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Author(s): Mehner, Thomas; Rapp, Tobias; Monk, Christopher T.; Beck, Mara E.; Trudeau, Ashley; Kiljunen, Mikko; Hilt, Sabine; Arlinghaus, Robert

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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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Key Words:	subsidy, human-derived food, stable isotopes, fish behaviour, fish growth, eutrophic lake



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16 17	8	Mikko Kiljunen ³ , Sabine Hilt ¹ , Robert Arlinghaus ^{1,2}
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19	9	
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22	11	¹ Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin
23	12	Germany
24 25	12	Germany
25 26	13	² Division of Integrative Fisheries Management, Faculty of Life Sciences, Humboldt Universität zu
20	14	Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany
28		, , ,
29	15	³ University of Jyväskylä, Department of Biological and Environmental Science, PO Box 35, FI-40014
30	16	University of Jyväskylä, Finland
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32	17	* Contact: mehner@igb-berlin.de
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18 Abstract

19	It is well documented that aquatic ecosystems may be subsidized by naturally-derived terrestrial
20	carbon sources. In contrast, the intentional or unintentional subsidy of animal populations by
21	human-derived feed resources and their ecosystem effects are poorly studied. We added ground
22	baits of the type, amount and temporal duration commonly applied by anglers targeting cyprinid
23	fishes to a small lake, and studied behaviour, diet composition and annual growth rate of the lake
24	fish community in response to the bait addition. Based on recordings by a high-resolution ultrasonic
25	telemetry array, common carp (Cyprinus carpio) as a model benthivore spend more time at the sites
26	where ground baits were added, and they significantly reduced their home range relative to the
27	period before bait addition. Furthermore, many omnivorous cyprinid fish species were regularly
28	caught by angling at the feeding sites, indicating active ingestion of the artificially added food items.
29	Stable istotope analyses of ¹³ C and ¹⁵ N showed that in particular larger specimens of common carp,
30	bream (Abramis brama), white bream (Blicca bjoerkna), tench (Tinca tinca), roach (Rutilus rutilus)
31	and rudd (Scardinius erythropthalmus) included substantial amounts of angler baits into their diet.
32	There was also a significant acceleration of growth in bream and white bream after bait addition,
33	most likely attributable to the energetic benefits from bait addition. In contrast, there was no
34	response in annual growth rate in top predators, suggesting they did not benefit from the subsidy.
35	The amount of carbon introduced was very low (about 1%) relative to an estimate of in-lake C
36	fixation by autotrophs. However, if the C added by bait was compared with the coarsely estimated
37	secondary production of benthic macroinvertebrates in the lake, the C available to benthivorous and
38	omnivorous fishes was comparable between natural resources and angler baits. We conclude that
39	human-derived feed resources associated with recreational fishing may constitute a substantial
40	subsidy to omnivorous fishes in lakes, in particular if the food is provided in form of particles, which
41	are readily accessible and found at repeatable feeding places and over sufficiently long time periods
42	during a year. The long-term consequences for the receiving ecosystems still have to be elucidated.

43 Key words: subsidy, human-derived food, stable isotopes, fish behaviour, fish growth

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44 Introduction

45	Aquatic ecosystems are connected with their terrestrial surroundings by a reciprocal flux of
46	inorganic nutrients, dead organic matter and living organisms (Cole et al., 2006; Schindler and Smits,
47	2017). The contribution of terrestrial resources (i.e. allochthonous organic matter produced outside
48	of the aquatic system) to the aquatic secondary production of bacteria, invertebrates and
49	vertebrates remains hotly debated (reviewed by Brett et al., 2017). Among other factors, the
50	connectivity between aquatic and terrestrial ecosystems, the size of the receiving ecosystems, and
51	their productivity were suggested as contributing to the degree of allochthony of lakes and rivers
52	(Cole et al., 2002; Pace et al., 2004; Tanentzap et al., 2017). Another highly influential aspect
53	determining the contribution of allochthonous resources to aquatic secondary production is the
54	biochemical quality of the subsidy and the trophic level that is subsidized (Marcarelli et al., 2011;
55	Brett et al., 2017). Terrestrial dissolved and particulate organic matter (t-DOM and t-POM,
56	respectively) enter at the base of the food web and mostly need to be incorporated by primary
57	consumers before ultimately being available to fish (Cole et al., 2002; Pace et al., 2004; Scharnweber
58	et al., 2014a). They are both considered poor quality for aquatic consumers due to their high carbon
59	(C) to nutrient ratios and low energy content (Marcarelli et al., 2011). In contrast, terrestrial animals
60	are often a high-quality prey type for aquatic predators (Mehner et al., 2005; Marcarelli et al., 2011).
61	However, the effect size of subsidy for consumer density or biomass was lower for predators than for
62	detritivores, producers or omnivores, suggesting that subsidy by allochthonous prey is often spatially
63	or temporally limited and only affects selected trophic groups (Marczak et al., 2007; Marcarelli et al.,
64	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 et al., 2013). Humans intentionally or unintentionally dispose waste, food remains, crop residuals and animal carcasses into the environment, providing a predictable resource to animal populations with

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effects on food-web interactions and ecosystem processes (Oro et al., 2013). Examples for highquality human subsidy of aquatic ecosystems are food remains from open-water fish farms (Grey et
al., 2004; Wang et al., 2018), waste from landfills supporting the diet of sea birds (Osterback et al.,
2015), or the intentional feeding of aquatic organisms, such as water birds, by recreationists, in
particular in urban habitats (Oro et al., 2013).

75 Another specific form of intentional human subsidy of aquatic systems is the application of 76 ground bait by recreational coarse (i.e. non salmonid) freshwater anglers. Ground baiting is common 77 practice in freshwater recreational fisheries for cyprinid fishes all over Europe (Wolos et al., 1992; 78 Arlinghaus and Mehner, 2003; Amaral et al., 2013; Roberts et al., 2017), and is increasingly used 79 beyond Europe (e.g., North America or South Africa) where specialized angling for large cyprinids 80 such as common carp (Cyprinus carpio) is becoming locally fashionable. Recreational angling for 81 cyprinids is often based on the introduction of ground bait for several days prior to and during the 82 fishing day to attract the fish on the fishing sites (Wolos et al., 1992; Arlinghaus and Mehner, 2003). 83 In Europe, specialized common carp and barbel (Barbus barbus) anglers regularly apply more than 1 84 kg of ground bait per day, usually in form of food particles (corn, pellets, boilies - a special carp bait) 85 (Arlinghaus, 2004; Niesar et al., 2004; Basic and Britton, 2015). However, ground baiting is also 86 standard practice in competitive fishing for small-bodied cyprinids such as roach (*Rutilus rutilus*) 87 (Amaral et al., 2013). The average annual dispersal of ground baits per freshwater angler in Germany 88 was estimated to be 7.3 kg (Arlinghaus, 2004), which easily scales to several thousand tons of ground 89 bait introduced to aquatic ecosystems by about 3.3 million anglers in Germany alone. These 90 considerable volumes of angler baits and their high nutritional quality evidenced by very high 91 digestibility of all classes of macronutrients (protein, lipids, carbohydrates) (Arlinghaus and Niesar, 92 2005) and positive growth responses in laboratory experiments with common carp (Niesar et al., 93 2004) may form a relevant direct subsidy to benthivorous and omnivorous fish in lakes and rivers 94 exposed to high use-intensity by recreational coarse anglers. Some individuals of the benthivorous 95 cyprinid barbel in rivers indeed expressed a strong preference for the angler ground bait relative to

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96	natural food, as indicated by shifts in the population isotopic niches (Basic and Britton, 2015; Roberts
97	et al., 2017). However, these studies were inconclusive with respect to a mechanistic understanding
98	of the consequences of subsidizing a fish community by ground bait. In particular, studies testing
99	whether benthivorous fish are behaviorally attracted by the baits and benefit from their ingestion by
100	accelerated growth are lacking. It is also unknown whether the anthropogenic subsidy affects top
101	predators that are unlikely to feed directly on the angler bait. Importantly, for a quantitative
102	evaluation of the effect of bait additions on the lake ecosystem, a comparison of C loads from baits
103	relative to in-lake C fixation by autotrophs (Mehner et al., 2016) and to production by primary
104	consumers is needed.

105 We performed a whole-lake experiment in an eutrophic lake to test for a chain-of-action response 106 of a fish community to an intentional addition of resources, by providing ground baits of the type, 107 amount and temporal duration commonly applied by specialized cyprinid anglers. We used a fine-108 scale acoustic telemetry system (Baktoft et al., 2015), which facilitated studying the individual 109 behaviour 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 δ^{15} N and δ^{13} C 110 111 signatures of several benthivorous/omnivorous and piscivorous fish species, before and after bait 112 addition, to estimate the proportion of baits in their diet composition. Finally, we measured the 113 annual growth rates of a sample of cyprinid and top predatory species to elucidate whether there 114 was a discernible effect of ground-bait ingestion on the individual growth rates of fishes, serving as 115 an indicator of a potential contribution of bait to secondary production. We hypothesized that even 116 modest amounts of ground bait introduced to a lake ecosystem would generate substantial changes 117 within the benthivorous and omnivorous fish community. We expect this because ground bait is of 118 high nutritional quality, provided continuously during the growing season and not accessible by other 119 consumers than large cyprinid fish. Ground bait additions could thus significantly modify behaviour, 120 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 121

3	122	ground baits to the diet of omnivorous fish, but not in piscivorous fish or invertebrate consumers as
4 5	123	these groups do not directly consume particle-based ground bait, and (iii) growth of fishes directly
6 7	124	feeding on ground bait is accelerated. Overall, we expected a subsidy effect from bait addition
8 9 10	125	despite its low share in C loading relative to high C fixation in the eutrophic lake.
11 12 13	126	
14 15 16	127	Methods
17 18 19	128	Study lake and subsidy experiment
20 21	129	Lake Kleiner Döllnsee (subsequently referred to as Döllnsee, 52°99'N, 13°58'E) is situated about
22 23	130	80 km north of Berlin (Germany). It has an area of 0.25 km ² and a mean depth of 4.1 m. The lake is
24 25 26	131	stratified and eutrophic with a total phosphorus (TP) concentration of about 50 mg m ⁻³ (arithmetic
20 27 28	132	average of 12 monthly samples from the epilimnion in 2014), resulting in an average Secchi depth of
29 30	133	2.1 m. The shoreline is characterized by a dense reed (<i>Phragmites</i> spp., <i>Typha</i> spp.) belt; sparse
31 32	134	patches of submerged macrophytes cover the littoral and sub-littoral zones. The fish community
33 34	135	consists mainly of benthivorous or omnivorous species, namely cyprinids (roach, rudd Scardinius
35 36	136	erythrophthalmus, bream Abramis brama, white bream Blicca bjoerkna, bleak Alburnus alburnus,
37 38	137	tench, crucian carp Carassius carassius, and stocked common carp) and the percid species ruffe
39 40	138	(Gymnocephalus cernuus). Naturally occurring facultative piscivorous species are perch (Perca
41 42 43	139	fluviatilis) and pike (Esox lucius), whereas European catfish (Silurus glanis), eel (Anguilla anguilla) and
44 45	140	zander (Sander lucioperca) have been stocked and occur in low numbers.
46 47	141	Between July and October 2014, a total of 750 kg dry mass of soaked and cooked corn (Zea mays),
48 49	142	reflecting the typical bait preparation by specialized cyprinid anglers targeting carp, tench or large
50 51 52	143	bream, was introduced on eight sub-littoral feeding sites that were equally spaced around the
52 53 54	144	shoreline. Corn was introduced twice daily during four days per week. Furthermore, 189 kg of fish
55 56	145	mix boilies and 89 kg of sweet mix boilies were introduced together with corn. Boilies are specially
57 58 59	146	designed boiled paste balls commonly used in carp, tench and increasingly large bream fishing, and 6

are typically mixed with cereals such as corn as ground baits (Niesar et al., 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 et al., 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 et al., 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 et al. (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 et al., 2013a; Mehner et al., 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.

164 Behavioral observation of fish

As a model cyprinids, 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 highresolution, 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 et al., 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 et al., 2009; Hühn et al., 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 to 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 seconds were added to the feeding time. The reason is that after 335 seconds 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, four days per week between August

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2 3	198	12 and October 15, 2014, to study which species were ingesting the bait types and thus were
4 5	199	vulnerable to capture by angling. Note that we did not attempt to use angling data to measure the
6 7 8	200	use of feeding sites as opposed to other sites, but rather as source of information on whether the
9 10	201	fish indeed ingested the feedstuffs. More details of the angling can be found in Digital Appendix 1.
11 12 13	202	
14 15 16	203	Stable isotope analyses of natural resources and fish
17 18	204	To estimate the contributions of ground bait to the diet of fish, stable isotope (SI) values (δ^{13} C and
20 21	205	δ^{15} N) of ground bait as well as natural resources (zooplankton and benthic invertebrates) and fish
22	206	(benthivorous/omnivorous and piscivorous fish) were measured twice before bait addition (autumn
23 24 25	207	2013, summer 2014) and once after bait addition (autumn 2014). This sampling scheme takes the
26 27	208	seasonality of SI values into account and hence facilitates the comparison of SI values before and
28 29	209	after feed addition in autumn (2013 vs. 2014) and the direct before-after comparison of SI values in
30 31	210	response to feed addition (summer 2014 vs. autumn 2014). For more details of sampling, see Digital
32 33	211	Appendix 1.
35 36	212	A total of 749 samples for SI analysis were processed, including broad size ranges of fish (Digital
37 38	213	Appendix 2). Samples were dried at 60°C for 48 h to constant weight, and subsequently ground with
39 40	214	mortar and pestle into a fine powder. For analysis, 0.6 (\pm 0.1) mg of animal tissue was weighed into
41 42	215	tin capsules. Stable isotopes analyses were conducted using a Finnigan DELTA _{plus} Advantage mass
43 44	216	spectrometer (Thermo Fisher Scientific Corporation, Waltham, MA, U.S.A.) coupled to a FlashEA 1112
45 46	217	elemental analyser at the University of Jyväskylä, Finland. Stable nitrogen and carbon ratios are
47 48 40	218	expressed as delta values (δ^{15} N and δ^{13} C, respectively) relative to the international standards for
49 50 51	219	nitrogen (atmospheric nitrogen) and carbon (Vienna PeeDeeBelemnite). Analytical precision was
52 53	220	always better than ±0.33‰ and ±0.23‰ for $\delta^{^{15}}$ N and $\delta^{^{13}}$ C, respectively, and was based on repeated
54 55	221	analysis of working standards (pike white muscle tissue, birch leaves and Spirulina spp.) inserted in
56 57 59	222	each run after every five samples.
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224	To test for potential elevations of C stable isotope value after bait addition, we compared δ^{13} C
225	values of natural resources between the three sampling periods by ANOVA and Tukey HSD post-hoc
226	tests. In cases when the data did not meet the assumptions for parametric tests, we applied Kruskal-
227	Wallis tests with Nemenyi post-hoc tests. For comparison of δ^{13} C values of fish between the sampling
228	periods, we applied ANCOVA, with total length of fish added as covariate. Fish length had to be
229	included because corn and boilies are particles usually not accessible to smaller fishes because of
230	gape limitation and due to the hard texture, and hence we expected strong effects only for fish > 10
231	cm length. We first calculated the full ANCOVA model including the interaction between sampling
232	period and fish length, but removed non-significant interaction terms from the full model. We
233	plotted the least squares means of $\delta^{\rm 13}C$ for the three sampling periods, which take into account the
234	variable lengths of fish in the sampling periods. For species for which the interaction between
235	sampling period and fish length was significant, we tested whether there were significant differences
236	of intercepts and slopes between autumn 2014 (after bait addition) and either autumn 2013 or
237	summer 2014 (both before bait addition). Higher intercepts after than before bait addition would
238	suggest that all individuals of this species independent of length have included ground bait. Higher
239	slopes in the period after bait addition would suggest that in particular larger (positive slope) or
240	smaller (negative slope) individuals have ingested added food. All calculations were done in R 3.3.2 (R
241	Development Core Team, 2016).
242	To calculate the proportion of corn and boilies in the diets of those fish species, which showed

elevated δ¹³C 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, i.e. a valid

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3	249	mixing geometry and distinct resource isotope values were fulfilled (Digital Appendix 3). Mixing
4 5	250	modelling was conducted using fractionation factors of 0.4 \pm 1.3 for $\delta^{13}C$ and 3.4 \pm 1.0 for $\delta^{15}N$ (Post,
6 7	251	2002) and concentration dependence (Phillips and Koch, 2002). Initially we included zooplankton,
o 9 10	252	zebra mussels and benthic macroinvertebrates (larvae of Chironomidae, Ephemeroptera,
10 11 12	253	Trichoptera, Odonata, and Isopoda mixed because of similar isotopic signatures) as potential natural
13 14	254	sources of the diet of benthivorous or omnivorous fish. Furthermore, we considered corn, fish mix
15 16	255	boilies and sweet mix boilies separately as artificially added potential food sources (Digital Appendix
17 18	256	3). The artificial food sources could not be combined because of their distinctly separate δ^{13} C and
19 20	257	δ^{15} N values. However, to reduce the uncertainty in the mixing model output, we combined a priori
21 22	258	zooplankton, insect larvae and zebra mussels into a single category 'Natural Food'. This was justified
23 24	259	because the $\delta^{15}N$ values did not differ between these groups (ANOVA F_{2,83}=1.01, p=0.37), but $\delta^{13}C$
25 26 27	260	differed between the natural resource groups (ANOVA F _{2,83} =74.1, p<0.0001).
28 29	261	To address the potential uncertainty in the mixing model with four remaining sources and two
30 31 22	262	tracers, we included a hypothetical baseline fish with an isotopic signature, which reflected a pure
32 33 34	263	natural diet, and evaluated the contribution of ground bait to this baseline fish. By using the
35 36	264	posterior distributions, we calculated the probabilities for the differences in contributions of natural
37 38	265	food and angling baits between the baseline and the seven fish species, as based on 1000 repetitions
39 40	266	of the Bayesian mixing model. We did not analyze stomach or gut content from the fish in Döllnsee,
41 42	267	and hence we assumed equal contributions of the three natural sources to the diet of fish. However,
43 44	268	to reflect the uncertainty introduced by this assumption, we ran the same mixing models with each
45 46	269	natural food source separately, and provide the respective median source contributions in
47 48 49	270	comparison with the assumption of the equal mix.
50 51	271	We evaluated the diet composition of all carp (n=6) and tench (n=23) caught in autumn 2014
52 53	272	because in these species the δ^{13} C values did not vary with fish length (see results). In the other
54 55	273	species, there was a strong positive length dependency of δ^{13} C values, and hence we included only
56 57 58	274	individuals beyond a certain size threshold for which feeding on ground baits was likely, namely large

275	roach (TL >10 cm, n=17), large rudd (TL >10 cm, n=15), large white bream (TL >10 cm, n=19) and large
276	bream (TL > 28 cm, n=27). In perch, the statistical results indicated a negative slope of δ^{13} C values
277	with length, and hence we included only small perch (TL < 15 cm, n=5) into the mixing model
278	analyses.
279	
280	Growth rate analysis
281	After the bait addition period ended, fish were sampled by angling from 4 May to 29 May 2015 at
282	a time where the winter growth ring in scales was clearly developed and positive growth was visible
283	on the scales starting in spring. We focused the growth rate analyses on two fish species for which
284	uptake of added bait was likely, and which were frequent in the lake. Bream (n=59) and white bream
285	(n=30) were regularly angled at the locations on which bait was added; hence it was reasonable to
286	assume that they ate corn and boilies. Further, the piscivorous pike (n=34) served as "control"
287	because we assumed that piscivores should show no immediate benefit from our bait addition. Four
288	additional pike were caught on November 26, 2015 to increase the length gradient of the analysis
289	and sample size. For more details of scale reading and estimates by the growth model, see Digital
290	Appendix 1.
291	We used the growth model to predict the expected length of each fish one year later (i.e., in
292	spring 2015) assuming that this length would represent the typical growth of that individual for each
293	species in the study lake without a bait addition effect. We then estimated the linear difference
294	(residuals) between observed (back-calculated) length in spring 2015 and the predicted theoretical
295	length in spring 2015 to evaluate systematic deviations from predictions in response to bait addition.
296	Finally, we fitted a general linear model to examine the effect of treatment (spring 2015 = after bait
297	addition vs. spring 2014 = before addition), total length in spring 2014 and total length × year on the
298	growth residuals in 2015 by species. We choose the interaction of year with fish length because we
299	assumed that the bait addition would particularly benefit the larger size classes of the omnivorous
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300	fishes, which should in turn show the greatest growth increase. A significant interaction effect with a
301	positive slope would support our hypothesis that growth of the fish differed in response to bait
302	addition. This analysis was completed in SPSS, version 22.0 (SPSS Inc., Chicago, U.S.A.).
303	We present subsequently the results from the whole-lake experiment without having similar data
304	from an untreated reference lake. Lakes are rarely identical enough that differences between
305	treatment and control lakes can be ascribed exclusively to the treatment. Therefore, we base our
306	arguments on temporal references within the same system, by comparing fish stable isotope data,
307	fish growth and behavior and distribution of tagged fish before and after the experimental bait
308	addition. Further, by temporally limiting the experiment and analyses, we can compare the isotopic
309	changes of omnivorous fish (hypothesized to respond fast) with the isotopic changes in piscivorous
310	fish (hypothesized to respond only weakly within the study period), thus providing an internal
311	reference. Further, we combine behavioural studies with growth and diet analyses of fish, to
312	strengthen the argument that the treatment has caused an effect. This expanded approach is broad
313	and hence we do not have to rely on a single snapshot sample to infer that fish have profited from
314	the bait addition.
315	
316	Results
317	Occurrence of fish on feeding sites
318	Common carp used feeding sites significantly more often after bait was added (paired t-test, t = -
319	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
320	sites (Fig. 1A, see video documentary in the digital appendix), which were regularly spaced around
321	the entire littoral area. The feeding site usage varied among individual carp, but all individuals
322	showed an increase after the addition of baits (from <1% for all individuals before addition to
323	between 1.5% and 14.1% after addition). An increase in feeding site use following bait introduction
324	was robust to the assumption that carp swimming within 15 m of a feeding site constituted a visit, 13
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325 because comparative calculations for 5 m or 30 m distances gave similar results (Digital Appendix 4). 326 In contrast, the corresponding mean residence times at (future) feeding sites prior to the addition of 327 angler ground bait were close to zero. Prior to the initiation of the bait addition, the carp readily used 328 the eastern and northern areas of the lake and were never seen in the west and rarely on the 329 southern banks (Fig. 1 B,C) and rarely were seen to pause at the future locations of the feeding sites. 330 Throughout the bait addition period, however, the carp home ranges collapsed (56% decline in the 331 50% home range area after feeding commenced) around the eight feeding sites (Fig. 1 B,C; see video 332 in digital appendix). Similar behaviour at the feeding sites was observed for tench after bait addition 333 (Digital Appendix 5).

334 A range of species were captured by angling at the feeding sites, indicating active ingestion of the 335 angling bait (Digital Appendix 6). We also used sample feed in bags to study the uptake of the feed 336 and almost always found all the food consumed within a few hours. The most frequently captured 337 species was common bream, captured 616 times at a mean TL of 430 ± 57 mm (mean \pm sd). Carp 338 were captured 28 times (TL 580 \pm 76 mm), and tench were captured 32 times (433 \pm 52mm). We also 339 captured 62 roach (TL = 238 ± 59 mm mean \pm sd), 40 rudd (TL = 260 ± 53 mm mean \pm sd), 31 white 340 bream (TL= 205 ± 34 mm), four perch (TL= 393 ± 12 mm) and one pike (TL = 615 mm). The cyprinid 341 species were caught by all three baits types (corn, fish mix boilies, sweet mix boilies).

342

343 Stable isotope values of resources

The mean δ^{13} C values of corn (-12.0‰ ± 0.17 SD, n=17), fish mix boilies (-24.1‰ ± 0.29, n=6) and sweet mix boilies (-25.7‰ ± 0.23, n=4) confirmed that the ground baits were more enriched in ¹³C than natural resources for benthivorous fish (zooplankton, -39.5‰ ± 2.5; zebra mussels, -35.2‰ ± 1.0; benthic insect larvae, -31.6‰ ± 2.7) (Digital Appendix 3). Fish mix boilies were strongly ¹⁵Nenriched (7.27‰ ± 0.24), attributable to contributions of fish meal and oil, as compared to sweet mix boilies (3.19‰ ± 0.21) and corn (4.90‰ ± 1.44), which are rich in carbohydrate and plant-meal

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2 3	350	(Digital Appendix 2). δ^{13} C values of zooplankton, benthic insect larvae and zebra mussels were not
4 5	351	affected by bait additions, while crayfish δ^{13} C values were significantly elevated in the period after
6 7 8	352	bait addition (Fig. 2A-D, Table 1).
9 10 11	353	
12 13 14	354	Stable isotope signatures of fish and contribution of ground bait to fish diet
15 16	355	Among fishes, the δ^{13} C values of carp and tench were significantly elevated after bait addition in
17 18	356	autumn 2014 compared to the samplings before addition, independent of fish size (interaction
19 20	357	between fish length and sampling period not significant) (Fig. 3A,B; Table 1). Both species were also
21 22 23	358	regularly caught during experimental angling (Digital Appendix 6), revealing active feeding on the
25 24 25	359	feeding spots and bait types. Similarly, the $\delta^{13}\text{C}$ signatures of white bream, bream, rudd and roach
25 26 27	360	were higher in autumn 2014 than in autumn 2013, attributable to higher δ^{13} C of the larger
28 29	361	individuals after bait addition (significantly steeper slope of δ^{13} C with TL in autumn 2014 vs. autumn
30 31	362	2013) (Fig. 3C-F; Table 1). Again, angling experiments regularly revealed catches of bream and white
32 33	363	bream and to a smaller degree of large rudd and roach on the feeding spots (Digital Appendix 6). The
34 35	364	δ^{13} C of pike, which served as a control, remained unaffected (Fig. 3G; Table 1), and only one pike was
36 37	365	captured by angling (Digital Appendix 6). In perch, the intercepts of the δ^{13} C-TL relationships were
38 39	366	higher after bait addition than before, but the slope was lower in autumn 2014 than in autumn 2013,
40 41	367	suggesting that only the non-piscivorous smaller perch had on average higher δ^{13} C after bait addition
42 43	368	(Fig. 3H, Table 1). Note, however, that we captured only few, but large, perch at the feeding sites by
44 45 46	369	angling (Digital Appendix 6).
47 48	370	Due to the size-dependency of δ^{13} C values for several fish species, we calculated the contribution
49 50	371	of ground bait types to the diet only for fishes caught in autumn 2014, namely for common carp and
51 52	372	tench (all individuals independent of TL), large (TL >10 cm) roach, rudd and white bream, large bream
55 54 55	373	(TL > 28 cm) and small perch (TL < 15 cm). Isotopic biplots revealed that all seven fish species had
56 57	374	isotopic $\delta^{13}C$ values between the strongly $\delta^{13}C$ -enriched bait and the more $\delta^{13}C$ -depleted signatures
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375	of natural resources (Digital Appendix 7). Carp had the most enriched δ^{13} C, whereas a few individuals
376	of bream and white bream had high $\delta^{\rm 15}N$ values, corresponding with the high $\delta^{\rm 15}N$ of fish mix boilies
377	(Digital Appendix 7). The mixing models, which used the isotopic signature of natural food combined
378	from zebra mussels, zooplankton and insect larvae, revealed substantial contributions of angling bait
379	to the diet of fishes. Although the posterior distributions of the proportions in the diet were in part
380	flat (Digital Appendix 8), the results suggested that all seven fish species used at least one of the
381	three angling baits. Corn contributed substantially to the diet of common carp, but was of minor
382	importance for the diet of the other fish species (Fig. 4A). Fish mix boilies contributed significantly to
383	the diet of white bream, bream, rudd and roach (Fig. 4B), whereas sweet mix boilies were eaten
384	primarily by common carp, tench and rudd (Fig. 4C). Natural food sources combined contributed up
385	to 50% of the diet, in particular in bream and roach (Fig. 4D). To address the potential uncertainty in
386	the mixing models, we included a baseline fish with an isotopic signature, which reflected a pure
387	natural diet. The median contribution of natural food to this baseline fish was 74% (Digital Appendix
388	8H), whereas the calculated sum of contributions from angling baits was 26%, reflecting basic
389	uncertainty of the model. However, the median contribution of natural food was much higher, and
390	median contributions for all angling baits much lower in the baseline as compared to the seven fish
391	species (Fig. 4). By using the posterior distributions, we calculated the probabilities for the
392	differences in contributions of natural food and angling baits between the baseline and the seven fish
393	species. There was an average probability of near 1.0 that all fish species had eaten less natural food
394	than the baseline fish (Digital Appendix 9). In turn, the model suggested a high probability that the
395	seven species fed more fish mix boilies (average probability 0.926) and sweet mix boilies (average
396	probability 0.802) than the baseline fish (Digital Appendix 9). The model did not give clear evidence
397	for a stronger use of corn in the seven fish species in comparison to the baseline (average probability
398	0.405), but a strong signal was found for common carp (probability 0.996) (Digital Appendix 9).
399	To elucidate the uncertainty with respect to the assumption of equal use of the three natural food
400	sources by the fish, we ran the same mixing models with only one of the natural sources each. The

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2 3	401	potential composition of the natural food had strong effects on the results of the mixing models in
4 5	402	white bream and bream, whereas for the other fish species, the differences between the scenario
6 7	403	with a mix of natural food sources and the three scenarios with only one natural food source were
8 9 10	404	small to moderate (Digital Appendix 10).
11 12 13	405	
14 15 16	406	Growth rate effects
17 18 10	407	The older age classes of bream, white bream and pike had positive residuals from the population-
20 21	408	wide von Bertalanffy growth equation in spring 2015, whereas younger age classes tended to reveal
21 22 22	409	negative residuals (Digital Appendix 11). When examining the full linear model on the residual
25 24 25	410	variation, the main effects of year and TL were significant in all three species, but significant
25 26 27	411	interactions among year × TL were only revealed in the two omnivorous species bream and white
28 29	412	bream (Table 2). This suggests that older bream and white bream grew faster in 2014 until early 2015
30 31	413	during the feeding experiment than predicted from the population-wide von Bertalanffy growth
32 33	414	model estimated to data collected prior to feeding (Table 2). As the partial effect size plots show (Fig.
34 35	415	5), the slope of size effect on residuals was much steeper in 2014-2015 (after) compared to 2013-
36 37	416	2014 (before) in bream (Fig. 5A) and white bream (Fig. 5B), indicating that the larger conspecifics
38 39	417	achieved a size above average in spring 2015, six to nine months after bait addition. By contrast, the
40 41 42	418	size effect on residuals was similar in pike in the two study years and the interaction was non-
43 44	419	significant (Fig. 5C).
45 46 47	420	
48 49 50	421	Discussion
51 52	422	Our whole-lake experiment demonstrated that the addition of ground baits by recreational
53 54	423	cyprinid anglers caused a cascade of changes in the omnivorous fish community of the receiving lake.
55 56 57	424	Exemplified by position records of tagged common carp as a model species, the fish changed their
58 59 60		17

425	swimming behaviour and got attracted to the feeding sites. Angling catches revealed regular uptake
426	of bait by a range of cyprinid fishes, indicating active foraging on the feedstuffs. We also found the
427	added bait constituted a substantial proportion of the diet of all benthivorous and omnivorous fish
428	beyond certain size thresholds. Finally, the behavioral and diet changes induced higher annual
429	growth rates of the individual fish that preferentially used the bait. Angling baits thus significantly
430	subsidized omnivorous fish, but not piscivorous fish and invertebrates, despite a low contribution to
431	the lake C budget. Together these results suggest that the addition of human-derived ground bait by
432	anglers may change the structure and dynamics of lake fish communities, particularly of the
433	omnivorous feeding guilds, potentially accompanied by further, so far undocumented, consequences
434	for the entire lake ecosystem.
435	
436	Ground bait changed home range of large benthivorous and omnivorous fish
437	Our results obtained by fine-scale acoustic telemetry demonstrate an immediate behavioural
438	response of tagged common carp to the addition of bait and a strong attraction to the feeding sites.
439	Specifically, the carp spent more time at the feeding sites after bait had been added, and this
440	conditioning effect to feeding sites is also well known from pond aquaculture (Füllner, 2015). The
441	carp reduced their home range size substantially during the bait addition period, indicating that the
442	offered bait affected the food-search behaviour of the carp population at the lake scale. Carp can be
443	attracted rapidly to feed patches within days after the initiation of feeding (Bajer et al., 2010), for
444	example by olfaction and gustation from amino acids and other food attractants in the ground baits
445	(Kasumyan and Morsi, 1996) and by social learning (Bajer et al., 2010). Unfortunately, we have no
446	behavioural data for non-domesticated wild benthivorous fish for both the before and after periods,
447	but the home range behaviour of wild tench shown during feeding was similar to the behaviour of
448	carp and these fish also concentrated around the feeding spots. Furthermore, intense angling on the
449	feeding locations revealed that also other fish species were foraging on the added bait. We thus
450	tentatively conclude that the carp behaviour may represent the behaviour of other cyprinids,
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451 although it is possible that the large degree of domestication of carp resulted in this species being452 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 δ^{13} 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, δ^{13} 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 δ^{13} C values by feeding on those natural resources. For most of the fish species (except common carp and tench), the elevation in δ^{13} C values was stronger for larger individuals (as indicated by the significant positive interaction between fish length and δ^{13} 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, δ^{13} 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 δ^{13} 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 δ^{13} C was significant only for rudd. A similar effect of fish length on the uptake of angler baits has recently been reported in riverine barbel (Roberts et al., 2017).

474 Another reason for weaker δ^{13} C signals from ground bait in some individuals in autumn 2014 may 475 be found in the turnover time needed to assimilate the ¹³C-enhanced diet until equilibrium in the 476 muscle tissue of fish. The half-life of ¹³C in muscle tissue of adult fish is about three up to five months

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477	(Weidel et al., 2011), and hence only individuals, which started feeding on ground bait immediately
478	after the first introduction, may have achieved tissue equilibrium until the sampling in autumn 2014.
479	Accordingly, the contributions from ground baits to the fish diet calculated by mixing models may
480	even underestimate the true ingestion during the experimental phase. The piscivorous large perch
481	and pike served as a natural control for the effect of ground bait feeding on tissue $\delta^{13}\text{C}$, and we did
482	not find heavier δ^{13} C in these fishes and size classes. Accordingly, the predatory fish species as well as
483	the invertebrates neither directly (by feeding on added bait) nor indirectly (by feeding on prey, which
484	has fed upon bait) ingested the C from corn or boilies in the time frame of three months of our study.
485	
486	Ground bait substantially contributed to fish diet and enhanced fish growth rates
487	The mixing models indicated that for the fish individuals beyond a species-specific size threshold.

4 488 the contribution from the added bait particles to their diet was substantial. There was a very clear signal of the distinct δ^{13} C value of corn (attributable to its C₄ photosynthetic pathway) in common 489 490 carp. Therefore, terrestrial subsidy to aquatic food webs and vice versa can be traced in animal 491 tissues after addition of corn compounds (Scharnweber et al., 2014a; Scharnweber et al., 2014b). The 492 heavy reliance on corn by carp can be explained by the greater amylase activities in the intestine of 493 carp compared to other cyprinids such as tench (Hidalgo et al., 1999), which is decisive to break 494 down the starch in corn. Furthermore, there was strong evidence of feeding upon fish mix boilies by 495 some large bream and white bream, as indicated by their elevated δ^{15} N values after bait addition. A similar tracing of fish meal and oil from fishmeal pellets used as angling bait has been demonstrated 496 497 recently for barbel and chub (Squalius cephalus) in English rivers (Roberts et al., 2017). In contrast, 498 the sweet food mix was preferentially ingested by tench, carp and rudd, confirming earlier studies 499 that the common cyprinid species have differing preferences for certain types of angling bait 500 (Specziar et al., 1997). It is possible that these three species have better ability to break down 501 carbohydrates than the other cyprinids, which may have contributed to the larger fraction of both 502 corn and sweet mix boilies in tench, carp and rudd.

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2 3	503	In Döllnsee, the three bait particles contributed substantially to the diet of the omnivorous and
4 5	504	benthivorous fish species in the lake. A similarly strong reliance of barbel and chub on fishmeal
6 7 8	505	pellets has been shown in experiments where a mix of natural and artificial food was offered
9 10	506	(Roberts et al., 2017). We do not rely too strongly on the medians of the posterior distributions from
11 12	507	each of the bait types in the Bayesian mixing models, because the distributions were often flat and
13 14	508	hence had substantial uncertainty. However, the intermediate position of all fish in the isospace
15 16	509	(Digital Appendix 7) and the uncertainty analyses of the model (Table 2, Digital Appendices 9, 10)
17 18	510	suggest that the angler baits must have contributed at least to some extent to the diet of all species.
19 20 21	511	We showed that the individual growth rates of bream and white bream were enhanced in the
22 23	512	feeding year compared with the previous non-feeding year, in particular for larger individuals of both
24 25	513	species. In contrast, we did not find a similar growth response in the piscivorous pike. These results
26 27	514	suggest that the higher growth rates are at least partly attributable to the uptake of added bait. Corn
28 29	515	and other cereals have been used traditionally in pond aquaculture because the addition of
30 31 32	516	carbohydrates bound in cereals increases carp production substantially (Kestemont, 1995; Füllner,
33 34	517	2015). The main mechanisms by which supplementary feeding with corn elevates pond production of
35 36	518	fishes relates to the more efficient use of essential macro- und micronutrients from natural food and
37 38	519	the delayed depletion of natural food towards the end of the summer growing season (Füllner, 2015;
39 40	520	Hlavac et al., 2016). The growth rates of carp achievable by feeding upon boilies were even higher
41 42	521	than those achieved by feeding on seed particles like corn, indicating that different feedstuffs used
43 44	522	by anglers have different nutritional value to the fish (Niesar et al., 2004). However, the energy
45 46	523	density of the ground bait is comparable to that of natural animal food (about 20 kJ g ⁻¹ dry mass)
47 48	524	(Niesar et al., 2004), suggesting that ground baits are energetically not superior to natural food.
49 50	525	Moreover, if natural food of the same dry matter amount is given to carp compared to the same dry
51 52	526	matter of angling baits such as boilies, the growth on natural food is larger (Niesar et al., 2004).
55 54	527	However, natural food is often limited in natural ecosystems, particularly towards the end of the
55 56 57	528	growing season and the readily available angling bait can be found and ingested easily and provides a
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529	compact form of energy and nutrients that likely demands much less food search activity and sorting
530	than feeding on natural macrozoobenthos. Therefore, the nutrients bound in baits and the energy
531	supply seems to come on top of what an ecosystem naturally offers, and the accelerated growth
532	rates found in our experiment are indicative of a subsidy above the natural animal production,
533	similar to findings from the substantial increase of production in food-supplemented pond
534	aquaculture with cyprinids (Kestemont, 1995; Füllner, 2015). The ground baiting-induced increase in
535	growth is facilitated by the high digestibility of macronutrients from all ground baits, even of corn for
536	carp (Arlinghaus and Niesar, 2005), the reduction in energy needed for food search and feeding when
537	angling baits are available on predictable food patches, and very likely the more efficient use of
538	natural food similar to the case in pond aquaculture (Füllner, 2015).
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540	Can ground bait additions subsidize fish?
541	A surprising result is the discrepancy between the strong effects of ground bait addition on the
542	omnivorous fish and the modest contribution of these baits to the C budget of the lake. Organic C
543	budgets in eutrophic lakes are dominated by autochthonous primary production (Carpenter et al.,
544	2005; Brothers et al., 2013b). Consequently, additions of terrestrial particulate organic matter could
545	be traced in eutrophic aquatic food webs (Bartels et al., 2012; Scharnweber et al., 2014a), but had
546	little effects on consumer production and biomass (Mehner et al., 2016). In our previous whole-lake
547	experiments, we added maize leaves to the treatment halves of two divided lakes (about 25 g C m $^{-2}$)
548	accounting for only <10% of the C fixed by annual PPr in the lakes, making a weak effect on
549	secondary production plausible (Mehner et al., 2016). In the current experiment, angler baits
550	containing mainly terrestrial-plant derived material added even less than 1% to the estimated annual
551	net PPr, but induced high diet contributions and enhanced growth rates in fish, suggesting a
552	substantial subsidy effect. The allochthonous C was offered at high concentrations, at predictable
553	locations over long time spans of several months, and was bound in relatively large, easily accessible
554	particles with energy densities similar to the naturally available food, such as zooplankton or benthic
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2 3	555	macroinvertebrates. Subsidy by high-quality resources often shifts the diet preferences of consumers
4 5 6	556	towards the subsidy, and hence can have strong production effects (Marczak et al., 2007; Marcarelli
7 8	557	et al., 2011). Furthermore, in contrast to terrestrial particulate or dissolved organic C inputs entering
8 9 10	558	higher trophic levels via the microbial loop or benthic shortcuts (Attermeyer et al., 2013), the bait
10 11 12	559	particles can be considered prey supplied directly to fish consumers, similar to the allochthonous
13 14	560	natural prey subsidizing aquatic food webs (Mehner et al., 2005; Milardi et al., 2016). Indeed, added
15 16	561	baits were in the same order of magnitude as biomass (1 g C m $^{-2}$) and production of
17 18	562	macrozoobenthos (1 to 2 g C m ⁻² y ⁻¹) in lakes of similar morphometry and trophic state in this region
19 20	563	(Brauns et al., 2011; Lischke et al., 2017). From that perspective, the strong effects found in our study
21 22	564	can be compared to those of pulsed subsidies on the structure and dynamics of aquatic consumer
23 24	565	populations (Nowlin et al., 2008; Trebilco et al., 2016).
25 26		
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29 30	567	Conclusions
31 32	568	Ground baiting with mainly terrestrial plant-derived organic matter by recreational cyprinid
33 34	569	anglers has strong subsidy effects on a major component of a fish community, particularly on
35 36	570	omnivorous species, in eutrophic lakes despite high internal primary production. The shift in diet
37 38	571	composition and increased growth rates in fish detected in our study may eventually elevate fish
39 40	572	production and thus the carrying capacity of the aquatic systems to fish consumers, similar to the
41 42	573	case previously documented in feed-enhanced pond aquaculture with cyprinid fishes. Thus, longer-
43 44 45	574	term subsidy may result in higher biomasses of consumer populations (Trebilco et al., 2016) and
43 46 47	575	decouple predator-prey relationships (Rodewald et al., 2011). We confined our analysis to freshwater
48 49	576	cyprinid angling, but ground baiting and the addition of feed to attract fish is also commonplace e.g.
50 51	577	in coastal angling. Thus, our work can be considered as a motivation to further study the response of
52 53	578	consumers and entire ecosystems to the subsidy effect of angling-induced feed introduction over
54 55	579	longer time frames than completed in our experiment.
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58	86	study design, data collection and analysis, decision to publish, or preparation of the manuscript. The
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58	88	responsible State Animal Welfare and Animal Experimentation Agency (Landesamt fur Umwelt,
58	39	Gesundheit und Verbraucherschutz) in Brandenburg, Germany (project reference 2347-21-2014)
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Table 1: Statistical comparisons of δ^{13} 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 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 δ^{13} C or the interaction between TL and period on δ^{13} C were significant (ANCOVA), and therefore the comparison of groups may include differences of both intercept and slope.

Group	Test	Test statistics	Р	post-hoc test	Group differences	Р
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< td=""><td><0.0001</td></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< td=""><td>0.047</td></aut14<>	0.047
Carp	ANOVA	F _{1,24} =40.7	<0.0001	Tukey HSD	Sum14 <aut14< td=""><td>< 0.0001</td></aut14<>	< 0.0001
Tench	ANOVA	F _{2,26} =9.36	0.0008	Tukey HSD	Aut13 <aut14< td=""><td>0.03</td></aut14<>	0.03
					Sum14 <aut14< td=""><td>0.003</td></aut14<>	0.003
White bream	ANCOVA	F _{5,60} =25.2	<0.0001	Slope with TL	Aut13 <aut14< td=""><td>0.007</td></aut14<>	0.007
Bream	ANCOVA	F _{5,56} =9.58	<0.0001	Intercept with TL	Aut13>Aut14	0.0001
				Slope with TL	Aut13 <aut14< td=""><td>0.0003</td></aut14<>	0.0003
Rudd	ANCOVA	F _{5,51} =10.2	<0.0001	Slope with TL	Aut13 <aut14< td=""><td>0.003</td></aut14<>	0.003
Roach	ANCOVA	F _{5,111} =12.9	<0.0001	Intercept with TL	Aut13>Aut14	0.004
				Slope with TL	Aut13 <aut14< td=""><td><0.0001</td></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< td=""><td>0.0001</td></aut14<>	0.0001
				Intercept with TL	Sum14 <aut14< td=""><td><0.0001</td></aut14<>	<0.0001
				Slope with TL	Sum14>Aut14	0.0004

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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. The partial effects of the size × 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.

	df	F	р	В	S.E.	t	р
Bream, Adj.R ² =0.437	1						
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
White bream, Adj. R	²=0.227						
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
Pike, Adj. R²=0.300							
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 5 7 6	0 1 1 3				

3	763	Captions of figures
4 5	764	Figure 1: Boxplot of the mean daily percentages of time spent within 15 m of feeding sites for 22
6 7	765	individual carp before and during bait addition (A). Thick bars represent the median and whiskers
8	766	represent 1.5 times the interquartile range, and outliers are represented by points. Home ranges of
9 10	767	carp before (B) and during (C) bait addition. The black outline represents the shoreline of Döllnsee.
10	768	Shaded areas from lightest to darkest show the 50%, 25% and 5% carp home range areas
12 13 14	769	respectively. Locations of the eight feeding sites are shown by crosses.
15	770	Figure 2: Boxplots (median, box=25% and 75% percentiles, whiskers 10% and 90% percentiles,
16 17	771	dots=outliers) of δ^{13} C (‰) of natural resources (A) zooplankton, (B) benthic insect larvae, (C) zebra
18	772	mussels and (D) crayfish in Lake Döllnsee. Samples were taken in autumn 2013 and summer 2014
19 20 21	773	(both before bait addition) and in autumn 2014 (after bait addition).
22	774	Figure 3: Least squares means (blue dots, corrected for differing fish lengths between the three
23 24	775	sampling periods) of δ^{13} C of eight fish species (A) common carp, B) tench, C) white bream, D) bream,
25 26	776	E) rudd, F) roach, G) pike, H) perch) during the three sampling periods (autumn 2013, summer 2014:
20	777	before bait addition; autumn 2014: after bait addition) (no values available for carp, Before(Aut13)).
28 29	778	The blue lines indicate the 95% confidence intervals, non-overlapping red arrows between sampling
30	779	periods denote significant differences in δ^{13} C (not corrected for potential interactions between δ^{13} C
31 32 33	780	and fish length, see Table 1).
34	781	Figure 4: Posterior distributions of contribution of corn (A), fish mix boilie (B), sweet mix boilie (C),
35 36	782	and Natural Food (zooplankton, zebra mussels and insect larvae/Isopoda combined) (D) to the diet of
37	783	the seven fish species, as estimated from stable isotope values (δ^{13} C, δ^{15} N) by Bayesian mixing
38 39	784	models. As baseline, we provide the results of the same mixing model for a fish, which has fed
40	785	exclusively on natural food. The boxes represent the interquartile range (25 th and 75 th percentile),
41	786	and whiskers represent 1.5 times the interquartile range distant from the box. Dots are outlying
43 44	787	points, and represent the full range of solutions of the Byesian model. For detailed density plots, see
45	788	Digital Appendix 8.
46 47		
48	789	Figure 5: The partial effect sizes of the interactions of year and total length (mm) on the residuals
49 50	790	from the population level von Bertalanffy equation in 2014 and 2015 in bream (A), white bream (B)
51	791	and pike (C) from Döllnsee.
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Ecosystems



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.



(both before bait addition) and in autumn 2014 (after bait addition).



818 and fish length, see Table 1).



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 (δ^{13} C, δ^{15} 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 Byesian model. For detailed density plots, see **Digital Appendix 8.**

