

Feeding Aquatic Ecosystems: Whole-Lake Experimental Addition of Angler's Ground Bait Strongly Affects Omnivorous Fish Despite Low Contribution to Lake Carbon Budget

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ABSTRACT

It is well documented that aquatic ecosystems may be subsidized by naturally derived terrestrial carbon sources. In contrast, the intentional or unintentional subsidy of animal populations by human-derived feed resources and their ecosystem effects are poorly studied. We added ground baits of the type, amount and temporal duration commonly applied by anglers targeting cyprinid fishes to a small lake, and studied behavior, diet composition and annual growth rate of the lake fish community in response to the bait addition. Based on recordings by a high-resolution ultrasonic telemetry array, common carp (*Cyprinus carpio*) as a model benthivore spend more time at the

sites where ground baits were added, and they significantly reduced their home range relative to the period before bait addition. Furthermore, many omnivorous cyprinid fish species were regularly caught by angling at the feeding sites, indicating active ingestion of the artificially added food items. Stable isotope analyses of ¹³C and ¹⁵N showed that in particular larger specimens of common carp, bream (*Abramis brama*), white bream (*Blicca bjoerkna*), tench (*Tinca tinca*), roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*) included substantial amounts of angler baits into their diet. There was also a significant acceleration of growth in bream and white bream after bait addition, most likely attributable to the energetic benefits from bait addition. In contrast, there was no response in annual growth rate in top predators, suggesting they did not benefit from the subsidy. The amount of carbon introduced was very low (about 1%) relative to an estimate of in-lake C fixation by autotrophs. However, if the C added by bait was compared with the coarsely estimated secondary production of benthic macroinvertebrates in the lake, the C available to benthivorous and omnivorous fishes was compara-

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ble between natural resources and angler baits. We conclude that human-derived feed resources associated with recreational fishing may constitute a substantial subsidy to omnivorous fishes in lakes, in particular if the food is provided in form of particles, which are readily accessible and found at repeatable feeding places and over sufficiently long time periods during a year. The long-term consequences for the receiving ecosystems still have to be elucidated.

Key words: subsidy; human-derived food; stable isotopes; fish behavior; fish growth.

INTRODUCTION

Aquatic ecosystems are connected with their terrestrial surroundings by a reciprocal flux of inorganic nutrients, dead organic matter and living organisms (Cole and others 2006; Schindler and Smits 2017). The contribution of terrestrial resources (that is, allochthonous organic matter produced outside of the aquatic system) to the aquatic secondary production of bacteria, invertebrates and vertebrates remains hotly debated (reviewed by Brett and others 2017). Among other factors, the connectivity between aquatic and terrestrial ecosystems, the size of the receiving ecosystems, and their productivity were suggested as contributing to the degree of allochthony of lakes and rivers (Cole and others 2002; Pace and others 2004; Tanentzap and others 2017). Another highly influential aspect determining the contribution of allochthonous resources to aquatic secondary production is the biochemical quality of the subsidy and the trophic level that is subsidized (Marcarelli and others 2011; Brett and others 2017). Terrestrial dissolved and particulate organic matter (t-DOM and t-POM, respectively) enter at the base of the food web and mostly need to be incorporated by primary consumers before ultimately being available to fish (Cole and others 2002; Pace and others 2004; Scharnweber and others 2014a). They are both considered poor quality for aquatic consumers due to their high carbon (C) to nutrient ratios and low energy content (Marcarelli and others 2011). In contrast, terrestrial animals are often a high-quality prey type for aquatic predators (Mehner and others 2005; Marcarelli and others 2011). However, the effect size of subsidy for consumer density or biomass was lower for predators than for detritivores, producers or omnivores, suggesting that subsidy by al-

lochthonous prey is often spatially or temporally limited and only affects selected trophic groups (Marczak and others 2007; Marcarelli and others 2011).

Anthropogenic feed resources of high nutritional quality and energetic density likewise subsidize consumers in all types of ecosystems as a consequence of world-wide increase in human population density, recreational use of natural ecosystem, aquaculture and global economic development (Oro and others 2013). Humans intentionally or unintentionally dispose of waste, food remains, crop residuals and animal carcasses into the environment, providing a predictable resource to animal populations with effects on food-web interactions and ecosystem processes (Oro and others 2013). Examples for high-quality human subsidy of aquatic ecosystems are food remains from open-water fish farms (Grey and others 2004; Wang and others 2018), waste from landfills supporting the diet of sea birds (Osterback and others 2015), or the intentional feeding of aquatic organisms, such as water birds, by recreationists, in particular in urban habitats (Oro and others 2013).

Another specific form of intentional human subsidy of aquatic systems is the application of ground bait by recreational coarse (that is, non-salmonid) freshwater anglers. Ground baiting is common practice in freshwater recreational fisheries for cyprinid fishes all over Europe (Wolos and others 1992; Arlinghaus and Mehner 2003; Amaral and others 2013; Roberts and others 2017) and is increasingly used beyond Europe (for example, North America or South Africa) where specialized angling for large cyprinids such as common carp (*Cyprinus carpio*) is becoming locally fashionable. Recreational angling for cyprinids is often based on the introduction of ground bait for several days prior to and during the fishing day to attract the fish on the fishing sites (Wolos and others 1992; Arlinghaus and Mehner 2003). In Europe, specialized common carp and barbel (*Barbus barbus*) anglers regularly apply more than 1 kg of ground bait per day, usually in form of food particles (corn, pellets, boilies—a special carp bait) (Arlinghaus 2004; Niesar and others 2004; Basic and Britton 2015). However, ground baiting is also standard practice in competitive fishing for small-bodied cyprinids such as roach (*Rutilus rutilus*) (Amaral and others 2013). The average annual dispersal of ground baits per freshwater angler in Germany was estimated to be 7.3 kg (Arlinghaus 2004), which easily scales to several thousand tons of ground bait introduced to aquatic ecosystems by about 3.3 million anglers in Germany alone. These considerable volumes of angler baits and their high

nutritional quality evidenced by very high digestibility of all classes of macronutrients (protein, lipids, carbohydrates) (Arlinghaus and Niesar 2005) and positive growth responses in laboratory experiments with common carp (Niesar and others 2004) may form a relevant direct subsidy to benthivorous and omnivorous fish in lakes and rivers exposed to high use-intensity by recreational coarse anglers. Some individuals of the benthivorous cyprinid barbel in rivers indeed expressed a strong preference for the angler ground bait relative to natural food, as indicated by shifts in the population isotopic niches (Basic and Britton 2015; Roberts and others 2017). However, these studies were inconclusive with respect to a mechanistic understanding of the consequences of subsidizing a fish community by ground bait. In particular, studies testing whether benthivorous fish are behaviorally attracted by the baits and benefit from their ingestion by accelerated growth are lacking. It is also unknown whether the anthropogenic subsidy affects top predators that are unlikely to feed directly on the angler bait. Importantly, for a quantitative evaluation of the effect of bait additions on the lake ecosystem, a comparison of C loads from baits relative to in-lake C fixation by autotrophs (Mehner and others 2016) and to production by primary consumers is needed.

We performed a whole-lake experiment in an eutrophic lake to test for a chain-of-action response of a fish community to an intentional addition of resources, by providing ground baits of the type, amount and temporal duration commonly applied by specialized cyprinid anglers. We used a fine-scale acoustic telemetry system (Baktoft and others 2015), which facilitated studying the individual behavior of common carp as a model cyprinid fish species as well as tench (*Tinca tinca*) in response to subsidized feeding. Furthermore, we applied stable isotope analyses to compare the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of several benthivorous/omnivorous and piscivorous fish species, before and after bait addition, to estimate the proportion of baits in their diet composition. Finally, we measured the annual growth rates of a sample of cyprinid and top predatory species to elucidate whether there was a discernible effect of ground-bait ingestion on the individual growth rates of fishes, serving as an indicator of a potential contribution of bait to secondary production. We hypothesized that even modest amounts of ground bait introduced to a lake ecosystem would generate substantial changes within the benthivorous and omnivorous fish community. We expect this because ground bait is of high nutritional quality, provided continuously during the growing season and not accessible by

other consumers than large cyprinid fish. Ground bait additions could thus significantly modify behavior, diet composition and growth of fish. Specifically, we predicted that (i) introduced ground bait attracts fish to spend more time on the feeding sites, (ii) stable isotopes reflect strong contributions of ground baits to the diet of omnivorous fish, but not in piscivorous fish or invertebrate consumers as these groups do not directly consume particle-based ground bait, and (iii) growth of fishes directly feeding on ground bait is accelerated. Overall, we expected a subsidy effect from bait addition despite its low share in C loading relative to high C fixation in the eutrophic lake.

METHODS

Study Lake and Subsidy Experiment

Lake Kleiner Döllnsee (subsequently referred to as Döllnsee, 52°99'N, 13°58'E) is situated about 80 km north of Berlin (Germany). It has an area of 0.25 km² and a mean depth of 4.1 m. The lake is stratified and eutrophic with a total phosphorus (TP) concentration of about 50 mg m⁻³ (arithmetic average of 12 monthly samples from the epilimnion in 2014), resulting in an average Secchi depth of 2.1 m. The shoreline is characterized by a dense reed (*Phragmites* spp., *Typha* spp.) belt; sparse patches of submerged macrophytes cover the littoral and sub-littoral zones. The fish community consists mainly of benthivorous or omnivorous species, namely cyprinids (roach, rudd *Scardinius erythrophthalmus*, bream *Abramis brama*, white bream *Blicca bjoerkna*, bleak *Alburnus alburnus*, tench, crucian carp *Carassius carassius*, and stocked common carp) and the percid species ruffe (*Gymnocephalus cernuus*). Naturally occurring facultative piscivorous species are perch (*Perca fluviatilis*) and pike (*Esox lucius*), whereas European catfish (*Silurus glanis*), eel (*Anguilla anguilla*) and zander (*Sander lucioperca*) have been stocked and occur in low numbers.

Between July and October 2014, a total of 750 kg dry mass of soaked and cooked corn (*Zea mays*), reflecting the typical bait preparation by specialized cyprinid anglers targeting carp, tench or large bream, was introduced on eight sub-littoral feeding sites that were equally spaced around the shoreline. Corn was introduced twice daily during 4 days per week. Furthermore, 189 kg of fish mix boilies and 89 kg of sweet mix boilies were introduced together with corn. Boilies are specially designed boiled paste balls commonly used in carp, tench and increasingly large bream fishing, and are typi-

cally mixed with cereals such as corn as ground baits (Niesar and others 2004). For more information on boilie composition, see Digital Appendix 1.

The amount of corn and boilies introduced to the lake corresponded to the yearly bait addition of about five highly specialized carp anglers, each using about 215 kg bait per year (Niesar and others 2004). Other anthropogenic subsidies beyond the controlled corn and boilie introductions during the study period can be excluded because there are no commercial or recreational fisheries on the lake, and public access to Döllnsee is blocked. According to P contents of bait types determined earlier (Niesar and others 2004), the corn and boilie addition contributed about 15.4% (18.6 mg P m⁻² during the experimental period) to the P budget relative to the critical P load (Vollenweider 1976) of the lake (120 mg P m⁻² y⁻¹), which was calculated similarly as in Mehner and others (2007). Therefore, a substantial eutrophication effect by the experimental bait addition was not expected. The contribution of C to the lake C budget by corn and boilie addition (about 1.5 g C m⁻² during the experimental period) was estimated to be low relative to in-lake primary production (PPr) by phytoplankton and vascular plants. Two morphologically similar small lakes with comparable total P concentrations of 35–50 mg m⁻³ situated close (< 30 km) to Döllnsee had PPr values between 260 and 350 g C m⁻² y⁻¹ (Brothers and others 2013a; Mehner and others 2016). Assuming a PPr of about 300 g C m⁻² y⁻¹ suggests that the ground bait contributed less than 1% to the C budget of Döllnsee.

Behavioral Observation of Fish

As a model cyprinid, we tracked 91 common carp (total length: 40.6–72.2 cm; wet weight: 945–6934 g), released in June 2014 (Monk and Arlinghaus 2017) prior to the bait addition with a high-resolution, whole-lake acoustic telemetry system to study whether fish were preferentially using the eight feeding sites. The fine-scale acoustic telemetry system records 3D positions of fish at a high resolution and accuracy (5 m average error) at the scale of the whole lake (Baktoft and others 2015). Common carp were hatchery-raised and spent their life in earthen ponds surviving on natural food supplemented by formulated pellet feed. Acoustic transmitters were surgically implanted into carp body cavities following earlier protocols (Kobler and others 2009; Hühn and others 2014). We anaesthetized carp with a 9:1 EtOH:clove oil solution added in water at 1 mL L⁻¹. Surgical tools

and transmitters were sterilized with 7.5% povidone-iodine mixed in water, and each fish received four to five sutures using PDS-II adsorbable monofilament suture material and FS-1 3-0 needles (Ethicon, USA). We also inserted a passive integrated transponder (PIT) tag (23 mm length, Oregon RFID, OR USA) into the body cavity during surgeries for later identification upon recapture. Tagged carp were released into Döllnsee following recovery from surgery.

The carp experienced high tag loss (Monk and Arlinghaus 2017), and therefore, we focused our analysis on 22 individuals that retained the tags and generated behavioral data from tagging until the end of the bait additions (24–25 days before feeding and 79–108 days during feeding). We evaluated whether carp increased their presence at those littoral sites at which ground bait was added (feeding sites) in comparison with the presence before bait addition. We considered a carp to be present at a feeding site when positions were within 5, 15 or 30 m of a feeding site. Total time at feeding sites was summed daily. If a carp was detected at a feeding site and then there was a long period without a new detection, 335 s were added to the feeding time. The reason is that after 335 s, there is near certainty that the fish has left the last position based on known detection probabilities of fixed beacon transmitters (Monk and Arlinghaus 2017). We compared the average percentage of each day present at a feeding site before and during the bait addition for each carp with a paired *t* test. To compare space usage, we calculated the collective home range of the 22 individual carp before and during feeding. Specifically, the areas of the 5, 25 and 50% kernel utilization densities were calculated based on a 200 by 104 cell grid representing the lake, with a cell size of 5.78 m and a 10 m smoothing parameter in R using the *adehabitatHR* package (Calenge 2011). Besides carp, we also tagged a sample of wild captured tench (Monk and Arlinghaus 2017), but we lacked data from the period before the bait introduction and hence present the data after bait introduction in the supplement. Subsequently, angling pressure was applied at four of the eight designated feeding sites at equal spacing around the shoreline, 4 days per week between August 12 and October 15, 2014, to study which species were ingesting the bait types and thus were vulnerable to capture by angling. Note that we did not attempt to use angling data to measure the use of feeding sites as opposed to other sites, but rather as source of information on whether the fish indeed ingested the feedstuffs.

More details of the angling can be found in Digital Appendix 1.

Stable Isotope Analyses of Natural Resources and Fish

To estimate the contributions of ground bait to the diet of fish, stable isotope (SI) values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of ground bait as well as natural resources (zooplankton and benthic invertebrates) and fish (benthivorous/omnivorous and piscivorous fish) were measured twice before bait addition (autumn 2013, summer 2014) and once after bait addition (autumn 2014). This sampling scheme takes the seasonality of SI values into account and hence facilitates the comparison of SI values before and after feed addition in autumn (2013 vs. 2014) and the direct before–after comparison of SI values in response to feed addition (summer 2014 vs. autumn 2014). For more details of sampling, see Digital Appendix 1.

A total of 749 samples for SI analysis were processed, including broad size ranges of fish (Digital Appendix 2). Samples were dried at 60°C for 48 h to constant weight, and subsequently ground with mortar and pestle into a fine powder. For analysis, 0.6 (\pm 0.1) mg of animal tissue was weighed into tin capsules. Stable isotopes analyses were conducted using a Finnigan DELTA_{plus} Advantage mass spectrometer (Thermo Fisher Scientific Corporation, Waltham, MA, U.S.A.) coupled to a FlashEA 1112 elemental analyser at the University of Jyväskylä, Finland. Stable nitrogen and carbon ratios are expressed as delta values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) relative to the international standards for nitrogen (atmospheric nitrogen) and carbon (Vienna PeeDeeBelemnite). Analytical precision was always better than \pm 0.33‰ and \pm 0.23‰ for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively, and was based on repeated analysis of working standards (pike white muscle tissue, birch leaves and *Spirulina* spp.) inserted in each run after every five samples.

Statistical Comparisons and Mixing Models

To test for potential elevations of C stable isotope value after bait addition, we compared $\delta^{13}\text{C}$ values of natural resources between the three sampling periods by ANOVA and Tukey HSD post hoc tests. In cases when the data did not meet the assumptions for parametric tests, we applied Kruskal–Wallis tests with Nemenyi post hoc tests. For comparison of $\delta^{13}\text{C}$ values of fish between the

sampling periods, we applied ANCOVA, with total length of fish added as covariate. Fish length had to be included because corn and boilies are particles usually not accessible to smaller fishes because of gape limitation and due to the hard texture, and hence, we expected strong effects only for fish > 10 cm length. We first calculated the full ANCOVA model including the interaction between sampling period and fish length, but removed non-significant interaction terms from the full model. We plotted the least squares means of $\delta^{13}\text{C}$ for the three sampling periods, which take into account the variable lengths of fish in the sampling periods. For species for which the interaction between sampling period and fish length was significant, we tested whether there were significant differences of intercepts and slopes between autumn 2014 (after bait addition) and either autumn 2013 or summer 2014 (both before bait addition). Higher intercepts after than before bait addition would suggest that all individuals of this species independent of length have included ground bait. Higher slopes in the period after bait addition would suggest that in particular larger (positive slope) or smaller (negative slope) individuals have ingested added food. All calculations were done in R 3.3.2 (R Development Core Team 2016).

To calculate the proportion of corn and boilies in the diets of those fish species, which showed elevated $\delta^{13}\text{C}$ values after bait addition, we used Bayesian stable isotope mixing models as implemented in the *simmr* package (Parnell 2017) in R 3.3. Bayesian mixing provides posterior probability distributions instead of single point estimates of source contributions. Therefore, we always show the full posterior distributions and provide all estimates with their Bayesian credibility intervals, which can be considered equivalent to the confidence intervals of frequentist's statistics. Prior to mixing model analysis, we visually inspected whether preconditions of the model, that is, a valid mixing geometry and distinct resource isotope values were fulfilled (Digital Appendix 3). Mixing modeling was conducted using fractionation factors of 0.4 ± 1.3 for $\delta^{13}\text{C}$ and 3.4 ± 1.0 for $\delta^{15}\text{N}$ (Post, 2002) and concentration dependence (Phillips and Koch 2002). Initially, we included zooplankton, zebra mussels and benthic macroinvertebrates (larvae of Chironomidae, Ephemeroptera, Trichoptera, Odonata, and Isopoda mixed because of similar isotopic signatures) as potential natural sources of the diet of benthivorous or omnivorous fish. Furthermore, we considered corn, fish mix

boilies and sweet mix boilies separately as artificially added potential food sources (Digital Appendix 3). The artificial food sources could not be combined because of their distinctly separate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. However, to reduce the uncertainty in the mixing model output, we combined a priori zooplankton, insect larvae and zebra mussels into a single category 'Natural Food'. This was justified because the $\delta^{15}\text{N}$ values did not differ between these groups (ANOVA $F_{2,83} = 1.01$, $p = 0.37$), but $\delta^{13}\text{C}$ differed between the natural resource groups (ANOVA $F_{2,83} = 74.1$, $p < 0.0001$).

To address the potential uncertainty in the mixing model with four remaining sources and two tracers, we included a hypothetical baseline fish with an isotopic signature, which reflected a pure natural diet, and evaluated the contribution of ground bait to this baseline fish. By using the posterior distributions, we calculated the probabilities for the differences in contributions of natural food and angling baits between the baseline and the seven fish species, as based on 1000 repetitions of the Bayesian mixing model. We did not analyze stomach or gut content from the fish in Döllnsee, and hence, we assumed equal contributions of the three natural sources to the diet of fish. However, to reflect the uncertainty introduced by this assumption, we ran the same mixing models with each natural food source separately and provide the respective median source contributions in comparison with the assumption of the equal mix.

We evaluated the diet composition of all carp ($n = 6$) and tench ($n = 23$) caught in autumn 2014 because in these species the $\delta^{13}\text{C}$ values did not vary with fish length (see results). In the other species, there was a strong positive length dependency of $\delta^{13}\text{C}$ values, and hence, we included only individuals beyond a certain size threshold for which feeding on ground baits was likely, namely large roach (TL > 10 cm, $n = 17$), large rudd (TL > 10 cm, $n = 15$), large white bream (TL > 10 cm, $n = 19$) and large bream (TL > 28 cm, $n = 27$). In perch, the statistical results indicated a negative slope of $\delta^{13}\text{C}$ values with length, and hence, we included only small perch (TL < 15 cm, $n = 5$) into the mixing model analyses.

Growth Rate Analysis

After the bait addition period ended, fish were sampled by angling from 4 May to 29 May 2015 at a time where the winter growth ring in scales was clearly developed and positive growth was visible on the scales starting in spring. We focused the

growth rate analyses on two fish species for which uptake of added bait was likely, and which were frequent in the lake. Bream ($n = 59$) and white bream ($n = 30$) were regularly angled at the locations on which bait was added; hence, it was reasonable to assume that they ate corn and boilies. Further, the piscivorous pike ($n = 34$) served as "control" because we assumed that piscivores should show no immediate benefit from our bait addition. Four additional pikes were caught on November 26, 2015, to increase the length gradient of the analysis and sample size. For more details of scale reading and estimates by the growth model, see Digital Appendix 1.

We used the growth model to predict the expected length of each fish 1 year later (that is, in spring 2015) assuming that this length would represent the typical growth of that individual for each species in the study lake without a bait addition effect. We then estimated the linear difference (residuals) between observed (back-calculated) length in spring 2015 and the predicted theoretical length in spring 2015 to evaluate systematic deviations from predictions in response to bait addition. Finally, we fitted a general linear model to examine the effect of treatment (spring 2015 = after bait addition vs. spring 2014 = before addition), total length in spring 2014 and total length \times year on the growth residuals in 2015 by species. We chose the interaction of year with fish length because we assumed that the bait addition would particularly benefit the larger size classes of the omnivorous fishes, which should in turn show the greatest growth increase. A significant interaction effect with a positive slope would support our hypothesis that growth of the fish differed in response to bait addition. This analysis was completed in SPSS, version 22.0 (SPSS Inc., Chicago, U.S.A.).

We present subsequently the results from the whole-lake experiment without having similar data from an untreated reference lake. Lakes are rarely identical enough that differences between treatment and control lakes can be ascribed exclusively to the treatment. Therefore, we base our arguments on temporal references within the same system, by comparing fish stable isotope data, fish growth and behavior and distribution of tagged fish before and after the experimental bait addition. Further, by temporally limiting the experiment and analyses, we can compare the isotopic changes of omnivorous fish (hypothesized to respond fast) with the isotopic changes in piscivorous fish (hypothesized to respond only weakly within the study period), thus providing an internal reference. Further, we combine behavioral studies with growth and diet

analyses of fish, to strengthen the argument that the treatment has caused an effect. This expanded approach is broad, and hence, we do not have to rely on a single snapshot sample to infer that fish have profited from the bait addition.

RESULTS

Occurrence of Fish on Feeding Sites

Common carp used feeding sites significantly more often after bait was added (paired *t* test, $t = -10.8$, $df = 21$, $p < 0.001$), spending on average $5.5 \pm 9.15\%$ (mean \pm SD) of a given day on the feeding sites (Figure 1A, see video documentary in the digital appendix), which were regularly spaced around the entire littoral area. The feeding site usage varied among individual carp, but all individuals showed an increase after the addition of baits (from $< 1\%$ for all individuals before addition to between 1.5% and 14.1% after addition). An increase in feeding site use following bait introduction was robust to the assumption that carp swimming within 15 m of a feeding site constituted a visit, because comparative calculations for 5 m or 30 m distances gave similar results

(Digital Appendix 4). In contrast, the corresponding mean residence times at (future) feeding sites prior to the addition of angler ground bait were close to zero. Prior to the initiation of the bait addition, the carp readily used the eastern and northern areas of the lake and were never seen in the west and rarely on the southern banks (Figure 1B, C) and rarely were seen to pause at the future locations of the feeding sites. Throughout the bait addition period, however, the carp home ranges collapsed (56% decline in the 50% home range area after feeding commenced) around the eight feeding sites (Figure 1B, C; see video in digital appendix). Similar behavior at the feeding sites was observed for tench after bait addition (Digital Appendix 5).

A range of species were captured by angling at the feeding sites, indicating active ingestion of the angling bait (Digital Appendix 6). We also used sample feed in bags to study the uptake of the feed and almost always found all the food consumed within a few hours. The most frequently captured species was common bream, captured 616 times at a mean TL of 430 ± 57 mm (mean \pm SD). Carp were captured 28 times (TL 580 ± 76 mm), and

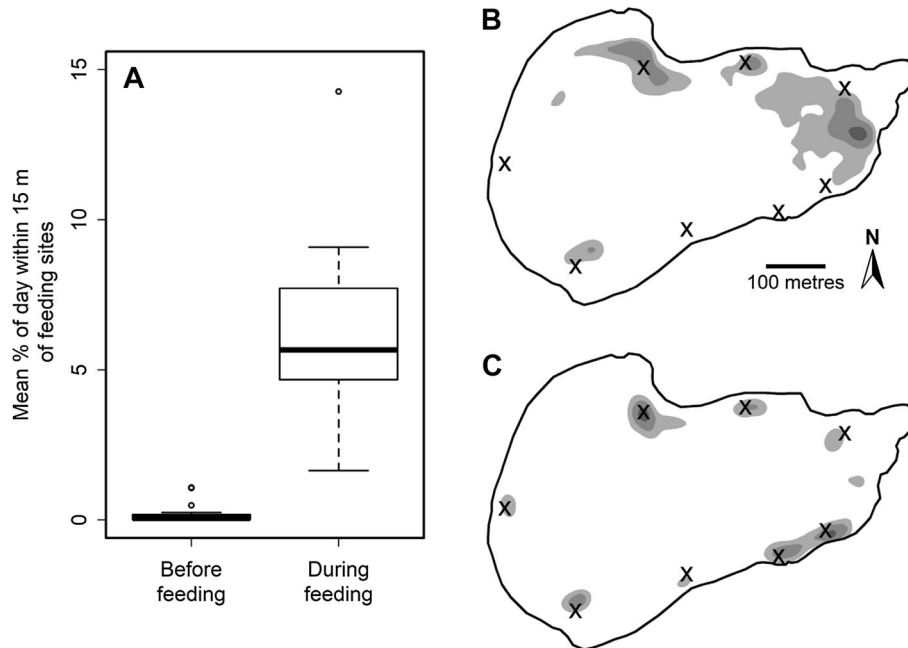


Figure 1. Boxplot of the mean daily percentages of time spent within 15 m of feeding sites for 22 individual carp before and during bait addition (**A**). Thick bars represent the median and whiskers represent 1.5 times the interquartile range, and outliers are represented by points. Home ranges of carp before (**B**) and during (**C**) bait addition. The black outline represents the shoreline of Döllnsee. Shaded areas from lightest to darkest show the 50, 25 and 5% carp home range areas respectively. Locations of the eight feeding sites are shown by crosses.

tench were captured 32 times (433 ± 52 mm). We also captured 62 roach (TL = 238 ± 59 mm mean \pm SD), 40 rudd (TL = 260 ± 53 mm mean \pm SD), 31 white bream (TL = 205 ± 34 mm), four perch (TL = 393 ± 12 mm) and one pike (TL = 615 mm). The cyprinid species were caught by all three baits types (corn, fish mix boilies, sweet mix boilies).

Stable Isotope Values of Resources

The mean $\delta^{13}\text{C}$ values of corn ($-12.0\text{‰} \pm 0.17$ SD, $n = 17$), fish mix boilies ($-24.1\text{‰} \pm 0.29$, $n = 6$) and sweet mix boilies ($-25.7\text{‰} \pm 0.23$, $n = 4$) confirmed that the ground baits were more enriched in ^{13}C than natural resources for benthivorous fish (zooplankton, $-39.5\text{‰} \pm 2.5$; zebra mussels, $-35.2\text{‰} \pm 1.0$; benthic insect larvae, $-31.6\text{‰} \pm 2.7$) (Digital Appendix 3). Fish mix boilies were strongly ^{15}N -enriched ($7.27\text{‰} \pm 0.24$), attributable to contributions of fish meal and oil, as compared to sweet mix boilies ($3.19\text{‰} \pm 0.21$) and corn ($4.90\text{‰} \pm 1.44$), which are rich in carbohydrate and plant-meal (Digital Appendix 2). $\delta^{13}\text{C}$ values of zooplankton, benthic insect larvae and zebra mussels were not affected by bait additions,

whereas crayfish $\delta^{13}\text{C}$ values were significantly elevated in the period after bait addition (Figure 2A–D, Table 1).

Stable Isotope Signatures of Fish and Contribution of Ground Bait to Fish Diet

Among fishes, the $\delta^{13}\text{C}$ values of carp and tench were significantly elevated after bait addition in autumn 2014 compared to the samplings before addition, independent of fish size (interaction between fish length and sampling period not significant) (Figure 3A, B; Table 1). Both species were also regularly caught during experimental angling (Digital Appendix 6), revealing active feeding on the feeding spots and bait types. Similarly, the $\delta^{13}\text{C}$ signatures of white bream, bream, rudd and roach were higher in autumn 2014 than in autumn 2013, attributable to higher $\delta^{13}\text{C}$ of the larger individuals after bait addition (significantly steeper slope of $\delta^{13}\text{C}$ with TL in autumn 2014 vs. autumn 2013) (Figure 3C–F; Table 1). Again, angling experiments regularly revealed catches of bream and white bream and to a smaller degree of large rudd and roach on the feeding spots (Digital Appendix 6).

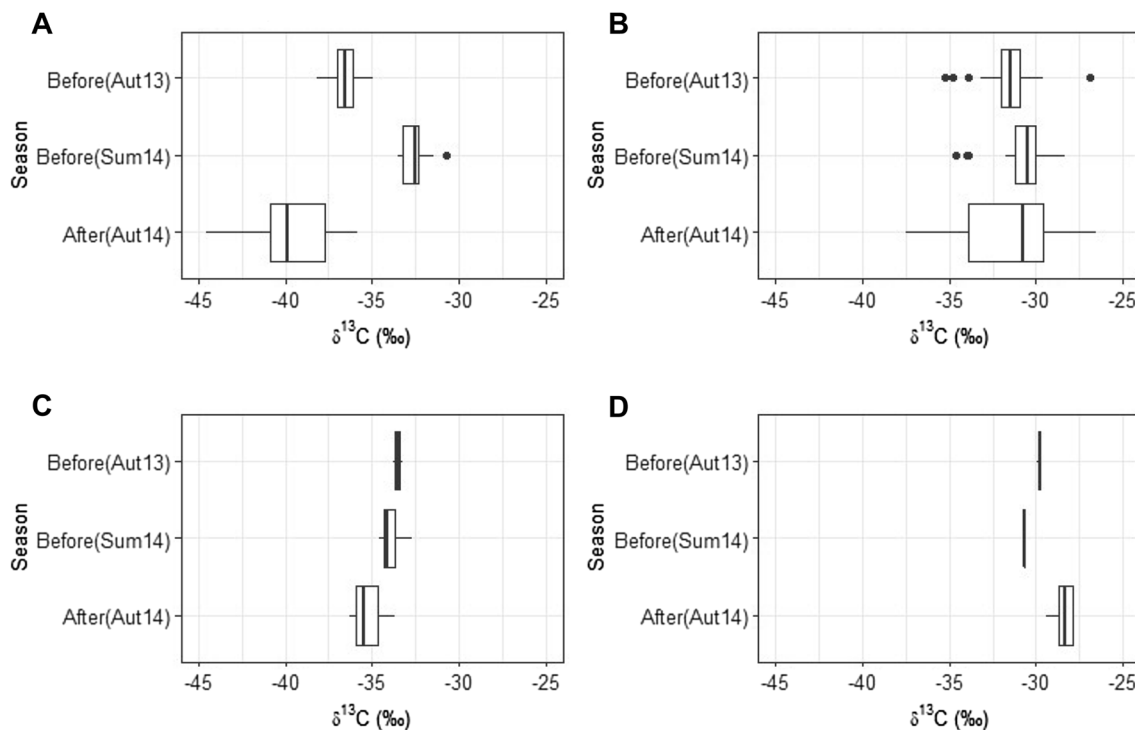


Figure 2. Boxplots (median, box = 25% and 75% percentiles, whiskers 10% and 90% percentiles, dots = outliers) of $\delta^{13}\text{C}$ (‰) of natural resources **A** zooplankton, **B** benthic insect larvae, **C** zebra mussels and **D** crayfish in Lake Döllnsee. Samples were taken in autumn 2013 and summer 2014 (both before bait addition) and in autumn 2014 (after bait addition).

Table 1. Statistical comparisons of $\delta^{13}\text{C}$ Values of Primary Consumers and Fish From Sampling Periods Before (Autumn 2013 = Aut13, Summer 2014 = Sum14) and After (Autumn 2014 = Aut14) the Experimental Addition of Bait into Döllnsee.

Group	Test	Test statistics	<i>P</i>	post hoc test	Group differences	<i>P</i>
Zooplankton	Kruskal–Wallis	$\chi^2(2) = 49.8$	< 0.0001	Nemenyi	Sum14 > Aut14	< 0.0001
Insect larvae	Kruskal–Wallis	$\chi^2(2) = 6.87$	0.032	Nemenyi	Aut13 < Aut14	< 0.0001
Zebra mussels	ANOVA	$F_{2,15} = 7.67$	0.0051	Tukey HSD	Aut13 > Aut14	0.012
					Sum14 > Aut14	0.012
Crayfish	ANOVA	$F_{2,5} = 7.54$	0.031	Tukey HSD	Sum14 < Aut14	0.047
Carp	ANOVA	$F_{1,24} = 40.7$	< 0.0001	Tukey HSD	Sum14 < Aut14	< 0.0001
Tench	ANOVA	$F_{2,26} = 9.36$	0.0008	Tukey HSD	Aut13 < Aut14	0.03
					Sum14 < Aut14	0.003
White bream	ANCOVA	$F_{5,60} = 25.2$	< 0.0001	Slope with TL	Aut13 < Aut14	0.007
Bream	ANCOVA	$F_{5,56} = 9.58$	< 0.0001	Intercept with TL	Aut13 > Aut14	0.0001
				Slope with TL	Aut13 < Aut14	0.0003
Rudd	ANCOVA	$F_{5,51} = 10.2$	< 0.0001	Slope with TL	Aut13 < Aut14	0.003
Roach	ANCOVA	$F_{5,111} = 12.9$	< 0.0001	Intercept with TL	Aut13 > Aut14	0.004
				Slope with TL	Aut13 < Aut14	< 0.0001
Pike	ANCOVA	$F_{5,74} = 4.45$	0.001	n.s.		
Perch	ANCOVA	$F_{5,100} = 13.4$	< 0.0001	Intercept with TL	Aut13 < Aut14	0.0001
				Intercept with TL	Sum14 < Aut14	< 0.0001
				Slope with TL	Sum14 > Aut14	0.0004

Group differences are given only for significant pairwise post hoc tests relative to autumn 2014. For all fish species, total length (TL) was initially included as covariate, but was not retained as significant predictor for carp and tench (ANOVA). In the other fish species, the effect of TL on $\delta^{13}\text{C}$ or the interaction between TL and period on $\delta^{13}\text{C}$ were significant (ANCOVA), and therefore the comparison of groups may include differences of both intercept and slope.

The $\delta^{13}\text{C}$ of pike, which served as a control, remained unaffected (Figure 3G; Table 1), and only one pike was captured by angling (Digital Appendix 6). In perch, the intercepts of the $\delta^{13}\text{C}$ -TL relationships were higher after bait addition than before, but the slope was lower in autumn 2014 than in autumn 2013, suggesting that only the non-piscivorous smaller perch had on average higher $\delta^{13}\text{C}$ after bait addition (Figure 3H, Table 1). Note, however, that we captured only few, but large, perch at the feeding sites by angling (Digital Appendix 6).

Due to the size-dependency of $\delta^{13}\text{C}$ values for several fish species, we calculated the contribution of ground bait types to the diet only for fishes caught in autumn 2014, namely for common carp and tench (all individuals independent of TL), large (TL > 10 cm) roach, rudd and white bream, large bream (TL > 28 cm) and small perch (TL < 15 cm). Isotopic biplots revealed that all seven fish species had isotopic $\delta^{13}\text{C}$ values between the strongly $\delta^{13}\text{C}$ -enriched bait and the more $\delta^{13}\text{C}$ -depleted signatures of natural resources (Digital Appendix 7). Carp had the most enriched $\delta^{13}\text{C}$, whereas a few individuals of bream and white bream had high $\delta^{15}\text{N}$ values, corresponding with the high $\delta^{15}\text{N}$ of fish mix boilies (Digital Appendix 7). The mixing models, which used the isotopic

signature of natural food combined from zebra mussels, zooplankton and insect larvae, revealed substantial contributions of angling bait to the diet of fishes. Although the posterior distributions of the proportions in the diet were in part flat (Digital Appendix 8), the results suggested that all seven fish species used at least one of the three angling baits. Corn contributed substantially to the diet of common carp, but was of minor importance for the diet of the other fish species (Figure 4A). Fish mix boilies contributed significantly to the diet of white bream, bream, rudd and roach (Figure 4B), whereas sweet mix boilies were eaten primarily by common carp, tench and rudd (Figure 4C). Natural food sources combined contributed up to 50% of the diet, in particular in bream and roach (Figure 4D). To address the potential uncertainty in the mixing models, we included a baseline fish with an isotopic signature, which reflected a pure natural diet. The median contribution of natural food to this baseline fish was 74% (Digital Appendix 8H), whereas the calculated sum of contributions from angling baits was 26%, reflecting basic uncertainty of the model. However, the median contribution of natural food was much higher, and median contributions for all angling baits much lower in the baseline as compared to the seven fish species (Figure 4). By using the posterior distributions, we

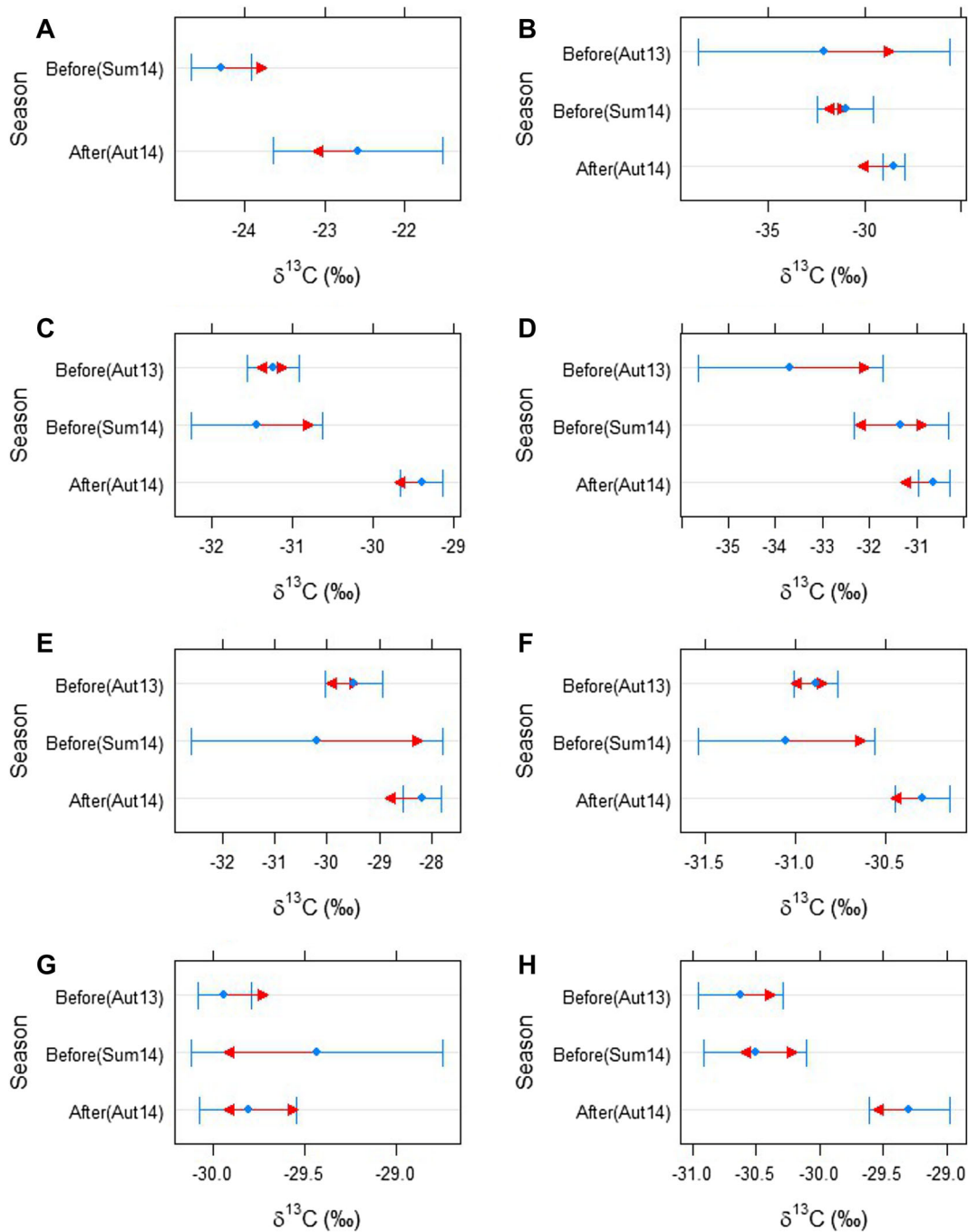


Figure 3. Least squares means (blue dots, corrected for differing fish lengths between the three sampling periods) of $\delta^{13}\text{C}$ of eight fish species **A** common carp, **B** tench, **C** white bream, **D** bream, **E** rudd, **F** roach, **G** pike, **H** perch) during the three sampling periods (autumn 2013, summer 2014: before bait addition; autumn 2014: after bait addition) (no values available for carp, Before(Aut13)). The blue lines indicate the 95% confidence intervals, non-overlapping red arrows between sampling periods denote significant differences in $\delta^{13}\text{C}$ (not corrected for potential interactions between $\delta^{13}\text{C}$ and fish length, see Table 1).

calculated the probabilities for the differences in contributions of natural food and angling baits between the baseline and the seven fish species. There was an average probability of near 1.0 that

all fish species had eaten less natural food than the baseline fish (Digital Appendix 9). In turn, the model suggested a high probability that the seven species fed more fish mix boilies (average proba-

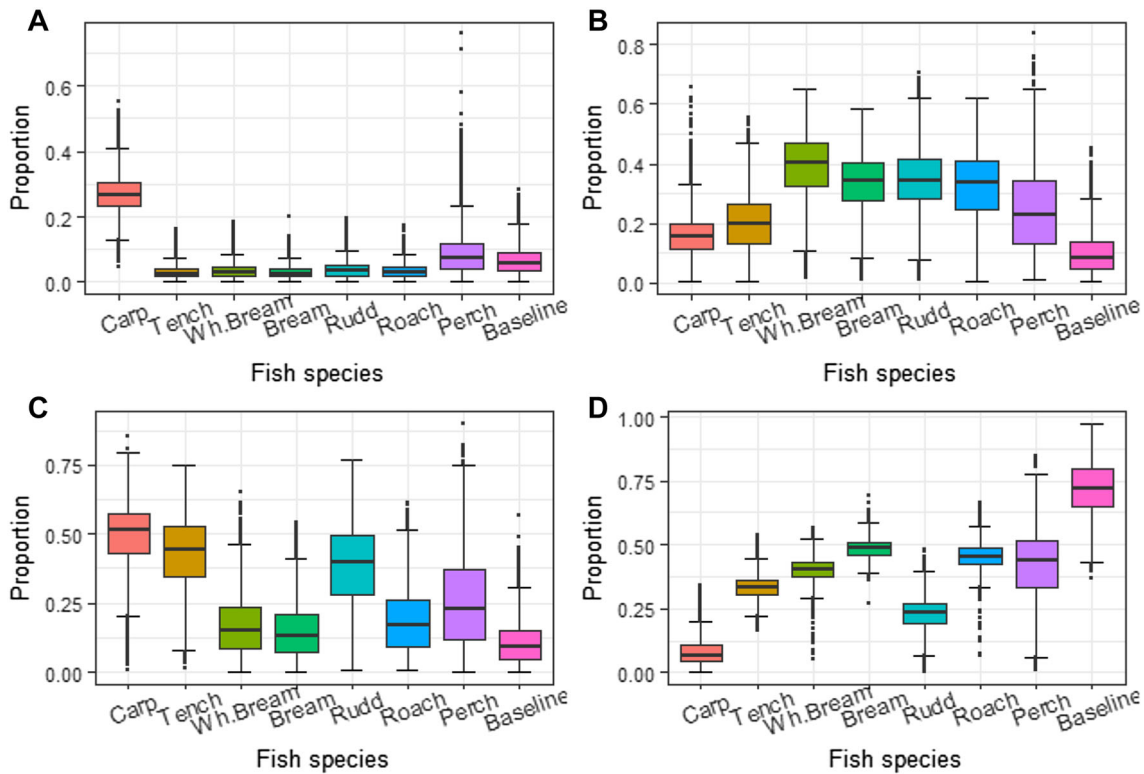


Figure 4. Posterior distributions of contribution of corn (**A**), fish mix boilie (**B**), sweet mix boilie (**C**), and Natural Food (zooplankton, zebra mussels and insect larvae/Isopoda combined) (**D**) to the diet of the seven fish species, as estimated from stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) by Bayesian mixing models. As baseline, we provide the results of the same mixing model for a fish, which has fed exclusively on natural food. The boxes represent the interquartile range (25th and 75th percentile), and whiskers represent 1.5 times the interquartile range distant from the box. Dots are outlying points, and represent the full range of solutions of the Bayesian model. For detailed density plots, see Digital Appendix 8.

bility 0.926) and sweet mix boilies (average probability 0.802) than the baseline fish (Digital Appendix 9). The model did not give clear evidence for a stronger use of corn in the seven fish species in comparison with the baseline (average probability 0.405), but a strong signal was found for common carp (probability 0.996) (Digital Appendix 9).

To elucidate the uncertainty with respect to the assumption of equal use of the three natural food sources by the fish, we ran the same mixing models with only one of the natural sources each. The potential composition of the natural food had strong effects on the results of the mixing models in white bream and bream, whereas for the other fish species, the differences between the scenario with a mix of natural food sources and the three scenarios with only one natural food source were small to moderate (Digital Appendix 10).

Growth Rate Effects

The older age classes of bream, white bream and pike had positive residuals from the population-wide von Bertalanffy growth equation in spring 2015, whereas younger age classes tended to reveal negative residuals (Digital Appendix 11). When examining the full linear model on the residual variation, the main effects of year and TL were significant in all three species, but significant interactions among year \times TL were only revealed in the two omnivorous species bream and white bream (Table 2). This suggests that older bream and white bream grew faster in 2014 until early 2015 during the feeding experiment than predicted from the population-wide von Bertalanffy growth model estimated to data collected prior to feeding (Table 2). As the partial effect size plots show (Figure 5), the slope of size effect on residuals was much steeper in 2014–2015 (after) compared to 2013–2014 (before) in bream (Figure 5A) and white bream (Figure 5B), indicating that the larger

Table 2. ANCOVA Model Results Testing the Residuals of Individual Level Size-at-Age in 2014 Prior to Bait Addition and the Residuals 2015 After Bait Addition as Deviation from the Population-level von Bertalanffy Model for Size-at-Age Prior to Bait Addition as a Function of Total Length (TL) and Year as well as the Interaction.

	df	F	p	B	S.E.	t	p
<i>Bream, Adj. R² = 0.437</i>							
Corrected model	3.102	28.1	< 0.001				
Intercept	1	69.0	< 0.001	- 103.7	11.2	- 9.2	< 0.001
Year	1	26.2	< 0.001				
2014 (relative to 2015)				79.1	15.4	5.1	< 0.001
TL	1	57.3	< 0.001				
Year*TL	1	14.9	< 0.001				
2014*TL				0.094	0.037	2.54	0.013
2015*TL				0.29	0.035	8.37	< 0.001
<i>White bream, Adj. R² = 0.227</i>							
Corrected model	3.50	7.77	< 0.001				
Intercept		11.7	0.001	- 61.7	13.9	- 4.42	< 0.001
Year		9.64	0.003				
2014 (relative to 2015)	1			58.7	18.9	3.10	0.003
TL		7.22	0.010				
Year*TL		4.83	0.033				
2014*TL	1			0.030	0.091	0.33	0.740
2015*TL	1			0.302	0.084	3.60	0.001
<i>Pike, Adj. R² = 0.300</i>							
Corrected model	3.64	10.5	< 0.001				
Intercept	1	29.4	< 0.001	- 181.9	35.047	- 5.19	< 0.001
Year	1	6.15	0.016				
2014 (relative to 2015)				114.1	46.035	2.48	0.016
TL	1	23.830	< 0.001				
Year*TL	1	2.576	0.113				

The partial effects of the size \times year interaction are shown in Figure 5. The columns on the left represent the statistics of the full model, whereas the last four columns reflect coefficient estimates (B) and their standard errors (S.E.), together with their t- and p-values.

conspecifics achieved a size above average in spring 2015, 6–9 months after bait addition. By contrast, the size effect on residuals was similar in pike in the two study years, and the interaction was non-significant (Figure 5C).

DISCUSSION

Our whole-lake experiment demonstrated that the addition of ground baits by recreational cyprinid anglers caused a cascade of changes in the omnivorous fish community of the receiving lake. Exemplified by position records of tagged common carp as a model species, the fish changed their swimming behavior and got attracted to the feeding sites. Angling catches revealed regular uptake of bait by a range of cyprinid fishes, indicating active foraging on the feedstuffs. We also found the added bait constituted a substantial proportion of the diet of all benthivorous and omnivorous fish beyond certain size thresholds. Finally, the behavioral and

diet changes induced higher annual growth rates of the individual fish that preferentially used the bait. Angling baits thus significantly subsidized omnivorous fish, but not piscivorous fish and invertebrates, despite a low contribution to the lake C budget. Together, these results suggest that the addition of human-derived ground bait by anglers may change the structure and dynamics of lake fish communities, particularly of the omnivorous feeding guilds, potentially accompanied by further, so far undocumented, consequences for the entire lake ecosystem.

Ground Bait Changed Home Range of Large Benthivorous and Omnivorous Fish

Our results obtained by fine-scale acoustic telemetry demonstrate an immediate behavioral response of tagged common carp to the addition of bait and a strong attraction to the feeding sites. Specifically, the carp spent more time at the feeding

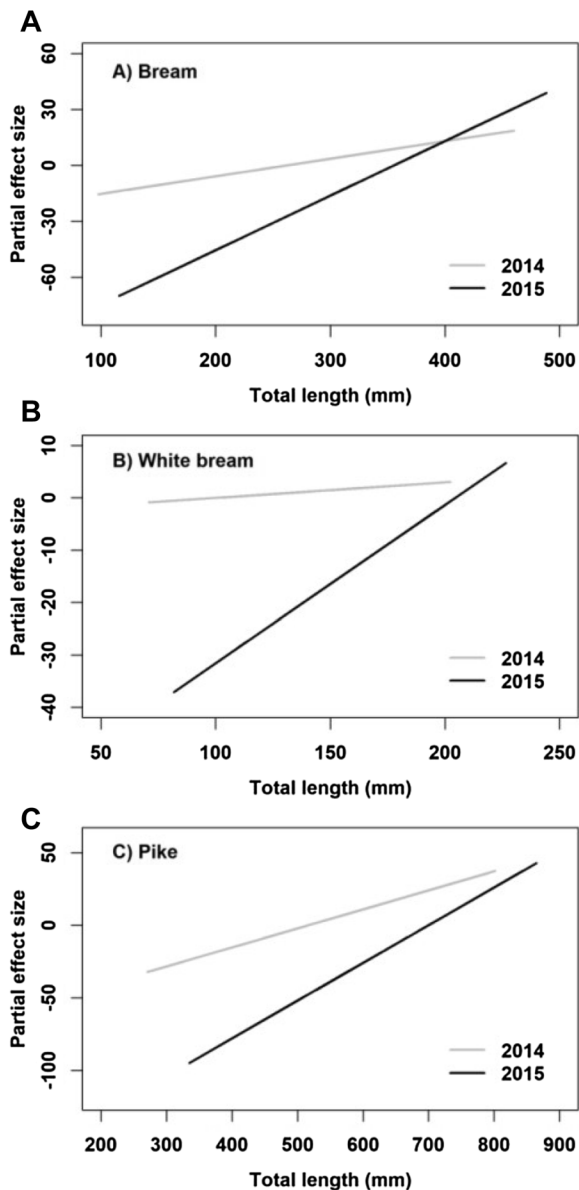


Figure 5. The partial effect sizes of the interactions of year and total length (mm) on the residuals from the population-level von Bertalanffy equation in 2014 and 2015 in bream (A), white bream (B) and pike (C) from Döllnsee.

sites after bait had been added, and this conditioning effect to feeding sites is also well known from pond aquaculture (Füllner 2015). The carp reduced their home range size substantially during the bait addition period, indicating that the offered bait affected the food-search behavior of the carp population at the lake scale. Carp can be attracted rapidly to feed patches within days after the initiation of feeding (Bajer and others 2010), for example by olfaction and gustation from amino acids and other food attractants in the ground baits

(Kasumyan and Morsi 1996) and by social learning (Bajer and others 2010). Unfortunately, we have no behavioral data for non-domesticated wild benthivorous fish for both the before and after periods, but the home range behavior of wild tench shown during feeding was similar to the behavior of carp and these fish also concentrated around the feeding spots. Furthermore, intense angling on the feeding locations revealed that also other fish species were foraging on the added bait. We thus tentatively conclude that the carp behavior may represent the behavior of other cyprinids, although it is possible that the large degree of domestication of carp resulted in this species being particularly attracted to the feeding sites.

The above conclusion of active uptake of angling bait by omnivorous fish was confirmed by the stable isotope analyses of the fish. We found significantly elevated $\delta^{13}\text{C}$ values of common carp, tench, bream, white bream, roach and rudd at the end of the bait addition period, in comparison with values obtained before bait addition. In contrast, $\delta^{13}\text{C}$ values of the natural resources (zooplankton and benthic macroinvertebrates) were not affected by bait additions, suggesting that the omnivorous fish cannot have obtained their elevated $\delta^{13}\text{C}$ values by feeding on those natural resources. For most of the fish species (except common carp and tench), the elevation in $\delta^{13}\text{C}$ values was stronger for larger individuals (as indicated by the significant positive interaction between fish length and $\delta^{13}\text{C}$ in the ANCOVAs). The size-dependency of bait uptake is most likely attributable to the large diameter of the rather hard-texture particles (10–14 mm boilies and ~ 8 mm corn) that can only be eaten by large cyprinids when fitting through the pharyngeal jaws (Sibbing 1988). Thus, gape constraints likely prevented small cyprinids with small gape width from feeding upon the added bait particles. For some of the fish species, $\delta^{13}\text{C}$ was significantly higher only for the comparison between autumn 2013 and autumn 2014, whereas the difference between summer 2014 and autumn 2014 was weaker. The heterogeneous size distribution of sampled fish across the three sampling periods probably contributed to these in part ambiguous results. If only fishes with similar size ranges per species in all three periods were included into statistical comparisons, there were strong differences of $\delta^{13}\text{C}$ values also between summer 2014 and autumn 2014 in carp, roach, rudd and white bream (Digital Appendix 12), whereas the interaction between fish length and $\delta^{13}\text{C}$ was significant only for rudd. A similar effect of fish length on the up-

take of angler baits has recently been reported in riverine barbel (Roberts and others 2017).

Another reason for weaker $\delta^{13}\text{C}$ signals from ground bait in some individuals in autumn 2014 may be found in the turnover time needed to assimilate the ^{13}C -enhanced diet until equilibrium in the muscle tissue of fish. The half-life of ^{13}C in muscle tissue of adult fish is about three up to five months (Weidel and others 2011), and hence only individuals, which started feeding on ground bait immediately after the first introduction, may have achieved tissue equilibrium until the sampling in autumn 2014. Accordingly, the contributions from ground baits to the fish diet calculated by mixing models may even underestimate the true ingestion during the experimental phase. The piscivorous large perch and pike served as a natural control for the effect of ground bait feeding on tissue $\delta^{13}\text{C}$, and we did not find heavier $\delta^{13}\text{C}$ in these fishes and size classes. Accordingly, the predatory fish species as well as the invertebrates neither directly (by feeding on added bait) nor indirectly (by feeding on prey, which has fed upon bait) ingested the C from corn or boilies in the time frame of 3 months of our study.

Ground Bait Substantially Contributed to Fish Diet and Enhanced Fish Growth Rates

The mixing models indicated that for the fish individuals beyond a species-specific size threshold, the contribution from the added bait particles to their diet was substantial. There was a very clear signal of the distinct $\delta^{13}\text{C}$ value of corn (attributable to its C_4 photosynthetic pathway) in common carp. Therefore, terrestrial subsidy to aquatic food webs and vice versa can be traced in animal tissues after addition of corn compounds (Scharnweber and others 2014a, b). The heavy reliance on corn by carp can be explained by the greater amylase activities in the intestine of carp compared to other cyprinids such as tench (Hidalgo and others 1999), which is decisive to break down the starch in corn. Furthermore, there was strong evidence of feeding upon fish mix boilies by some large bream and white bream, as indicated by their elevated $\delta^{15}\text{N}$ values after bait addition. A similar tracing of fish meal and oil from fishmeal pellets used as angling bait has been demonstrated recently for barbel and chub (*Squalius cephalus*) in English rivers (Roberts and others 2017). In contrast, the sweet food mix was preferentially ingested by tench, carp and rudd, confirming earlier studies that the common cyprinid species have

differing preferences for certain types of angling bait (Specziar and others 1997). It is possible that these three species have better ability to break down carbohydrates than the other cyprinids, which may have contributed to the larger fraction of both corn and sweet mix boilies in tench, carp and rudd.

In Döllnsee, the three bait particles contributed substantially to the diet of the omnivorous and benthivorous fish species in the lake. A similarly strong reliance of barbel and chub on fishmeal pellets has been shown in experiments where a mix of natural and artificial food was offered (Roberts and others 2017). We do not rely too strongly on the medians of the posterior distributions from each of the bait types in the Bayesian mixing models, because the distributions were often flat and hence had substantial uncertainty. However, the intermediate position of all fish in the isospace (Digital Appendix 7) and the uncertainty analyses of the model (Table 2, Digital Appendices 9, 10) suggest that the angler baits must have contributed at least to some extent to the diet of all species.

We showed that the individual growth rates of bream and white bream were enhanced in the feeding year compared with the previous non-feeding year, in particular for larger individuals of both species. In contrast, we did not find a similar growth response in the piscivorous pike. These results suggest that the higher growth rates are at least partly attributable to the uptake of added bait. Corn and other cereals have been used traditionally in pond aquaculture because the addition of carbohydrates bound in cereals increases carp production substantially (Kestemont 1995; Füllner 2015). The main mechanisms by which supplementary feeding with corn elevates pond production of fishes relates to the more efficient use of essential macro- and micronutrients from natural food and the delayed depletion of natural food toward the end of the summer growing season (Füllner 2015; Hlavac and others 2016). The growth rates of carp achievable by feeding upon boilies were even higher than those achieved by feeding on seed particles like corn, indicating that different feedstuffs used by anglers have different nutritional value to the fish (Niesar and others 2004). However, the energy density of the ground bait is comparable to that of natural animal food (about 20 kJ g^{-1} dry mass) (Niesar and others 2004), suggesting that ground baits are energetically not superior to natural food. Moreover, if natural food of the same dry matter amount is given to carp compared to the same dry matter of

angling baits such as boilies, the growth on natural food is larger (Niesar and others 2004). However, natural food is often limited in natural ecosystems, particularly toward the end of the growing season and the readily available angling bait can be found and ingested easily and provides a compact form of energy and nutrients that likely demands much less food-search activity and sorting than feeding on natural macrozoobenthos. Therefore, the nutrients bound in baits and the energy supply seems to come on top of what an ecosystem naturally offers, and the accelerated growth rates found in our experiment are indicative of a subsidy above the natural animal production, similar to findings from the substantial increase of production in food-supplemented pond aquaculture with cyprinids (Kestemont 1995; Füllner 2015). The ground baiting-induced increase in growth is facilitated by the high digestibility of macronutrients from all ground baits, even of corn for carp (Arlinghaus and Niesar 2005), the reduction in energy needed for food search and feeding when angling baits are available on predictable food patches, and very likely the more efficient use of natural food similar to the case in pond aquaculture (Füllner 2015).

Can Ground Bait Additions Subsidize Fish?

A surprising result is the discrepancy between the strong effects of ground bait addition on the omnivorous fish and the modest contribution of these baits to the C budget of the lake. Organic C budgets in eutrophic lakes are dominated by autochthonous primary production (Carpenter and others 2005; Brothers and others 2013b). Consequently, additions of terrestrial particulate organic matter could be traced in eutrophic aquatic food webs (Bartels and others 2012; Scharnweber and others 2014a), but had little effects on consumer production and biomass (Mehner and others 2016). In our previous whole-lake experiments, we added maize leaves to the treatment halves of two divided lakes (about 25 g C m^{-2}) accounting for only less than 10% of the C fixed by annual PPr in the lakes, making a weak effect on secondary production plausible (Mehner and others 2016). In the current experiment, angler baits containing mainly terrestrial-plant-derived material added even less than 1% to the estimated annual net PPr, but induced high diet contributions and enhanced growth rates in fish, suggesting a substantial subsidy effect. The allochthonous C was offered at high concentrations, at predictable locations over long time spans of several months, and was bound in relatively

large, easily accessible particles with energy densities similar to the naturally available food, such as zooplankton or benthic macroinvertebrates. Subsidy by high-quality resources often shifts the diet preferences of consumers toward the subsidy and hence can have strong production effects (Marczak and others 2007; Marcarelli and others 2011). Furthermore, in contrast to terrestrial particulate or dissolved organic C inputs entering higher trophic levels via the microbial loop or benthic shortcuts (Attermeyer and others 2013), the bait particles can be considered prey supplied directly to fish consumers, similar to the allochthonous natural prey subsidizing aquatic food webs (Mehner and others 2005; Milardi and others 2016). Indeed, added baits were in the same order of magnitude as biomass (1 g C m^{-2}) and production of macrozoobenthos ($1\text{--}2 \text{ g C m}^{-2} \text{ y}^{-1}$) in lakes of similar morphometry and trophic state in this region (Brauns and others 2011; Lischke and others 2017). From that perspective, the strong effects found in our study can be compared to those of pulsed subsidies on the structure and dynamics of aquatic consumer populations (Nowlin and others 2008; Trebilco and others 2016).

CONCLUSIONS

Ground baiting with mainly terrestrial-plant-derived organic matter by recreational cyprinid anglers has strong subsidy effects on a major component of a fish community, particularly on omnivorous species, in eutrophic lakes despite high internal primary production. The shift in diet composition and increased growth rates in fish detected in our study may eventually elevate fish production and thus the carrying capacity of the aquatic systems to fish consumers, similar to the case previously documented in feed-enhanced pond aquaculture with cyprinid fishes. Thus, longer-term subsidy may result in higher biomasses of consumer populations (Trebilco and others 2016) and decouple predator–prey relationships (Rodewald and others 2011). We confined our analysis to freshwater cyprinid angling, but ground baiting and the addition of feed to attract fish is also commonplace, for example, in coastal angling. Thus, our work can be considered as a motivation to further study the response of consumers and entire ecosystems to the subsidy effect of angling-induced feed introduction over longer time frames than completed in our experiment.

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