

Return of the apex predator — how brown trout (*Salmo trutta*) re-establishment shapes an ecosystem

Tommi Perälä*, Silva Uusi-Heikkilä & Anna Kuparinen

*Department of Biological and Environmental Science, P.O. Box 35, FI-40014 University of Jyväskylä, Finland (*corresponding author's e-mail: tommy.a.perala@jyu.fi)*

Received 25 Sep. 2020, final version received 24 Nov. 2020, accepted 22 Jan. 2021

Perälä, T., Uusi-Heikkilä, S. & Kuparinen, A. 2021: Return of the apex predator — how brown trout (*Salmo trutta*) re-establishment shapes an ecosystem. — *Ann. Zool. Fennici* 58: 231–242.

Re-establishment of a declined apex predator fish species in a lake ecosystem may have dramatic effects on other fish and plankton community already inhabiting the ecosystem. We studied mechanistically potential impacts of re-establishment of the brown trout (*Salmo trutta*) in the west-central European Lake Constance focusing on two commercially important fish species: whitefish and Eurasian perch. We compared simulation model outputs from two versions of an allometric trophic network model for Lake Constance, one with and one without the trout as the apex predator. The re-establishment of the declined brown trout reduced the perch population directly by predation and indirectly by increased resource competition, whereas the whitefish population was directly affected by increased predation. The decrease in fish biomass densities was highly sensitive to trout larval survivability. Both species showed strong compensatory behaviour by achieving higher per capita resource consumption when the populations decreased in the presence of brown trout.

Introduction

High fishing pressure and broad-scale habitat alterations have led to dramatic declines of many freshwater fish species (Collen *et al.* 2014, Darwall & Freyhof 2016; <https://www.iucnredlist.org/>). In Europe, migratory freshwater fish species have been declining particularly fast, with populations falling by 93% in the past five decades (Deinet *et al.* 2020). The decline has been attributed to overfishing and construction of dams, which have blocked the migration paths of the fish (Barbarossa *et al.* 2020, Deinet *et al.* 2020). The brown trout (*Salmo trutta*) is an iconic species valued by recreational anglers. The species shows numerous migratory behav-

ious but here we focused on trout that migrate from their natal river to a lake to feed and back again to spawn (i.e., adfluvial type). In Finland, for example, spawning migrations of large brown trout attract thousands of anglers threatening the sustainability of these populations (Syrjänen *et al.* 2017). In a west-central European lake (Lake Constance), the decline in migrating brown trout was initiated by the construction of a dam which resulted in blocking the access of fish to the most important spawning grounds (Ruhlé 1996). Detrimental management decisions, such as reductions of minimum size limits and stocking of the rainbow trout (*Oncorhynchus mykiss*), further impaired the natural reproduction of the brown trout in that ecosystem. The brown trout dem-

onstrates considerable plasticity and adaptability (reviewed in Klemetsen *et al.* 2003, L'Abée-Lund & Vøllestad 2017), thus long-term conservation measures can lead to re-establishment of declined populations (e.g., Birnie-Gauvin *et al.* 2017, 2018, Brink *et al.* 2018). However, a species' recovery or re-establishment in an ecosystem after decades of absence can affect other species in the ecosystem, particularly those that have overtaken the niche of the nearly extinct species. For example, in a Finnish lake, Oulujärvi, re-establishment of pikeperch led to a drastic decline in the abundance and length-at-age of native whitefish (*Coregonus lavaretus*) forms (Vainikka *et al.* 2017). In Lake Constance, the invasion of three-spined stickleback (*Gasterosteus aculeatus*) heavily affected the abundance and growth of pelagic whitefish (*C. wartmanni*; Rösch *et al.* 2018). Therefore, when we aimed to predict the impacts of anthropogenic pressures, such as fisheries, fish stocking and/or re-establishment of declined populations, we had to consider the complex interactions among numerous species that constitute the ecosystem to fully comprehend the possible changes in that system.

Including a more holistic view of the ecosystem in management practices is an effective approach to manage fish stocks and fisheries (Zhou *et al.* 2010). However, the focus is typically on a single target species while the predators and the prey of the target species as well as other ecosystem components and interactions are often ignored (Pikitch *et al.* 2004). Understanding how an ecosystem consisting of a complex set of interactions and feedbacks responds to species removal and/or introduction, requires consideration of indirect effects related to changes in the flow of energy through the ecosystem (Hollowed *et al.* 2000). Food-web characterization has emerged as a promising tool and a first step in understanding species' roles and interactions within the ecosystem (Link 2002, Montoya *et al.* 2006, Braga *et al.* 2012). This is important particularly in mixed fisheries, where catches consist of many different fish species and age and size classes. Furthermore, it is not an uncommon scenario that while the system is exploited by mixed fisheries, more fish is simultaneously added into the system either via stocking or re-establishment (Ruhlé 1996, Vain-

ikka *et al.* 2017). The use of food-web models is typically limited by the lack of ecological data needed to validate the models and they often include a large amount of confounding environmental parameters.

We used an allometric trophic network (ATN) model to study mechanistically food-web dynamics and feeding interactions in an extensively harvested freshwater system, into which the brown trout was being re-established. In particular, we examined how re-establishment of a large piscivorous fish species valuable to recreational fisheries (i.e., brown trout) would affect the biomass densities of other species in the system (fish and zooplankton) and whether it would compromise management objectives (i.e., increase in fisheries catches). The ATN model we used was parametrized and validated for the pelagic food web of a west-central European alpine lake, Lake Constance (LC), by Boit *et al.* (2012) and modified by Kuparinen *et al.* (2016) to better address the life-history structure of fishes. We studied the ecological consequences of brown trout re-establishment for two key species in LC, which are both important to commercial fisheries — whitefish *Coregonus wartmanni* and Eurasian perch *Perca fluviatilis*; in particular (i) the abundances of whitefish, perch and associated (zooplankton) species, and (ii) the mechanisms underlying the potential changes in their abundances.

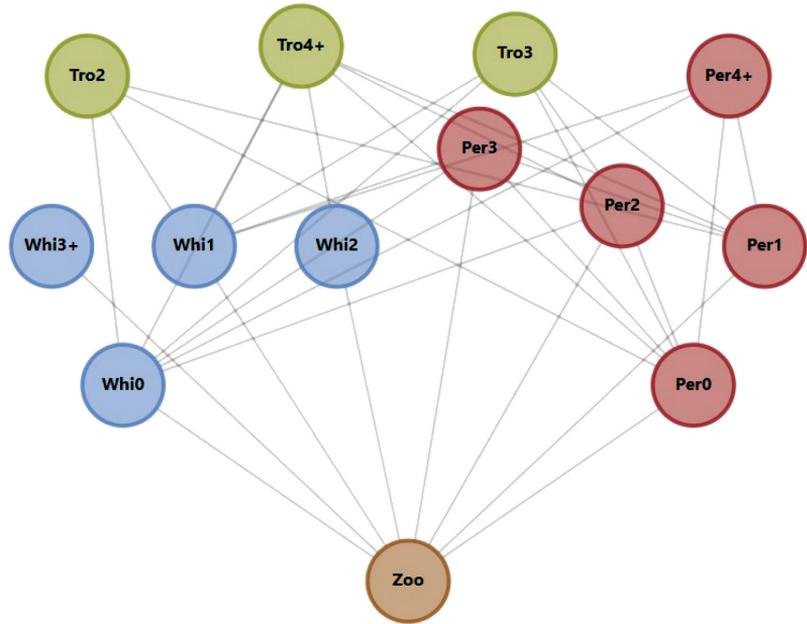
Material and methods

Food web and its dynamics

To explore the effects of trout re-establishment on the abundances of whitefish and perch and on fishery catches, we used the ATN model for the LC ecosystem (Boit *et al.* 2012) with fish life-history structure included (Kuparinen *et al.* 2016, 2019). The functional response parameters were determined according to the algorithm presented in Bland *et al.* (2019). Fish larvae were treated as invertebrates, and fish reproduction was modelled using piecewise-defined model to enforce impaired reproduction under starvation (Perälä & Kuparinen 2020).

We compared the model outputs for two scenarios of the LC food web. Both scenarios had

Fig. 1. A simplified illustration of the Lake Constance food web focusing on the fish life-stages and their interactions. The prey-averaged trophic level of the node in the food web is indicated by its vertical position. Per = perch, Whi = whitefish, Tro = trout, Zoo = all the zooplankton species consumed by the fish combined; numbers following fish species abbreviations refer to age classes. For complete food web, see Fig. 2.



the same plankton community (six basal producers, seven heterotrophic microbes, and seven invertebrates) as well as five life-history stages of both perch and whitefish (Kuparinen *et al.* 2016, 2019, Perälä & Kuparinen 2020). One of the two scenarios included three age classes of brown trout (2-, 3-, and +4-year-old). Trout larvae (age 0 year) and juvenile (age 1 year) were not included in the food web as they live in the river Rhine and are thought to migrate to the lake as smolts at two years of age. The adult trout age classes interact with the rest of the LC food web in a similar manner to the other fish species by consuming their prey and allocating portion of the gained biomass for reproduction. At the end of the growth season, they migrate to the river to spawn and return to the lake for the next growth season to feed. The amount of biomass allocated for reproduction becomes the new larvae biomass, which after gaining biomass for two years in the river turns into the smolt biomass, which joins the LC food web as the 2-year-old age class. The biomass gained by the larvae during their two-year river-life-history stage before becoming the new smolts was calculated deterministically by multiplying the larval biomass by the estimate of the fraction of the number of trout larvae surviving to age two (0.12%–1.23%) multiplied by

the ratio of the estimate of the average body mass of a trout smolt to the average body mass of a trout larva ($51362.4/37.5 = 1370$; Huusko *et al.* 2017, Syrjänen *et al.* 2017)

In the new version of the food web model, trout sits at the top of the food web as the new apex predator. It is a piscivore and feeds on the larvae, juvenile and two-year-old age classes of both whitefish and perch (Figs. 1 and 2) while having no predators itself. The trout competes for food with the adult perch as they also consume fish larvae and juveniles.

Simulation design

Each simulation year consisted of a 90-day growth season simulating the bioenergetic dynamics of the food web. The dynamics describes the carbon flow in the food web via feeding interactions between the guilds, maintenance of bodily functions for fish and zooplankton, reproductive investment of adult fish, and possible adult biomass removal by fishing. After the growth season, the fish reproduce and transfer their biomass to the next life-history stage as they age. The simulation consisted of 100 years where the first 50 years did not include

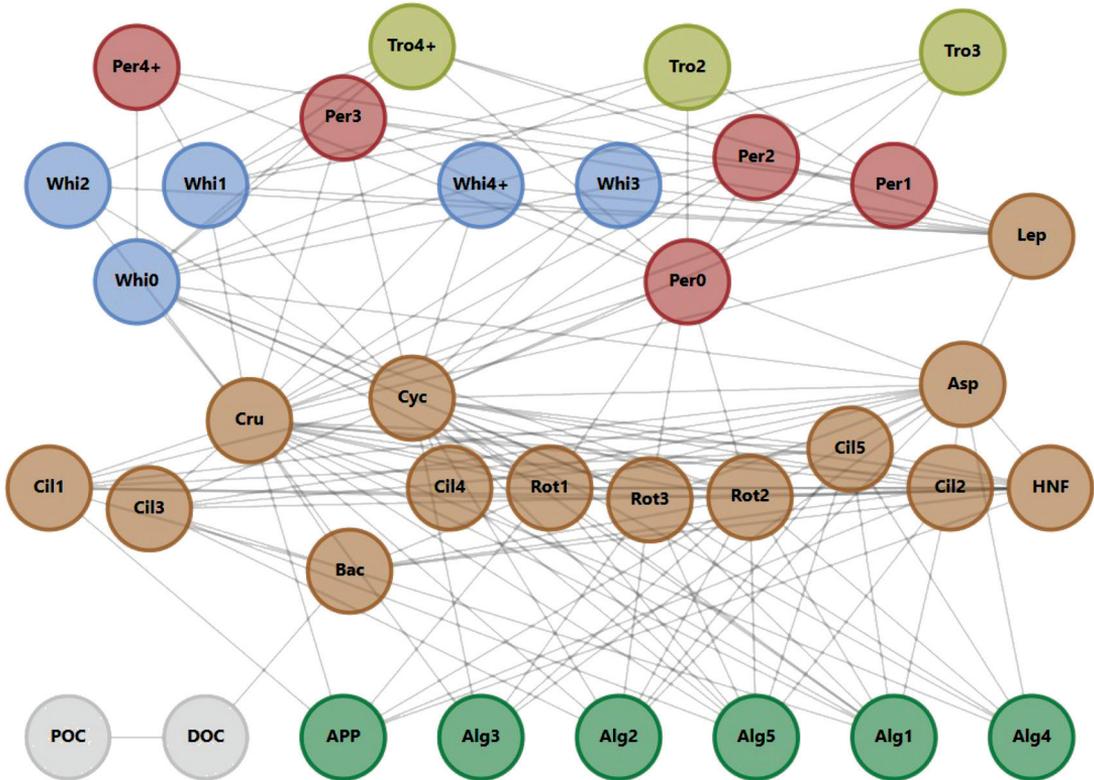


Fig. 2. The complete Lake Constance food web. The prey-averaged trophic level of the node in the food web is indicated by its vertical position. POC = particulate organic carbon, DOC = dissolved organic carbon, Alg1 = single-cell algae, Alg2 = large, single-cell algae or colonies, Alg3 = filamentous blue and green algae, Alg4 = diatoms, algal colonies, Alg5 = small, coccal algae, APP = autotrophic picoplankton, Bac = heterotrophic bacteria, HNF = heterotrophic nanoflagellates, Cil1 = small ciliates, Cil2 = small ciliates, Cil3 = medium-size ciliates, Cil4 = medium-size ciliates, Cil5 = larger ciliates, Rot1 = small rotifers, Rot2 = medium-size rotifers, Rot3 = large rotifers, Asp = large rotifers, Cru = mostly cladocerans (*Daphnia*), Cyc = cyclopoid copepods, Lep = large, carnivorous cladocerans, Whi = whitefish, Per = perch, Tro = trout. Numbers following the fish species abbreviations refer to age classes.

fishing and were considered a burn-in period to ensure the system reaches an equilibrium. For the next 50 years, different levels of fishing intensity (0.25, 0.50, 0.75) were applied to the system by subjecting all adult fish age classes to the same fishing intensity (i.e. selectivity was the same for each species and age class). The first 20 years of the fishing period were discarded, as we were not interested in the transient dynamics but instead in the yearly averages of biomasses, and total catches and consumption gains in the last 30 years. The consumption gains were further normalized by dividing them by the average biomass density of the predator guild to obtain consumption gains per unit of predator biomass density. This measure was then used to examine the energy flow through specific species interac-

tions in the food web. As there was considerable uncertainty in the parameter estimate for the fraction of the trout larvae surviving to the age of two years (0.12%–1.23%), we tested the sensitivity of the model to this parameter by testing three values for this parameter given by the minimum, midpoint and maximum of the interval (i.e., 0.12%, 0.68% and 1.23%).

Results

The re-establishment of the brown trout at the proportions of 16%–40% decreased the proportions of whitefish and perch in the fish community (Table 1). The biomass densities of both perch and whitefish adults (i.e., 2-, 3-, and

+4-year-old) decreased after the re-establishment of brown trout in LC (Table 2). Trout feeds on larval, juvenile, and 2-year-old perch (Figs. 1 and 2) and this partly explains the decreased abundance of adult perch. Furthermore, trout competes with adult perch for the same resources (i.e., prey species: larval and juvenile fish; Figs. 1 and 2). Unlike perch and trout, adult whitefish feed on zooplankton (Figs. 1 and 2). The decreased abundance of adult whitefish after the re-establishment of trout is thus not caused by competition for the same prey but by trout feeding on larval, juvenile, and 2-year-old whitefish (Figs. 1 and 2). In spite of perch experiencing both direct and indirect pressures from brown trout, the abundance of adult perch decreased only slightly more than the abundance of adult whitefish except for the oldest age class in which the differences in the relative changes in their

biomass densities were the highest (Table 2). The re-establishment of the brown trout affected only slightly the biomass densities of the zooplankton species in LC (Table 3), and the effect on the biomass density of the whole ecosystem was practically absent (Table 3). The fish community was most affected with the greatest change in the total fish biomass density being -11.8% (Table 3), with the change generally increasing with increasing fishing intensity and decreasing trout river-life-history-stage survivability.

Despite trout feeding on larval perch and whitefish, the relative biomass densities of fish larvae were affected less by the re-establishment of trout than those of the adult fish (Table 2). The reduced abundance of adult whitefish decreased the feeding competition as larval and juvenile fish feed on the same prey items as adult whitefish (Figs. 1 and 2). Indeed, the relative consumption

Table 1. Proportions of fish species (%) with and without brown trout in the food web model under the three fishing intensities and three trout river-life-history stage survival fractions.

Fishing intensity	Trout river-life-history stage survival fraction											
	Without trout			0.12%			0.68%			1.23%		
	0.25	0.50	0.75	0.25	0.50	0.75	0.25	0.50	0.75	0.25	0.50	0.75
Whitefish	34.9	36.3	37.6	28.4	30.8	33.1	25.3	27.7	30.1	23.8	26.2	28.6
Perch	65.1	63.7	62.4	47.2	49.6	51.2	39.7	42.8	45.0	36.6	39.7	42.1
Trout				24.4	19.7	15.8	34.9	29.5	24.9	39.6	34.1	29.3

Table 2. Relative changes in biomass densities (%) of whitefish and perch after the re-establishment of brown trout in Lake Constance under different fishing intensities and trout river-life-history stage survival fractions; Whi = whitefish, Per = perch.

Fishing intensity	Trout river-life-history stage survival fraction								
	0.12%			0.68%			1.23%		
	0.25	0.50	0.75	0.25	0.50	0.75	0.25	0.50	0.75
Whi0	-10.3	-9.36	-8.33	-14.3	-13.4	-12.4	-15.6	-14.7	-13.7
Whi1	-31.5	-29.0	-26.5	-40.7	-38.6	-35.5	-43.3	-41.5	-39.6
Whi2	-51.9	-47.8	-43.7	-60.7	-57.4	-54.0	-63.1	-60.1	-57.1
Whi3	-50.8	-46.5	-42.5	-57.5	-53.7	-50.2	-59.5	-55.8	-52.2
Whi4+	-22.5	-24.2	-25.7	-23.3	-25.9	-28.7	-23.4	-26.3	-29.4
Per0	-12.2	-10.9	-9.75	-16.8	-15.6	-14.5	-18.2	-17.1	-16.0
Per1	-31.5	-29.0	-26.5	-40.6	-38.6	-36.6	-43.2	-41.4	-39.6
Per2	-55.9	-51.7	-47.4	-65.4	-62.1	-58.7	-68.0	-65.0	-61.9
Per3	-55.3	-51.2	-47.1	-64.5	-61.4	-58.2	-67.1	-64.3	-61.4
Per4+	-36.4	-33.9	-31.5	-45.2	-43.4	-41.9	-47.7	-46.2	-45.1

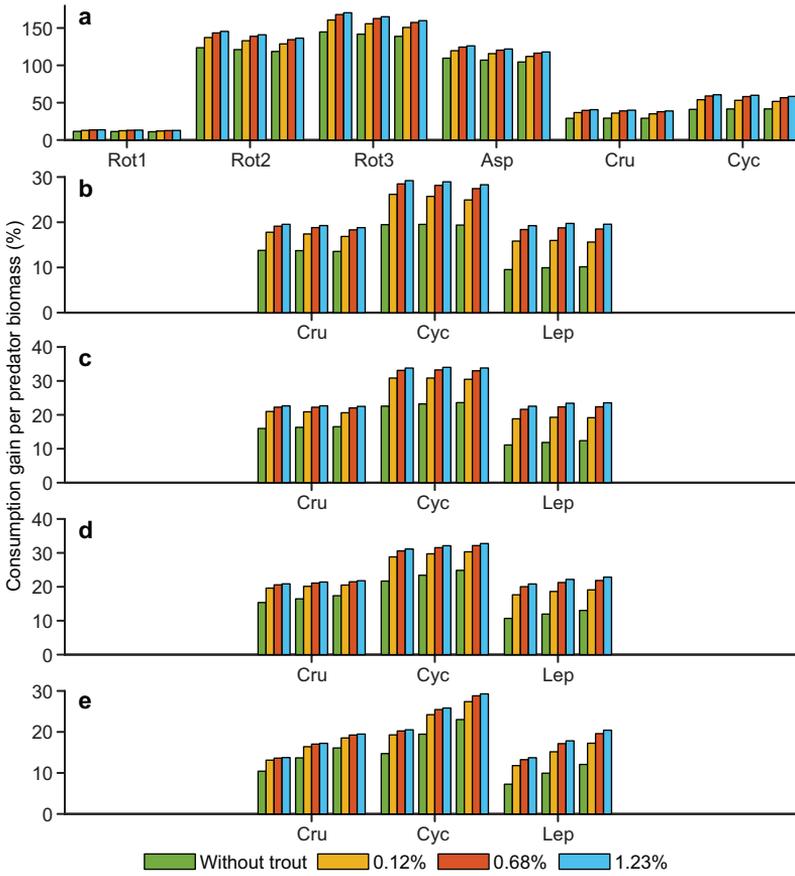


Fig. 3. Consumption gains of whitefish age classes from their respective prey guilds without trout in the model and for three different trout river life-history stage survival fractions (0.12%, 0.68% and 1.23%); (a) larvae, (b) juveniles, (c) adults of 2 years of age, (d) adults of 3 years of age, and (e) adults of +4 years of age. Three bars of each prey guild represent different fishing intensities, which are from left to right 0.25, 0.50 and 0.75, respectively. The prey guilds are Rot1 = small rotifers, Rot2 = medium-size rotifers, Rot3 = large rotifers, Asp = large rotifers, Cru = mostly cladocerans (*Daphnia*), Cyc = cyclopoid copepods, Lep = large, carnivorous cladocerans.

gains of larval fish increased in the presence of trout (Figs. 3 and 4). Similarly, relative consumption gains among juvenile and adult whitefish and perch systematically increased in the presence of trout (Figs. 3 and 4). The biomass densities of all life stages of whitefish and perch decreased as a result of the re-establishment of the brown trout and consequently the per-capita feeding rate

increased leading to the increase in consumption gains per unit of predator biomass.

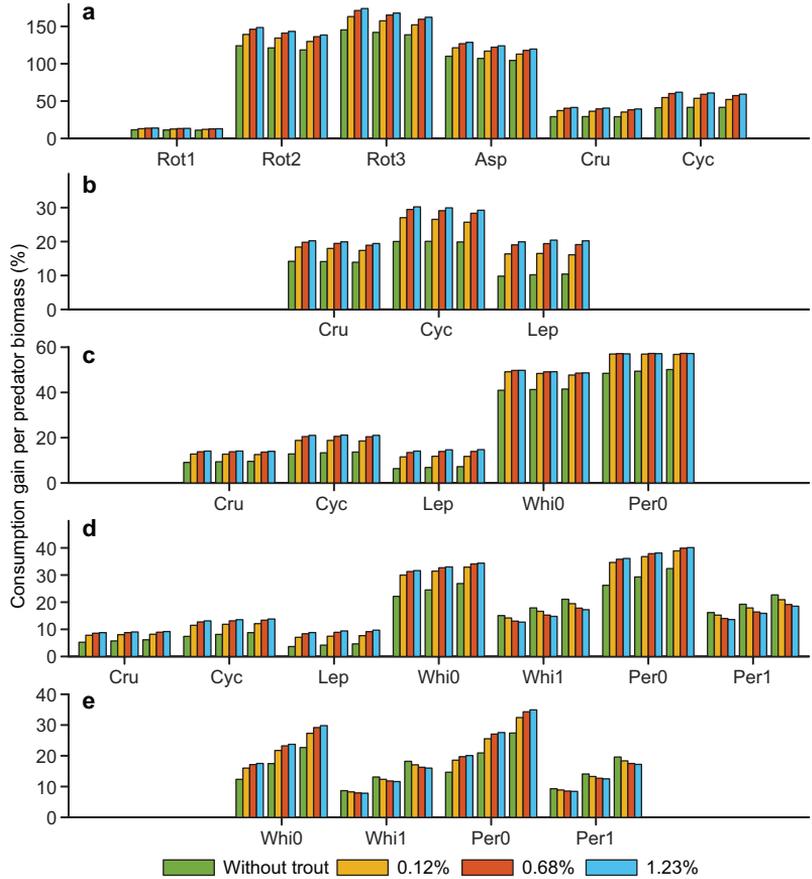
Discussion

The re-establishment of declined brown trout population in LC affected not only the exist-

Table 3 Relative changes in the biomass density (%) of the whole ecosystem, the zooplankton community and the fish community after the re-establishment of brown trout in Lake Constance under different fishing intensities and for different trout river-life-history stage survival fractions.

	Trout river-life-history stage survival fraction								
	0.12%			0.68%			1.23%		
	0.25	0.50	0.75	0.25	0.50	0.75	0.25	0.50	0.75
Fishing intensity									
Ecosystem	-0.089	-0.062	-0.041	-0.31	-0.22	-0.17	-0.46	-0.33	-0.25
Zooplankton	2.0	1.9	1.7	2.7	2.7	2.6	3.0	3.0	2.9
Fishes	-9.5	-11.2	-11.7	-5.8	-9.6	-11.8	-1.9	-6.8	-9.8

Fig. 4. Consumption gains of perch age classes from their respective prey guilds without trout in the model and for three different trout river life-history stage survival fractions (0.12%, 0.68% and 1.23%); (a) larvae, (b) juveniles, (c) adults of 2 years of age, (d) adults of 3 years of age, and (e) adults of +4 years of age. Three bars of the same colour for each prey guild represent different fishing intensities, which are from left to right 0.25, 0.50 and 0.75, respectively. The prey guilds are Rot1 = small rotifers, Rot2 = medium-size rotifers, Rot3 = large rotifers, Asp = large rotifers, Cru = mostly cladocerans (*Daphnia*), Cyc = cyclopoid copepods, Lep = large, carnivorous cladocerans, Whi0 = whitefish larvae, Whi1 = whitefish juveniles, Per0 = perch larvae, Per1 = perch juveniles.



ing perch population, with which trout shares resources, but also the whitefish population, which feeds on entirely different prey than brown trout. Reductions in the adult whitefish and perch biomass densities were substantial and were reflected in fisheries' catches (Table 4). Brown trout feeds on whitefish and perch larvae and juveniles, yet their biomass densities were least affected by the re-establishment of trout likely due to the decreased feeding competition with adult whitefish. The consumption gains systematically increased among whitefish and perch in the presence of trout suggesting that re-establishment of this piscivorous top predator led to (lower densities of) better-conditioned fish.

The brown trout affects species interacting in the LC ecosystem and their population dynamics through direct and indirect mechanisms. Trout directly reduces whitefish and perch biomass densities by feeding on their larvae, juveniles and 2-year-old adults (Figs. 1 and 2). Despite

the trout feeding intensively on fish larvae (i.e., consumption gains are relatively high; Fig. 5), its effect on their biomass densities is relatively minor (Table 1). This is partly because the average biomass of fish larvae in the lake is substantially greater than that of any other life-history stage. Furthermore, the abundant food supply for the larvae help maintaining a strong cohort even at high levels of predation. The indirect mechanism is seen in resource competition. Trout feeds on 2-year-old whitefish and consequently reduces the biomass densities of 3- and +4-year-old whitefish. These older age classes feed mainly on *Daphnia* and cyclopoid copepods, which are the main prey items of juvenile and larval whitefish and perch (Fig. 2). Lesser feeding competition leads to a potentially better body condition and lower starvation mortality of larval and juvenile fish. Despite trout having both direct and indirect effects on perch population dynamics, perch biomass densities were

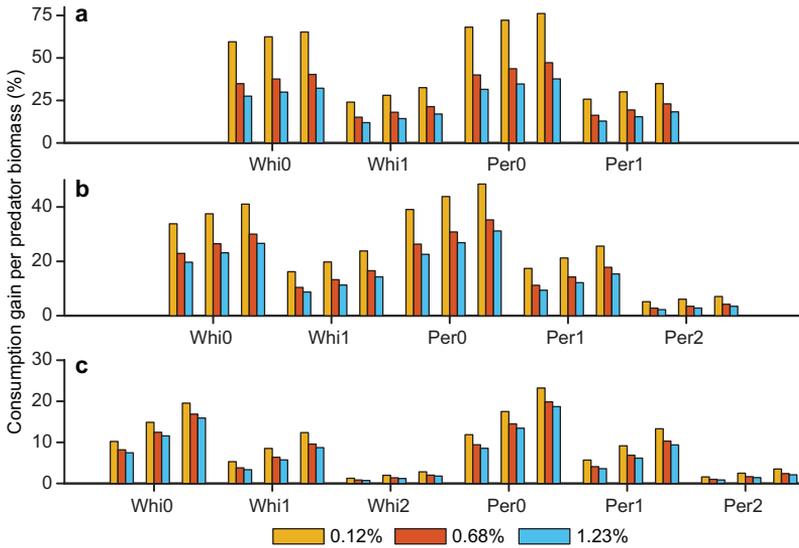


Fig. 5. Consumption gains of trout age classes from their respective prey for three different trout river life-history stage survival fractions (0.12%, 0.68% and 1.23%); (a) adults of 2 years of age, (b) adults of 3 years of age, and (c) adults of +4 years of age. Three bars of the same colour for each prey guild represent different fishing intensities, which are from left to right 0.25, 0.50 and 0.75, respectively. The prey guilds are Whi0 = whitefish larvae, Whi1 = whitefish juveniles, Whi2 = whitefish adults of 2 years of age, Per0 = perch larvae, Per1 = perch juveniles, Per2 = perch adults of 2 years of age.

not substantially lower than those of whitefish (Table 1). This is likely because perch diet does not fully overlap with that of the trout. While trout feeds on fish larvae and juveniles, 3-year-old perch, for example, feeds also on zooplankton species (Fig. 2). This diet diversification could potentially help perch to maintain similar biomass densities as those of the whitefish.

The effects of trout re-establishment on the total ecosystem biomass density were negligible (Table 3). However, changes at different trophic

levels were of varying magnitude and direction; the further away from the trout in terms of the trophic level the species were the lesser the cascading effect they experienced. The total biomass density of the phytoplankton community was not affected at all (data not shown), whereas the total biomass density of the zooplankton community increased slightly due to decreased predation by the younger perch and whitefish (Table 3). Interestingly, the total biomass density of the fish community decreased up to 11.8% (Table 3), and

Table 4. Relative changes in fish catches after the re-establishment of brown trout in Lake Constance under different fishing intensities and trout river-life-history stage survival fractions; Whi = whitefish, Per = perch.

Fishing intensity	Trout river-life-history stage survival fraction								
	0.12%			0.68%			1.23%		
	0.25	0.50	0.75	0.25	0.50	0.75	0.25	0.50	0.75
Whi2	-51.9	-47.8	-43.7	-60.7	-57.4	-54.1	-63.2	-60.1	-57.1
Whi3	-50.8	-46.5	-42.5	-57.5	-53.7	-50.2	-59.4	-55.8	-52.5
Whi4	-22.5	-24.2	-25.7	-23.3	-25.9	-28.6	-23.4	-26.3	-29.4
Per2	-55.9	-51.7	-47.4	-65.4	-62.1	-58.7	-68.0	-65.0	-61.9
Per3	-55.3	-51.2	-47.1	-64.5	-61.4	-58.2	-67.1	-64.3	-61.4
Per4	-36.4	-33.9	-31.5	-45.2	-43.4	-41.9	-47.7	-46.2	-45.1

it was highly dependent on the trout river-life-history-stage survivability and the fishing intensity. The decrease in the total fish biomass density was caused by inefficiencies in the biomass transfer in the trophic interactions, and introducing brown trout at the top of the food web increased the mean trophic level of the fish community as trout also feeds on 2-year-old whitefish and perch. On the other hand, decreasing trout river-life-history-stage survivability resulted in a decrease in total fish biomass densities, which at first might seem contradictory, but the reason for this is simply that much less trout smolt biomass returns to the lake when the trout river-life-history-stage survivability is lower.

The whitefish population in LC is largely dependent on stocking (Eckmann *et al.* 2007), hence lower biomass densities of adult whitefish had little effect on larval production. Perch, on the other hand, reproduces naturally in LC and lowered abundance of adult perch in the presence of trout should affect larval production negatively. Indeed, depending on the scenario, the larval production decreased by 22.6%–36.1% in the presence of trout (data not shown) but the average larval biomass decreased slightly less (Table 1) due to heavier larvae of better condition. In Oulujärvi, re-established pikeperch caused a steep decline in whitefish populations, but had no effect on whitefish recruitment (Vainikka *et al.* 2017). While in that study, the indirect temperature effect could have explained this, in our study the effect of trout re-establishment on perch recruitment was likely masked by the decrease in resource competition. In LC, the native fish (particularly whitefish) have recently suffered from the presence of a species different than brown trout. The three-spined stickleback was established in LC approximately a decade ago, and today constitutes almost 30% of fish biomass in the pelagic zone (Rösch *et al.* 2018). The presence of this species has caused a steep decline in whitefish catches directly through predation of whitefish eggs and larvae, and indirectly through interspecific feeding competition (particularly of *Daphnia*; Roch *et al.* 2018). The brown trout, on the other hand, has been shown to feed on sticklebacks (Björnsson 2001a, 2001b, Sánchez-Hernández *et al.* 2016), and future re-establishment of the brown trout might

potentially reduce the abundance of sticklebacks in LC, hence helping whitefish populations to recover without further costly investments in whitefish stocking.

We simulated scenarios with three fishing intensities and showed that in the presence of the brown trout the catches did not always increase with increasing fishing intensities (Table 4). For example, in the case of moderate trout river-life-history-stage survival (0.68%), at the fishing intensity of 0.5 the catches of +4-year-old whitefish decreased by almost 26% in the presence of trout, but at a higher fishing intensity of 0.75, the catches decreased even more, almost by 29% (Table 4). Similarly, the catches of +4-year-old trout did not markedly increase with the fishing intensity (Table 5). This suggests that the maximum sustainable yield in our case was achieved with fishing intensity lower than our maximum of 0.75. Gobin *et al.* (2016) suggested that in Lake Huron, whitefish populations that declined were not exposed to instantaneous fishing mortality rates exceeding 0.5. In Oulujärvi, the instantaneous fishing mortality rates were on average 0.68 (Vainikka *et al.* 2017), which was close to the highest fishing intensity simulated in our study (i.e., 0.75). Vainikka and colleagues suggested that the fishing mortality rate of 0.68 might be unsustainably high for whitefish in an environment with re-established pikeperch.

To our knowledge the effects of species re-establishment in a freshwater ecosystem have not been studied before using ecosystem simulation models. The ATN models used in this work are able to incorporate the mechanisms by which the species interact with each other and their dynamics as well as their interplay with anthropogenic

Table 5. Catches ($\mu\text{g C m}^{-3}$) of +4-year-old trout in Lake Constance under different fishing intensities (0.25, 0.50, 0.75) and trout river-life-history stage survivals (0.12%, 0.68%, 1.23%).

Fishing intensity	Trout river-life-history stage survival fraction		
	0.12%	0.68%	1.23%
0.25	4540	5620	6150
0.50	5670	6790	7310
0.75	5780	6780	7220

pressures such as fishing and stocking (e.g., Uusi-Heikkilä *et al.* 2018). Instead of relying on single-species models, in which information about other species (usually only the main prey or predator) is incorporated as a covariate, implicitly assuming unidirectional effect, or modelling simple predator–prey systems while ignoring the bigger picture, a more holistic ecosystem model approach is advisable when managing natural resources. Here, for example, instead of assuming some fixed level of increased natural mortality for the other fish species due to re-establishment of the brown trout, the increase in their mortality is the emergent property of the changes in the food web structure and the energy flows among the species in the lake ecosystem. The ATN model used in this study has hundreds of parameters some of which are known with high accuracy, some are derived using allometric scaling laws from the well-known parameters, while others are reasonable estimates (Bland *et al.* 2019). Clearly, there is great uncertainty about some of the model parameters, especially the parameter estimates of the functional response controlling the feeding interactions. Thus, quantitatively the results presented here are also uncertain. However, we feel that qualitatively the results can be trusted and they demonstrate well the possible effects of brown trout re-establishment. If more precise estimates of the reductions in fish catches are needed, for example, for management purposes, more rigorous sensitivity analysis for the key unknown parameters should be conducted. Here, we studied the model's sensitivity to the fishing intensity and trout larval survivability parameters, and the results were in line with our prior expectations confirming that the model performs properly. Moreover, we focused only on the pelagic food web and thus zoobenthos as well as birds and aquatic mammals were excluded from the study. However, we do not believe that this simplification affected the conclusions of the study.

In summary, the present study demonstrates that while re-establishment of the brown trout has some negative effects on the biomass of the other fish species, it has little effect on the overall structure and functioning of the ecosystem, including its productivity and plankton community. Instead, from a more general biological perspective, the re-establishment of an apex preda-

tor can have several positive effects as they have been shown to play a disproportionate role in the dynamics of their communities. They structure communities through top-down regulation effects (Estes *et al.* 2011), have been shown to increase community stability (Ripple & Beschta 2007, Estes *et al.* 2011), promote higher community diversity (Crooks & Soulé 1999, Beschta & Ripple 2014), and maintain natural community trophic cascades (Power *et al.* 1985, Estes & Duggins 1995). From a societal perspective, our results suggest that the re-establishment of the brown trout could negatively affect professional fishermen through decreased whitefish and perch catches but, on the other hand, benefits to recreational fishing targeting brown trout might balance the situation. Finally, from a conservational perspective, the brown trout re-establishment increases biodiversity in the lake, and restores it towards its state prior to large-scale human-induced alterations (Ruhlé 1996).

Acknowledgements

This study was funded by the Academy of Finland (grants 317495, 317940 to AK and 328953 to SUH), H2020 European Research Council (COMPLEX-FISH 770884 to AK), and Natural Sciences and Engineering Research Council of Canada (Discovery Grant to AK). The views presented in this study are those of the authors only, and the European Research Council is not responsible for the use which might be made of the information given in the paper.

References

- Barbarossa, V., Schmitt, R. J. P., Huijbregts, M. A. J., Zarfl, C., King, H. & Schipper, A. M. 2020: Impacts of current and future large dams on the geographic range connectivity of freshwater fish worldwide. — *Proceedings of the National Academy of Sciences of the USA* 117: 3648–3655.
- Beschta, R. L. & Ripple, W. J. 2014: Divergent patterns of riparian cottonwood recovery after the return of wolves in Yellowstone, USA. — *Ecology* 95: 58–66.
- Birnie-Gauvin, K., Larsen, M. H., Nielsen, J. & Aarestrup, K. 2017: 30 years of data reveal dramatic increase in abundance of brown trout following the removal of a small hydrodam. — *Journal of Environmental Management* 204: 467–471.
- Birnie-Gauvin, K., Candee, M. M., Baktoft, H., Larsen, M. H., Koed, A. & Aarestrup, K. 2018: River connectivity reestablished: Effects and implications of six weir

- removals on brown trout smolt migration. — *River Research and Applications* 34: 548–554.
- Björnsson, B. 2001a: Diel changes in the feeding behaviour of Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Ellidavatn, a small lake in southwest Iceland. — *Limnologica* 31: 281–288.
- Björnsson, B. 2001b: The trophic ecology of Arctic char (*Salvelinus alpinus*) and brown trout (*Salmo trutta*) in Ellidavatn, a small lake in southwest Iceland. — *Limnologica* 31: 199–207.
- Bland, S., Valdovinos, F. S., Hutchings, J. A. & Kuparinen, A. 2019: The role of fish life histories in allometrically scaled food-web dynamics. — *Ecology and Evolution* 9: 3651–3660.
- Braga, R. R., Bornatowski, H. & Vitule, J. R. S. 2012: Feeding ecology of fishes: an overview of worldwide publications. — *Reviews in Fish Biology and Fisheries* 22: 915–929.
- Brink, K., Gough, P., Royte, J., Schollemma, P. & Wanningen, H. 2018: *From Sea to Source 2.0. Protection and restoration of fish migration in rivers worldwide*. — World Fish Migration Foundation, Groningen, The Netherlands.
- Boit, A., Martinez, M. D., Williams, R. J. & Gaedke, U. 2012: Mechanistic theory and modeling of complex food web dynamics in Lake Constance. — *Ecology Letters* 15: 594–602.
- Collen, B., Whittton, F., Dyer, E. E., Baillie, J. E. M., Cumberlidge, N., Darwall, W. R. T., Pollock, C., Richman, N. I., Soulsby, A.-M. & Böhm, M. 2014: Global patterns of freshwater species diversity, threat and endemism. — *Global Ecology and Biogeography* 23: 40–51.
- Crooks, K. R. & Soulé, M. E. 1999: Mesopredator release and avifaunal extinctions in a fragmented system. — *Nature* 400: 563–566.
- Darwall, W. R. T. & Freyhof, J. 2016: Lost fishes, who is counting? The extent of the threat to freshwater fish biodiversity. — In: Closs, G. P., Krkosek, M. & Olden, J. D. (eds.), *Conservation of freshwater fishes*: 1–36. Cambridge University Press.
- Deinet, S., Scott-Gatty, K., Rotton, H., Twardek, W.M., Marconi, V., McRae, L., Baumgartner, L. J., Brink, K., Claussen, J. E., Cooke, S. J., Darwall, W., Eriksson, B. K., Garcia de Leaniz, C., Hogan, Z., Royte, J., Silva, L. G. M., Thieme, M. L., Tickner, D., Waldman, J., Wanningen, H., Weyl, O. L. F. & Berkhuisen, A. 2020: *The Living Planet Index (LPI) for migratory freshwater fish*. — Technical Report, World Fish Migration Foundation, Groningen, The Netherlands.
- Eckmann, R., Kugler, M. & Ruhlé, C. 2007: Evaluating the success of large-scale whitefish stocking at Lake Constance. — *Advances in Limnology* 60: 361–368.
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pickett, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E., Virtanen, R. & Wardle, D. A. 2011: Trophic downgrading of planet earth. — *Science* 333: 301–306.
- Estes, J. A. & Duggins, D. O. 1995: Sea otters and kelp forests in Alaska: generality and variation in a community ecology paradigm. — *Ecological Monographs* 65: 75–100.
- Gobin, J., Lester, N. P., Fox, M. G. & Dunlop, E. S. 2016: Effects of changes in density-dependent growth and recruitment on sustainable harvest of lake whitefish. — *Journal of Great Lakes Research* 42: 871–882.
- Hollowed, A. B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J. & Rice, J. C. 2000: Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? — *ICES Journal of Marine Science* 57: 707–719.
- Huusko, A., Vainikka, A., Syrjänen, J. T., Orell, P., Louhi, P. & Vehanen, T. 2017: Life history of the adfluvial brown trout (*Salmo trutta* L.) in eastern Fennoscandia. — In: Lobón-Cerviá, J. & Sanz, N. (eds.), *Brown trout: biology, ecology and management*: 267–295. Wiley, Hoboken, NJ.
- Klemetsen, A., Amundsen, P.-A., Dempson, J. B., Jonsson, B., Jonsson, N., O’Connell, M. F. & Mortensen, E. 2003: Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. — *Ecology of Freshwater Fish* 12: 1–59.
- Kuparinen, A., Boit, A., Valdovinos, F. S., Lassaux, H. & Martinez, N. D. 2016: Fishing-induced life-history changes degrade and destabilize harvested ecosystems. — *Scientific Reports* 6, 22245, <https://doi.org/10.1038/srep22245>.
- Kuparinen, A., Perälä, T., Martinez, N. D. M. & Valdovinos, F. S. 2019: Environmentally-induced noise dampens and reddens with increasing trophic level in a complex food web. — *Oikos* 128: 608–620.
- L’Abée-Lund, J. H. & Vøllestad, L. A. 2017: Life-history plasticity in anadromous brown trout. A Norwegian perspective. — In: Lobón-Cerviá, J. & Sanz, N. (eds.), *Brown trout: biology, ecology and management*: 251–265. Wiley, Hoboken, NJ.
- Link, J. 2002: Does food web theory work for marine ecosystems? — *Marine Ecology Progress Series* 230: 1–9.
- Montoya, J. M., Pimm, S. L. & Solé, R. V. 2006: Ecological networks and their fragility. — *Nature* 442: 259–264.
- Perälä, T. & Kuparinen, A. 2020: Eco-evolutionary dynamics driven by fishing: from single species models to dynamic evolution within complex food webs. — *Evolutionary Applications*. <https://doi.org/10.1111/eva.13058>.
- Pickett, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E. D., Link, J., Livingston, P. A., Mangel, M., McAllister, M. K., Pope, J. & Sainsbury, K. J. 2004: Ecosystem-based fishery management. — *Science* 305: 346–347.
- Power, M. E., Matthews, W. J. & Stewart, A. J. 1985: Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. — *Ecology* 66: 1448–1456.
- Ripple, W. J. & Beschta, R. L. 2007: Restoring Yellowstone’s aspen with wolves. — *Biological Conservation* 138: 514–519.
- Roch, S., von Ammon, L., Geist, J. & Brinker, A. 2018:

- Foraging habits of invasive three-spined sticklebacks (*Gasterosteus aculeatus*) – impacts on fisheries yield in Upper Lake Constance. — *Fisheries Research* 204: 172–180.
- Ruhlé, C. 1996: Decline and conservation of migrating brown trout (*Salmo trutta f. lacustris* L.) of Lake Constance. — In: Kirchhofer, A. & Hefti, D. (eds.), *Conservation of endangered freshwater fish in Europe*: 203–211. Birkhäuser Verlag, Basel, Boston, Berlin.
- Rösch, R., Baer, J. & Brinker, A. 2018: Impact of the invasive three-spined stickleback (*Gasterosteus aculeatus*) on relative abundance and growth of native pelagic whitefish (*Coregonus wartmanni*) in Upper Lake Constance. — *Hydrobiologia* 284: 243–254.
- Sánchez-Hernández, J., Eloranta, A. P., Finstad, A. G. & Amundsen, P.-A. 2016: Community structure affects trophic ontogeny in a predatory fish. — *Ecology and Evolution* 7: 358–367.
- Syrjänen, J. T., Vainikka, A., Louhi, P., Huusko, A., Orell, P. & Vehanen, T. 2017: History, conservation and management of adfluvial brown trout stocks in Finland. — In: Lobón-Cerviá, J. & Sanz, N. (eds.), *Brown trout: biology, ecology and management*: 697–733. Wiley, Hoboken, NJ.
- Uusi-Heikkilä, S., Perälä, T. & Kuparinen, A. 2018: Species' ecological functionality alters the outcome of fish stocking success predicted by a food-web model. — *Royal Society Open Science* 5, 180465, <https://www.doi.org/10.1098/rsos.180465>.
- Vainikka, A., Jakubaviciute, E. & Hyvärinen, P. 2017: Synchronous decline of three morphologically distinct whitefish (*Coregonus lavaretus*) stocks in Lake Oulujärvi with concurrent changes in the fish community. — *Fisheries Research* 196: 34–46.
- Zhou, S., Smith, A. D. M., Punt, A. E., Richardson, A. J., Gibbs, M., Fulton, E. A., Pascoe, S., Bulman, C., Bayliss, P. & Sainsbury, K. 2010: Ecosystem-based fisheries management requires a change to the selective fishing philosophy. — *Proceedings of the National Academy of Sciences of the USA* 107: 9485–9489.