

This is a self-archived version of an original article. This version may differ from the original in pagination and typographic details.

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

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

Year: 2019

Version: Accepted version (Final draft)

Copyright: © Springer Science+Business Media, LLC, part of Springer Nature 2018

Rights: In Copyright

Rights url: <http://rightsstatements.org/page/InC/1.0/?language=en>

Please cite the original version:

Mehner, T., Rapp, T., Monk, C. T., Beck, M. E., Trudeau, A., Kiljunen, M., Hilt, S., & Arlinghaus, R. (2019). Feeding Aquatic Ecosystems : Whole-Lake Experimental Addition of Angler's Ground Bait Strongly Affects Omnivorous Fish Despite Low Contribution to Lake Carbon Budget. *Ecosystems*, 22(2), 346-362. <https://doi.org/10.1007/s10021-018-0273-x>



Feeding aquatic ecosystems: whole-lake experimental addition of angler's ground bait strongly affects omnivorous fish despite low contribution to lake carbon budget

Journal:	<i>Ecosystems</i>
Manuscript ID	ECO-17-0378.R2
Types:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Mehner, Thomas; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Biology and Ecology of Fishes Rapp, Tobias; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Biology and Ecology of Fishes Monk, Christopher; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Biology and Ecology of Fishes Beck, Mara; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Biology and Ecology of Fishes Trudeau, Ashley; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Biology and Ecology of Fishes Kiljunen, Mikko; University of Jyväskylä, Department of Biological and Environmental Science Hilt, Sabine; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Limnology of Shallow Lakes Arlinghaus, Robert; Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Biology and Ecology of Fishes; Humboldt-Universität zu Berlin, Division of Integrative Fisheries Management, Faculty of Life Sciences
Key Words:	subsidy, human-derived food, stable isotopes, fish behaviour, fish growth, eutrophic lake

1
2
3 1
4
5 2 **Feeding aquatic ecosystems: whole-lake experimental addition of angler's**
6 3 **ground bait strongly affects omnivorous fish despite low contribution to lake**
7 4 **carbon budget**
8
9

10 5
11 6
12
13
14 7 Thomas Mehner^{1,*}, Tobias Rapp¹, Christopher T. Monk¹, Mara E. Beck¹, Ashley Trudeau¹,
15 8 Mikko Kiljunen³, Sabine Hilt¹, Robert Arlinghaus^{1,2}
16 9
17 10

18
19
20
21
22 11 ¹ Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin,
23 12 Germany

24
25 13 ² Division of Integrative Fisheries Management, Faculty of Life Sciences, Humboldt Universität zu
26 14 Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany

27
28 15 ³ University of Jyväskylä, Department of Biological and Environmental Science, PO Box 35, FI-40014
29 16 University of Jyväskylä, Finland

30
31
32 17 * Contact: mehner@igb-berlin.de
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

1
2
3 18 **Abstract**
4

5 19 It is well documented that aquatic ecosystems may be subsidized by naturally-derived terrestrial
6
7 20 carbon sources. In contrast, the intentional or unintentional subsidy of animal populations by
8
9 21 human-derived feed resources and their ecosystem effects are poorly studied. We added ground
10
11 22 baits of the type, amount and temporal duration commonly applied by anglers targeting cyprinid
12
13 23 fishes to a small lake, and studied behaviour, diet composition and annual growth rate of the lake
14
15 24 fish community in response to the bait addition. Based on recordings by a high-resolution ultrasonic
16
17 25 telemetry array, common carp (*Cyprinus carpio*) as a model benthivore spend more time at the sites
18
19 26 where ground baits were added, and they significantly reduced their home range relative to the
20
21 27 period before bait addition. Furthermore, many omnivorous cyprinid fish species were regularly
22
23 28 caught by angling at the feeding sites, indicating active ingestion of the artificially added food items.
24
25 29 Stable isotope analyses of ^{13}C and ^{15}N showed that in particular larger specimens of common carp,
26
27 30 bream (*Abramis brama*), white bream (*Blicca bjoerkna*), tench (*Tinca tinca*), roach (*Rutilus rutilus*)
28
29 31 and rudd (*Scardinius erythrophthalmus*) included substantial amounts of angler baits into their diet.
30
31 32 There was also a significant acceleration of growth in bream and white bream after bait addition,
32
33 33 most likely attributable to the energetic benefits from bait addition. In contrast, there was no
34
35 34 response in annual growth rate in top predators, suggesting they did not benefit from the subsidy.
36
37 35 The amount of carbon introduced was very low (about 1%) relative to an estimate of in-lake C
38
39 36 fixation by autotrophs. However, if the C added by bait was compared with the coarsely estimated
40
41 37 secondary production of benthic macroinvertebrates in the lake, the C available to benthivorous and
42
43 38 omnivorous fishes was comparable between natural resources and angler baits. We conclude that
44
45 39 human-derived feed resources associated with recreational fishing may constitute a substantial
46
47 40 subsidy to omnivorous fishes in lakes, in particular if the food is provided in form of particles, which
48
49 41 are readily accessible and found at repeatable feeding places and over sufficiently long time periods
50
51 42 during a year. The long-term consequences for the receiving ecosystems still have to be elucidated.
52
53
54
55
56

57 43 **Key words:** subsidy, human-derived food, stable isotopes, fish behaviour, fish growth
58
59
60

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).

65 Anthropogenic feed resources of high nutritional quality and energetic density likewise subsidize
66 consumers in all types of ecosystems as a consequence of world-wide increase in human population
67 density, recreational use of natural ecosystem, aquaculture and global economic development (Oro
68 et al., 2013). Humans intentionally or unintentionally dispose waste, food remains, crop residuals and
69 animal carcasses into the environment, providing a predictable resource to animal populations with

1
2
3 70 effects on food-web interactions and ecosystem processes (Oro et al., 2013). Examples for high-
4
5 71 quality human subsidy of aquatic ecosystems are food remains from open-water fish farms (Grey et
6
7 72 al., 2004; Wang et al., 2018), waste from landfills supporting the diet of sea birds (Osterback et al.,
8
9 73 2015), or the intentional feeding of aquatic organisms, such as water birds, by recreationists, in
10
11 74 particular in urban habitats (Oro et al., 2013).

12
13
14 75 Another specific form of intentional human subsidy of aquatic systems is the application of
15
16 76 ground bait by recreational coarse (i.e. non salmonid) freshwater anglers. Ground baiting is common
17
18 77 practice in freshwater recreational fisheries for cyprinid fishes all over Europe (Wolos et al., 1992;
19
20 78 Arlinghaus and Mehner, 2003; Amaral et al., 2013; Roberts et al., 2017), and is increasingly used
21
22 79 beyond Europe (e.g., North America or South Africa) where specialized angling for large cyprinids
23
24 80 such as common carp (*Cyprinus carpio*) is becoming locally fashionable. Recreational angling for
25
26 81 cyprinids is often based on the introduction of ground bait for several days prior to and during the
27
28 82 fishing day to attract the fish on the fishing sites (Wolos et al., 1992; Arlinghaus and Mehner, 2003).
29
30
31 83 In Europe, specialized common carp and barbel (*Barbus barbus*) anglers regularly apply more than 1
32
33 84 kg of ground bait per day, usually in form of food particles (corn, pellets, boilies - a special carp bait)
34
35 85 (Arlinghaus, 2004; Niesar et al., 2004; Basic and Britton, 2015). However, ground baiting is also
36
37 86 standard practice in competitive fishing for small-bodied cyprinids such as roach (*Rutilus rutilus*)
38
39 87 (Amaral et al., 2013). The average annual dispersal of ground baits per freshwater angler in Germany
40
41 88 was estimated to be 7.3 kg (Arlinghaus, 2004), which easily scales to several thousand tons of ground
42
43 89 bait introduced to aquatic ecosystems by about 3.3 million anglers in Germany alone. These
44
45 90 considerable volumes of angler baits and their high nutritional quality evidenced by very high
46
47 91 digestibility of all classes of macronutrients (protein, lipids, carbohydrates) (Arlinghaus and Niesar,
48
49 92 2005) and positive growth responses in laboratory experiments with common carp (Niesar et al.,
50
51 93 2004) may form a relevant direct subsidy to benthivorous and omnivorous fish in lakes and rivers
52
53 94 exposed to high use-intensity by recreational coarse anglers. Some individuals of the benthivorous
54
55 95 cyprinid barbel in rivers indeed expressed a strong preference for the angler ground bait relative to
56
57
58
59
60

1
2
3 96 natural food, as indicated by shifts in the population isotopic niches (Basic and Britton, 2015; Roberts
4
5 97 et al., 2017). However, these studies were inconclusive with respect to a mechanistic understanding
6
7 98 of the consequences of subsidizing a fish community by ground bait. In particular, studies testing
8
9 99 whether benthivorous fish are behaviorally attracted by the baits and benefit from their ingestion by
10
11 100 accelerated growth are lacking. It is also unknown whether the anthropogenic subsidy affects top
12
13 101 predators that are unlikely to feed directly on the angler bait. Importantly, for a quantitative
14
15 102 evaluation of the effect of bait additions on the lake ecosystem, a comparison of C loads from baits
16
17 103 relative to in-lake C fixation by autotrophs (Mehner et al., 2016) and to production by primary
18
19 104 consumers is needed.

21
22 105 We performed a whole-lake experiment in an eutrophic lake to test for a chain-of-action response
23
24 106 of a fish community to an intentional addition of resources, by providing ground baits of the type,
25
26 107 amount and temporal duration commonly applied by specialized cyprinid anglers. We used a fine-
27
28 108 scale acoustic telemetry system (Baktoft et al., 2015), which facilitated studying the individual
29
30 109 behaviour of common carp as a model cyprinid fish species as well as tench (*Tinca tinca*) in response
31
32 110 to subsidized feeding. Furthermore, we applied stable isotope analyses to compare the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$
33
34 111 signatures of several benthivorous/omnivorous and piscivorous fish species, before and after bait
35
36 112 addition, to estimate the proportion of baits in their diet composition. Finally, we measured the
37
38 113 annual growth rates of a sample of cyprinid and top predatory species to elucidate whether there
39
40 114 was a discernible effect of ground-bait ingestion on the individual growth rates of fishes, serving as
41
42 115 an indicator of a potential contribution of bait to secondary production. We hypothesized that even
43
44 116 modest amounts of ground bait introduced to a lake ecosystem would generate substantial changes
45
46 117 within the benthivorous and omnivorous fish community. We expect this because ground bait is of
47
48 118 high nutritional quality, provided continuously during the growing season and not accessible by other
49
50 119 consumers than large cyprinid fish. Ground bait additions could thus significantly modify behaviour,
51
52 120 diet composition and growth of fish. Specifically, we predicted that (i) introduced ground bait attracts
53
54 121 fish to spend more time on the feeding sites, (ii) stable isotopes reflect strong contributions of
55
56
57
58
59
60

1
2
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
9 125 despite its low share in C loading relative to high C fixation in the eutrophic lake.
10
11
12 126

13 14 15 127 **Methods**

16 17 18 128 *Study lake and subsidy experiment*

19
20 129 Lake Kleiner Döllnsee (subsequently referred to as Döllnsee, 52°99'N, 13°58'E) is situated about
21
22 130 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
23
24 131 stratified and eutrophic with a total phosphorus (TP) concentration of about 50 mg m⁻³ (arithmetic
25
26 132 average of 12 monthly samples from the epilimnion in 2014), resulting in an average Secchi depth of
27
28 133 2.1 m. The shoreline is characterized by a dense reed (*Phragmites* spp., *Typha* spp.) belt; sparse
29
30 134 patches of submerged macrophytes cover the littoral and sub-littoral zones. The fish community
31
32 135 consists mainly of benthivorous or omnivorous species, namely cyprinids (roach, rudd *Scardinius*
33
34 136 *erythrophthalmus*, bream *Abramis brama*, white bream *Blicca bjoerkna*, bleak *Alburnus alburnus*,
35
36 137 tench, crucian carp *Carassius carassius*, and stocked common carp) and the percid species ruffe
37
38 138 (*Gymnocephalus cernuus*). Naturally occurring facultative piscivorous species are perch (*Perca*
39
40 139 *fluviatilis*) and pike (*Esox lucius*), whereas European catfish (*Silurus glanis*), eel (*Anguilla anguilla*) and
41
42 140 zander (*Sander lucioperca*) have been stocked and occur in low numbers.
43
44
45

46 141 Between July and October 2014, a total of 750 kg dry mass of soaked and cooked corn (*Zea mays*),
47
48 142 reflecting the typical bait preparation by specialized cyprinid anglers targeting carp, tench or large
49
50 143 bream, was introduced on eight sub-littoral feeding sites that were equally spaced around the
51
52 144 shoreline. Corn was introduced twice daily during four days per week. Furthermore, 189 kg of fish
53
54 145 mix boilies and 89 kg of sweet mix boilies were introduced together with corn. Boilies are specially
55
56 146 designed boiled paste balls commonly used in carp, tench and increasingly large bream fishing, and
57
58
59
60

1
2
3 147 are typically mixed with cereals such as corn as ground baits (Niesar et al., 2004). For more
4
5 148 information on boilie composition, see Digital Appendix 1.
6
7

8 149 The amount of corn and boilies introduced to the lake corresponded to the yearly bait addition of
9
10 150 about five highly specialized carp anglers, each using about 215 kg bait per year (Niesar et al., 2004).
11
12 151 Other anthropogenic subsidies beyond the controlled corn and boilie introductions during the study
13
14 152 period can be excluded because there are no commercial or recreational fisheries on the lake, and
15
16 153 public access to Döllnsee is blocked. According to P contents of bait types determined earlier (Niesar
17
18 154 et al., 2004), the corn and boilie addition contributed about 15.4% (18.6 mg P m^{-2} during the
19
20 155 experimental period) to the P budget relative to the critical P load (Vollenweider, 1976) of the lake
21
22 156 ($120 \text{ mg P m}^{-2} \text{ y}^{-1}$), which was calculated similarly as in Mehner et al. (2007). Therefore, a substantial
23
24 157 eutrophication effect by the experimental bait addition was not expected. The contribution of C to
25
26 158 the lake C budget by corn and boilie addition (about 1.5 g C m^{-2} during the experimental period) was
27
28 159 estimated to be low relative to in-lake primary production (PPr) by phytoplankton and vascular
29
30 160 plants. Two morphologically similar small lakes with comparable total P concentrations of 35-50 mg
31
32 161 m^{-3} situated close (<30 km) to Döllnsee had PPr values between 260 and $350 \text{ g C m}^{-2} \text{ y}^{-1}$ (Brothers et
33
34 162 al., 2013a; Mehner et al., 2016). Assuming a PPr of about $300 \text{ g C m}^{-2} \text{ y}^{-1}$ suggests that the ground bait
35
36 163 contributed less than 1% to the C budget of Döllnsee.
37
38
39

40 164 *Behavioral observation of fish*

41
42

43 165 As a model cyprinids, we tracked 91 common carp (total length: 40.6-72.2 cm; wet weight: 945-
44
45 166 6934 g), released in June 2014 (Monk and Arlinghaus, 2017) prior to the bait addition with a high-
46
47 167 resolution, whole-lake acoustic telemetry system to study whether fish were preferentially using the
48
49 168 eight feeding sites. The fine-scale acoustic telemetry system records 3D positions of fish at a high
50
51 169 resolution and accuracy (5 m average error) at the scale of the whole lake (Baktoft et al., 2015).
52
53 170 Common carp were hatchery-raised and spent their life in earthen ponds surviving on natural food
54
55 171 supplemented by formulated pellet feed. Acoustic transmitters were surgically implanted into carp
56
57
58
59
60

1
2
3 172 body cavities following earlier protocols (Kobler et al., 2009; Hühn et al., 2014). We anaesthetized
4
5 173 carp with a 9:1 EtOH:clove oil solution added in water at 1 mL L⁻¹. Surgical tools and transmitters
6
7 174 were sterilized with 7.5% povidone-iodine mixed in water, and each fish received four to five sutures
8
9 175 using PDS-II adsorbable monofilament suture material and FS-1 3-0 needles (Ethicon, USA). We also
10
11 176 inserted a passive integrated transponder (PIT) tag (23 mm length, Oregon RFID, OR USA) into the
12
13 177 body cavity during surgeries for later identification upon recapture. Tagged carp were released into
14
15 178 Döllnsee following recovery from surgery.

179 The carp experienced high tag loss (Monk and Arlinghaus, 2017), and therefore we focused our
180 analysis on 22 individuals that retained the tags and generated behavioral data from tagging until the
181 end of the bait additions (24-25 days before feeding and 79 to 108 days during feeding). We
182 evaluated whether carp increased their presence at those littoral sites at which ground bait was
183 added (feeding sites) in comparison with the presence before bait addition. We considered a carp to
184 be present at a feeding site when positions were within 5, 15 or 30 m of a feeding site. Total time at
185 feeding sites was summed daily. If a carp was detected at a feeding site and then there was a long
186 period without a new detection, 335 seconds were added to the feeding time. The reason is that
187 after 335 seconds there is near certainty that the fish has left the last position based on known
188 detection probabilities of fixed beacon transmitters (Monk and Arlinghaus, 2017). We compared the
189 average percentage of each day present at a feeding site before and during the bait addition for each
190 carp with a paired t-test. To compare space usage, we calculated the collective home range of the 22
191 individual carp before and during feeding. Specifically, the areas of the 5%, 25% and 50% kernel
192 utilization densities were calculated based on a 200 by 104 cell grid representing the lake, with a cell
193 size of 5.78 m and a 10 m smoothing parameter in R using the adehabitatHR package (Calenge,
194 2011). Besides carp, we also tagged a sample of wild captured tench (Monk and Arlinghaus, 2017),
195 but we lacked data from the period before the bait introduction and hence present the data after
196 bait introduction in the supplement. Subsequently, angling pressure was applied at four of the eight
197 designated feeding sites at equal spacing around the shoreline, four days per week between August

1
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
7 200 use of feeding sites as opposed to other sites, but rather as source of information on whether the
8
9 201 fish indeed ingested the feedstuffs. More details of the angling can be found in Digital Appendix 1.
10

11
12 202

13
14
15 203 *Stable isotope analyses of natural resources and fish*

16
17 204 To estimate the contributions of ground bait to the diet of fish, stable isotope (SI) values ($\delta^{13}\text{C}$ and
18
19 205 $\delta^{15}\text{N}$) of ground bait as well as natural resources (zooplankton and benthic invertebrates) and fish
20
21 206 (benthivorous/omnivorous and piscivorous fish) were measured twice before bait addition (autumn
22
23 207 2013, summer 2014) and once after bait addition (autumn 2014). This sampling scheme takes the
24
25 208 seasonality of SI values into account and hence facilitates the comparison of SI values before and
26
27 209 after feed addition in autumn (2013 vs. 2014) and the direct before-after comparison of SI values in
28
29 210 response to feed addition (summer 2014 vs. autumn 2014). For more details of sampling, see Digital
30
31 211 Appendix 1.
32
33
34

35 212 A total of 749 samples for SI analysis were processed, including broad size ranges of fish (Digital
36
37 213 Appendix 2). Samples were dried at 60°C for 48 h to constant weight, and subsequently ground with
38
39 214 mortar and pestle into a fine powder. For analysis, 0.6 (\pm 0.1) mg of animal tissue was weighed into
40
41 215 tin capsules. Stable isotopes analyses were conducted using a Finnigan DELTA_{plus} Advantage mass
42
43 216 spectrometer (Thermo Fisher Scientific Corporation, Waltham, MA, U.S.A.) coupled to a FlashEA 1112
44
45 217 elemental analyser at the University of Jyväskylä, Finland. Stable nitrogen and carbon ratios are
46
47 218 expressed as delta values ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) relative to the international standards for
48
49 219 nitrogen (atmospheric nitrogen) and carbon (Vienna PeeDeeBelemnite). Analytical precision was
50
51 220 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
52
53 221 analysis of working standards (pike white muscle tissue, birch leaves and *Spirulina* spp.) inserted in
54
55 222 each run after every five samples.
56
57
58
59
60

1
2
3 223 *Statistical comparisons and mixing models*
4

5 224 To test for potential elevations of C stable isotope value after bait addition, we compared $\delta^{13}\text{C}$
6
7 225 values of natural resources between the three sampling periods by ANOVA and Tukey HSD post-hoc
8
9 226 tests. In cases when the data did not meet the assumptions for parametric tests, we applied Kruskal-
10
11 227 Wallis tests with Nemenyi post-hoc tests. For comparison of $\delta^{13}\text{C}$ values of fish between the sampling
12
13 228 periods, we applied ANCOVA, with total length of fish added as covariate. Fish length had to be
14
15 229 included because corn and boilies are particles usually not accessible to smaller fishes because of
16
17 230 gape limitation and due to the hard texture, and hence we expected strong effects only for fish > 10
18
19 231 cm length. We first calculated the full ANCOVA model including the interaction between sampling
20
21 232 period and fish length, but removed non-significant interaction terms from the full model. We
22
23 233 plotted the least squares means of $\delta^{13}\text{C}$ for the three sampling periods, which take into account the
24
25 234 variable lengths of fish in the sampling periods. For species for which the interaction between
26
27 235 sampling period and fish length was significant, we tested whether there were significant differences
28
29 236 of intercepts and slopes between autumn 2014 (after bait addition) and either autumn 2013 or
30
31 237 summer 2014 (both before bait addition). Higher intercepts after than before bait addition would
32
33 238 suggest that all individuals of this species independent of length have included ground bait. Higher
34
35 239 slopes in the period after bait addition would suggest that in particular larger (positive slope) or
36
37 240 smaller (negative slope) individuals have ingested added food. All calculations were done in R 3.3.2 (R
38
39 241 Development Core Team, 2016).
40
41
42
43

44 242 To calculate the proportion of corn and boilies in the diets of those fish species, which showed
45
46 243 elevated $\delta^{13}\text{C}$ values after bait addition, we used Bayesian stable isotope mixing models as
47
48 244 implemented in the *simmr* package (Parnell, 2017) in R 3.3. Bayesian mixing provides posterior
49
50 245 probability distributions instead of single point estimates of source contributions. Therefore, we
51
52 246 always show the full posterior distributions, and provide all estimates with their Bayesian credibility
53
54 247 intervals, which can be considered equivalent to the confidence intervals of frequentist's statistics.
55
56 248 Prior to mixing model analysis, we visually inspected whether preconditions of the model, i.e. a valid
57
58
59
60

1
2
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 ± 1.3 for $\delta^{13}\text{C}$ and 3.4 ± 1.0 for $\delta^{15}\text{N}$ (Post,
6
7 251 2002) and concentration dependence (Phillips and Koch, 2002). Initially we included zooplankton,
8
9 252 zebra mussels and benthic macroinvertebrates (larvae of Chironomidae, Ephemeroptera,
10
11 253 Trichoptera, Odonata, and Isopoda mixed because of similar isotopic signatures) as potential natural
12
13 254 sources of the diet of benthivorous or omnivorous fish. Furthermore, we considered corn, fish mix
14
15 255 boilies and sweet mix boilies separately as artificially added potential food sources (Digital Appendix
16
17 256 3). The artificial food sources could not be combined because of their distinctly separate $\delta^{13}\text{C}$ and
18
19 257 $\delta^{15}\text{N}$ values. However, to reduce the uncertainty in the mixing model output, we combined a priori
20
21 258 zooplankton, insect larvae and zebra mussels into a single category 'Natural Food'. This was justified
22
23 259 because the $\delta^{15}\text{N}$ values did not differ between these groups (ANOVA $F_{2,83}=1.01$, $p=0.37$), but $\delta^{13}\text{C}$
24
25 260 differed between the natural resource groups (ANOVA $F_{2,83}=74.1$, $p<0.0001$).

26
27
28
29 261 To address the potential uncertainty in the mixing model with four remaining sources and two
30
31 262 tracers, we included a hypothetical baseline fish with an isotopic signature, which reflected a pure
32
33 263 natural diet, and evaluated the contribution of ground bait to this baseline fish. By using the
34
35 264 posterior distributions, we calculated the probabilities for the differences in contributions of natural
36
37 265 food and angling baits between the baseline and the seven fish species, as based on 1000 repetitions
38
39 266 of the Bayesian mixing model. We did not analyze stomach or gut content from the fish in Döllnsee,
40
41 267 and hence we assumed equal contributions of the three natural sources to the diet of fish. However,
42
43 268 to reflect the uncertainty introduced by this assumption, we ran the same mixing models with each
44
45 269 natural food source separately, and provide the respective median source contributions in
46
47 270 comparison with the assumption of the equal mix.

48
49
50 271 We evaluated the diet composition of all carp ($n=6$) and tench ($n=23$) caught in autumn 2014
51
52 272 because in these species the $\delta^{13}\text{C}$ values did not vary with fish length (see results). In the other
53
54 273 species, there was a strong positive length dependency of $\delta^{13}\text{C}$ values, and hence we included only
55
56 274 individuals beyond a certain size threshold for which feeding on ground baits was likely, namely large

1
2
3 275 roach (TL >10 cm, n=17), large rudd (TL >10 cm, n=15), large white bream (TL >10 cm, n=19) and large
4
5 276 bream (TL > 28 cm, n=27). In perch, the statistical results indicated a negative slope of $\delta^{13}\text{C}$ values
6
7 277 with length, and hence we included only small perch (TL < 15 cm, n=5) into the mixing model
8
9 278 analyses.

10
11
12 279

13
14
15 280 *Growth rate analysis*

16
17
18 281 After the bait addition period ended, fish were sampled by angling from 4 May to 29 May 2015 at
19
20 282 a time where the winter growth ring in scales was clearly developed and positive growth was visible
21
22 283 on the scales starting in spring. We focused the growth rate analyses on two fish species for which
23
24 284 uptake of added bait was likely, and which were frequent in the lake. Bream (n=59) and white bream
25
26 285 (n=30) were regularly angled at the locations on which bait was added; hence it was reasonable to
27
28 286 assume that they ate corn and boilies. Further, the piscivorous pike (n=34) served as “control”
29
30 287 because we assumed that piscivores should show no immediate benefit from our bait addition. Four
31
32 288 additional pike were caught on November 26, 2015 to increase the length gradient of the analysis
33
34 289 and sample size. For more details of scale reading and estimates by the growth model, see Digital
35
36 290 Appendix 1.

37
38
39 291 We used the growth model to predict the expected length of each fish one year later (i.e., in
40
41 292 spring 2015) assuming that this length would represent the typical growth of that individual for each
42
43 293 species in the study lake without a bait addition effect. We then estimated the linear difference
44
45 294 (residuals) between observed (back-calculated) length in spring 2015 and the predicted theoretical
46
47 295 length in spring 2015 to evaluate systematic deviations from predictions in response to bait addition.
48
49 296 Finally, we fitted a general linear model to examine the effect of treatment (spring 2015 = after bait
50
51 297 addition vs. spring 2014 = before addition), total length in spring 2014 and total length \times year on the
52
53 298 growth residuals in 2015 by species. We choose the interaction of year with fish length because we
54
55 299 assumed that the bait addition would particularly benefit the larger size classes of the omnivorous
56
57
58
59
60

1
2
3 300 fishes, which should in turn show the greatest growth increase. A significant interaction effect with a
4
5 301 positive slope would support our hypothesis that growth of the fish differed in response to bait
6
7 302 addition. This analysis was completed in SPSS, version 22.0 (SPSS Inc., Chicago, U.S.A.).
8
9

10 303 We present subsequently the results from the whole-lake experiment without having similar data
11
12 304 from an untreated reference lake. Lakes are rarely identical enough that differences between
13
14 305 treatment and control lakes can be ascribed exclusively to the treatment. Therefore, we base our
15
16 306 arguments on temporal references within the same system, by comparing fish stable isotope data,
17
18 307 fish growth and behavior and distribution of tagged fish before and after the experimental bait
19
20 308 addition. Further, by temporally limiting the experiment and analyses, we can compare the isotopic
21
22 309 changes of omnivorous fish (hypothesized to respond fast) with the isotopic changes in piscivorous
23
24 310 fish (hypothesized to respond only weakly within the study period), thus providing an internal
25
26 311 reference. Further, we combine behavioural studies with growth and diet analyses of fish, to
27
28 312 strengthen the argument that the treatment has caused an effect. This expanded approach is broad
29
30 313 and hence we do not have to rely on a single snapshot sample to infer that fish have profited from
31
32 314 the bait addition.
33
34
35
36 315

38 316 **Results**

41 317 *Occurrence of fish on feeding sites*

44 318 Common carp used feeding sites significantly more often after bait was added (paired t-test, $t = -$
45
46 319 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
47
48 320 sites (Fig. 1A, see video documentary in the digital appendix), which were regularly spaced around
49
50 321 the entire littoral area. The feeding site usage varied among individual carp, but all individuals
51
52 322 showed an increase after the addition of baits (from $<1\%$ for all individuals before addition to
53
54 323 between 1.5% and 14.1% after addition). An increase in feeding site use following bait introduction
55
56 324 was robust to the assumption that carp swimming within 15 m of a feeding site constituted a visit,
57
58
59
60

1
2
3 325 because comparative calculations for 5 m or 30 m distances gave similar results (Digital Appendix 4).
4
5 326 In contrast, the corresponding mean residence times at (future) feeding sites prior to the addition of
6
7 327 angler ground bait were close to zero. Prior to the initiation of the bait addition, the carp readily used
8
9 328 the eastern and northern areas of the lake and were never seen in the west and rarely on the
10
11 329 southern banks (Fig. 1 B,C) and rarely were seen to pause at the future locations of the feeding sites.
12
13 330 Throughout the bait addition period, however, the carp home ranges collapsed (56% decline in the
14
15 331 50% home range area after feeding commenced) around the eight feeding sites (Fig. 1 B,C; see video
16
17 332 in digital appendix). Similar behaviour at the feeding sites was observed for tench after bait addition
18
19 333 (Digital Appendix 5).

20
21
22 334 A range of species were captured by angling at the feeding sites, indicating active ingestion of the
23
24 335 angling bait (Digital Appendix 6). We also used sample feed in bags to study the uptake of the feed
25
26 336 and almost always found all the food consumed within a few hours. The most frequently captured
27
28 337 species was common bream, captured 616 times at a mean TL of 430 ± 57 mm (mean \pm sd). Carp
29
30 338 were captured 28 times (TL 580 ± 76 mm), and tench were captured 32 times (433 ± 52 mm). We also
31
32 339 captured 62 roach (TL = 238 ± 59 mm mean \pm sd), 40 rudd (TL = 260 ± 53 mm mean \pm sd), 31 white
33
34 340 bream (TL= 205 ± 34 mm), four perch (TL= 393 ± 12 mm) and one pike (TL = 615 mm). The cyprinid
35
36 341 species were caught by all three baits types (corn, fish mix boilies, sweet mix boilies).

37
38
39
40 342

41 42 43 343 *Stable isotope values of resources*

44
45 344 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
46
47 345 sweet mix boilies ($-25.7\text{‰} \pm 0.23$, n=4) confirmed that the ground baits were more enriched in ^{13}C
48
49 346 than natural resources for benthivorous fish (zooplankton, $-39.5\text{‰} \pm 2.5$; zebra mussels, $-35.2\text{‰} \pm$
50
51 347 1.0 ; benthic insect larvae, $-31.6\text{‰} \pm 2.7$) (Digital Appendix 3). Fish mix boilies were strongly ^{15}N -
52
53 348 enriched ($7.27\text{‰} \pm 0.24$), attributable to contributions of fish meal and oil, as compared to sweet mix
54
55 349 boilies ($3.19\text{‰} \pm 0.21$) and corn ($4.90\text{‰} \pm 1.44$), which are rich in carbohydrate and plant-meal

1
2
3 350 (Digital Appendix 2). $\delta^{13}\text{C}$ values of zooplankton, benthic insect larvae and zebra mussels were not
4
5 351 affected by bait additions, while crayfish $\delta^{13}\text{C}$ values were significantly elevated in the period after
6
7 352 bait addition (Fig. 2A-D, Table 1).
8
9

10 353

11
12
13 354 *Stable isotope signatures of fish and contribution of ground bait to fish diet*

14
15 355 Among fishes, the $\delta^{13}\text{C}$ values of carp and tench were significantly elevated after bait addition in
16
17 356 autumn 2014 compared to the samplings before addition, independent of fish size (interaction
18
19 357 between fish length and sampling period not significant) (Fig. 3A,B; Table 1). Both species were also
20
21 358 regularly caught during experimental angling (Digital Appendix 6), revealing active feeding on the
22
23 359 feeding spots and bait types. Similarly, the $\delta^{13}\text{C}$ signatures of white bream, bream, rudd and roach
24
25 360 were higher in autumn 2014 than in autumn 2013, attributable to higher $\delta^{13}\text{C}$ of the larger
26
27 361 individuals after bait addition (significantly steeper slope of $\delta^{13}\text{C}$ with TL in autumn 2014 vs. autumn
28
29 362 2013) (Fig. 3C-F; Table 1). Again, angling experiments regularly revealed catches of bream and white
30
31 363 bream and to a smaller degree of large rudd and roach on the feeding spots (Digital Appendix 6). The
32
33 364 $\delta^{13}\text{C}$ of pike, which served as a control, remained unaffected (Fig. 3G; Table 1), and only one pike was
34
35 365 captured by angling (Digital Appendix 6). In perch, the intercepts of the $\delta^{13}\text{C}$ -TL relationships were
36
37 366 higher after bait addition than before, but the slope was lower in autumn 2014 than in autumn 2013,
38
39 367 suggesting that only the non-piscivorous smaller perch had on average higher $\delta^{13}\text{C}$ after bait addition
40
41 368 (Fig. 3H, Table 1). Note, however, that we captured only few, but large, perch at the feeding sites by
42
43 369 angling (Digital Appendix 6).
44
45

46
47
48 370 Due to the size-dependency of $\delta^{13}\text{C}$ 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
53
54 373 (TL > 28 cm) and small perch (TL < 15 cm). Isotopic biplots revealed that all seven fish species had
55
56 374 isotopic $\delta^{13}\text{C}$ values between the strongly $\delta^{13}\text{C}$ -enriched bait and the more $\delta^{13}\text{C}$ -depleted signatures
57
58
59
60

1
2
3 375 of natural resources (Digital Appendix 7). Carp had the most enriched $\delta^{13}\text{C}$, whereas a few individuals
4
5 376 of bream and white bream had high $\delta^{15}\text{N}$ values, corresponding with the high $\delta^{15}\text{N}$ of fish mix boilies
6
7 377 (Digital Appendix 7). The mixing models, which used the isotopic signature of natural food combined
8
9 378 from zebra mussels, zooplankton and insect larvae, revealed substantial contributions of angling bait
10
11 379 to the diet of fishes. Although the posterior distributions of the proportions in the diet were in part
12
13 380 flat (Digital Appendix 8), the results suggested that all seven fish species used at least one of the
14
15 381 three angling baits. Corn contributed substantially to the diet of common carp, but was of minor
16
17 382 importance for the diet of the other fish species (Fig. 4A). Fish mix boilies contributed significantly to
18
19 383 the diet of white bream, bream, rudd and roach (Fig. 4B), whereas sweet mix boilies were eaten
20
21 384 primarily by common carp, tench and rudd (Fig. 4C). Natural food sources combined contributed up
22
23 385 to 50% of the diet, in particular in bream and roach (Fig. 4D). To address the potential uncertainty in
24
25 386 the mixing models, we included a baseline fish with an isotopic signature, which reflected a pure
26
27 387 natural diet. The median contribution of natural food to this baseline fish was 74% (Digital Appendix
28
29 388 8H), whereas the calculated sum of contributions from angling baits was 26%, reflecting basic
30
31 389 uncertainty of the model. However, the median contribution of natural food was much higher, and
32
33 390 median contributions for all angling baits much lower in the baseline as compared to the seven fish
34
35 391 species (Fig. 4). By using the posterior distributions, we calculated the probabilities for the
36
37 392 differences in contributions of natural food and angling baits between the baseline and the seven fish
38
39 393 species. There was an average probability of near 1.0 that all fish species had eaten less natural food
40
41 394 than the baseline fish (Digital Appendix 9). In turn, the model suggested a high probability that the
42
43 395 seven species fed more fish mix boilies (average probability 0.926) and sweet mix boilies (average
44
45 396 probability 0.802) than the baseline fish (Digital Appendix 9). The model did not give clear evidence
46
47 397 for a stronger use of corn in the seven fish species in comparison to the baseline (average probability
48
49 398 0.405), but a strong signal was found for common carp (probability 0.996) (Digital Appendix 9).

50
51
52
53
54 399 To elucidate the uncertainty with respect to the assumption of equal use of the three natural food
55
56 400 sources by the fish, we ran the same mixing models with only one of the natural sources each. The

1
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
9 404 small to moderate (Digital Appendix 10).

10
11
12 405

13
14
15 406 *Growth rate effects*

16
17 407 The older age classes of bream, white bream and pike had positive residuals from the population-
18
19 408 wide von Bertalanffy growth equation in spring 2015, whereas younger age classes tended to reveal
20
21 409 negative residuals (Digital Appendix 11). When examining the full linear model on the residual
22
23 410 variation, the main effects of year and TL were significant in all three species, but significant
24
25 411 interactions among year \times TL were only revealed in the two omnivorous species bream and white
26
27 412 bream (Table 2). This suggests that older bream and white bream grew faster in 2014 until early 2015
28
29 413 during the feeding experiment than predicted from the population-wide von Bertalanffy growth
30
31 414 model estimated to data collected prior to feeding (Table 2). As the partial effect size plots show (Fig.
32
33 415 5), the slope of size effect on residuals was much steeper in 2014-2015 (after) compared to 2013-
34
35 416 2014 (before) in bream (Fig. 5A) and white bream (Fig. 5B), indicating that the larger conspecifics
36
37 417 achieved a size above average in spring 2015, six to nine months after bait addition. By contrast, the
38
39 418 size effect on residuals was similar in pike in the two study years and the interaction was non-
40
41 419 significant (Fig. 5C).

42
43
44
45
46 420

47
48
49 421 **Discussion**

50
51 422 Our whole-lake experiment demonstrated that the addition of ground baits by recreational
52
53 423 cyprinid anglers caused a cascade of changes in the omnivorous fish community of the receiving lake.
54
55 424 Exemplified by position records of tagged common carp as a model species, the fish changed their
56
57
58
59
60

1
2
3 425 swimming behaviour and got attracted to the feeding sites. Angling catches revealed regular uptake
4
5 426 of bait by a range of cyprinid fishes, indicating active foraging on the feedstuffs. We also found the
6
7 427 added bait constituted a substantial proportion of the diet of all benthivorous and omnivorous fish
8
9 428 beyond certain size thresholds. Finally, the behavioral and diet changes induced higher annual
10
11 429 growth rates of the individual fish that preferentially used the bait. Angling baits thus significantly
12
13 430 subsidized omnivorous fish, but not piscivorous fish and invertebrates, despite a low contribution to
14
15 431 the lake C budget. Together these results suggest that the addition of human-derived ground bait by
16
17 432 anglers may change the structure and dynamics of lake fish communities, particularly of the
18
19 433 omnivorous feeding guilds, potentially accompanied by further, so far undocumented, consequences
20
21 434 for the entire lake ecosystem.
22
23
24
25

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,

1
2
3 451 although it is possible that the large degree of domestication of carp resulted in this species being
4
5 452 particularly attracted to the feeding sites.
6

7
8 453 The above conclusion of active uptake of angling bait by omnivorous fish was confirmed by the
9
10 454 stable isotope analyses of the fish. We found significantly elevated $\delta^{13}\text{C}$ values of common carp,
11
12 455 tench, bream, white bream, roach and rudd at the end of the bait addition period, in comparison
13
14 456 with values obtained before bait addition. In contrast, $\delta^{13}\text{C}$ values of the natural resources
15
16 457 (zooplankton and benthic macroinvertebrates) were not affected by bait additions, suggesting that
17
18 458 the omnivorous fish cannot have obtained their elevated $\delta^{13}\text{C}$ values by feeding on those natural
19
20 459 resources. For most of the fish species (except common carp and tench), the elevation in $\delta^{13}\text{C}$ values
21
22 460 was stronger for larger individuals (as indicated by the significant positive interaction between fish
23
24 461 length and $\delta^{13}\text{C}$ in the ANCOVAs). The size-dependency of bait uptake is most likely attributable to
25
26 462 the large diameter of the rather hard-texture particles (10 - 14 mm boilies and ~8 mm corn) that can
27
28 463 only be eaten by large cyprinids when fitting through the pharyngeal jaws (Sibbing, 1988). Thus, gape
29
30 464 constraints likely prevented small cyprinids with small gape width from feeding upon the added bait
31
32 465 particles. For some of the fish species, $\delta^{13}\text{C}$ was significantly higher only for the comparison between
33
34 466 autumn 2013 and autumn 2014, whereas the difference between summer 2014 and autumn 2014
35
36 467 was weaker. The heterogeneous size distribution of sampled fish across the three sampling periods
37
38 468 probably contributed to these in part ambiguous results. If only fishes with similar size ranges per
39
40 469 species in all three periods were included into statistical comparisons, there were strong differences
41
42 470 of $\delta^{13}\text{C}$ values also between summer 2014 and autumn 2014 in carp, roach, rudd and white bream
43
44 471 (Digital Appendix 12), whereas the interaction between fish length and $\delta^{13}\text{C}$ was significant only for
45
46 472 rudd. A similar effect of fish length on the uptake of angler baits has recently been reported in
47
48 473 riverine barbel (Roberts et al., 2017).
49
50

51
52 474 Another reason for weaker $\delta^{13}\text{C}$ signals from ground bait in some individuals in autumn 2014 may
53
54 475 be found in the turnover time needed to assimilate the ^{13}C -enhanced diet until equilibrium in the
55
56 476 muscle tissue of fish. The half-life of ^{13}C in muscle tissue of adult fish is about three up to five months
57
58
59
60

1
2
3 477 (Weidel et al., 2011), and hence only individuals, which started feeding on ground bait immediately
4
5 478 after the first introduction, may have achieved tissue equilibrium until the sampling in autumn 2014.
6
7 479 Accordingly, the contributions from ground baits to the fish diet calculated by mixing models may
8
9 480 even underestimate the true ingestion during the experimental phase. The piscivorous large perch
10
11 481 and pike served as a natural control for the effect of ground bait feeding on tissue $\delta^{13}\text{C}$, and we did
12
13 482 not find heavier $\delta^{13}\text{C}$ in these fishes and size classes. Accordingly, the predatory fish species as well as
14
15 483 the invertebrates neither directly (by feeding on added bait) nor indirectly (by feeding on prey, which
16
17 484 has fed upon bait) ingested the C from corn or boilies in the time frame of three months of our study.
18
19

20 485

21
22
23 486 *Ground bait substantially contributed to fish diet and enhanced fish growth rates*

24
25 487 The mixing models indicated that for the fish individuals beyond a species-specific size threshold,
26
27 488 the contribution from the added bait particles to their diet was substantial. There was a very clear
28
29 489 signal of the distinct $\delta^{13}\text{C}$ value of corn (attributable to its C_4 photosynthetic pathway) in common
30
31 490 carp. Therefore, terrestrial subsidy to aquatic food webs and *vice versa* can be traced in animal
32
33 491 tissues after addition of corn compounds (Scharnweber et al., 2014a; Scharnweber et al., 2014b). The
34
35 492 heavy reliance on corn by carp can be explained by the greater amylase activities in the intestine of
36
37 493 carp compared to other cyprinids such as tench (Hidalgo et al., 1999), which is decisive to break
38
39 494 down the starch in corn. Furthermore, there was strong evidence of feeding upon fish mix boilies by
40
41 495 some large bream and white bream, as indicated by their elevated $\delta^{15}\text{N}$ values after bait addition. A
42
43 496 similar tracing of fish meal and oil from fishmeal pellets used as angling bait has been demonstrated
44
45 497 recently for barbel and chub (*Squalius cephalus*) in English rivers (Roberts et al., 2017). In contrast,
46
47 498 the sweet food mix was preferentially ingested by tench, carp and rudd, confirming earlier studies
48
49 499 that the common cyprinid species have differing preferences for certain types of angling bait
50
51 500 (Specziar et al., 1997). It is possible that these three species have better ability to break down
52
53 501 carbohydrates than the other cyprinids, which may have contributed to the larger fraction of both
54
55 502 corn and sweet mix boilies in tench, carp and rudd.
56
57
58
59
60

1
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
7 505 pellets has been shown in experiments where a mix of natural and artificial food was offered
8
9 506 (Roberts et al., 2017). We do not rely too strongly on the medians of the posterior distributions from
10
11 507 each of the bait types in the Bayesian mixing models, because the distributions were often flat and
12
13 508 hence had substantial uncertainty. However, the intermediate position of all fish in the isospace
14
15 509 (Digital Appendix 7) and the uncertainty analyses of the model (Table 2, Digital Appendices 9, 10)
16
17 510 suggest that the angler baits must have contributed at least to some extent to the diet of all species.

19
20 511 We showed that the individual growth rates of bream and white bream were enhanced in the
21
22 512 feeding year compared with the previous non-feeding year, in particular for larger individuals of both
23
24 513 species. In contrast, we did not find a similar growth response in the piscivorous pike. These results
25
26 514 suggest that the higher growth rates are at least partly attributable to the uptake of added bait. Corn
27
28 515 and other cereals have been used traditionally in pond aquaculture because the addition of
29
30 516 carbohydrates bound in cereals increases carp production substantially (Kestemont, 1995; Füllner,
31
32 517 2015). The main mechanisms by which supplementary feeding with corn elevates pond production of
33
34 518 fishes relates to the more efficient use of essential macro- und micronutrients from natural food and
35
36 519 the delayed depletion of natural food towards the end of the summer growing season (Füllner, 2015;
37
38 520 Hlavac et al., 2016). The growth rates of carp achievable by feeding upon boilies were even higher
39
40 521 than those achieved by feeding on seed particles like corn, indicating that different feedstuffs used
41
42 522 by anglers have different nutritional value to the fish (Niesar et al., 2004). However, the energy
43
44 523 density of the ground bait is comparable to that of natural animal food (about 20 kJ g⁻¹ dry mass)
45
46 524 (Niesar et al., 2004), suggesting that ground baits are energetically not superior to natural food.
47
48 525 Moreover, if natural food of the same dry matter amount is given to carp compared to the same dry
49
50 526 matter of angling baits such as boilies, the growth on natural food is larger (Niesar et al., 2004).
51
52 527 However, natural food is often limited in natural ecosystems, particularly towards the end of the
53
54 528 growing season and the readily available angling bait can be found and ingested easily and provides a

1
2
3 529 compact form of energy and nutrients that likely demands much less food search activity and sorting
4
5 530 than feeding on natural macrozoobenthos. Therefore, the nutrients bound in baits and the energy
6
7 531 supply seems to come on top of what an ecosystem naturally offers, and the accelerated growth
8
9 532 rates found in our experiment are indicative of a subsidy above the natural animal production,
10
11 533 similar to findings from the substantial increase of production in food-supplemented pond
12
13 534 aquaculture with cyprinids (Kestemont, 1995; Füllner, 2015). The ground baiting-induced increase in
14
15 535 growth is facilitated by the high digestibility of macronutrients from all ground baits, even of corn for
16
17 536 carp (Arlinghaus and Niesar, 2005), the reduction in energy needed for food search and feeding when
18
19 537 angling baits are available on predictable food patches, and very likely the more efficient use of
20
21 538 natural food similar to the case in pond aquaculture (Füllner, 2015).
22
23
24
25

539

27 540 *Can ground bait additions subsidize fish?*

29 541 A surprising result is the discrepancy between the strong effects of ground bait addition on the
30
31 542 omnivorous fish and the modest contribution of these baits to the C budget of the lake. Organic C
32
33 543 budgets in eutrophic lakes are dominated by autochthonous primary production (Carpenter et al.,
34
35 544 2005; Brothers et al., 2013b). Consequently, additions of terrestrial particulate organic matter could
36
37 545 be traced in eutrophic aquatic food webs (Bartels et al., 2012; Scharnweber et al., 2014a), but had
38
39 546 little effects on consumer production and biomass (Mehner et al., 2016). In our previous whole-lake
40
41 547 experiments, we added maize leaves to the treatment halves of two divided lakes (about 25 g C m⁻²)
42
43 548 accounting for only <10% of the C fixed by annual PPr in the lakes, making a weak effect on
44
45 549 secondary production plausible (Mehner et al., 2016). In the current experiment, angler baits
46
47 550 containing mainly terrestrial-plant derived material added even less than 1% to the estimated annual
48
49 551 net PPr, but induced high diet contributions and enhanced growth rates in fish, suggesting a
50
51 552 substantial subsidy effect. The allochthonous C was offered at high concentrations, at predictable
52
53 553 locations over long time spans of several months, and was bound in relatively large, easily accessible
54
55 554 particles with energy densities similar to the naturally available food, such as zooplankton or benthic
56
57
58
59
60

1
2
3 555 macroinvertebrates. Subsidy by high-quality resources often shifts the diet preferences of consumers
4
5 556 towards the subsidy, and hence can have strong production effects (Marczak et al., 2007; Marcarelli
6
7 557 et al., 2011). Furthermore, in contrast to terrestrial particulate or dissolved organic C inputs entering
8
9 558 higher trophic levels via the microbial loop or benthic shortcuts (Attermeyer et al., 2013), the bait
10
11 559 particles can be considered prey supplied directly to fish consumers, similar to the allochthonous
12
13 560 natural prey subsidizing aquatic food webs (Mehner et al., 2005; Milardi et al., 2016). Indeed, added
14
15 561 baits were in the same order of magnitude as biomass (1 g C m^{-2}) and production of
16
17 562 macrozoobenthos ($1 \text{ to } 2 \text{ g C m}^{-2} \text{ y}^{-1}$) in lakes of similar morphometry and trophic state in this region
18
19 563 (Brauns et al., 2011; Lischke et al., 2017). From that perspective, the strong effects found in our study
20
21 564 can be compared to those of pulsed subsidies on the structure and dynamics of aquatic consumer
22
23 565 populations (Nowlin et al., 2008; Trebilco et al., 2016).

24
25
26
27 566

28 29 567 *Conclusions*

30
31 568 Ground baiting with mainly terrestrial plant-derived organic matter by recreational cyprinid
32
33 569 anglers has strong subsidy effects on a major component of a fish community, particularly on
34
35 570 omnivorous species, in eutrophic lakes despite high internal primary production. The shift in diet
36
37 571 composition and increased growth rates in fish detected in our study may eventually elevate fish
38
39 572 production and thus the carrying capacity of the aquatic systems to fish consumers, similar to the
40
41 573 case previously documented in feed-enhanced pond aquaculture with cyprinid fishes. Thus, longer-
42
43 574 term subsidy may result in higher biomasses of consumer populations (Trebilco et al., 2016) and
44
45 575 decouple predator-prey relationships (Rodewald et al., 2011). We confined our analysis to freshwater
46
47 576 cyprinid angling, but ground baiting and the addition of feed to attract fish is also commonplace e.g.
48
49 577 in coastal angling. Thus, our work can be considered as a motivation to further study the response of
50
51 578 consumers and entire ecosystems to the subsidy effect of angling-induced feed introduction over
52
53 579 longer time frames than completed in our experiment.

580 Acknowledgments

581 We would like to thank Leander Höhne for helping with scale reading, Asja Vogt for help with
582 sample preparation, and Andreas Mühlbradt, Alexander Türck and Jan Hallermann for technical
583 assistance with field sampling and tracking. We thank reviewers for their valuable feedback that
584 helped improve our article. We also would like to acknowledge support by Shimano and SPRO with
585 donating some angling equipment to support our study. Shimano and SPRO, however, had no role in
586 study design, data collection and analysis, decision to publish, or preparation of the manuscript. The
587 invasive animal procedures (including surgeries and recaptures) were ethically approved by the
588 responsible State Animal Welfare and Animal Experimentation Agency (Landesamt für Umwelt,
589 Gesundheit und Verbraucherschutz) in Brandenburg, Germany (project reference 2347-21-2014)
590 according to the German Animal Protection Act. Financial support was provided by the German
591 Academic Exchange Service (DAAD PPP Finland).

592

593 References

- 594 Amaral SD, Brito D, Ferreira MT, Neves R, Franco A. 2013. Modeling water quality in reservoirs used
595 for angling competition: Can groundbait contribute to eutrophication? *Lake and Reservoir*
596 *Management* 29: 257-269.
- 597 Arlinghaus R. 2004. Recreational fisheries in Germany - a social and economic analysis. *Berichte des*
598 *IGB (ISSN 1432-508X)* 18: 1-168.
- 599 Arlinghaus R, Mehner T. 2003. Socio-economic characterisation of specialised common carp
600 (*Cyprinus carpio* L.) anglers in Germany, and implications for inland fisheries management
601 and eutrophication control. *Fisheries Research* 61: 19-33.
- 602 Arlinghaus R, Niesar M. 2005. Nutrient digestibility of angling baits for carp, *Cyprinus carpio*, with
603 implications for groundbait formulation and eutrophication control. *Fisheries Management*
604 *and Ecology* 12: 91-97.
- 605 Attermeyer K, Premke K, Hornick T, Hilt S, Grossart HP. 2013. Ecosystem-level studies of terrestrial
606 carbon reveal contrasting bacterial metabolism in different aquatic habitats. *Ecology* 94:
607 2754-2766.
- 608 Bajer PG, Lim H, Travaline MJ, Miller BD, Sorensen PW. 2010. Cognitive aspects of food searching
609 behavior in free-ranging wild Common Carp. *Environmental Biology of Fishes* 88: 295-300.
- 610 Baktoft H, Zajicek P, Klefoth T, Svendsen JC, Jacobsen L, Pedersen MW, Morla DM, Skov C, Nakayama
611 S, Arlinghaus R. 2015. Performance assessment of two whole-lake acoustic positional
612 telemetry systems - is reality mining of free-ranging aquatic animals technologically possible?
613 *Plos One* 10: ARTN e0126534.

- 1
2
3 614 Bartels P, Cucherousset J, Gudasz C, Jansson M, Karlsson J, Persson L, Premke K, Rubach A, Steger K,
4 615 Tranvik LJ, Eklov P. 2012. Terrestrial subsidies to lake food webs: an experimental approach.
5 616 *Oecologia* 168: 807-818.
- 6 617 Basic T, Britton JR. 2015. Utility of fish scales from stock assessment surveys in stable isotope analysis
7 618 for initial assessments of trophic relationships in riverine fish communities. *Journal of*
8 619 *Applied Ichthyology* 31: 296-300.
- 9 620 Brauns M, Gücker B, Wagner C, Garcia XF, Walz N, Pusch MT. 2011. Human lakeshore development
10 621 alters the structure and trophic basis of littoral food webs. *Journal of Applied Ecology* 48:
11 622 916-925.
- 12 623 Brett MT, Bunn SE, Chandra S, Galloway AWE, Guo F, Kainz MJ, Kankaala P, Lau DCP, Moulton TP,
13 624 Power ME, Rasmussen JB, Taipale SJ, Thorp JH, Wehr JD. 2017. How important are terrestrial
14 625 organic carbon inputs for secondary production in freshwater ecosystems? *Freshwater*
15 626 *Biology* 62: 833-853.
- 16 627 Brothers SM, Hilt S, Meyer S, Köhler J. 2013a. Plant community structure determines primary
17 628 productivity in shallow, eutrophic lakes. *Freshwater Biology* 58: 2264-2276.
- 18 629 Brothers SM, Hilt S, Attermeyer K, Grossart HP, Kosten S, Lischke B, Mehner T, Meyer N,
19 630 Scharnweber K, Köhler J. 2013b. A regime shift from macrophyte to phytoplankton
20 631 dominance enhances carbon burial in a shallow, eutrophic lake. *Ecosphere* 4 (137): Doi
21 632 10.1890/Es1813-00247.00241.
- 22 633 Calenge C. 2011. Home range estimation in R: the adehabitatHR package. Saint Benoist, Auffargis:
23 634 Office national de la classe et de la faune sauvage.
- 24 635 Carpenter SR, Cole JJ, Pace ML, Van de Bogert M, Bade DL, Bastviken D, Gille CM, Hodgson JR, Kitchell
25 636 JF, Kritzberg ES. 2005. Ecosystem subsidies: Terrestrial support of aquatic food webs from C-
26 637 13 addition to contrasting lakes. *Ecology* 86: 2737-2750.
- 27 638 Cole JJ, Carpenter SR, Kitchell JF, Pace ML. 2002. Pathways of organic carbon utilization in small lakes:
28 639 Results from a whole-lake C-13 addition and coupled model. *Limnology and Oceanography*
29 640 47: 1664-1675.
- 30 641 Cole JJ, Carpenter SR, Pace ML, Van de Bogert MC, Kitchell JL, Hodgson JR. 2006. Differential support
31 642 of lake food webs by three types of terrestrial organic carbon. *Ecology Letters* 9: 558-568.
- 32 643 Füllner G. 2015. Traditional feeding of common carp and strategies of replacement of fish meal.
33 644 Pietsch C, Hirsch PE editors. *Biology and ecology of carp*. Boca Raton: Taylor & Francis, p135-
34 645 163.
- 35 646 Grey J, Waldron S, Hutchinson R. 2004. The utility of carbon and nitrogen isotope analyses to trace
36 647 contributions from fish farms to the receiving communities of freshwater lakes: a pilot study
37 648 in Esthwaite Water, UK. *Hydrobiologia* 524: 253-262.
- 38 649 Hidalgo MC, Urea E, Sanz A. 1999. Comparative study of digestive enzymes in fish with different
39 650 nutritional habits. Proteolytic and amylase activities. *Aquaculture* 170: 267-283.
- 40 651 Hlavac D, Anton-Pardo M, Masilko J, Hartman P, Regenda J, Vejsada P, Baxa M, Pechar L, Valentova
41 652 O, Vsetickova L, Drozd B, Adamek Z. 2016. Supplementary feeding with thermally treated
42 653 cereals in common carp (*Cyprinus carpio* L.) pond farming and its effects on water quality,
43 654 nutrient budget and zooplankton and zoobenthos assemblages. *Aquaculture International*
44 655 24: 1681-1697.
- 45 656 Hühn D, Klefoth T, Pagel T, Zajicek P, Arlinghaus R. 2014. Impacts of external and surgery-based
46 657 tagging techniques on small northern pike under field conditions. *North American Journal of*
47 658 *Fisheries Management* 34: 322-334.
- 48 659 Kasumyan AO, Morsi AMK. 1996. Taste sensitivity of common carp *Cyprinus carpio* to free amino
49 660 acids and classical taste substances. *Journal of Applied Ichthyology* 36: 391-403.
- 50 661 Kestemont P. 1995. Different systems of carp production and their impacts on the environment.
51 662 *Aquaculture* 129: 347-372.
- 52 663 Kobler A, Klefoth T, Mehner T, Arlinghaus R. 2009. Coexistence of behavioural types in an aquatic top
53 664 predator: a response to resource limitation? *Oecologia* 161: 837-847.

- 1
2
3 665 Lischke B, Mehner T, Hilt S, Attermeyer K, Brauns M, Brothers S, Grossart HP, Köhler J, Scharnweber
4 666 K, Gaedke U. 2017. Benthic carbon is inefficiently transferred in the food webs of two
5 667 eutrophic shallow lakes. *Freshwater Biology* 62: 1693-1706.
- 6 668 Marcarelli AM, Baxter CV, Mineau MM, Hall RO. 2011. Quantity and quality: unifying food web and
7 669 ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* 92: 1215-
8 670 1225.
- 9 671 Marczak LB, Thompson RM, Richardson JS. 2007. Meta-analysis: Trophic level, habitat, and
10 672 productivity shape the food web effects of resource subsidies. *Ecology* 88: 140-148.
- 11 673 Mehner T, Attermeyer K, Brauns M, Brothers S, Diekmann J, Gaedke U, Grossart HP, Köhler J, Lischke
12 674 B, Meyer N, Scharnweber K, Syväranta J, Vanni MJ, Hilt S. 2016. Weak response of animal
13 675 allochthony and production to enhanced supply of terrestrial leaf litter in nutrient-rich lakes.
14 676 *Ecosystems* 19: 311-325.
- 15 677 Mehner T, Ihlau J, Dörner H, Hölker F. 2005. Can feeding of fish on terrestrial insects subsidize the
16 678 nutrient pool of lakes? *Limnology and Oceanography* 50: 2022-2031.
- 17 679 Mehner T, Ihlau J, Dörner H, Hupfer M, Hölker F. 2007. The role of insectivorous fish in fostering the
18 680 allochthonous subsidy of lakes. *Limnology and Oceanography* 52: 2718-2721.
- 19 681 Milardi M, Kakela R, Weckstrom J, Kahilainen KK. 2016. Terrestrial prey fuels the fish population of a
20 682 small, high-latitude lake. *Aquatic Sciences* 78: 695-706.
- 21 683 Monk CT, Arlinghaus R. 2017. Encountering a bait is necessary but insufficient to explain individual
22 684 variability in vulnerability to angling in two freshwater benthivorous fish in the wild. *Plos One*
23 685 12: ARTN e0173989.
- 24 686 Niesar M, Arlinghaus R, Rennert B, Mehner T. 2004. Coupling insights from a carp, *Cyprinus carpio*,
25 687 angler survey with feeding experiments to evaluate composition, quality and phosphorus
26 688 input of groundbait in coarse fishing. *Fisheries Management and Ecology* 11: 225-235.
- 27 689 Nowlin WH, Vanni MJ, Yang LH. 2008. Comparing resource pulses in aquatic and terrestrial
28 690 ecosystems. *Ecology* 89: 647-659.
- 29 691 Oro D, Genovart M, Tavecchia G, Fowler MS, Martinez-Abraín A. 2013. Ecological and evolutionary
30 692 implications of food subsidies from humans. *Ecology Letters* 16: 1501-1514.
- 31 693 Osterback AMK, Frechette DM, Hayes SA, Shaffer SA, Moore JW. 2015. Long-term shifts in
32 694 anthropogenic subsidies to gulls and implications for an imperiled fish. *Biological*
33 695 *Conservation* 191: 606-613.
- 34 696 Pace ML, Cole JJ, Carpenter SR, Kitchell JF, Hodgson JR, Van de Bogart MC, Bade DL, Kritzberg ES,
35 697 Bastviken D. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food
36 698 webs. *Nature* 427: 240-243.
- 37 699 Parnell A. 2017. simmr: A Stable Isotope Mixing Model. R package version 0.3. [http://CRAN.R-](http://CRAN.R-project.org/package=simmr)
40 700 [project.org/package=simmr](http://CRAN.R-project.org/package=simmr).
- 41 701 Phillips DL, Koch PL. 2002. Incorporating concentration dependence in stable isotope mixing models.
42 702 *Oecologia* 130: 114-125.
- 43 703 Post DM. 2002. Using stable isotopes to estimate trophic position: Models, methods, and
44 704 assumptions. *Ecology* 83: 703-718.
- 45 705 Roberts CG, Basic T, Trigo FA, Britton JR. 2017. Trophic consequences for riverine cyprinid fishes of
46 706 angler subsidies based on marine-derived nutrients. *Freshwater Biology* 62: 894-905.
- 47 707 Rodewald AD, Kearns LJ, Shustack DP. 2011. Anthropogenic resource subsidies decouple predator-
48 708 prey relationships. *Ecological Applications* 21: 936-943.
- 49 709 Scharnweber K, Syväranta J, Hilt S, Brauns M, Vanni MJ, Brothers SM, Köhler J, Knezevic-Jaric J,
50 710 Mehner T. 2014a. Whole-lake experiments reveal the fate of terrestrial particulate organic
51 711 carbon in benthic food webs of shallow lakes. *Ecology* 95: 1496-1505.
- 52 712 Scharnweber K, Vanni MJ, Hilt S, Syväranta J, Mehner T. 2014b. Boomerang ecosystem fluxes: organic
53 713 carbon inputs from land to lakes are returned to terrestrial food webs via aquatic insects.
54 714 *Oikos* 123: 1439-1448.
- 55 715 Schindler DE, Smits AP. 2017. Subsidies of aquatic resources in terrestrial ecosystems. *Ecosystems* 20:
56 716 78-93.

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

717 Sibbing FA. 1988. Specializations and limitations in the utilization of food resources by the carp,
718 *Cyprinus carpio* - a study of oral food-processing. Environmental Biology of Fishes 22: 161-
719 178.

720 Specziar A, Tolg L, Biro P. 1997. Feeding strategy and growth of cyprinids in the littoral zone of Lake
721 Balaton. Journal of Fish Biology 51: 1109-1124.

722 Tanentzap AJ, Kielstra BW, Wilkinson GM, Berggren M, Craig N, del Giorgio PA, Grey J, Gunn JM,
723 Jones SE, Karlsson J, Solomon CT, Pace ML. 2017. Terrestrial support of lake food webs:
724 Synthesis reveals controls over cross-ecosystem resource use. Science Advances 3: ARTN
725 e1601765.

726 Trebilco R, Dulvy NK, Anderson SC, Salomon AK. 2016. The paradox of inverted biomass pyramids in
727 kelp forest fish communities. Proceedings of the Royal Society B-Biological Sciences 283:
728 20160816.

729 Vollenweider RA. 1976. Advances in defining critical loading levels for phosphorus in lake
730 eutrophication. Memorie dell'Istituto Italiano di Idrobiologia 33 53-83.

731 Wang YMV, Wan AHL, Lock EJ, Andersen N, Winter-Schuh C, Larsen T. 2018. Know your fish: A novel
732 compound-specific isotope approach for tracing wild and farmed salmon. Food Chemistry
733 256: 380-389.

734 Weidel BC, Carpenter SR, Kitchell JF, Vander Zanden MJ. 2011. Rates and components of carbon
735 turnover in fish muscle: insights from bioenergetics models and a whole-lake C-13 addition.
736 Canadian Journal of Fisheries and Aquatic Sciences 68: 387-399.

737 Wolos A, Theodorowicz M, Grabowska K. 1992. Effect of ground-baiting on anglers' catches and
738 nutrient budget of water bodies as exemplified by Polish lakes. Aquaculture and Fisheries
739 Management 23: 499-509.

740

741

742

743

744 Table 1: Statistical comparisons of $\delta^{13}\text{C}$ values of primary consumers and fish from sampling periods
 745 before (autumn 2013=Aut13, summer 2014=Sum14) and after (autumn 2014=Aut14) the
 746 experimental addition of bait into Döllnsee. Group differences are given only for significant pairwise
 747 post-hoc tests relative to autumn 2014. For all fish species, total length (TL) was initially included as
 748 covariate, but was not retained as significant predictor for carp and tench (ANOVA). In the other fish
 749 species, the effect of TL on $\delta^{13}\text{C}$ or the interaction between TL and period on $\delta^{13}\text{C}$ were significant
 750 (ANCOVA), and therefore the comparison of groups may include differences of both intercept and
 751 slope.

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

752

753

754 Table 2: ANCOVA model results testing the residuals of individual level size-at-age in 2014 prior to
 755 bait addition and the residuals 2015 after bait addition as deviation from the population-level von
 756 Bertalanffy model for size-at-age prior to bait addition as a function of total length (TL) and year as
 757 well as the interaction. The partial effects of the size \times year interaction are shown in Figure 5. The
 758 columns on the left represent the statistics of the full model, whereas the last four columns reflect
 759 coefficient estimates (B) and their standard errors (S.E.), together with their t- and p-values.

760

	df	F	p	B	S.E.	t	p
Bream, Adj. R²=0.437							
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. R²=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	2.576	0.113				

761

762

1
2
3 763 **Captions of figures**

4 764 Figure 1: Boxplot of the mean daily percentages of time spent within 15 m of feeding sites for 22
5 765 individual carp before and during bait addition (A). Thick bars represent the median and whiskers
6 766 represent 1.5 times the interquartile range, and outliers are represented by points. Home ranges of
7 767 carp before (B) and during (C) bait addition. The black outline represents the shoreline of Döllnsee.
8 768 Shaded areas from lightest to darkest show the 50%, 25% and 5% carp home range areas
9 769 respectively. Locations of the eight feeding sites are shown by crosses.

10
11 770 Figure 2: Boxplots (median, box=25% and 75% percentiles, whiskers 10% and 90% percentiles,
12 771 dots=outliers) of $\delta^{13}\text{C}$ (‰) of natural resources (A) zooplankton, (B) benthic insect larvae, (C) zebra
13 772 mussels and (D) crayfish in Lake Döllnsee. Samples were taken in autumn 2013 and summer 2014
14 773 (both before bait addition) and in autumn 2014 (after bait addition).

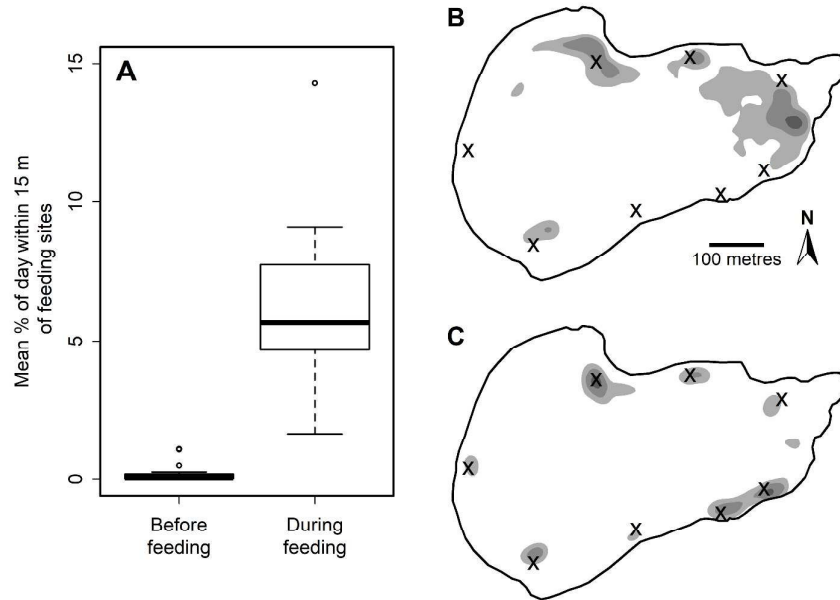
15 774 Figure 3: Least squares means (blue dots, corrected for differing fish lengths between the three
16 775 sampling periods) of $\delta^{13}\text{C}$ of eight fish species (A) common carp, B) tench, C) white bream, D) bream,
17 776 E) rudd, F) roach, G) pike, H) perch) during the three sampling periods (autumn 2013, summer 2014:
18 777 before bait addition; autumn 2014: after bait addition) (no values available for carp, Before(Aut13)).
19 778 The blue lines indicate the 95% confidence intervals, non-overlapping red arrows between sampling
20 779 periods denote significant differences in $\delta^{13}\text{C}$ (not corrected for potential interactions between $\delta^{13}\text{C}$
21 780 and fish length, see Table 1).

22 781 Figure 4: Posterior distributions of contribution of corn (A), fish mix boilie (B), sweet mix boilie (C),
23 782 and Natural Food (zooplankton, zebra mussels and insect larvae/Isopoda combined) (D) to the diet of
24 783 the seven fish species, as estimated from stable isotope values ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) by Bayesian mixing
25 784 models. As baseline, we provide the results of the same mixing model for a fish, which has fed
26 785 exclusively on natural food. The boxes represent the interquartile range (25th and 75th percentile),
27 786 and whiskers represent 1.5 times the interquartile range distant from the box. Dots are outlying
28 787 points, and represent the full range of solutions of the Bayesian model. For detailed density plots, see
29 788 Digital Appendix 8.

30 789 Figure 5: The partial effect sizes of the interactions of year and total length (mm) on the residuals
31 790 from the population level von Bertalanffy equation in 2014 and 2015 in bream (A), white bream (B)
32 791 and pike (C) from Döllnsee.

33
34
35
36
37
38
39
40
41
42
43
44
45
46
47 792

48
49
50
51
52
53
54
55 793



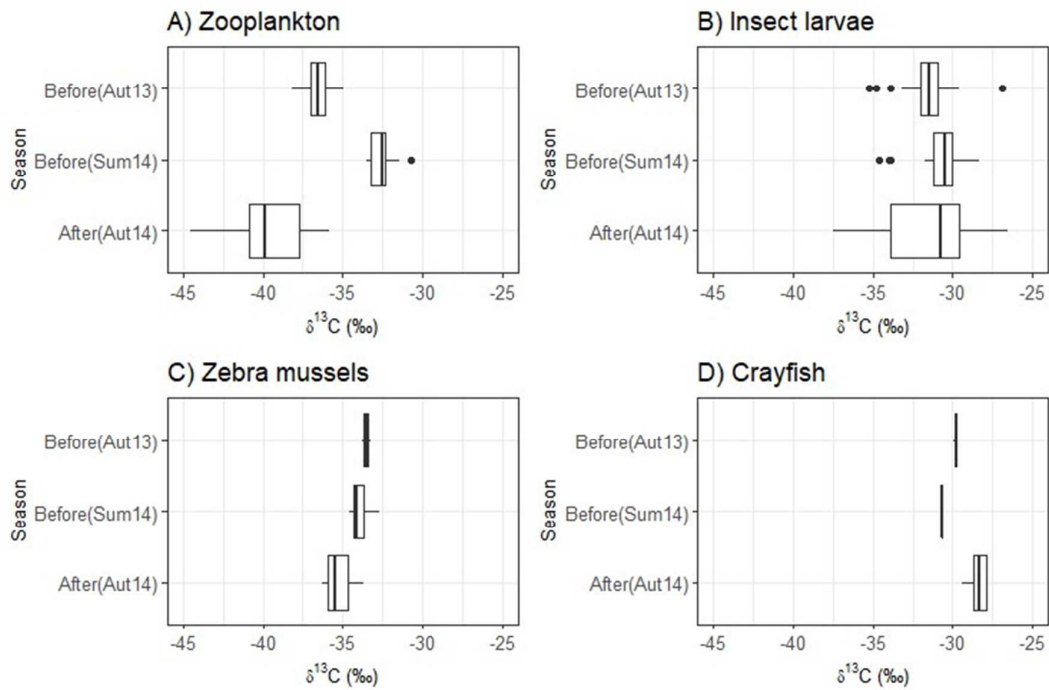
794

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

801

802

803

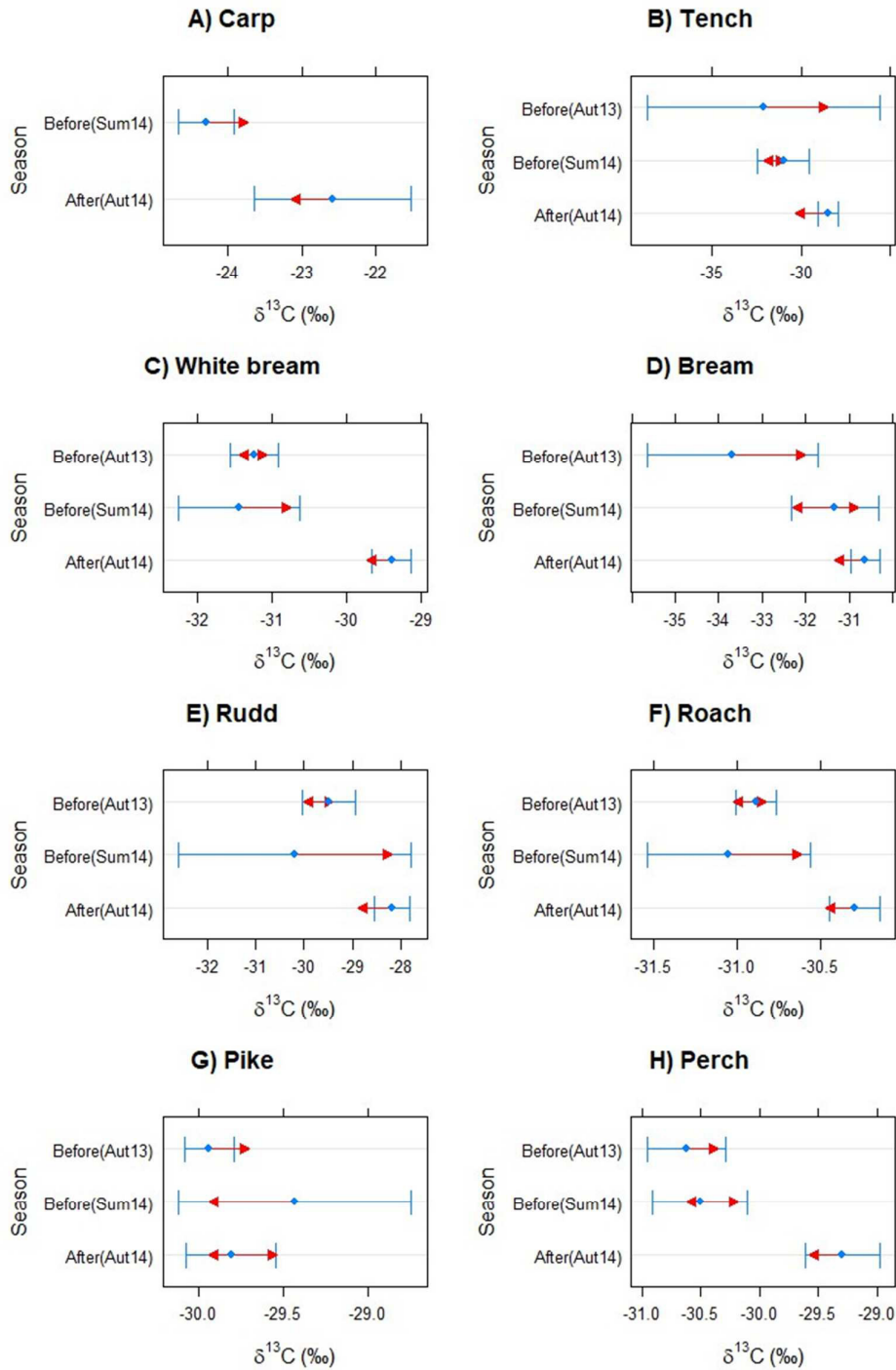


804

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

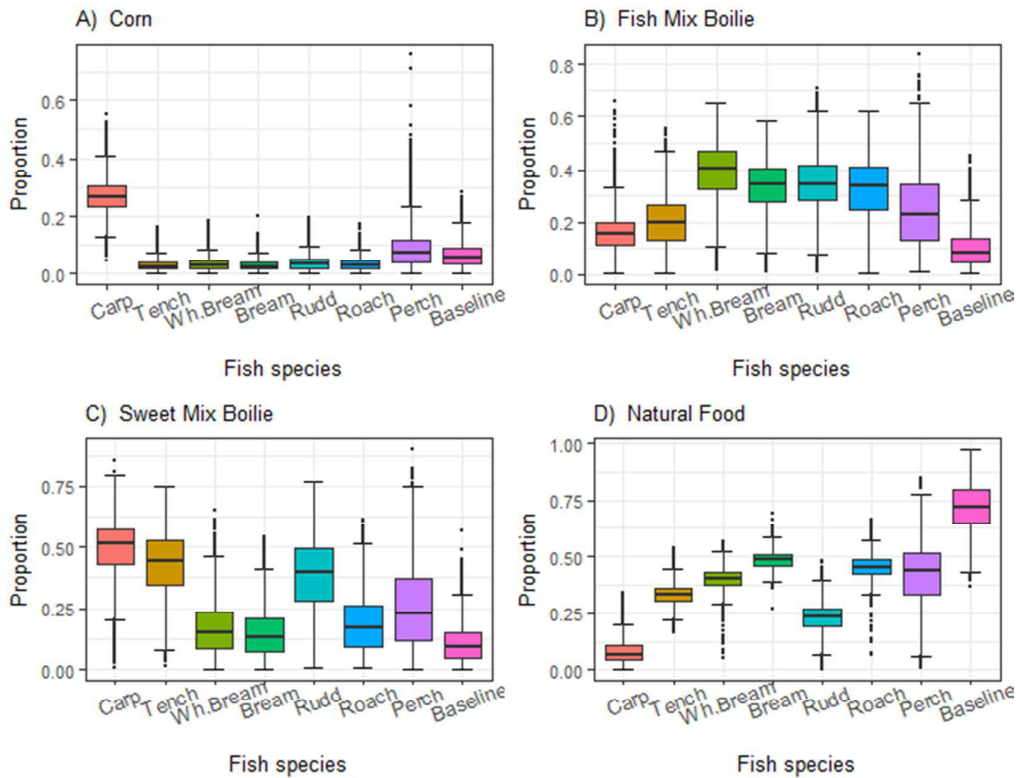
809

810



811

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



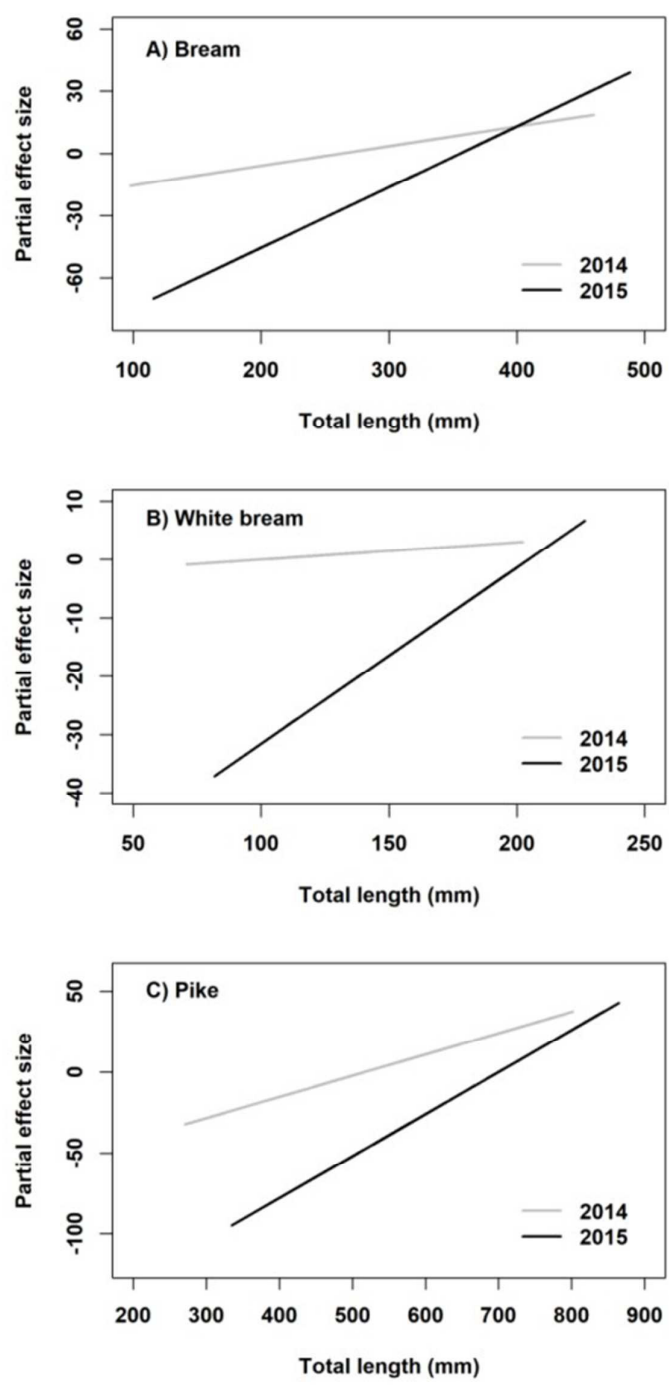
819

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

828

829

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



830

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

834

835