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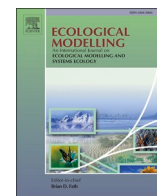
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# Effects of top predator re-establishment and fishing on a simulated food web: Allometric Trophic Network model for Lake Oulujärvi

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## ABSTRACT

Fish communities face changes in environmental conditions and fishing that affects the abundances and structures of the populations. Before 1960s there were abundant stocks of both pikeperch (*Stizostedion lucioperca*) and whitefish (*Coregonus lavaretus*) in Lake Oulujärvi, but in 1960s–1970s the stock of pikeperch declined to very low levels while whitefish stock remained abundant. Due to massive re-introductions, pikeperch recovered since 1999 and is again common while whitefish stock has declined. To understand the ecosystem-level changes observed along the recovery of the pikeperch stock, we constructed a food web model capturing the two most recent states of pikeperch abundance in Lake Oulujärvi. We used Allometric Trophic Network (ATN) model to simulate the pelagic food web in the presence and absence of pikeperch and in the presence and absence of fishing. To parametrize ATN model based on body masses and food web interactions, we used data collections of fish cohort analyses, fish individuals, fish stomach contents, zooplankton, and phytoplankton in Lake Oulujärvi. Pikeperch decreased the biomasses of its planktivorous prey. Fishing truncated the age distribution of planktivorous fish. Pikeperch and fishing had synergistic negative effects on vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*) percentages of fish biomass, and antagonistic negative effect on whitefish and brown trout (*Salmo trutta*) percentages of fish biomass. *Mysis relicta*, *Chaoborus flavicans*, *Leptodora* and other predatory zooplankton, and Cyclopoida zooplankton guilds increased with fishing and pikeperch. Fishing, and pikeperch in the presence of fishing, increased biomass of Crustacean zooplankton guild. There were marked differences between the ATN model simulations and empirically observed time series of fish stock abundances suggesting that the observed changes are partially caused by environmental or fishing-related factors that were not included in the model.

## 1. Introduction

Population abundances fluctuate naturally due to variable environmental conditions (Coulson et al., 2021) but fish communities have also faced large structural changes in recent decades (e.g., Heithaus et al., 2008; Jeppesen et al., 2012). Abundant species in fish communities may change due to altered environmental conditions or shifts in fisheries (e.g., Colby and Lehtonen, 1994; Pycha, 1962). Often, fishing has strongest

effects on top predator species (Myers and Worm, 2003; Pauly et al., 1998). These species are important members of their ecosystems and valued by fishers and common people. Management efforts and changing environmental conditions can also sometimes lead to re-establishment of populations that have declined due to temporally unfavorable conditions or overfishing. Yet, it is not known if the ecosystems recover to their previous state when the top predators return or whether they could reach a novel stable state, for example, due to altered environment. It is important to study what are the effects of

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### Abbreviations

1AN period 1	pikeperch absent, fishing absent
1AF period 1	pikeperch absent, fishing present
1PN period 1	pikeperch present, fishing absent
1PF period 1	pikeperch present, fishing present
2PN period 2	pikeperch present, fishing absent
2PF period 2	pikeperch present, fishing present
2AN period 2	pikeperch absent, fishing absent
2AF period 2	pikeperch absent, fishing present

re-established top predator species in the ecosystems they inhabit after recovering from relatively low abundances.

Declines and increases of top predator species can have large effects in the food webs or even induce trophic cascades (Heithaus et al., 2008; Martin et al., 2022). Trophic cascades are indirect effects into nonadjacent trophic levels in a food web (Carpenter et al., 1985). For example, piscivorous fish may reduce planktivorous fish which then leads to more abundant zooplankton and less abundant phytoplankton (Carpenter et al., 1985). When piscivorous fish are exposed to high fishing mortality, they are not able to limit their prey populations (Mehner et al., 2001). Further, body size and edibility of the organisms consumed, affect the trophic cascades (Brooks and Dodson, 1965; McCauley et al., 1988; Wetzel, 2001). Trophic cascades are usually more often found in freshwaters than in other ecosystems (Shurin et al., 2002; but see Kokkonen et al., 2019; Mehner et al., 2010). In biomanipulation efforts the success of inducing a trophic cascade also varies (Bernes et al., 2015). It is important to consider the complex dynamics of food webs, including for example predation, intraspecific and interspecific competition, avoidance of predation, maturation, reproduction, and ontogenetic diet shifts.

In this study, we examine the effects of a top predator fish, pikeperch (*Stizostedion lucioperca*, Percidae), and fishing on the structure of the pelagic food web in northern boreal Lake Oulujärvi, using an Allometric Trophic Network (ATN) model parameterized for the lake. Lake Oulujärvi has experienced large changes in fish community composition and water temperature (Vainikka et al. 2017a). Lake Oulujärvi is the fifth largest lake in Finland located in the northern central Finland. The lake is of major importance for regional commercial and recreational fisheries. Pikeperch and the coregonids (including vendace *Coregonus albula*, Salmonidae, and whitefish *Coregonus lavaretus*, Salmonidae) can be categorized as key species in the Lake Oulujärvi ecosystem, based on their commonness, their importance to fisheries and their ecological roles in the lake. We asked how a boreal lake ecosystem changes in response to the re-establishment of the pikeperch, thriving in warm and eutrophic waters (Hokansson, 1977; Heikinheimo et al., 2014; Olin et al., 2002; Persson et al., 1991; Veneranta et al., 2011). We hypothesized that the increased pikeperch population could contribute to the decline of the coregonids, especially whitefish, and smelt (*Osmerus eperlanus*, Osmeridae) and changes in the age distributions of vendace (Huusko and Hyvärinen 2005; Vehanen et al., 1998; Vainikka et al., 2017a).

We constructed the pelagic food web model of Lake Oulujärvi and used it as a model system to study how the re-establishment of a top predatory fish and changes in fishing pressure modify the food web structure and function. Extensive time series data on the fish stocks in Lake Oulujärvi is available from the 1970s. Before 1960s there were viable populations of both pikeperch and whitefish. At the beginning of the time series, pikeperch was at a very low abundance in Lake Oulujärvi (Colby and Lehtonen, 1994). We consider pikeperch as being re-established since 1999, when its natural reproduction started again on a large scale (Sutela and Hyvärinen, 2002; Vainikka and Hyvärinen, 2012) after stocking efforts that started in 1985 (Salminen et al., 2012).

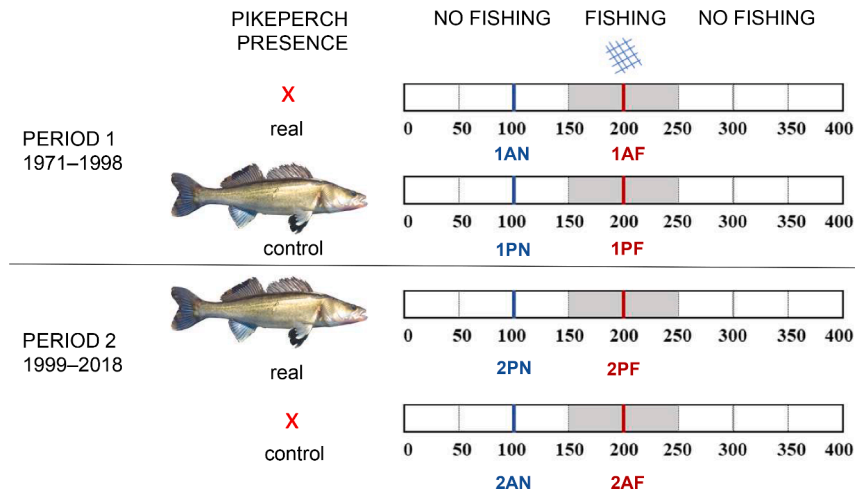
Thus, we divide the available empirical data into two periods based on pikeperch occurrence: 1) 1971–1998 (period 1, before pikeperch re-establishment), and 2) 1999–2018 (period 2, after pikeperch re-establishment). We used an ATN model to simulate a pelagic lake ecosystem before and after the re-establishment of this native piscivorous top predator species. ATN models (Berlow, et al., 2009; Brose et al., 2006; Martinez, et al., 2006; Otto et al., 2007) are modern tools to simulate complex size-structured aquatic food webs. ATN models are based on the metabolic theory of ecology (Brown et al., 2004), and they use the metabolic rates and growth rates of organismal guilds as the basis of the food web function (Boit et al., 2012; Kuparinen et al., 2016). This is the first time an ATN model is used for a northern boreal lake. We performed the ATN simulation in the presence and absence of pikeperch for both periods (Fig. 1). In addition, we studied the food web in the presence and absence of fishing. For control purposes, we also applied scenarios where pikeperch was included in the period 1 (before re-establishment) and excluded from the period 2 (after re-establishment), so that we could separate the effects of the two periods (Fig. 1). The results of the simulations were compared to the species-specific results from Pope's cohort analysis (Fig. 2) or to averaged initial biomasses when data was available. Throughout simulations, we sought to resolve 1) how the re-establishment of a top predator affects the food web, and 2) how fishing affects the food web and 3) what are the combined effects of these two factors. We studied these effects in established equilibrium states of the ATN model. We looked at the strengths of the combined effects of pikeperch and fishing and classified them as additive (sum of effects when alone), synergistic (larger than additive effects), or antagonistic (smaller than additive effects) (see Folt et al., 1999).

We specifically predicted that pikeperch presence would reduce the biomass of its planktivorous prey species (smelt, vendace, whitefish, and European perch (*Perca fluviatilis*, Percidae)). Consequently, pikeperch was expected to indirectly increase the biomass of pelagic invertebrates (except for *Mysis* that is a direct prey for pikeperch) and zooplankton and reduce the biomass of phytoplankton as expected based on trophic cascades theory (Carpenter et al., 1985). We expected that fishing would decrease the biomass of the target species, i.e., all fish species in the food web; pikeperch, vendace, smelt, whitefish, perch, and brown trout (*Salmo trutta*, Salmonidae). We also expected that fishing could have indirect effects. In general, fishing in period 2 was expected to have larger negative effects on the biomass of its target species than in period 1, as there were commonly larger fishing mortalities in period 2 than in period 1. Compensating density related intraspecific effects (Rose et al., 2001) of predation and fishing could be expected by different age classes of fish species, that could reduce the effects of both fishing and pikeperch. In addition, fishing and pikeperch were expected to have interspecific effects on the competition between different fish species, so that the fish species that had lower fishing mortality, or those that were not as much consumed by pikeperch, would benefit from the presence of fishing or the presence of pikeperch or the presence of both fishing and pikeperch.

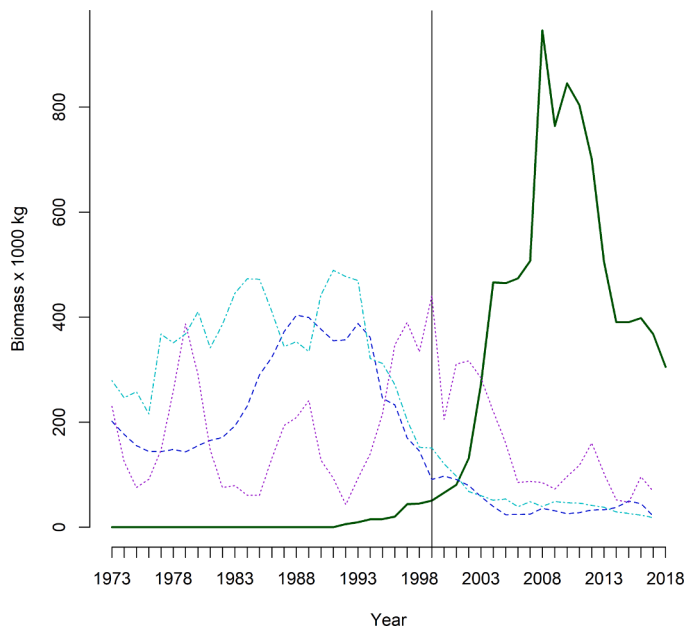
## 2. Methods

### 2.1. Study site – foundation for the simulation

Lake Oulujärvi (928 km<sup>2</sup>, 27°10'E, 64°20') represents a large humic lake with a good ecological status based on the criteria set for surface water quality by the EU Water Framework Directive. The lake has been regulated for hydropower production in the river Oulujoki since 1951 and supports significant commercial and recreational fisheries (up to 817 tons of annual catches). In the contemporary pelagic Lake Oulujärvi community, pikeperch is the most important top predator, and vendace and smelt are its main pelagic prey species (Vehanen et al., 1998). Kainuu Fisheries Research Station of Natural Resources Institute Finland (Luke) and private companies have collected fisheries data as part of the



**Fig. 1.** Graphical representation of the model periods and simulation scenarios. Models were studied in two periods: period 1 in the upper panel and period 2 in the lower panel, that had their own parametrizations based on the data from that period (growth rates of phytoplankton, metabolic rates of fish, fishing mortalities, see more specifically from the **Appendix A.**). Pikeperch is either present or absent in the models, in the real-world pikeperch is rare in the first study period 1, and it is considered re-established in the second study period 2. Model was run for 400 years (each having 90 timesteps from the growth season) and we looked at the equilibrium situation in year 100 (fishing absent) marked with blue line and in year 200 marked with red line (fishing present) from the 90th timestep. Notice that number of years is not crucial as the result of equilibrium state was studied.



**Fig. 2.** Biomass ( $\times 1000$  kg) fluctuations based on Pope's cohort analysis shown for pikeperch ages 3– $\geq 12$  (solid dark green line), whitefish ages 0– $\geq 12$  (dot-dashed turquoise line), smelt ages 0– $\geq 7$  (dashed blue line) and vendace ages 1– $\geq 4$  (dotted purple line) in the two study periods divided by a vertical line (at 1999); periods are 1971–1998 (period 1, before pikeperch re-establishment), and 2) 1999–2018 (period 2, after pikeperch re-establishment). Notice that the most recent years of the cohort analysis are more unreliable.

monitoring program set to follow the effects of the water level regulation (Vehanen et al., 2020). Catch statistics were collected using postal questionnaires and by bookkeeping of selected active fishers (Vehanen et al., 2020). As part of the monitoring program individual fish data from the different species has been collected from the catches (**Appendix B., Table B1.**).

## 2.2. Allometric Trophic Network (ATN) model

The biomass dynamics of the food web consisted of two parts. The

dynamics were first simulated for the growth season after which the fish biomass densities were moved up one age guild, and the fish larvae for the next growth season were born.

The growth season of year  $Y$  was modelled with a set of ordinary differential equations (ODEs). The biomass density ( $\mu\text{g C m}^{-3}$ ), hereafter biomass, of guild  $i$  and its rate of change were denoted by  $B_{Y,i}(t)$  and  $\dot{B}_{Y,i}(t)$ , respectively. Individual body masses are in  $\mu\text{g C}$  and biomasses are modelled as  $\mu\text{g C m}^{-3}$ . The biomasses of all guilds were collected in the vector  $\mathbf{B}_Y(t)$ . The length of the growth season was set to 90 time-steps, and thus  $t \in [0, t^{\text{end}}]$ . The models were run for 400 years, so that in the years 150–250 fishing was applied. In the following description of the growth season dynamics, we omitted the time and year indices for notational simplicity.

We denoted the set of producer, consumer, and fish guild indices by  $\mathcal{S}_P$ ,  $\mathcal{S}_C$  and  $\mathcal{S}_F$ , respectively. The biomass of producer  $i \in \mathcal{S}_P$  was affected by two factors: it grew with rate  $\mathcal{G}_i^{\text{growth}}$  and it lost biomass to its herbivore consumer  $j \in \mathcal{S}_i^{\text{consumers}}$  with rate  $\mathcal{L}_{ij}^{\text{consumption}}$ , where  $\mathcal{S}_i^{\text{consumers}}$  denotes the set of indices of the consumers of the guild  $i$ . The rate of change of the biomass of producer guild  $i$  was thus,

$$\dot{B}_i = \mathcal{G}_i^{\text{growth}} - \sum_{j \in \mathcal{S}_i^{\text{consumers}}} \mathcal{L}_{ij}^{\text{consumption}} \quad (1)$$

The intrinsic growth of the producers was modelled using a logistic growth model,

$$\mathcal{G}_i^{\text{growth}} = (1 - s_i)r_i B_i \left( 1 - \frac{1}{K} \frac{N_p}{N_p + 1} \sum_{j \in \mathcal{S}_P} c_{ij} B_j \right) \quad (2)$$

where  $s_i(0.2)$  is the fraction of exudation,  $r_i$  (1 timestep $^{-1}$ ) is the intrinsic growth rate,  $K$  ( $540,000 \mu\text{g C m}^{-3}$ ) is the shared carrying capacity of the producer community,  $N_p$  is the number of producer guilds, and  $c_{ij}$  (1 when  $i \neq j$ , 2 when  $i = j$ ) is the producer competition coefficient describing the competition between producers  $i$  and  $j$ . The  $\frac{N_p}{N_p + 1}$  term in the equation is required to scale the producer competition coefficients so that the parameter  $K$  coincides with the realized carrying capacity of the model. This is needed because all  $c_{ij}$  are not one, instead we expect intra-guild competition to be stronger than inter-guild competition. The carrying capacity  $K$  is defined for the producer species and it can be thought of as the maximum attainable biomass of the producer species in the absence of consumers. The biomass loss of producer  $i$  due to being eaten

by consumer  $j$  is

$$\mathcal{L}_{ij}^{\text{consumption}} = \frac{1}{e_{j,i}} \mathcal{G}_{ij}^{\text{consumption}} \quad (3)$$

where  $e_{j,i}$  is the assimilation efficiency, and the consumption gain for consumer guild  $i$  from the consumption of its resource guild  $j \in \mathcal{J}_i^{\text{resources}}$  is

$$\mathcal{G}_{ij}^{\text{consumption}} = f_a x_i B_i y_{ij} \text{FR}_{ij}(\mathbf{B}) \quad (4)$$

where  $f_a$  (for Bac 0.2, otherwise 0.4) is the fraction of assimilated carbon used for production of consumers biomass ( $1-f_a$  is the part of the assimilated biomass that is respired and does not become part of consumer biomass as this energy is used in feeding, predation and digestion),  $x_i$  (1 timestep<sup>-1</sup>) is the mass-specific metabolic rate (that is constant within a growth season) (Appendix A., Tables A1.–A2.),  $y_{ij}$  (Appendix A., Table A3.) is the maximum feeding rate scaling factor of guild  $i$  consuming on guild  $j$ , and

$$\dot{B}_i = \sum_{j \in \mathcal{J}_i^{\text{resources}}} \mathcal{G}_{ij}^{\text{consumption}} - \mathcal{L}_i^{\text{maintenance}} - \sum_{k \in \mathcal{J}_i^{\text{consumers}}} \mathcal{L}_{ik}^{\text{consumption}} - \mathcal{L}_i^{\text{fishing}} - \mathcal{L}_i^{\text{investment}} \quad (8)$$

$$\text{FR}_{ij}(\mathbf{B}) = \frac{\omega_{ij} B_j^q}{B_0^{q_{ij}} + d_{ij} B_0^{q_{ij}} B_i + \sum_{k \in \mathcal{J}_i^{\text{resources}}} \omega_{ik} B_k^q} \quad (5)$$

is the consumer guild's normalized functional response to its resource species densities, where  $\omega_{ij} = 1/|\mathcal{J}_i^{\text{resources}}|$  is the consumer's relative resource preference and  $|\mathcal{J}_i^{\text{resources}}|$  is the number of resource items of guild  $i$ . The exponent  $q = 1.2$  was chosen to form a relatively stable functional response (nonchaotic system dynamics, reaching equilibrium, small fluctuations during the growth season, no extinctions), intermediate between the Holling Type II and III functional responses (Williams and Martinez, 2004). The half saturation density  $B_{0ij}$  ( $\mu\text{gC m}^{-3}$ ) describes the biomass of the resource at which the consumer achieves half of its maximum feeding rate when consuming only resource  $j$  and in the absence of feeding interference, and  $d_{ij}$  ( $\text{m}^3 \mu\text{gC}^{-1}$ ) is the coefficient of intraspecific feeding interference of guild  $i$  when feeding on guild  $j$  (Appendix A., Table A3.). The intraspecific feeding inference models competition and other forms of inference between the individuals within the same guild. The functional response parameters  $B_{0ij}$  and  $d_{ij}$  were determined using the algorithm of Bland et al. (2019) with the exception that fish larvae were treated as invertebrates, except those fish larvae that ate fish (Appendix A., Table A3.). We set the maximum feeding rate scaling factor  $y_{ij}$  to 4 for ectotherm vertebrates and to 8 for invertebrate consumers, and the assimilation efficiencies  $e_{ij}$  were 0.45 and 0.85 for plant and animal/bacteria resources, respectively (Brose et al., 2006). As Bland et al. (2019) did not consider detritivores, we decided to use  $e_{ij} = 0.45$ ,  $B_{0ij} = 150,000 \mu\text{gC m}^{-3}$  and  $d_{ij} = 0.01 \text{ m}^3 \mu\text{gC}^{-1}$  for detritivores feeding on dissolved organic carbon.

The biomass of consumer guild  $i \in \mathcal{J}_C$  increases due to its consumption rates  $\mathcal{G}_{ij}^{\text{consumption}}$  on its resource species  $j \in \mathcal{J}_i^{\text{resources}}$  and decreases due to the maintenance of bodily functions  $\mathcal{L}_i^{\text{maintenance}}$  and by getting fed on by their consumers  $\mathcal{L}_{ik}^{\text{consumption}}$ ,  $k \in \mathcal{J}_i^{\text{consumers}}$ . The rate of change of the biomass of consumer guild  $i \in \mathcal{J}_C$  was thus

$$\dot{B}_i = \sum_{j \in \mathcal{J}_i^{\text{resources}}} \mathcal{G}_{ij}^{\text{consumption}} - \mathcal{L}_i^{\text{maintenance}} - \sum_{k \in \mathcal{J}_i^{\text{consumers}}} \mathcal{L}_{ik}^{\text{consumption}}. \quad (6)$$

where the maintenance loss is

$$\mathcal{L}_i^{\text{maintenance}} = f_m x_i B_i \quad (7)$$

and  $f_m(0.1)$  is the maintenance respiration coefficient. The maintenance respiration coefficient  $f_m$  is not related to feeding, but it describes the carbon lost when changing biomass of the consumer into energy for the upkeep of bodily functions.

The fish guilds ( $i \in \mathcal{J}_F$ ) are treated like the consumer guilds with the exception that they suffer additional losses due to fishing and reproduction (excluding larval and juvenile fish guilds). The fish biomass is also divided into two parts: the first part represents the fishes' "own" biomass ( $B_i$ ), and the latter part consists of the biomass of their gonads ( $B_i^+$ ) which is available for the reproduction of the next years larvae at the end of the growth season. The loss due to reproduction was considered because the biomass is transferred from the adult fish guilds to the larvae guilds. The rate of change of the biomass of fish guild  $i$  is thus

The reproduction loss was modelled with a piecewise function to enforce impaired reproduction when the maintenance losses are greater than the consumption gains (Perälä and Kuparinen, 2020; Uusi-Heikkilä et al., 2022) as

$$\mathcal{L}_i^{\text{investment}} = \begin{cases} P_i I_i \frac{\mathcal{G}_i^2}{2 \mathcal{L}_i^{\text{maintenance}}}, & \mathcal{G}_i < \mathcal{L}_i^{\text{maintenance}} \\ P_i I_i \left( \mathcal{G}_i - \frac{1}{2} \mathcal{L}_i^{\text{maintenance}} \right), & \mathcal{G}_i \geq \mathcal{L}_i^{\text{maintenance}} \end{cases} \quad (9)$$

where  $P_i$  denotes the proportion of mature biomass in guild  $i$ , and  $I_i$  denotes the strength of the reproductive investment (Appendix A., Tables A1.–A2.), and

$$\mathcal{G}_i = \sum_{j \in \mathcal{J}_i^{\text{resources}}} \mathcal{G}_{ij}^{\text{consumption}}$$

is the sum of consumption gains of guild  $i$  from all its prey guilds.

The fish biomass loss to fishing occurred at a rate

$$\mathcal{L}_i^{\text{fishing}} = F_i B_i \quad (10)$$

The guild specific fishing mortalities  $F_i$  were based on the empirical data from Lake Oulujärvi and are shown in Appendix A., Tables A1.–A2. Natural mortality of the fish was not modelled, but natural mortality through predation is included in the model through the feeding interactions.

The losses to gonads due to fishing are

$$\mathcal{L}_i^{\text{fishing gonads}} = F_i B_i^+ \quad (11)$$

The larvae biomass for the next year was calculated from the information, that the same amount of biomass invested to reproduction goes to gonads

$$\dot{B}_i^+(t) = \mathcal{L}_i^{\text{investment}} - \mathcal{L}_i^{\text{fishing gonads}} \quad (12)$$

which was added to the system of ODEs.



The particulate organic carbon guild ( $i = i_{\text{POC}}$ ) biomass is determined by egestion caused by consumer and fish feeding, producer exudation, and its dissolution into dissolved organic carbon with rate  $\alpha$

$$\dot{B}_{i_{\text{POC}}} = \sum_{i \in \mathcal{J}_C \cup \mathcal{J}_F} \left( \sum_{j \in \mathcal{J}_{\text{resource}}} \mathcal{L}_{j,i}^{\text{consumption}} (1 - e_{ij}) \right) + \sum_{j \in \mathcal{J}_P} \frac{S_j}{1 - S_j} \mathcal{L}_i^{\text{growth}} - \alpha B_{i_{\text{POC}}}. \quad (13)$$

The dissolved organic carbon guild ( $i = i_{\text{DOC}}$ ) dynamics were governed by the dissolution of particulate organic carbon and loss to consumption by detritivores:

$$\dot{B}_{i_{\text{DOC}}} = \alpha B_{i_{\text{POC}}} - \left( \sum_{k \in \mathcal{J}_{\text{consumers}}} \mathcal{L}_{i,k}^{\text{consumption}} \right). \quad (14)$$

At the start of the simulation at year  $Y = 1$ , the initial biomasses (Appendix A., Tables A1.–A2.), and the initial value for  $B_{Y,i}^+(0) = 0, \forall i \in \mathcal{J}_F, \forall Y$ . The system of ODEs was then solved for the growth season  $t \in [0, t^{\text{end}}]$ .

After the growth season of year  $Y$ , the sum of the biomasses allocated to reproduction  $B_{Y,i}^+(t^{\text{end}})$  by the adult fish guilds of a given species become the initial larvae biomass for the growth season of year  $Y + 1$

$$B_{Y+1,i}(0) = \sum_{a=0}^n B_{Y,i+a}^+(t^{\text{end}}), \quad (15)$$

where  $n + 1$  is the number of age guilds of the particular fish species, and  $B_{Y,i+a}^+(t^{\text{end}})$  is non-zero only for the mature age guilds. The initial biomasses of the juveniles (age 1), and the  $n - 2$  first adult life stages (ages 2 to  $n - 1$ , except for vendace which become mature at age 1) for year  $Y + 1$  are the biomasses of the previous life stages at the end of the growth season of year  $Y$

$$B_{Y+1,i}(0) = B_{Y,i-1}(t^{\text{end}}). \quad (16)$$

The oldest life stage (age class  $n +$ ) consists of the  $n$ -year old fish and all the older fish, and thus the initial biomass of the  $n +$  group for year  $Y + 1$  is the sum of the  $n +$  and  $n - 1$  group biomasses at the end of the growth season of year  $Y$ ,

$$B_{Y+1,i}(0) = B_{Y,i}(t^{\text{end}}) + B_{Y,i-1}(t^{\text{end}}). \quad (17)$$

For non-fish guilds ( $i \in \mathcal{J}_P \cup \mathcal{J}_C$ ), the initial biomasses for year  $Y + 1$  are the biomasses at the end of the growth season of year  $Y$

$$B_{Y+1,i}(0) = B_{Y,i}(t^{\text{end}}). \quad (18)$$

To describe the reproduction success, we added parameter  $P_{\text{suc}}$  (Probability of success), which gets values between 0 and 1 (0=no success, 1=all successful).  $P_{\text{suc}}$  parameter was used for brown trout because its natural reproduction fails. When there is no natural reproduction, fish still invest to gonads and mature, but the reproduction is not successful. Gonad gain is multiplied by  $P_{\text{suc}}$ . When  $P_{\text{suc}}$  is zero, there comes no larvae from the gonads. We did not use  $P_{\text{suc}} = 0$  for pikeperch in period 1, because the preliminary result produced unconvincingly large pikeperch biomasses. Therefore, pikeperch was either included or excluded from the models.

Models were run with The MathWorks Inc (2020).

### 2.3. Phytoplankton

Phytoplankton data were derived from the open access database of the Finnish Environment Institute (SYKE). For period 1, data included the years: 1971, 1977, 1982, 1986, 1994 and 1996–1998, and for period 2, the years: 1999–2005, 2008, 2011, 2013–2016 and 2018. We included pelagic data (sampling stations: Niskanselkä 140, Paltaselkä 138, Ärjänselkä 139 and Ärjänselkä 27) from June to August because those were the most regularly sampled months in the data and the ATN

model implicitly models the dynamics during the growth season.

We grouped phytoplankton into guilds following the classification of Lang (1997), but we modified the classification by considering the fatty acid composition of the phytoplankton (Taipale et al., 2013). According to the applied classification, and with the help of the expert judgement we divided the phytoplankton into six guilds (Appendix A., Tables A1.–A2., Appendix C.). The new guild of phytoplankton guild 1A consisted of the Cryptophyceae. Phytoplankton taxonomy followed the taxonomy presented in algaebase.org (Guiry and Guiry 2020, searched on October 6th, 2020). For the modelling, we first calculated carbon content of each cell ( $\mu\text{g C cell}^{-1}$ ) for each phytoplankton sample by dividing carbon concentration ( $\mu\text{g C l}^{-1}$ ) by the number of cells ( $\text{cells l}^{-1}$ ) (to obtain individual body mass). We calculated summer season (June–August) averages for each guild by weighting the carbon content of the cells with the carbon concentration. Because in the modelling we simulated the growth season, summer season values were thought to best present it. Then, we calculated the averages from the summer season values for each guild for both periods 1 and 2. We estimated the initial biomasses ( $\mu\text{g C m}^{-3}$ ) as averages for each guild per sampling occasion (date and sampling station) and from these averages we calculated the averages for periods 1 and 2. We used the phytoplankton guild 1A as a reference guild, and therefore all growth rates for the producer species (Eq. (19)), and metabolic rates for the consumer species (Eq. (20), Eq. (24)) are calculated in proportion to this reference guild, as seen in the equations where the individual body mass of the reference guild term is included.

$$r_i = \left( \frac{Bm_{\text{ref}}}{Bm_i} \right)^{0.15} \quad (19)$$

Where the growth rate for species  $i$  is denoted as  $r_i$ ,  $Bm_{\text{ref}}$  is the individual body mass of the reference guild, and  $Bm_i$  is the individual body mass of guild  $i$  (Brose et al., 2006; de Castro and Gaedke, 2008; Boit et al. 2012).

### 2.4. Bacteria, heterotrophic nano-flagellates, and autotrophic picoplankton

The data for the smallest organisms were limited, although heterotrophic nano-flagellates were observed each year. Because of the limited data on heterotrophic nano-flagellates (HNF), bacteria (Bac) and autotrophic picoplankton (APP), we used the same average cell carbon contents as used in Lake Constance (Kuparinen et al., 2016). Yet, we lowered the metabolic rate of Bac (0.04), and the intrinsic growth rate of APP (0.6) according to Boit et al. (2012). The HNF metabolic rate (0.47 period 1, and 0.46 period 2) differed slightly from the Lake Constance values because of the different reference guilds. We calculated the metabolic rates for consumers as:

$$x_i = 0.314 \times \left( \frac{Bm_{\text{ref}}}{Bm_i} \right)^{0.15} \quad (20)$$

where the metabolic rates for invertebrate consumers is denoted as  $x_i$ ,  $Bm_{\text{ref}}$  is the individual body mass of the reference guild, and  $Bm_i$  is the individual body mass of the guild  $i$  (Brose et al. 2006; de Castro and Gaedke, 2008; Boit et al., 2012).

The initial biomasses of Lake Constance were used, except for HNF for which we calculated the initial biomasses (Appendix A., Tables A1.–A2.) in the same way as the initial biomasses for the phytoplankton.

### 2.5. Zooplankton and pelagic invertebrates

We expected the trophic linkages between the groups of zooplankton, phytoplankton, Bac, HNF, and APP to be similar as in Lake Constance, because the guilds were divided similarly and no Oulujärvi-specific data on the linkages were available. Data on the zooplankton

(species and their individual lengths) on the years 1982 and 1984 in Lake Oulujärvi were available (Sutela, 1985). We divided the observed zooplankton species into guilds (Appendix A., Tables A1.–A2., Appendix D., Table D1.) according to Lang (1997) but combining the adult and juvenile groups (Kuparinen et al., 2016). We calculated the carbon contents for the different species ( $\mu\text{g C individual}^{-1}$ ) with specific equations from the available length data from Lake Oulujärvi (Sutela, 1985) with depths 0–20 m averaged, or from the literature weight or length data, or we used the values of carbon content from the literature directly (Appendix D., Table D1.). We weighted the guild specific carbon contents ( $\mu\text{g C individual}^{-1}$ ) with the average volume ( $10^6 \mu\text{m}^3$ ) when it was known. For all zooplankton guilds, we used similar initial biomasses as in Lake Constance.

For the ciliates we used the carbon contents from Lake Constance study (Boit et al., 2012) but their metabolic rates were calculated relative to the Lake Oulujärvi reference guild (Eq. (20)). In Lake Oulujärvi, species from the ciliate guilds 2 and 3, had not been observed (Lang, 1997; Sutela, 1985). The small ciliates had not been the target in the Lake Oulujärvi study (Sutela, 1985). According to comparisons of Lake Constance with other northern lakes: Peipsi (Zingel and Haberman, 2007), Vörtsjärv (Zingel et al., 2019) and Köyliönjärvi (Wiackowski et al., 2001), species belonging to all five ciliate guilds, have been found in these lakes too.

Pelagic invertebrates included in the study were *Chaoborus flavicans* (Chaoboridae), hereafter called *Chaoborus* and *Mysis relicta* (Mysidae), hereafter called *Mysis* (Appendix A., Tables A1.–A2.). Sixteen individuals of *Chaoborus* had been observed in lake Oulujärvi in 1984 sampling (Sutela 1985). In lakes with abundant planktivorous fish stocks, *Chaoborus* may not be common, but occurrence of abundant piscivorous fish populations can support the coexistence of *Chaoborus* and fish (Liljendahl-Nurminen, 2006). We modelled the diet of *Chaoborus* based on the literature (Pekcan-Hekim et al., 2006) (Appendix E., Table E1.). *Mysis* had been recorded in the pikeperch diet and was also found in the Lake Oulujärvi in the study of Sutela (1985). The dry weights and the diet of *Mysis* (Appendix E., Table E1.) were taken from the literature (Horppila et al., 2003). We calculated the metabolic rates for the zooplankton and pelagic invertebrates (Eq. (20)). We gave initial biomasses for the *Mysis*  $100 \mu\text{g C m}^{-3}$  and for the *Chaoborus*  $10 \mu\text{g C m}^{-3}$ . Initial parameters for the zooplankton and pelagic invertebrate guilds were the same for both periods.

## 2.6. Fish community

We obtained data from pelagic fishes (pikeperch, vendace, smelt, whitefish, perch, and brown trout) from the Kainuu Fisheries Research Station (Härkönen et al., 2023 (chapter 4.2); Härkönen and Hyvärinen, 2024a, 2024b, 2024c; Härkönen and Hyvärinen, 2024d, 2024e, 2024f; Härkönen and Hyvärinen, 2024g, 2024h). We combined the different ecotypes of whitefish as they have shown similar stock development dynamics (Vainikka et al., 2017a), and they had broad diet categories. We omitted roach (*Rutilus rutilus*, Cyprinidae), burbot (*Lota lota*, Lotidae) and pike (*Esox lucius*, Esocidae) from the model due to the scarcity of the data and assumed lower relevance in the pelagic community (Appendix B., Table B1. on data of fish species included) than study species. We divided fish into functional guilds based on species and age classes. Pikeperch, smelt, whitefish, and perch had age classes from age 0 to age  $\geq 6$ , vendace had age guilds from 0 to age  $\geq 4$  and brown trout lake-age classes from age 0 to age  $\geq 3$ . Lake-age describes years, in which brown trout has been present in the lake. Number of the age classes in vendace and brown trout is smaller because they are generally very short-lived in the study system.

We obtained fishing mortality ( $F$ ) and biomass estimates from the cohort analyses (Appendix A., Tables A1.–A2.), except for perch the value was approximated based on old reports (Salojärvi et al., 1985). Cohort analyses were based on the previous studies (vendace: Huusko and Hyvärinen, 2005; pikeperch: Vainikka and Hyvärinen, 2012;

Vainikka et al., 2017b; whitefish: Vainikka et al., 2017a; smelt: Hyvärinen and Huusko, 2006) but updated with more recent years (Härkönen et al., 2023). For brown trout we obtained  $F$  and the biomasses for lake-ages by assuming that lake-age-0 contains brown trout at the ages 2–3, lake-age-1 contains brown trout at the ages 3–4, lake-age-2 contains brown trout at the ages 4–5 and lake-age-3 contains brown trout at the ages 5–6 (Hyvärinen and Huusko, 2005). For perch we used similar values for both periods. For smelt, vendace, and whitefish, old period  $F$  was the average over the years 1973–1998 and for pikeperch average over the years 1992–1998. Before 1992, pikeperch population size for cohort analysis was too low. For the new period,  $F$  for pikeperch, smelt, vendace, and whitefish, was the average over the years 2013–2017. Most recent years were used because we were interested in the newest  $F$  values. We calculated the initial biomasses as  $\mu\text{g C m}^{-3}$ , for the whole lake area as averaged over the years for whole periods. Initial biomasses per  $\text{m}^3$  are given for each guild as a starting point for the model. The model has been tested to be robust for the choice of the initial biomasses as the equilibrium state is independent of the initial biomass, whenever fish recruit naturally. When there is no natural reproduction, initial biomasses and hatchery inputs have an effect.

Brown trout, pikeperch, and whitefish have been stocked annually in Lake Oulujärvi. Correspondingly, we added a hatchery source of the fish for these species in the model. We assumed brown trout to lack natural reproduction. Yearly hatchery inputs for period 1 (calculated as yearly averages over period 1) were,  $153.859 \mu\text{g C m}^{-3}$  for brown trout lake-age-0 and  $104.173 \mu\text{g C m}^{-3}$  for whitefish age-0 and  $5.558 \mu\text{g C m}^{-3}$  for pikeperch age-0 (when included in the model). For period 2, yearly hatchery additions (calculated as yearly averages over the period 2) were  $13.699 \mu\text{g C m}^{-3}$  for pikeperch age-0,  $137.283 \mu\text{g C m}^{-3}$  for brown trout lake-age-0 and  $62.188 \mu\text{g C m}^{-3}$  for whitefish age-0.

We modified the fish ages so that the age 0 begins in the year of hatching. First year (age 0) last until 1st of June, when we considered the second year of life (age 1+) and all later years, and growth (due to increased temperature) to start. For pikeperch, brown trout, smelt, vendace, and whitefish we predicted lengths with a linear regression model with capture day as explanatory variable and grouped by age and study period (Example of the model equation for a fish species with five age classes (Eq. 21) :  $\text{Body length} = \beta_0 + \beta_1 \cdot \text{day}$  (running number of capture day counted from June 1st onwards)  $+ \beta_2 \cdot I(\text{age 1 period 1}) + \beta_3 \cdot I(\text{age 2 period 1}) + \beta_4 \cdot I(\text{age 3 period 1}) + \beta_5 \cdot I(\text{age 4 period 1}) + \beta_6 \cdot I(\text{age 0 period 2}) + \beta_7 \cdot I(\text{age 1 period 2}) + \beta_8 \cdot I(\text{age 2 period 2}) + \beta_9 \cdot I(\text{age 3 period 2}) + \beta_{10} \cdot I(\text{age 4 period 2}) + \beta_{11} \cdot \text{day} \times I(\text{age 1 period 1}) + \beta_{12} \cdot \text{day} \times I(\text{age 2 period 1}) + \beta_{13} \cdot \text{day} \times I(\text{age 3 period 1}) + \beta_{14} \cdot \text{day} \times I(\text{age 4 period 1}) + \beta_{15} \cdot \text{day} \times I(\text{age 0 period 2}) + \beta_{16} \cdot \text{day} \times I(\text{age 1 period 2}) + \beta_{17} \cdot \text{day} \times I(\text{age 2 period 2}) + \beta_{18} \cdot \text{day} \times I(\text{age 3 period 2}) + \beta_{19} \cdot \text{day} \times I(\text{age 4 period 2})$ . In the equation  $I(\cdot)$  is an indicator variable with a value 1 when the data point belongs to the given group and zero otherwise.) for 15th July (Appendix F., Table F1.) with The MathWorks Inc (2020). If there was only monthly information available for the time of capture, we set the day to 15th (140 cases in pikeperch and 3279 cases in whitefish). In the results, there were clear jumps in the lengths of pikeperch from age 3 to age 4. To avoid these jumps, we obtained the lengths for those ages from Von Bertalanffy (VB) growth curves fitted using the Ford–Walford plot estimation implemented in AV Bio-Statistics (Appendix F., Table F1.). In addition, we used VB to get 0–1-year-old perch lengths to avoid large differences between the study periods (see Appendix F., Table F1.). Since there were so few capture dates available in the perch data, we used the average length for each age guild for period 2 (instead of the linear model) (Appendix F., Table F1.). For the period 1, VB growth was available (Salojärvi et al., 1985) (Appendix F., Table F1.).

To calculate the metabolic rates for the model, we transcribed fish lengths into fresh weights. We fitted the equation

$$FW = a \times L^b \quad (22)$$

Where  $FW$ =fresh weight,  $L$ =length, using nonlinear least squares estimation in R 4.0.2 (R Core Team, 2020). (Appendix F., Table F1.) and took the starting parameter values for each species from the FishBase (<https://www.fishbase.de/home.htm>). We calculated the carbon contents ( $\mu\text{g C}$ ) for the fish for both periods as:

$$Bm_i = 0.2 \times 0.53 \times 10^6 \times FW_i \quad (23)$$

where the individual body mass of fish guild  $i$   $\mu\text{g C}$  is denoted as  $Bm_i$ ,  $FW_i$  is the individual weight of guild  $i$  in grams (Kuparinen et al., 2016).

From the carbon content we calculated the metabolic rate as:

$$x_i = 0.88 \times \left( \frac{Bm_{ref}}{Bm_i} \right)^{0.11} \quad (24)$$

where the metabolic rate is denoted as  $x_i$ ,  $Bm_{ref}$  is the individual body mass of the reference guild,  $Bm_i$  is the individual body mass of fish guild  $i$  (Killen et al. 2007, 2010; Kuparinen et al., 2016).

To determine the diets of each fish species for the food web construction, we used the data on stomach contents of Lake Oulujärvi fish (pikeperch and brown trout) and literature sources. We used the stomach content data to give suggestive information on the diets for the final assumed diets (Appendix E., Tables E4.–E9.). In the stomach data, the ages of the predator fishes were known, and we handled them similarly as in the length data (see determination of age 0 and age 1+ above). The lengths of the prey had been measured. The age of the prey was not observed, and we thus estimated it based on its length and a table of age guild specific length intervals (Appendix F. Table F2.). We obtained these length intervals from body lengths predicted for 15th July for each species age guild by using similar linear regressions as in equation 21, but now grouped by age only (Appendix F., Table F3.). So, we expected no differences in the possible diets in the different periods. For perch we used averages of the previously obtained period 1 and 2 length-values (Appendix F., Table F2.). We calculated the percentages of different prey fish in numbers. Calculation of the percentages only included species, and ages that were included in this study.

When the number of prey guild individuals in the diet was at least 5 % of the studied fish prey in the predator diet data, we included the guild as potential prey in the model. When the prey had over 5 % in an earlier and later predator age class diet, the prey was also included in the age classes in between even if falling under the 5 % limit. For whitefish we accepted any occurrence in the diet, as it was probably already rare when stomach content data had been collected. Mysis was found in pikeperch diet and therefore included.

We estimated the age at maturity of the fish for the model (Appendix A., Tables A1.–A2.). Pikeperch of Lake Oulujärvi typically matures at age 6. Vendace generally matures at age 1+ (Salojärvi, 1987) and both smelt and whitefish latest at age 4+ in Oulujärvi (Salojärvi et al., 1985; Salojärvi, 1992). For perch, we used maturity parameter values (95 % mature at age  $\geq 4$ ) similar to ATN models of Lake Constance (Kuparinen et al., 2016, Appendix A., Tables A1.–A2.), as there is no exact information on its age at maturation in Lake Oulujärvi. For brown trout we assumed half of the lake-age  $\geq 3$  guild mature (Appendix A., Tables A1.–A2.) so that part of the obtained energy goes to gonads although its reproduction fails due to lack of spawning areas or fishing mortality.

## 2.7. Calculation

We examined the equilibrium states as the model result. To reach this, we ran simulations for 400 years, first without fishing in years 0–149, then with fishing in years 150–250, and then again without fishing in years 251–400. Each growth season within a year included 90 timesteps. When fishing was applied in the model, all guilds of all fishes that had fishing mortality of at least 0.1 were fished. We made sure the whole system and reproduction total biomass reach equilibrium in the

absence of fishing (years 1–150), in the presence of fishing (years 151–250) and again in the absence of fishing (years 251–400) by studying a moving coefficient of variation using a window length of five years (similar method as used in (Uusi-Heikkilä et al., 2022) to study dampening of fishing-induced biomass variations). At a first look the equilibrium could also be seen by eye from the biomass figures, but to show this numerically we arbitrarily chose a small enough tolerance level of 0.0001 for the moving coefficient of variation which ensures that the system has reached its equilibrium state (this arbitrary choice was enough to ensure a stable model output). Number of years is only important for the reaching of equilibrium as results are shown in equilibrium state.

We simulated the food web dynamics for periods 1 and 2 in the presence of pikeperch (scenario P (as presence)) and absence of pikeperch (scenario A (as absence)). Pikeperch is considered re-established in period 2 (1999–2018), but we look at the presence of pikeperch in both periods to separate its effects from the other differences in parametrization between these periods. We present the results calculated for the last time step in the growth season of an equilibrium state year (100) and equilibrium state year (200). During these years the model was in equilibrium as measured by the variation in the beginning-of-year biomasses (although during the growth season fluctuations exist). We do not show the result of the second “no fishing” period (years 251–400) as it would be practically identical to the first “no fishing” period (years 1–150), because there were no extinctions in the fishing period (years 150–250), and after fishing ceased the non-evolving system returned to its pre-fishing equilibrium state. We calculated the results in the presence of fishing (using simulation year 200; scenario F (as fishing)) and in the absence of fishing (using simulation year 100, scenario N (as no fishing)). Therefore, we obtain results from the following four scenarios for period 1: 1PF, 1PN, 1AF, 1AN, and for period 2: 2PF, 2PN, 2AF, 2AN (Fig. 1). The most realistic scenario for period 1 would be 1AF and for period 2 it would be 2PF. The other scenarios are tested for comparison and control purposes so that we can understand how much the effects are explained by pikeperch, by fishing and how much by different period parametrizations. The four scenarios allow us to compare the situations when the different compositions are: pikeperch and fishing present (scenario PF), only pikeperch present (scenario PN), only fishing present (scenario AF) and both pikeperch and fishing absent (scenario AN).

We calculated path-based prey averaged trophic positions (Levine, 1980). We calculated them for all guilds, excluding bacteria. Trophic position of algae was 1. The trophic positions of all other guilds are the average trophic positions of their resources plus one. The trophic positions can be solved in a vector form as:

$$T = (I - Q)^{-1} \mathbf{1} \quad (25)$$

where  $I$  is the identity matrix,  $Q$  is matrix having elements  $Q_{ij} = 1/N_i^{\text{resources}}$  if  $i$  eats  $j$  and zero otherwise,  $N_i^{\text{resources}}$  being the number of resource guilds of guild  $i$ , and  $\mathbf{1}$  is a vector of ones (Levine, 1980).

We calculated the weighted average trophic position (WATP), were proportions of the biomass of each guild on the total biomass were used in weighting.

We calculated the proportions (%) over the total biomass for each guild and trophic levels. From the fish guilds we classified pikeperch, and brown trout guilds, and perch age-4– $\geq 6$  guilds as piscivorous fish. Rest of the fish guilds were classified as planktivorous fish. We calculated the proportions (%) of the fish biomass for each fish species. Simulations in the presence and absence of pikeperch and fishing in both periods were compared. Simulations in the presence and absence of pikeperch and fishing in both periods were compared to evaluate whether the effects were additive, or antagonistic or synergistic. Effects were classified as additive (sum of the effects of pikeperch and fishing when alone), synergistic (larger than additive effects), or antagonistic (smaller than additive effects) (see Folt et al., 1999). We preferred to



show the results as percentages as those are more easily understandable than carbon contents. Model is also better suitable for studying relative effects instead of actual biomasses.

We calculated ratios of the guild specific biomasses in period 2 to the guild specific biomasses in period 1 for each guild. In addition, we calculated similar ratios for comparisons of different model results. We also calculated ratios of initial biomass in the period 2 to initial biomass in period 1 for those biomasses of phytoplankton and fish that were totally data-based. Then we calculated Pinkham & Pearson's similarity index for the fish level (including guilds: smelt age-0, smelt age-1, smelt age-2, smelt age-3, smelt age-4, smelt age-5, smelt age $\geq$ 6, vendace age-1, vendace age-2, vendace age-3, vendace age $\geq$ 4, whitefish age-0, whitefish age-1, whitefish age-2, whitefish age-3, whitefish age-4, whitefish age-5 and whitefish age $\geq$ 6) and phytoplankton level (including guilds of all phytoplankton guilds except autotrophic picoplankton) and for the broader ecosystem level (including guild in the previous fish and phytoplankton level) to look how similar ratios based on initial biomass were to model results.

$$\text{Similarity index} = \sum_{i=1}^S \frac{\min(p_{ia}, p_{ib})}{\max(p_{ia}, p_{ib})} \times \frac{(p_{ia} + p_{ib})}{2}, \quad (25.a)$$

where  $p$  = proportion,  $a$  = model ratio of 2PF/1AF,  $b$  = data ratio of 2PF/1AF (phytoplankton data and Pope's cohort analysis data,  $S$  = guild. Largest possible similarity index value was 1.

We studied the results with R 4.0.2 (R Core Team, 2020). and The MathWorks Inc (2020).

### 3. Results

Phytoplankton comprised the largest proportion of the total biomass of the trophic guilds, and it was followed by zooplankton, planktivorous fish, piscivorous fish (in scenarios 1AN, 1PN, 1PF, 2AN, 2PN, and 2PF) or pelagic invertebrates (in scenarios 1AF and 2AF), and finally bacteria, and heterotrophic nano-flagellates (Table 1). In the 1AF there were more phytoplankton, zooplankton and planktivorous fish than in the 2PF, and less pelagic invertebrates and piscivorous fish (Table 1). In the 2PF there were more piscivorous fish and pelagic invertebrates than in the 1AF and less phytoplankton, zooplankton and planktivorous fish (Table 1).

Fishing had increasing effect on the proportion of phytoplankton, zooplankton, and pelagic invertebrates and decreasing effect on the proportion of the total biomass of planktivorous and piscivorous fish (Fig. 3). The presence of pikeperch increased the proportion of the total biomass of phytoplankton, zooplankton, pelagic invertebrates, and piscivorous fish and decreased the proportion of the total biomass of planktivorous fish (Fig. 3). Combined effects of fishing and pikeperch on the phytoplankton, zooplankton, and piscivorous fish proportions of the total biomass were antagonistic (Fig. 3). The combined effects of fishing and pikeperch on the pelagic invertebrates and planktivorous fish proportions of the total biomass were synergistic (Fig. 3). Division of the biomass among fishes was quite similar in both periods, largest effect of period was on perch percentage of biomass, where the body size of perch in these different periods can have affected results (Fig. 3). The proportion of pikeperch of all fish biomass was approximately 30 % in the absence of fishing and 41 % in the presence of fishing in both study periods. Effect of pikeperch was negative on the proportion of the fish biomass of brown trout, perch, smelt, vendace, and whitefish (Fig. 3). Effect of fishing was negative on the proportion of the fish biomass of brown trout and vendace in both periods, but on perch only in period 1 (Fig. 3.). The effect of fishing was positive on the proportion of the fish biomass of smelt, whitefish, and pikeperch in both periods and on perch in period 2 (Fig. 3). Combined effects of pikeperch and fishing were negative on the biomass proportion of all other fish species (Table 1, Fig. 3). Combined effects of pikeperch and fishing were antagonistic on the brown trout and whitefish proportions of the fish biomass in both periods, and on the proportion of perch of the fish biomass in period 1

**Table 1**

Percentages of biomass in different trophic levels, fish species and guilds in period 1AF (in the absence of pikeperch and presence of fishing) and period 2PF (in the presence of pikeperch and fishing). Other includes bacteria and heterotrophic nanoflagellates.

Trophic level		Period	
		1AF%	2PF%
Piscivorous fish		1.6	6.2
Planktivorous fish		13.2	6.8
Pelagic invertebrates		2.9	5.7
Zooplankton		29.8	29.1
Phytoplankton		52.5	52.2
Other		0.01	0.01
Fish species		Period	
		1AF%	2PF%
Brown trout		0.4	0.1
Perch		20.5	17.9
Pikeperch		–	41.2
Smelt		32.1	11.6
Vendace		18.3	12.2
Whitefish		28.7	16.9
Guild	Abbreviation	Period	
		1AF%	2PF%
Heterotrophic nanoflagellates	HNF	0.01	0.01
Autotrophic picoplankton	APP	0.1	0.1
Algae group 1A	Alg1A	1.5	1.6
Algae group 1B	Alg1B	1.2	1.0
Algae group 2	Alg2	6.3	5.0
Algae group 3	Alg3	22.9	23.7
Algae group 4	Alg4	17.1	17.2
Algae group 5	Alg5	3.5	3.6
Ciliate group 1	Cil1	0.01	0.01
Ciliate group 2	Cil2	1.5	1.5
Ciliate group 3	Cil3	3.4	3.0
Ciliate group 4	Cil4	2.6	2.6
Ciliate group 5	Cil5	6.3	5.9
Rotifer group 1	Rot1	0.9	0.9
Rotifer group 2	Rot2	5.0	5.0
Rotifer group 3	Rot3	5.7	5.7
Asplanchna	Asp	2.3	2.1
Crustacean zooplankton	Cru	0.8	0.8
Cyclopoida zooplankton	Cyc	1.0	1.1
Leptodora and other predatorous zooplankton	Lep	0.3	0.4
Mysis relicta	Mys	0.8	0.9
Chaoborus flavicans	Cha	2.1	4.8

Table 1. continues.

Guild	Abbreviation	Period	
		1AF%	2PF%
Brown trout lake-age-0	Br0	0.02	0.01
Brown trout lake-age-1	Br1	0.02	0.002
Brown trout lake-age-2	Br2	0.01	0.0004
Brown trout lake-age $\geq$ 3	Br3	0.01	0.0002
Perch age-0	Per0	0.6	0.7
Perch age-1	Per1	0.4	0.3
Perch age-2	Per2	0.3	0.3
Perch age-3	Per3	0.2	0.2
Perch age-4	Per4	0.3	0.2
Perch age-5	Per5	0.3	0.2
Perch age $\geq$ 6	Per6	1.0	0.5
Pikeperch age-0	Ppe0	–	0.6
Pikeperch age-1	Ppe1	–	0.7
Pikeperch age-2	Ppe2	–	0.8
Pikeperch age-3	Ppe3	–	0.9
Pikeperch age-4	Ppe4	–	0.9
Pikeperch age-5	Ppe5	–	0.8
Pikeperch age $\geq$ 6	Ppe6	–	0.7
Smelt age-0	Sme0	1.6	1.2
Smelt age-1	Sme1	1.3	0.2
Smelt age-2	Sme2	0.9	0.1
Smelt age-3	Sme3	0.6	0.03
Smelt age-4	Sme4	0.3	0.01
Smelt age-5	Sme5	0.1	0.0004
Smelt age $\geq$ 6	Sme6	0.001	0.00001

(continued on next page)

Table 1 (continued)

Guild	Abbreviation	Period	
		1AF%	2PF%
Vendace age-0	Ven0	1.7	1.3
Vendace age-1	Ven1	0.7	0.3
Vendace age-2	Ven2	0.3	0.04
Vendace age-3	Ven3	0.1	0.00004
Vendace age $\geq 4$	Ven4	0.03	0
Whitefish age-0	Whi0	1.6	1.2
Whitefish age-1	Whi1	1.1	0.5
Whitefish age-2	Whi2	0.7	0.3
Whitefish age-3	Whi3	0.5	0.1
Whitefish age-4	Whi4	0.2	0.03
Whitefish age-5	Whi5	0.1	0.01
Whitefish age $\geq 6$	Whi6	0.1	0.01

(Fig. 3). Combined effects of fishing and pikeperch were synergistic on the proportion of perch of the fish biomass in period 2, and on the proportions of smelt, and vendace of the fish biomass in both periods (Fig. 3).

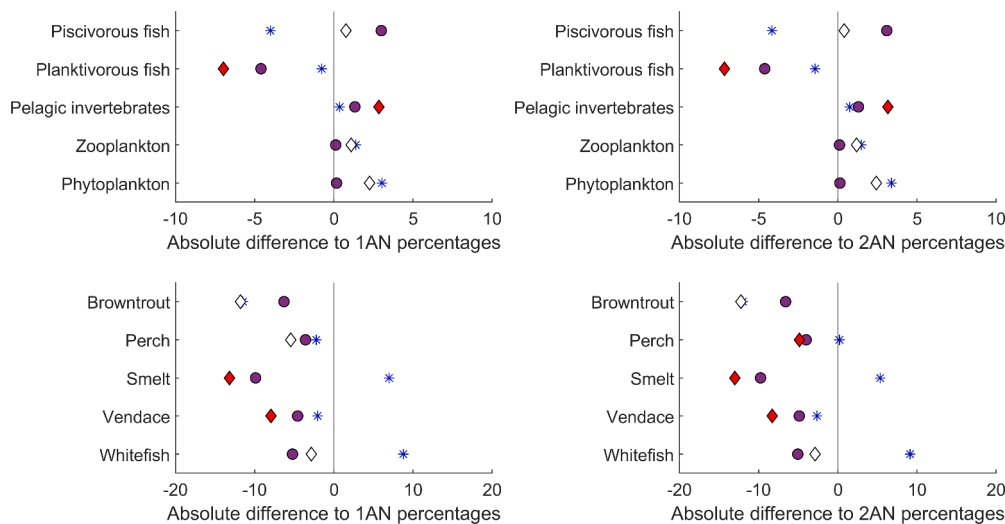
Presence of both pikeperch and fishing had negative effect on percentages of biomasses of *Asplanchna* guild, all whitefish guilds, all vendace guilds, all brown trout lake-age guilds, smelt guilds from smelt age-1 to smelt age  $\geq 6$ , perch guilds from perch age-3 to perch age-6 (Fig. 4). Most of the combined effects of the presence of fishing and pikeperch were antagonistic (Fig. 4). In both periods presence of both fishing and pikeperch had synergistic effects on *Asplanchna* guild, *Leptodora* and other predaceous zooplankton guild, *Chaoborus* guild, whitefish age-0, whitefish age-1, whitefish age-3, smelt age-1, smelt age-2, perch age-0 guilds (Fig. 4). In period 1 presence of both fishing and pikeperch also had synergistic effects on percentages of Crustacean zooplankton guild, Cyclopoida zooplankton guild, whitefish age-2, whitefish age-4, vendace age-1 guilds and smelt age-3 guilds (Fig. 4). In period 2 presence of both fishing and pikeperch also had synergistic effects on percentages of perch age-3, perch age-4 and perch age-5 guilds (Fig. 4).

Presence of the pikeperch increased the number of the guilds in the high trophic positions, because the pikeperch guilds in general, had the high trophic positions (approximately 4.3 (age-0 guild), 4.8 (age-1–2

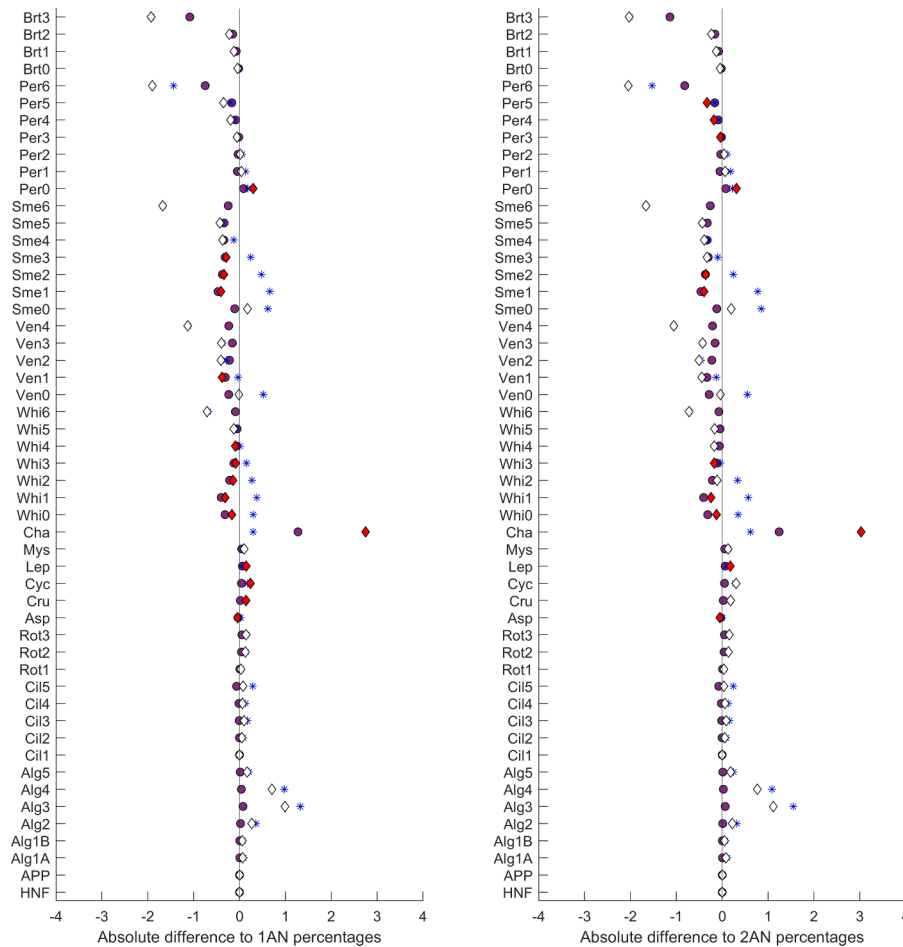
guilds), 4.9 (age-3 guild), 5 (age-4– $\geq 6$ -guilds)) (Appendix G., Table G1., Fig. G1.). Fishing decreased the proportion of the total biomass in the higher trophic positions (Appendix G., Fig. G1.). Algae guild 3 had the largest proportion of the total biomass (from approximately 22 % to 24 % depending on the simulation) followed by the algae guild 4 (from approximately 16 % to 18 % depending on the simulation) (Table 1., Appendix G., Table G1.). The weighted average trophic position (WATP) in period 1 was in the absence of fishing and pikeperch 2.10, and in the presence of fishing and absence of pikeperch 1.94. The WATP in period 2 was in the absence of fishing and presence of pikeperch 2.11, and in the presence of fishing and pikeperch 1.98.

Biomasses of the fish guilds in period 2 (in the simulations in the presence of pikeperch) were generally smaller than in period 1 (in the simulations in the absence of pikeperch), i.e., the ratio of period 2 biomass to period 1 biomass was smaller than one (Fig. 5., Appendix H., Table H1.). From the fish guild other than pikeperch, only perch age-0 guild and perch age-3 guild had larger biomass in period 2PF than in period 1AF (Fig. 5). The biomass in period 2PF was larger than in 1AF in the following lower trophic level guilds: in algae guilds Alg1A, Alg3–Alg5, autotrophic picoplankton, heterotrophic nano-flagellates, and bacteria guilds, in ciliate guilds Cil1, Cil2, and Cil4, in rotifer guilds Rot1–Rot3, in Crustacean zooplankton guild, in Cyclopoida zooplankton guild, in *Leptodora* and other predatory zooplankton guild, in pelagic invertebrates *Mysis*, and *Chaoborus* guilds (Fig. 5., Appendix H., Table H1.). In contrary, biomass in period 2PF was lower than in period 1AF in algae guilds Alg1B, and Alg2, in ciliate guilds Cil3, and Cil5, and in the *Asplanchna* guild (Fig. 5., Appendix H., Table H1.). The simultaneous presence of fishing and pikeperch increased the ratio especially in *Leptodora* and other predatory zooplankton guild and *Chaoborus* guild (Fig. 5., Appendix H., Table H1.).

Comparison of ratios from the model to the initial ratios was done to also get an idea how closely the results of model are to the data used (Fig. 5). This can also be seen as an evaluation of model quality, although the data did not include all guilds and is itself also a limited description of the reality. There were good matching cases, but also differences whether the calculated ratio was below or over one depending on the method (Fig. 5.). Pinkham and Pearson's similarity index values were for the fish comparisons 0.37, for the phytoplankton



**Fig. 3.** Absolute difference of trophic level percentages to the percentages of trophic levels in the scenario 1AN (upper left) and scenario 2AN (upper right) (scenario 1AN: period 1 in the absence of pikeperch and fishing and scenario 2AN: period 2 in the absence of pikeperch and fishing). Absolute difference of fish species percentages to the percentages of fish species in scenario 1AN (below left) and scenario 2AN (below right). Purple dot = effect of pikeperch (scenario 1PN when comparing to 1AN and scenario 2PN when comparing to 2AN), blue star = effect of fishing (scenario 1AF when comparing to 1AN and scenario 2AF when comparing to 2AN), white diamond = effect of both pikeperch and fishing (scenario 1PF when comparing to 1AN and scenario 2PF when comparing to 2AN), red diamond = synergistic effect of both pikeperch and fishing, and blue star = antagonistic effect of both pikeperch and fishing. Synergistic effect means that the effect of both pikeperch and fishing is larger than the sum of the effects of fishing alone and pikeperch alone.



**Fig. 4.** Absolute difference of guild percentages to the percentages of guilds in scenario 1AN (left) and scenario 2AN (right) (scenario 1AN: period 1 in the absence of pikeperch and fishing and scenario 2AN: period 2 in the absence of pikeperch and fishing). Purple dot = effect of pikeperch (scenario 1PN when comparing to 1AN and scenario 2PN when comparing to 2AN), blue star = effect of fishing (scenario 1AF when comparing to 1AN and scenario 2AF when comparing to 2AN), diamond = effect of both pikeperch and fishing (scenario 1PF when comparing to 1AN and scenario 2PF when comparing to 2AN), white diamond = antagonistic effect of both pikeperch and fishing, and red diamond = synergistic effect of both pikeperch and fishing. Antagonistic effect means that the effect of both pikeperch and fishing is smaller than the sum of the effects of fishing alone and pikeperch alone. Synergistic effect means that the effect of both pikeperch and fishing is larger than the sum of the effects of fishing alone and pikeperch alone.

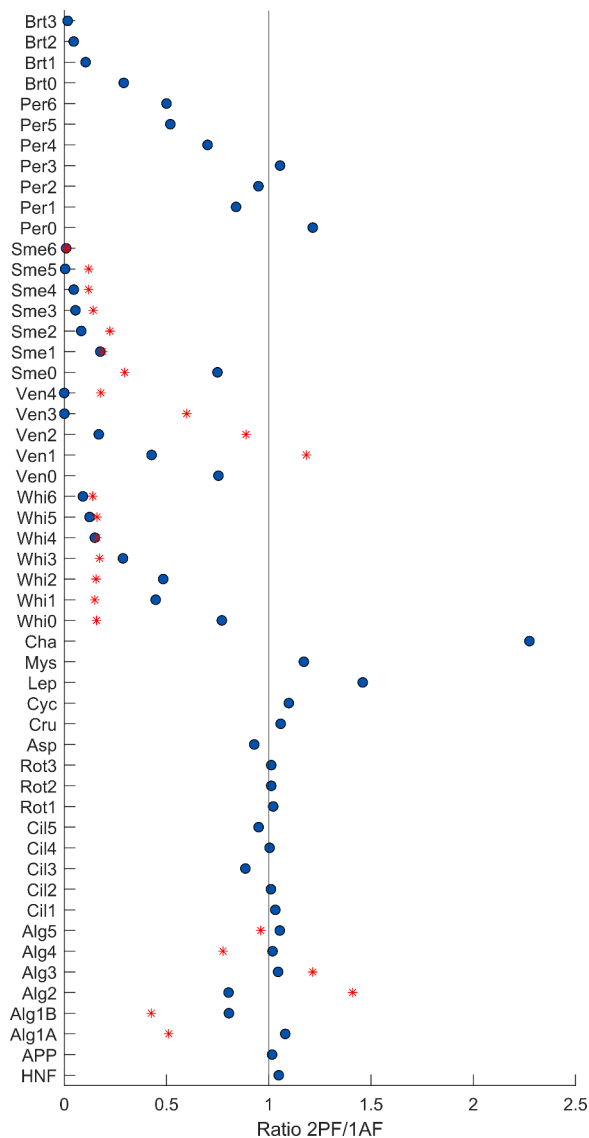
comparisons 0.58, and for the combined comparison of fish and phytoplankton 0.55.

Fishing altered the division of the biomasses of the fishes into different age guilds, i.e., caused typical age truncation (Figs. 6–7., Appendix I. Figures I1–I2.). In the presence of the fishing, and especially during generally higher fishing mortalities applied in the model in period 2 (Appendix A., Tables A1–A2.) most of the biomass was in the youngest age classes among the planktivorous fish (Fig. 6., Appendix I. Fig. I1.). In the absence of fishing, the largest biomasses of the planktivorous species were in the age-0 guild and in the oldest age guild (Fig. 6., Appendix I. Fig. I1.). In the absence of fishing, the piscivorous species had the largest biomass in their oldest age class (Fig. 7., Appendix I. Fig. I2.). In the presence of fishing, the biomass of the piscivorous fish was rather evenly distributed among the different age classes, except in the brown trout, which had the relatively largest biomass in the lake-age-0 guild (Fig. 7., Appendix I. Fig. I2.).

#### 4. Discussion

Our research builds upon the ongoing exploration of allometric relationships within food webs, as demonstrated by previous studies (e.g., Cózar et al., 2008; Abernethy, 2020), with a particular focus on Allometric Trophic Network (ATN) models, as reviewed by Martinez (2020).

While simulation studies have contributed significantly to theoretical food web construction (Abernethy, 2020; Nonaka and Kuparinen, 2023), our investigation distinguishes itself by constructing a singular food web grounded in extensive empirical data sourced from Lake Oulujärvi. This study marks the pioneering application of ATN modelling in a boreal lake ecosystem, characterized by a broader inclusion of age classes and fish species compared to previous models (Boit et al., 2012; Kuparinen et al., 2016), notably in Lake Constance. Abernethy's (2020) findings underscore the potential for cascading extinctions following the removal of specific species over time, particularly emphasizing the vulnerability to removal of rare third trophic level species with numerous prey items. However, in our investigation, the removal of pikeperch from the food web did not result in any extinctions. Additionally, as highlighted by Nonaka and Kuparinen (2023), fishing activities can introduce destabilizing impacts on fish biomasses, albeit without consistent outcomes across simulations. Our study examines the influence of the presence of pikeperch and fishing activities, both individually and in combination, on the food web composition under stable equilibrium conditions. Pikeperch negatively affected the youngest age classes of its prey species, while fishing was directed towards the oldest age classes of fish. Antagonistic effects of pikeperch and fishing together on guild biomass percentages were found more often than synergistic effects, while synergistic effects were also common. In



**Fig. 5.** Ratio of guilds in period 2 in the presence of pikeperch and fishing (2PF) to period 1 in the presence of fishing and absence of pikeperch (1AF). Blue dots = model results, red stars = Pope's cohort analysis or phytoplankton data-based averages (also initial biomass values for the model). If ratio is 1 there is no difference, if ratio is  $> 1$  guild had larger biomass in period 2PF than in period 1AF, and if ratio is  $< 1$  guild had smaller biomass in period 2PF than in period 1AF. Notice that Ven age  $\geq 4$  guild biomass was zero in the 2PF.

the experimental study of Folt et al., 1999 antagonistic effects of multiple stressors were also most common. Ecological modelling studies can benefit from classification of effects to additive, antagonistic, and synergistic effects. Currently, in Lake Oulujärvi pikeperch and fishing are present. It is therefore important to consider especially the synergistic negative effects they can have for vendace and smelt to ensure that they can sustain the fishing pressures. Smaller or larger effects than expected based on the additivity remind on the importance of the indirect effects in the food web.

Similarity tests between empirical time series and ATN model simulations yielded moderate similarities from 0.37 to 0.58, as highest possible similarity would have been 1. Especially, the ratio changes in the biomasses of whitefish guilds from age-3 to age-6, smelt guilds from age-1 to age-6, and algae guilds Alg3 and Alg5 from period 1 to period 2 matched well between ATN model and averaged initial biomasses reflecting the ability of the ATN model to capture some of the key trophic interactions. Pope's cohort analysis (for pikeperch, vendace, smelt

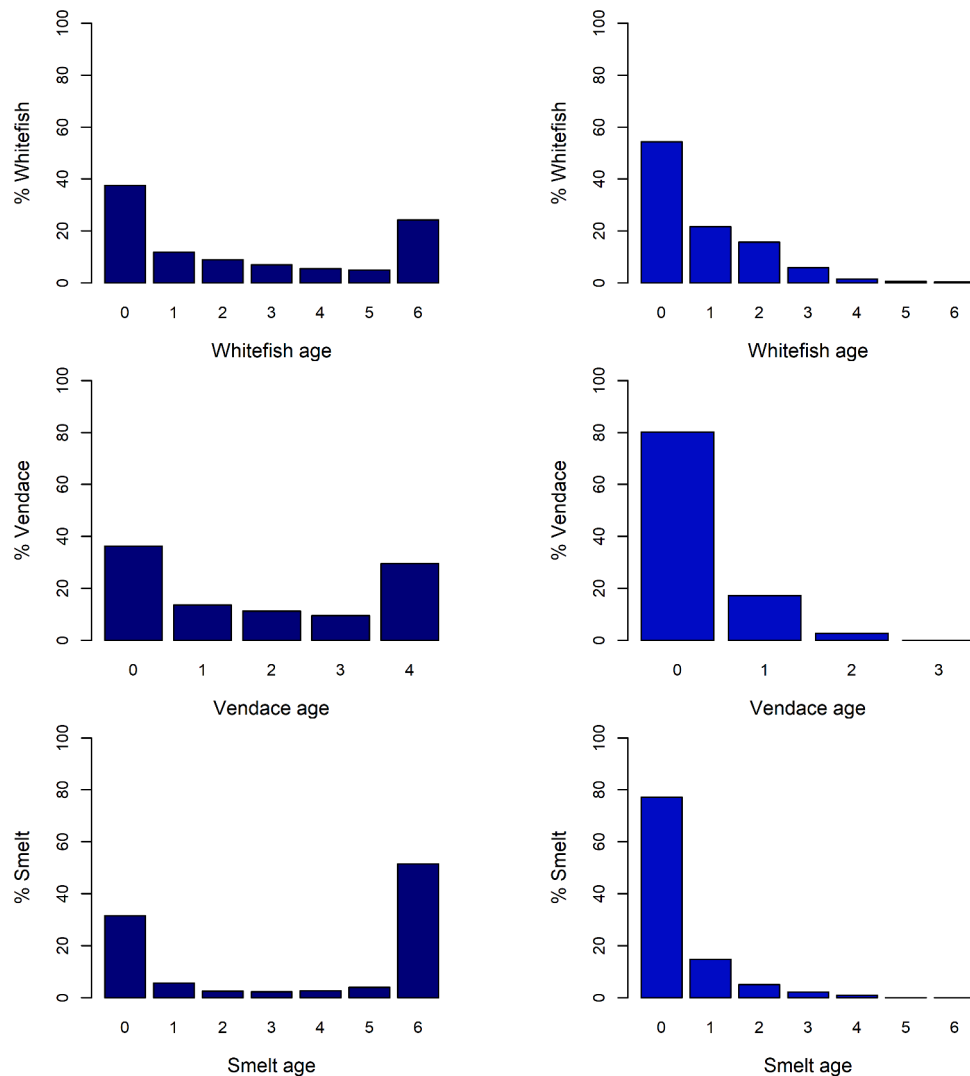
and whitefish) is an empirical analysis based on highly uncertain data on individual species, and as such the empirical results do not reflect the reality perfectly. Thus, the combined interpretation of the model simulations at theoretical equilibrium state and empirical time series can help to infer the reasons for the observed changes in the lake. Advancement in ATN model compared to more traditional modelling is the consideration of multiple species, trophic levels and interactions in the food web simultaneously.

Pikeperch and fishers are both at the top levels in the food web, but their effects on the fish community are different. The natural mortality caused by pikeperch predation was directed towards the youngest age classes of planktivorous fish, whilst fishing had the largest effects on the oldest age classes of fish. Gape size of the piscivorous fish limits the size of the prey they can feed but even predators with a large gape size include small prey in their diet (Juanes, 1994; Mittelbach and Persson, 1998; Vehanen et al. 1998). The typical prey of the predator might be highly affected by prey availability (Hyvärinen and Huusko, 2006). The effect of pikeperch on the weighted average trophic position was minor; in the absence of pikeperch some of the top predator biomass was replaced by other predatory fish, such as brown trout and large perch. Fishing affected the weighted average trophic level of the food web probably mostly through its effects on the biomass of older fish. Fishing often targets the oldest fish due to their larger size (Barnett et al., 2017) and the truncations of the mean size and age, and consequently reduction in average trophic level are the typical consequences of fishing (Pauly and Watson, 2005). In the fisheries management, it is possible to reduce the truncating effect of fishing on age distributions by for example lowering the fishing pressures so that larger number of older individuals can survive. The high-quality traits of old female fish were outlined by Hixon and others (2014) and included production of larger eggs, production of fast-growing and more starvation resistant larvae and, better survival of the females over unfavorable reproduction periods to reproduce again when the more favorable conditions return. Thereby, larger number of older individuals in the fish populations can enhance the production of larvae (Hixon et al., 2014), maintain the variability in the individuals of the population (Schindler et al., 2010; Wright and Trippel, 2009) and keep the population biomasses more stable (Anderson et al., 2008; Hsieh et al., 2006).

We did not observe that larger biomass of zooplankton would decrease biomass of phytoplankton as predicted by the trophic cascade theory (e.g., Carpenter et al., 1985). Clear trophic cascades are often missing in nature, as there exists many kinds of compensatory effects, including increases in types of species that are not eaten as much or increases in reproductive output when the biomass of older fish decreases (Rose et al., 2001; Wetzel, 2001). In Lake Oulujärvi the presence of predatory pikeperch appeared to increase the proportion of the pelagic invertebrates and consequently pelagic invertebrates fed increased amounts of zooplankton. It is known that pelagic invertebrates can have large effects on zooplankton (Liljendahl-Nurminen et al., 2003, 2008; Wissel and Benndorf, 1998). In the Lake Hiidenvesi, for example, *Chaoborus flavicans* was limiting the abundance of the Cladoceran zooplankton, and it affected even the body sizes of the Cladocerans that increased in average size after the relaxation of the predation pressure (Liljendahl-Nurminen et al., 2003). In addition, intraguild predation of zooplankton can affect the occurrence of trophic cascades (McCann et al., 1998) and bottom-up effects from phytoplankton to upper levels could also have a role. In this study, bottom-up effects could come from the periodic differences in the growth rates of the phytoplankton guilds. Although there were no clear trophic cascades, indirect effects of pikeperch and fishing on guild-specific compositions of community were found. Cyclopoida zooplankton and pelagic invertebrate Mysis belong to the diet of pikeperch, but pikeperch increased their biomass through indirect effects.

The importance of pikeperch in the food web was tracked by both Pope's cohort analysis and ATN model. According to the Pope's cohort analysis pikeperch biomass increased during period 2, because of



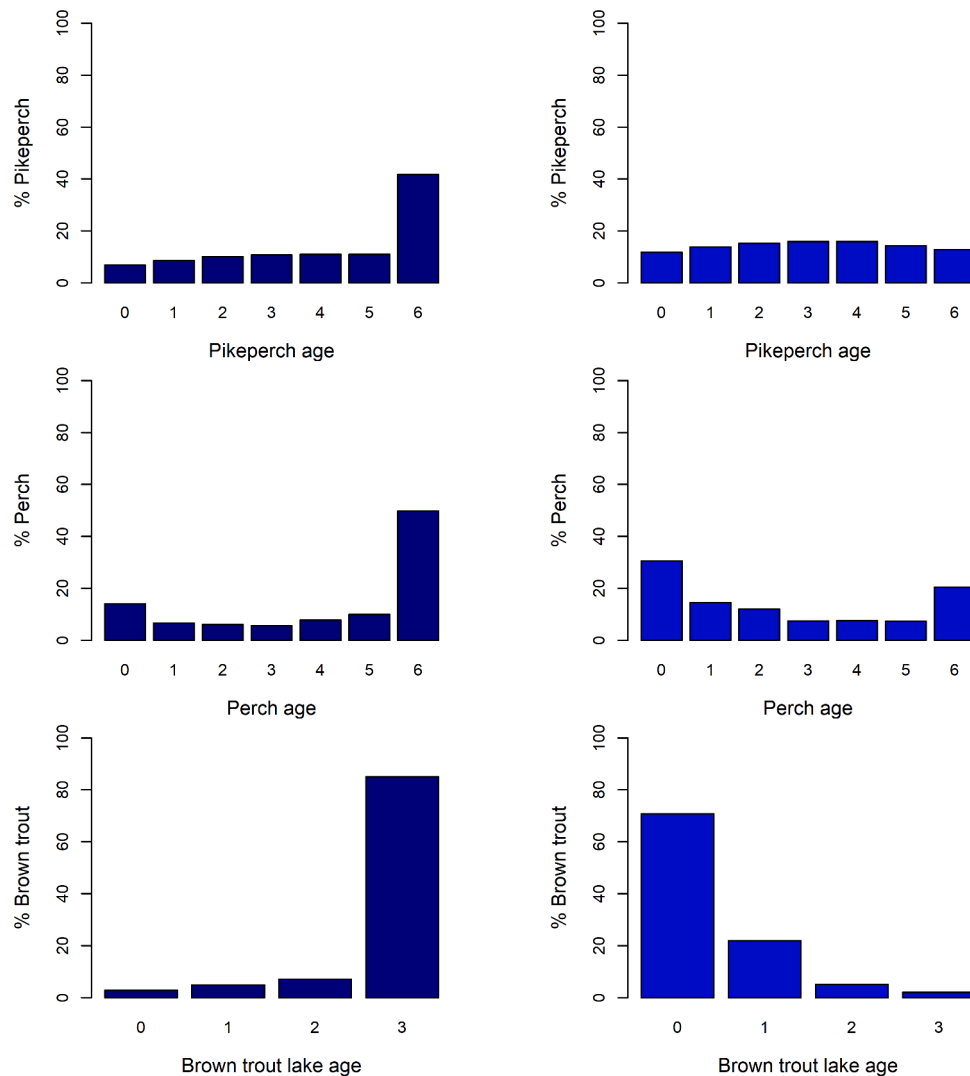


**Fig. 6.** The age structure of the mainly planktivorous fish guilds (although smelt age  $\geq 3$  can feed on smelt age-0) shown as proportion (%) of biomass in the different age guilds in scenario 2PN (dark blue; in the left column) and in scenario 2PF (blue; in the right column) in the end of the growth season. Age 6 means age  $\geq 6$ .

massive stockings and subsequent natural recruitment, and it rapidly became the most common fish species by biomass in the lake. Pikeperch comprised the largest biomass of the fish community also in the ATN model. Lately, pikeperch catches have increased (Laitala et al., 2022), but according to the cohort analysis pikeperch biomass was declining before the latest catch statistics. However, the last years of cohort analyses involves high uncertainty, and more recent cohorts need to be added to the analyses to see if the population is also increasing. In the ATN model, fishing did not cause large declines in the pikeperch biomass. Reason for this could be the compensatory mechanisms (Rose et al., 2001) like better growth of the remaining population after fishing due to decreased intraspecific feeding interference and more abundant prey. It is also possible that ATN model overestimated the proportion of pikeperch biomass (30 %/41 %). However, over 40 % of piscivorous biomass are possible in lakes. In biomanipulation literature for example over 25% (Mehner et al., 2004) and 30–40 % (Kasprzak et al., 2007) piscivore biomass have been recommended, although over 40 % biomass could cause increases in invertebrate planktivores (Benndorf et al., 2000).

ATN model partly captured the developments found in other fish species too, although some of the changes observed in the Pope's cohort analyses still need further studies. Low biomass of the oldest age guilds of vendace in the presence of fishing was consistent with an earlier study

in Lake Oulujärvi observing changes in age distributions after the trawling of vendace started in 1987 (Huusko and Hyvärinen, 2005). Compared to cohort analysis-based ratio calculations, ATN model was a bit more pessimistic on vendace declines in period 2. Vendace and smelt biomasses have also declined according to the cohort analysis during period 2, although in vendace there is some fluctuation into a higher biomass too (notice that age 0 vendace was not included in the cohort analysis, age 0 vendace can be more than 50 % of vendace biomass in the autumn). At least in the autumn season, vendace biomass can reach similar levels to pikeperch biomass (Huusko and Hyvärinen, 2005). Whitefish stocks have declined to very low levels despite that pikeperch and whitefish have likely coexisted in more equal abundances in the past (Vainikka et al., 2017a). According to the cohort analyses and observations of catch in unselective fishing methods (Laitala et al., 2022), population biomasses of the native whitefish forms have continuously decreased during period 2 (Vainikka et al. 2017a). The model simulations revealed that pikeperch alone, and pikeperch and fishing in combination can reduce the biomass of whitefish noticeably but less than observed in the lake. Whitefish had still very high percentages of fish biomass in the ATN model because in the model the intraspecific compensation by the growth of the young fish likely balanced the situation. Vendace and whitefish have competitive interactions, and vendace can have negative effects on young whitefish through competition



**Fig. 7.** The age structure of the piscivorous fish guilds (except perch < age-4 non-piscivorous) shown as proportion (%) of biomass in the different age guilds in scenario 2PN (dark blue, in the left column) and in scenario 2PF (blue, in the right column) in the end of the growth season. Age 6 means age  $\geq 6$ .

for food (e.g., Salojärvi, 1992). Accordingly, fishing had positive effects on whitefish in the absence of pikeperch, explained by higher fishing mortality for possible competitors; vendace and smelt, and higher fishing mortality for the predatory fish, brown trout. Brown trout diet included vendace, smelt, whitefish and perch, but brown trout biomasses in the ATN model were low (especially in the presence of fishing) as expected because the species show no natural reproduction in the Lake Oulujärvi system and has extremely high fishing mortality. Our parametrization of the whitefish fishing mortalities and the inclusion of whitefish into the diet of pikeperch could be affected by the fact that whitefish has become less abundant during the time scale of the cohort analysis. Perhaps some effects on whitefish are not explained by either fishing or pikeperch. Due to the climate change, it may be expected that boreal lakes may move from the abundant coregonid community to a community abundant of percids and cyprinids (Lehtonen et al., 1996). In a recent review, declines in cold water adapted species and increases in warm water species have also been found in European lakes (Jeppesen et al., 2012). In Lake Peipsi (Estonia), pikeperch abundance has increased, but vendace, smelt, whitefish and burbot abundances have declined (Kangur et al., 2007). Long-term changes of in Lake Peipsi were also related to multiple factors such as warming water, eutrophication, and fishing (Kangur et al., 2007). Changes in the fish community composition can also be reinforcing, so that for example in Lake Peipsi

increased pikeperch population together with environmental factors prevent the recovery of vendace (Kangur et al., 2007). Other example is from vendace in Lake Säkylän Pyhäjärvi, where vendace has not been recovered to as high levels as before overfishing, because part of the resources is nowadays used by other increased planktivorous fish species (perch, smelt and roach (*Rutilus rutilus*)) in the lake's fish community (Helminen and Sarvala, 2021). The case of whitefish in Lake Oulujärvi could be similarly affected by multiple effects. Even water level regulation could have negative consequences for whitefish breeding success depending on the sites of spawning (Sutela et al., 2002). In Lake Oulujärvi whitefish abundances can be mitigated by stocking, and whitefish abundance is also affected by the success of stockings.

In this ATN simulation study, we demonstrated how the re-establishment of a top predator species, pikeperch, and fishing mortality, could together affect the food web biomass distributions into different trophic levels, and age guilds of fish species. Nonetheless, our model included several uncertainties and simplifications that should be considered. Preliminary simulations suggested that top predators may be able to reach high biomass levels in the model even without natural reproduction if they lack natural predators in the constructed food web. This problem was solved by excluding pikeperch completely from the comparative simulations. The construction of food webs is characteristic on multiple difficult choices and question of the enough good resolution

(Pringle and Hutchinson, 2020). The inclusion of pike in the model could be useful in the future, as pike is another important predator for all the included prey fishes, for the stocked brown trout and for the juvenile pikeperch (Lake Oulujärvi data, Hyvärinen and Vehanen, 2004; Korhonen and Hyvärinen, 2004). Furthermore, the model did not include diet shifts, adaptive foraging, and spatial aspects and, similarly, the effects of environmental variables such as primary productivity or temperature were not included in the model. The inclusion of environmental effects, such as water temperature could be useful for considering the natural mortality of young fish and the growth of the fish. For example, warm water temperature in the first summer enhances the pikeperch recruitment (Heikinheimo et al., 2014). Since ATN model leaved the nutrients and environmental effects aside, we could better focus on the biotic dynamics within the ecosystem.

Extensive time series and diet data collection made it possible to build the current ATN model reflecting Lake Oulujärvi food web. Complex interactions of fishing and pikeperch in the food web were found. Further evaluation on the fish community interactions and environmental and/or anthropogenic effects are needed for understanding the current low population sizes of whitefish. Considering the food web interactions, and effects of fishing on fish age distributions are important for the ecosystem-based management of inland lakes.

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## Data statement

Data used in the simulations is available in the supplementary material. Original data sets of lake Oulujärvi fish data can be asked from Natural Resources Institute Finland (see also <https://dataportal.eu-interact.org/stations/kainuu-fisheries-research-station>) and phytoplankton data from Finnish Environment Institute.

## CRediT authorship contribution statement

**Evi Kokkonen:** . **Mikael Kuisma:** Writing – review & editing, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Pekka Hyvärinen:** Writing – review & editing, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Anssi Vainikka:** Writing – review & editing, Visualization, Supervision, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Kristiina Vuorio:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Tommi Perälä:** Writing – review & editing, Software, Methodology, Investigation,

Formal analysis, Data curation. **Laura S. Härkönen:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Satu Estlander:** Writing – review & editing, Methodology, Formal analysis. **Anna Kuparinen:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Data curation, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Original data can be asked from Natural Resources Institute Finland (see also <https://dataportal.eu-interact.org/stations/kainuu-fisheries-research-station>) and Finnish Environment Institute.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2024.110715](https://doi.org/10.1016/j.ecolmodel.2024.110715).

## References

- Abernethy, G.M., 2020. Allometry in an eco-evolutionary network model. *Ecol. Modell.* 427, 109090 <https://doi.org/10.1016/j.ecolmodel.2020.109090>.
- Anderson, C.N.K., Hsieh, C., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M., Sugihara, G., 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452, 835–838. <https://doi.org/10.1038/nature06851>.
- Barnett, L.A.K., Branch, T.A., Ranasinghe, R.A., Essington, T.A., 2017. Old-growth fishes become scarce under fishing. *Curr. Biol.* 27, 2843–2848. <https://doi.org/10.1016/j.cub.2017.07.069> e2.
- Benndorf, J., Wissel, B., Sell, A.F., Hornig, U., Ritter, P., Böing, W., 2000. Food web manipulation by extreme enhancement of piscivory: an invertebrate predator compensates for the effects of planktivorous fish on a plankton community. *Limnologia* 30, 235–245. [https://doi.org/10.1016/S0075-9511\(00\)80053-5](https://doi.org/10.1016/S0075-9511(00)80053-5).
- Berlow, E.L., Dunne, J.A., Martinez, N.D., Brose, U., 2009. Simple prediction of interaction strengths in complex food webs. *PNAS* 106 (1), 187–191. <https://doi.org/10.1073/pnas.0806823106>.
- Bernes, C., Carpenter, S., Gårdmark, A., Larsson, P., Persson, L., Skov, C., Speed, J.D.M., van Donk, E., 2015. What is the influence of a reduction of planktivorous and benthivorous fish on water quality in temperate eutrophic lakes? A systematic review. *Environ. Evid.* 4, 1–28. <https://doi.org/10.1186/s13750-015-0032-9>.
- Bland, S., Valdovinos, F.S., Hutchings, J.A., Kuparinen, A., 2019. The role of fish life histories in allometrically scaled food-web dynamics. *Ecol. Evol.* 9 (6), 3651–3660. <https://doi.org/10.1002/ece3.4996>.
- Boit, A., Martinez, N.D., Williams, R.J., Gaedke, U., 2012. Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. *Ecol. Lett.* 15 (6), 594–602. <https://doi.org/10.1111/j.1461-0248.2012.01777.x>.
- Brooks, J.L., Dodson, S.L., 1965. Predation, body size, and composition of plankton. *Science* 150, 28–35. <https://doi.org/10.1126/science.150.3692.28>.

- Brose, U., Williams, R.J., Martinez, N.D., 2006. Allometric scaling enhances stability in complex food webs. *Ecol. Lett.* 9 (11), 1228–1236. <https://doi.org/10.1111/j.1461-0248.2006.00978.x>.
- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85 (7), 1771–1789. <https://doi.org/10.1890/03-9000>.
- Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35, 634–639. <https://doi.org/10.2307/1309989>.
- Colby, P.J., Lehtonen, H., 1994. Suggested causes for the collapse of zander, *Stizostedion lucioperca* (L.), populations in northern and central Finland through comparisons with North American walleye, *Stizostedion vitreum* (Mitchill). *Boreal Environ. Res.* 24 (1), 9–20.
- Coulson, T., 2021. We live in a changing world, but that shouldn't mean we abandon the concept of equilibrium. *Ecol. Lett.* 24 (1), 3–5. <https://doi.org/10.1111/ele.13629>.
- Cózar, A., García, C.M., Gálvez, J.A., Echevarría, F., 2008. Structuring pelagic trophic networks from the biomass size spectra. *Ecol. Modell.* 215, 314–324. <https://doi.org/10.1016/j.ecolmodel.2008.02.038>.
- de Castro, F., Gaedke, U., 2008. The metabolism of lake plankton does not support the metabolic theory of ecology. *Oikos* 117, 1218–1226. <https://doi.org/10.1111/j.0030-1299.2008.16547.x>.
- Folt, C.L., Chen, C.Y., Moore, M.V., Burnaford, J., 1999. Synergism and antagonism among multiple stressors. *Limnol. Oceanogr.* 44 (3part2), 864–877. <https://doi.org/10.4319/lo.1999.44.3.part.2.0864>.
- Guiry, M.D., Guiry, G.M., 2020. AlgaeBase. World-wide electronic Publication. National University of Ireland, Galway. <https://www.algaebase.org>.
- Heikinheimo, O., Pekkan-Hekim, Z., Raitaniemi, J., 2014. Spawning stock–recruitment relationship in pikeperch *Sander lucioperca* (L.) in the Baltic Sea, with temperature as an environmental effect. *Fish. Res.* 155, 1–9. <https://doi.org/10.1016/j.fishres.2014.02.015>.
- Heithaus, M.R., Frid, A., Wirsing, A.J., Worm, B., 2008. Predicting ecological consequences of marine top predator declines. *Trends Ecol. Evol.* 23 (4), 202–210. <https://doi.org/10.1016/j.tree.2008.01.003>.
- Helminen, H., Sarvala, J., 2021. Trends in vendace (*Coregonus albula*) biomass in Pyhäjärvi (SW Finland) relative to trophic state, climate change, and abundance of other fish species. *Ann. Zool. Fenn.* 58, 255–269. <https://doi.org/10.5735/086.058.0411>.
- Hixon, M.A., Johnson, D.W., Sogard, S.M., 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. *ICES J. Mar. Sci.* 71 (8), 2171–2185. <https://doi.org/10.1093/icesjms/fst200>.
- Hokanson, K., 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. *J. Fish. Board Can.* 34, 1524–1550. <https://doi.org/10.1139/f77-217>.
- Horppila, J., Liljendahl-Nurminen, A., Malinen, T., Salonen, M., Tuomaala, A., Uusitalo, L., Vinni, M., 2003. *Mysis relicta* in a eutrophic lake: consequences of obligatory habitat shifts. *Limnol. Oceanogr.* 48 (3), 1214–1222. <https://doi.org/10.4319/lo.2003.48.3.1214>.
- Hsieh, C., Reiss, C.S., Hunter, J.R., Beddington, J.R., May, R.M., Sugihara, G., 2006. Fishing elevates variability in the abundance of exploited species. *Nature* 443, 859–862. <https://doi.org/10.1038/nature05232>.
- Huusko, A., Hyvärinen, P., 2005. A high harvest rate induces a tendency to generation cycling in a freshwater fish population. *J. Anim. Ecol.* 74 (3), 525–531. <https://doi.org/10.1111/j.1365-2656.2005.00951.x>.
- Hyvärinen, P., Vehanen, T., 2004. Effect of brown trout body size on post-stocking survival and pike predation. *Ecol. Freshw. Fish* 13 (2), 77–84. <https://doi.org/10.1111/j.1600-0633.2004.00050.x>.
- Hyvärinen, P., Huusko, A., 2005. Long-term variation in brown trout, *Salmo trutta* L., stocking success in a large lake: interplay between availability of suitable prey and size at release. *Ecol. Freshw. Fish* 14 (4), 303–310. <https://doi.org/10.1111/j.1600-0633.2005.00104.x>.
- Hyvärinen, P., Huusko, A., 2006. Diet of brown trout in relation to variation in abundance and size of pelagic fish prey. *J. Fish Biol.* 68 (1), 87–98. <https://doi.org/10.1111/j.0022-1112.2006.00879.x>.
- Härkönen, L.S., Hyvärinen, P., Rinnevali, R., van der Meer, O., Orell, P., Veneranta, L., Erkinaro, J., Louhi, P., 2023. Kalastonhoidon kehittäminen Oulujoen vesistöissä. Luonnonvara- ja biotalouden Tutkimus 47/2023. Luonnonvarakeskus. Helsinki, p. 138. <https://jukuri.luke.fi/handle/10024/553371>.
- Härkönen, L., Hyvärinen, P., 2024a. Pikeperch Catches in Lake Oulujärvi 1974–2021. Natural Resources Institute Finland. <https://doi.org/10.23729/ee7dfd3a-7087-4a19-9776-d6e62a83beab>.
- Härkönen, L., Hyvärinen, P., 2024b. Whitefish Catches in Lake Oulujärvi 1974–2020. Natural Resources Institute Finland. <https://doi.org/10.23729/58518080-2c0a-49a3-b792-294b8b41b5c5>.
- Härkönen, L., Hyvärinen, P., 2024c. Vendace Catches in Lake Oulujärvi 1974–2020. Natural Resources Institute Finland. <https://doi.org/10.23729/a309a735-e034-4c0d-9564-4f3a821b7b67>.
- Härkönen, L., Hyvärinen, P., 2024d. Smelt Catches in Lake Oulujärvi 1974–2017. Natural Resources Institute Finland. <https://doi.org/10.23729/13206886-5bc0-48d9-8026-e79555d305ef>.
- Härkönen, L., Hyvärinen, P., 2024e. Pikeperch Size Variation in Lake Oulujärvi Catches 1992–2018. Natural Resources Institute Finland. <https://doi.org/10.23729/4b51ddd7-1943-4831-82e6-8d6af670ce83>.
- Härkönen, L., Hyvärinen, P., 2024f. Whitefish Size Variation in Lake Oulujärvi Catches 1972–2017. Natural Resources Institute Finland. <https://doi.org/10.23729/87b66442-a8b6-4fe3-9b83-cddea4f06652>.
- Härkönen, L., Hyvärinen, P., 2024g. Vendace Size Variation in Lake Oulujärvi Catches 1973–2017. Natural Resources Institute Finland. <https://doi.org/10.23729/1c2daede-afa9-44e2-8600-78b1bf09f130>.
- Härkönen, L., Hyvärinen, P., 2024h. Smelt Size Variation in Lake Oulujärvi 1989–2017. Natural Resources Institute Finland. <https://doi.org/10.23729/d04bde23-8593-4286-9a12-9f47ac54e594>.
- Jeppesen, E., Mehner, T., Winfield, I.J., Kangur, K., Sarvala, J., Gerdeaux, T., Meerhoff, M., 2012. Impacts of climate warming on the long-term dynamics of key fish species in 24 European lakes. *Hydrobiologia* 694, 1–39. <https://doi.org/10.1007/s10750-012-1182-1>.
- Juanes, F., 1994. What determines prey size selectivity in piscivorous fishes? In: Stouder, K., Fresh, L., Feller, R.J. (Eds.), *Theory and Application in Fish Feeding ecology*. Belle W Baruch Library of Marine Sciences. University of South Carolina Press, Columbia, pp. 79–100.
- Kangur, K., Park, Y.-S., Kangur, A., Lek, S., 2007. Patterning long-term changes of fish community in large shallow Lake Peipsi. *Ecol. Modell.* 203, 34–44. <https://doi.org/10.1016/j.ecolmodel.2006.03.039>.
- Kasprzak, P., Benndorf, J., Gonsiorczyk, T., Koschel, R., Krienitz, L., Mehner, T., Hülsmann, S., Schultz, H., Wagner, A., 2007. Reduction of nutrient loading and biomanipulation as tools in water quality management: longterm observations on Bautzen Reservoir and Feldberger Haussee (Germany). *Lake Reserv. Manag.* 23, 410–427. <https://doi.org/10.1080/07438140709354027>.
- Killen, S.S., Costa, I., Brown, J.A., Gamperl, A., 2007. Little left in the tank: metabolic scaling in marine teleosts and its implications for aerobic scope. *Proc. R. Soc. B* 274 (1608), 431–438. <https://doi.org/10.1098/rspb.2006.3741>.
- Killen, S.S., Atkinson, D., Glazier, D.S., 2010. The intraspecific scaling of metabolic rate with body mass in 16 fishes depends on lifestyle and temperature. *Ecol. Lett.* 13 (2), 184–193. <https://doi.org/10.1111/j.1461-0248.2009.01415.x>.
- Kokkonen, E., Mitikka, S., Huuskonen, H., Olin, M., Ruuhijärvi, J., Vainikka, A., 2019. Structural equation models suggest that bottom-up processes override top-down processes in boreal pikeperch (*Sander lucioperca*) lakes. *Freshw. Biol.* 64 (5), 1054–1063. <https://doi.org/10.1111/fwb.13285>.
- Korhonen, K., Hyvärinen, P., 2004. Pienet kuhat petokalojen saalistuksen kohteena Oulujärvellä. Kala- ja riistaraportteja 335, 13 pp. (In Finnish). <https://urn.fi/URN:ISBN,951-776-472-3>.
- Kuparinen, A., Boit, A., Valdovinos, F.S., Lassaux, H., Martinez, N.D., 2016. Fishing-induced life-history changes degrade and destabilize harvested ecosystems. *Sci. Rep.* 6, 1–8. <https://doi.org/10.1038/srep22245>.
- Laitala, H., Alaja, H., Jokinen, J., 2022. Oulujärven yhteistarkkailu. Kalataloudellinen tarkkailu vuonna 2020. Eurofins Ahma Oy 73.
- Lang, M.M., 1997. Das Nahrungsnetz im Pelagial des Bodensees: eine Analyse auf Basis der Theorie der Nahrungsnetze. PhD Thesis. University of Konstanz., German.
- Lehtonen, H., 1996. Potential effects of global warming on northern European freshwater fish and fisheries. *Fish. Manag. Ecol.* 3 (1), 59–71. <https://doi.org/10.1111/j.1365-2400.1996.tb00130.x>.
- Levine, S., 1980. Several measures of trophic structure applicable to complex food webs. *J. Theor. Biol.* 83 (2), 195–207. [https://doi.org/10.1016/0022-5193\(80\)90288-X](https://doi.org/10.1016/0022-5193(80)90288-X).
- Liljendahl-Nurminen, A., Horppila, J., Malinen, T., Eloranta, P., Vinni, M., Alajärvi, E., Valtonen, S., 2003. The supremacy of invertebrate predators over fish – factors behind the unconventional seasonal dynamics of cladocerans in Lake Hiidenvesi. *Arch. Hydrobiol.* 158 (1), 75–96. <https://doi.org/10.1127/0003-9136/2003/0158-0075>.
- Liljendahl-Nurminen, A., 2006. Invertebrate Predation and Trophic Cascades in a Pelagic Food Web – The Multiple Roles of Chaoborus flavicans (Meigen) in a Clay-Turbid Lake. PhD Thesis. University of Helsinki.
- Liljendahl-Nurminen, A., Horppila, J., Uusitalo, L., Niemistö, J., 2008. Spatial variability in the abundance of pelagic invertebrate predators in relation to depth and turbidity. *Aquatic Ecol.* 42, 25–33. <https://doi.org/10.1007/s10452-006-9070-2>.
- Martin, B.E., Walsh, J.R., Vander Zanden, M.J., 2022. Rise of a native apex predator and an invasive zooplankton cause successive ecological regime shifts in a North Temperate Lake. *Limnol. Oceanogr.* 67, S163–S172. <https://doi.org/10.1002/lno.12049>.
- Martinez, N.D., Williams, R.J., Dunne, J.A., 2006. Diversity, complexity, and persistence in large model ecosystems. In: Pascual, M., Dunne, J.A. (Eds.), *Ecological networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, Oxford.
- Martinez, N.D., 2020. Allometric trophic networks from individuals to socio-ecosystems: consumer–resource theory of the ecological elephant in the room. *Front. Ecol. Evol.* 27 (8). <https://doi.org/10.3389/fevo.2020.00092>.
- McCann, K.S., Hastings, A., Strong, D.R., 1998. Trophic cascades and trophic trickles in pelagic food webs. *Proc. Royal Society B* 265, 205–209. <https://doi.org/10.1098/rspb.1998.0283>.
- McCauley, E., Murdoch, W.W., Watson, S., 1988. Simple models and variation in plankton densities among lakes. *Am. Nat.* 132 (3), 383–403. <https://doi.org/10.1086/284859>.
- Mehner, T., Kasprzak, P., Wysujack, K., Laude, U., Koschel, R., 2001. Restoration of a stratified lake (Feldberger Haussee, Germany) by a combination of nutrient load reduction and long-term biomanipulation. *Int. Rev. Hydrobiol.* 86, 253–265. [https://doi.org/10.1002/1522-2632\(200104\)86:2<253::AID-IROH253>3.0.CO;2-5](https://doi.org/10.1002/1522-2632(200104)86:2<253::AID-IROH253>3.0.CO;2-5).
- Mehner, T., Arlinghaus, R., Berg, S., Dörner, H., Jacobsen, L., Kasprzak, P., Koschel, R., Schulze, T., Skov, C., Wolter, C., Wysujack, K., 2004. How to link biomanipulation and sustainable fisheries management: a step-by-step guideline for lakes of the European temperate zone. *Fish. Manag. Ecol.* 11, 261–275. <https://doi.org/10.1111/j.1365-2400.2004.00401.x>.
- Mehner, T., 2010. No empirical evidence for community-wide top-down control of prey fish density and size by fish predators in lakes. *Limnol. Oceanogr.* 55 (1), 203–213. <https://doi.org/10.4319/lo.2010.55.1.0203>.



- Mittelbach, G.G., Persson, L., 1998. The ontogeny of piscivory and its ecological consequences. *Can. J. Fish. Aquat. Sci.* 55, 1454–1465. <https://doi.org/10.1139/f98-041>.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283. <https://doi.org/10.1038/nature01610>.
- Nonaka, E., Kuparinen, A., 2023. Limited effects of size-selective harvesting and harvesting-induced life-history changes on the temporal variability of biomass dynamics in complex food webs. *Ecol. Modell.* 476, 110150 <https://doi.org/10.1016/j.ecolmodel.2022.110150>.
- Olin, M., Rask, M., Ruuhijärvi, J., Kurkilahti, M., Ala-Opas, P., Ylönen, O., 2002. Fish community structure in mesotrophic and eutrophic lakes of southern Finland: the relative abundances of percids and cyprinids along a trophic gradient. *J. Fish Biol.* 60, 593–612. <https://doi.org/10.1111/j.1095-8649.2002.tb01687.x>.
- Otto, S.B., Rall, B.C., Brose, U., 2007. Allometric degree distributions facilitate food-web stability. *Nature* 450, 1226–1229. <https://doi.org/10.1038/nature06359>.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down marine food webs. *Science* 279, 860–863. <https://doi.org/10.1126/science.279.5352.8>.
- Pauly, D., Watson, R., 2005. Background and interpretation of the 'Marine Trophic Index' as a measure of biodiversity. *Philos. Trans. R. Soc. B* 360 (1454), 415–423. <https://doi.org/10.1098/rstb.2004.1597>.
- Pekcan-Hekim, Z., Liljendahl-Nurminen, A., Horppila, J., 2006. *Chaoborus flavicans* in the food web competitor or resource for fish? *Pol. J. Ecol.* 54 (4), 701–707.
- Persson, L., Diehl, S., Johansson, L., Andersson, G., Hamrin, S., 1991. Shifts in fish communities along the productivity gradient of temperate lakes—Patterns and the importance of size-structured interactions. *J. Fish Biol.* 38, 281–293. <https://doi.org/10.1111/j.1095-8649.1991.tb03114.x>.
- Perälä, T., Kuparinen, A., 2020. Eco-evolutionary dynamics driven by fishing: from single species models to dynamic evolution within complex food webs. *Evol. Appl.* 13 (10), 2507–2520. <https://doi.org/10.1111/eva.13058>.
- Pringle, R.M., Hutchinson, M.C., 2020. Resolving food-web structure. *Annu. Rev. Ecol. Syst.* 51, 55–80. <https://doi.org/10.1146/annurev-ecolsys-110218-024908>.
- Pycha, R.L., 1962. The relative efficiency of nylon and cotton gill nets for taking lake trout in lake superior. *J. Fish. Res. Board Can.* 19 (6) <https://doi.org/10.1139/f62-071>.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Rose, K.A., Cowan Jr, J.H., Winemiller, K.O., Myers, R.A., Hilborn, R., 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish Fish.* 2 (4), 293–327. <https://doi.org/10.1046/j.1467-2960.2001.00056.x>.
- Salminen, M., Koljonen, M.-L., Säisä, M., Ruuhijärvi, J., 2012. Genetic effects of supportive stockings on native pikeperch populations in boreal lakes – three cases, three different outcomes. *Hereditas* 149 (1), 1–15. <https://doi.org/10.1111/j.1601-5223.2011.02230.x>.
- Salojärvi, K., Partanen, H., Auvinen, H., Jurvelius, J., Jäntti-Huhtanen, Rajakallio, R., 1985. Oulujärven Kalatalouden Kehittämissuunnitelma Osa 1: Nykytila. Riista- ja Kalatalouden Tutkimuslaitos, Kalantutkimusosasto, 40. Monistettuja julkaisuja, Finnish, p. 278 pp. <http://urn.fi/URN:ISBN:951-9092-65-X>.
- Salojärvi, K., 1987. Why do vendace (*Coregonus albula* L.) populations fluctuate? *Aqua Fenn.* 17 (1), 17–26.
- Salojärvi, K., 1992. Compensation in whitefish (*Coregonus Lavaretus* L. s.l.) populations in Lake Oulujärvi, northern Finland. *Finnish Fish. Res.* 13, 31–48.
- Schindler, D.E., Hilborn, R., Chasco, B., Boatright, C.P., Quinn, T.P., Rogers, L.A., Webster, M.S., 2010. Population diversity and the portfolio effect in an exploited species. *Nature* 465, 609–613. <https://doi.org/10.1038/nature09060>.
- Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B., Halpern, B.S., 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* 5, 785–791. <https://doi.org/10.1046/j.1461-0248.2002.00381.x>.
- Sutela, T., 1985. Kalapredaation, Veden Lämpötilan Ja Liikaantumisen Vaikutukset Oulujärven eläinplanktoniin. Pro Gradu, University of Jyväskylä, Finnish.
- Sutela, T., Mutenia, A., Salonen, E., 2002. Relationship between annual variation in reservoir conditions and year-class strength of peled (*Coregonus peled*) and whitefish (*C. lavaretus*). *Hydrobiologia* 485, 213–221. <https://doi.org/10.1023/A:1021322025688>.
- Sutela, T., Hyvärinen, P., 2002. Diet and growth of stocked and wild 0+ pikeperch, *Stizostedion lucioperca* (L.). *Fish. Manag. Ecol.* 9 (1), 57–63. <https://doi.org/10.1046/j.1365-2400.2002.00251.x>.
- Taipale, S., Strandberg, U., Peltomaa, E., Galloway, A.W.E., Ojala, A., Brett, M.T., 2013. Fatty acid composition as biomarkers of freshwater microalgae: analysis of 37 strains of microalgae in 22 genera and in seven classes. *Aquat. Microb. Ecol.* 71, 165–178. <https://doi.org/10.3354/ame01671>.
- The MathWorks Inc, 2020. MATLAB version: 9.9 (R2020b). The MathWorks Inc, Natick, Massachusetts. <https://www.mathworks.com>.
- Uusi-Heikkilä, S., Perälä, T., Kuparinen, A., 2022. Fishing triggers trophic cascade in terms of variation, not abundance, in an allometric trophic network model. *Can. J. Fish. Aquat. Sci.* 79, 947–957. <https://doi.org/10.1139/cjfas-2021-0146>.
- Vainikka, A., Hyvärinen, P., 2012. Ecologically and evolutionarily sustainable fishing of the pikeperch *Sander lucioperca*: lake Oulujärvi as an example. *Fish. Res.* 113 (1), 8–20. <https://doi.org/10.1016/j.fishres.2011.09.004>.
- Vainikka, A., Jakubaviciūtė, E., Hyvärinen, P., 2017a. Synchronous decline of three morphologically distinct whitefish (*Coregonus lavaretus*) stocks in Lake Oulujärvi with concurrent changes in the fish community. *Fish. Res.* 196, 34–46. <https://doi.org/10.1016/j.fishres.2017.08.013>.
- Vainikka, A., Olin, M., Ruuhijärvi, J., Huuskonen, H., Eronen, R., Hyvärinen, P., 2017. Model-based evaluation of the management of pikeperch (*Sander lucioperca*) stocks using minimum and maximum size limits. *Boreal Environ. Res.* 22, 187–212. <http://urn.fi/URN:NBN:fi-fe201702171763>.
- Vehanen, T., Hyvärinen, P., Huusko, A., 1998. Food consumption and prey orientation of piscivorous brown trout (*Salmo trutta*) and pikeperch (*Stizostedion lucioperca*) in a large regulated lake. *J. Appl. Ichthyol.* 14 (1–2), 15–22. <https://doi.org/10.1111/j.1439-0426.1998.tb00608.x>.
- Vehanen, T., Piria, M., Kubečka, J., Skov, C., Kelly, F., Pokki, H., Eskelinen, P., Rahikainen, M., Keskinen, T., Artell, J., Romakkaniemi, A., Suić, J., Adámek, Z., Heimlich, R., Chalupa, P., Ženíšková, H., Lyach, R., Berg, S., Birnie-Gauvin, K., Jepsen, N., Koed, A., Pedersen, M.I., Rasmussen, G., Gargan, P., Roche, W., Arlinghaus, R., 2020. Data Collection Systems and Methodologies For the Inland Fisheries of Europe. FAO Fisheries and Aquaculture Technical Paper No. 649. Budapest, FAO. <https://doi.org/10.4060/ca7993en>.
- Veneranta, L., Urho, L., Lappalainen, A., Kallasvuori, M., 2011. Turbidity characterizes the reproduction areas of pikeperch (*Sander lucioperca* (L.)) in the northern Baltic Sea. *Estuar., Coast. Shelf Sci.* 95, 199–206. <https://doi.org/10.1016/j.ecss.2011.08.032>.
- Wetzel, R.G., 2001. *Limnology, Lake and River Ecosystems*, 3rd edition. Academic Press, London, p. 1006.
- Wiackowski, K., Ventelä, A.-M., Moilanen, M., Saarikari, V., Vuorio, K., Sarvala, J., 2001. What factors control planktonic ciliates during summer in a highly eutrophic lake? *Hydrobiologia* 443, 43–57. <https://doi.org/10.1023/A:1017592019513>.
- Williams, R.J., Martinez, N.D., 2004. Stabilization of chaotic and non-permanent food-web dynamics. *Eur. Phys. J. B* 38, 297–303. <https://doi.org/10.1140/epjb/e2004-00122-1>.
- Wissel, B., Benndorf, J., 1998. Contrasting effects of the invertebrate predator *Chaoborus* obscuripes and planktivorous fish on plankton communities of a long term biomanipulation experiment. *Arch. Hydrobiol.* 143 (2), 129–146. <https://doi.org/10.1127/archiv-hydrobiol/143/1998/129>.
- Wright, P.J., Trippel, E.A., 2009. Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. *Fish Fish.* 10, 283–304. <https://doi.org/10.1111/j.1467-2979.2008.00322.x>.
- Zingel P., Haberman J. 2007. A comparison of zooplankton densities and biomass in Lakes Peipsi and Võrtsjärv (Estonia): rotifers and crustaceans versus ciliates. In: Nöges T. et al. (eds) *European Large Lakes Ecosystem changes and their Ecological and Socioeconomic Impacts. Developments in Hydrobiology*. vol 199. Springer, Dordrecht. 10.1007/978-1-4020-8379-2\_18.
- Zingel P., Agasild, H., Karus, K., Buholce, L., Nöges, T., 2019. Importance of ciliates as food for fish larvae in a shallow sea bay and a large shallow lake. *Eur. J. Protistol.* 67, 59–70. <https://doi.org/10.1016/j.ejop.2018.10.004>.