooplankton, shown at all our sites, has been reported previously (Arnold, 1990; Rosecchi et al., 1993), along with a diet composed of benthic crustaceans (Rosecchi et al., 1993; Xie et al., 2000), chironomids (Declerck et al., 2002), phytoplankton and algae (Muchacheva, 1950). However, the reliance on plant seeds found at one of our

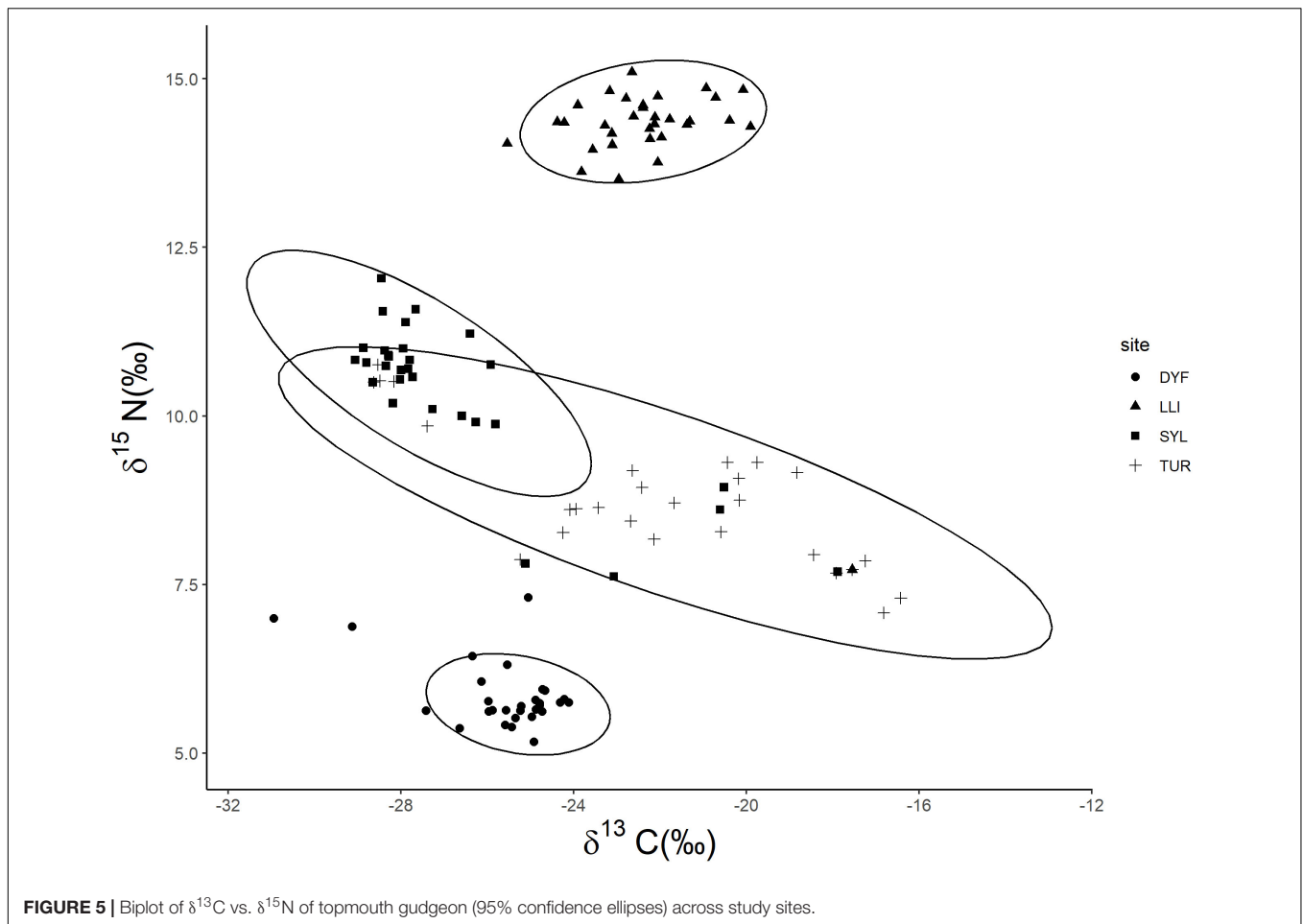


TABLE 3 | Comparison of isotope values for topmouth gudgeon across locations.

Mean length (\pm SE) or range (mm)	Habitat	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Country	Status	References
19–118	Pond (3,250 m ²)	-23.3 ± 0.7	8.4 ± 0.7	England	Invasive	Britton et al., 2010
20–108	Lake Izunuma (3.69 km ²)	-29.5 to -25.2	12.2–15.9	Japan	Native	Yasuno et al., 2012
60–90	Lake Taihu (2,338 km ²)	-24.0 ± 0.2	14.2 ± 0.2	China	Native	Mao et al., 2012
74 ± 2.2	Pond (600 m ²)	-38.6 ± 0.1	–	Belgium	Invasive	Tran et al., 2015
72 ± 2.3	Pond (1,900 m ²)	-35.8 ± 0.4	–	Belgium	Invasive	Tran et al., 2015
63 ± 3.9	Pond (3,000 m ²)	-25.5 ± 0.1	–	Wales	Invasive	Tran et al., 2015
–	8 ponds (240 m ² –400 m ²)	-32.8 ± 0.5	–	England	Invasive	Tran et al., 2015
90–110	3 polyculture ponds (6,000 m ²)	-21.9 ± 0.6	9.8 ± 0.2	China	Native	Mao et al., 2016
–	Lake Huizhou West (1.8 km ²)	-24.9 ± 0.2	17.5 ± 0.3	China	Native	Gao et al., 2017
63 ± 13.7	Dyfatty pond (3,800 m ²)	-25.6 ± 1.4	5.8 ± 0.5	Wales	Invasive	This study
54 ± 10.2	Lliedi reservoir (0.13 km ²)	-22.3 ± 1.5	14.1 ± 1.2	Wales	Invasive	This study
55 ± 10.1	Sylen pond (16,200 m ²)	-26.7 ± 2.7	10.3 ± 1.1	Wales	Invasive	This study
55 ± 14.3	Turbine pond (10,600 m ²)	-22.1 ± 3.8	8.8 ± 1.0	Wales	Invasive	This study

sites was unexpected, and may have been the consequence of strong inter-specific competition.

Results from stomach content analysis were largely confirmed by results from SIA and seemed to reflect the combined effects of food availability and competition. However, both techniques are needed to properly characterize individual variation in diet, as found for other lentic fish, for example the pumpkinseed sunfish (Locke et al., 2013). Thus, the widest variation in

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was observed at one of the small recreational ponds (TUR), which is consistent with a generalist diet largely unaffected by inter-specific competition as only one other fish was recorded (European eel, *Anguilla anguilla*). In contrast, at the other recreational pond (DYF) topmouth gudgeon coexisted with four other species (eel, perch *Perca fluviatilis*, rudd *Scardinius erythrophthalmus*, and roach *Rutilus rutilus*), displayed a very high occurrence of individuals with an empty stomach (84%)

and relied almost exclusively on plant seeds. This may explain why they attained a much lower condition factor, and displayed a lower trophic level, suggesting that plant seeds are nutritionally poor and not a preferred food resource. Britton et al. (2010) have shown that roach occupies a similar trophic position as topmouth gudgeon and this can result in competition for food, while rudd occupies a higher trophic level and may prey on topmouth gudgeon. Therefore, the presence of competitors and predators may have forced the topmouth gudgeon to adopt a more specialized feeding behavior in this pond. In a similar way, the narrow trophic position of TMG at the reservoir could be explained by high predatory pressure, since this reservoir is managed by an angling association which regularly stocks it with trout for recreational fishing.

We found that the body condition factor (a measure of growth performance – Froese, 2006) and the C:N ratio (a proxy for stored lipids – Jardine et al., 2008) was highest in the pond with the most diverse diet, widest diet breadth, and fewest competitors (Turbin pond where only eel was reported). This was also reflected in high carbon and nitrogen contents, as well as in high $\delta^{13}\text{C}$ values. In aquatic food webs, high $\delta^{13}\text{C}$ values tend to correlate with better feeding conditions and less competition (Hinz et al., 2017), which is consistent with our results. In contrast, TMG sampled in the much larger reservoir (LLI) where predatory salmonids abound, had the lowest C:N ratios, indicative of low lipid reserves, as well as low carbon and nitrogen contents, which are also consistent with poor feeding conditions (Vander Zanden et al., 1999).

Comparisons of SIA values from our study and other studies (Table 3) indicate that TMG in Wales generally have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (i.e., more enriched) than those reported in another study in Great Britain (Britton et al., 2010), indicating a higher trophic level ($\delta^{15}\text{N}$) and a different primary source of carbon ($\delta^{13}\text{C}$). Our $\delta^{13}\text{C}$ values are relatively high and closer to the ones reported in China – where topmouth gudgeon is a native species (Mao et al., 2012, 2016; Gao et al., 2017) than to values observed in Belgium where the species is invasive (Tran et al., 2015). High $\delta^{13}\text{C}$ values are more typical of benthic food pathways, compared to pelagic food pathways which tend to be more ^{13}C depleted (Pinnegar and Polunin, 1999). Variation in $\delta^{15}\text{N}$ was also greater in our study than those reported in the literature, and one of our sites (DYF) had the lowest $\delta^{15}\text{N}$ value reported for the species; this coincides with a diet dominated by plant seeds. In general, the variability among sites is so high that for example $\delta^{15}\text{N}$ values obtained from fish at one of our sites (LLI) are more similar to those found in fish from Lake Taihu in China (Mao et al., 2012) than to those at neighboring sites in Wales. This indicates that it is difficult to predict the diet or trophic position of TMG even within small geographical areas. Substantial spatial variation in stable isotope signatures have also been reported for other lentic fish (Locke et al., 2013).

CONCLUSION

Our study indicates that when the topmouth gudgeon colonizes a new area it may be difficult to predict its trophic impacts

from local information, since differences in diet are largely independent of geographical proximity. Populations living in neighboring water bodies can have diets more dissimilar than those from populations thousands of kilometers away. Given the importance diet information has on models that attempt to predict the risks posed by invasive fish, such as FISK (Copp et al., 2009; Mastitsky et al., 2010; Copp, 2013; Simonovic et al., 2013), uncertainty on the expected diet of the topmouth gudgeon could result in incorrect risk assessments. To improve the precision of risk assessments, information on trophic level seems to be important for predicting the diet, and therefore the likely feeding impacts, of topmouth gudgeon on native communities. As trophic impacts will likely vary widely from site to site, our study shows that SIA could be used, perhaps in combination with eDNA (Robinson et al., 2019), for species detection to prioritize control and eradication measures that consider variation in diet.

DATA AVAILABILITY STATEMENT

The datasets generated by this study are available on Figshare: 10.6084/m9.figshare.1197447.

ETHICS STATEMENT

The animal study was reviewed and approved by Swansea University College of Science Ethics Committee, Permit Student 210519/1544.

AUTHOR CONTRIBUTIONS

CG and SC designed the study and secured the samples and funding. MR collected the data and carried out the analyses with advice from CG. MR and CG wrote the manuscript with contributions from SC. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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