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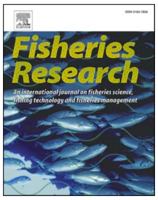

Biomass and sustainable yields of Eurasian perch (*Perca fluviatilis*) in small boreal lakes with respect to lake properties and water quality

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ABSTRACT

Understanding of factors that explain variation in potential fisheries yields is essential for the ecosystem-based management of lake fisheries. We used mark-recapture and Nordic survey net sampling to obtain estimates of Eurasian perch (*Perca fluviatilis*) abundance in 28 small (13.3 ha ± 11.4 ha, mean ± S.D.) boreal lakes. A size-structured population model was calibrated for each lake using further individual data to derive estimates of potential yields. Principal component scores formed from physical and chemical environmental parameters and a simple score reflecting the relative photic area of the lakes were then used to explain variation in theoretical yields to identify potential environmental proxies for fisheries management purposes. The estimated mean biomass of perch in the study lakes was 52.4 ± 51.2 kg ha^{-1}, and the maximum sustainable yield, obtained with environment-dependent recruitment size was estimated to be 9.4 ± 12.1 kg ha^{-1} yr^{-1}. The estimated yields were highest in shallow lakes with good oxygen saturation and with high percentage of euphotic bottom while excess nutrients decreased yields and alkalinity was marginally predictive for catch of large individuals. Our study provides quantitative estimates of potential yields of varyingly sized perch and helps to develop environmentally informed management for small lakes of which some are surprisingly productive.

1. Introduction

Although biological fish production capacity of waterbodies sets the ultimate boundaries for sustainable fisheries management, estimates of potential sustainable yields have been published for a low number of lakes (e.g. Ryder, 1965; Rask and Arvola, 1985; Mosindy et al., 1987; Downing et al., 1990). In addition, yield estimates have often been made by assuming a constant production to biomass ratio (e.g. Viljanen and Holopainen, 1982) or by accounting fish growth but without fisheries constraints such as size at which fish enter fishery or fishing intensity (e.g. Horppila et al., 2010; Karlsson et al., 2015; van Dorst et al., 2019). To incorporate ecosystem approach to fisheries management it would be desirable to understand how physical and limnological conditions and catchment properties shape the production of fish populations and the ways these populations could be optimally managed (e.g. Horppila et al., 2010; Karlsson et al., 2015; Seekell et al., 2018; van Dorst et al., 2019). Such knowledge is also a prerequisite to understand the past and forthcoming effects of climate change (Schindler et al., 1990; Lepistö et al., 2021) and intensive forestry practices on aquatic ecosystems (Laudon et al., 2009; Nieminen et al., 2015; Aaltonen et al., 2021).

Various methods have been developed to predict fish production from environmental variables (Leach et al., 1987; MacLeod et al., 2022). In general, fish production is limited by the availability of suitable habitats, oxygen and nutrients, and composition of the prey, predator and competitor community (MacLeod et al., 2022). Shallow lakes are typically more productive than deep ones (Rawson, 1952; Ryder, 1965; Chu et al., 2016), and coloured lakes with high nutrient contents can support higher level of primary production than nutrient-poor

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clear-water lakes (Nürnberg and Shaw, 1999). Still, visually hunting fish and algal production may be light limited in strongly humic waters (Karlsson et al., 2009; Benoît et al., 2016; Seekell et al., 2018). Lakes with high rates of primary production, measured as chlorophyll-*a* concentration, generally yield the highest catches in recreational fisheries (Jones and Hoyer, 1982) and show the highest catch-per-unit-effort (CPUE) indices for predatory fishes in experimental fishing by multi-mesh gillnets (Kokkonen et al., 2019b). Downing et al. (1990) concluded that primary production, total phosphorus concentration, and fish biomass best predicted fish production rates. However, many environmental contributions to the productivity of fish populations may be non-linear or related to the structure and function of the ecosystem more than to the concentrations of nutrients or other chemical substances (Trudeau et al., 2023). Ranta and Lindström (1993) argued that, in theory, fish production should show a bell-shaped relationship with environmental variables such as nutrient concentrations or water colour. Because different fish species have different preferences for environmental variables, production of certain species may show linear relationships only at limited ranges of environmental variables (Finstad et al., 2014; Jarvis et al., 2020). Despite the inherent complexity of aquatic ecosystems, easily measurable environmental metrics may still offer relevant predictors of fish growth, recruitment and size structure (Holmgren and Appelberg, 2005; Höhne et al., 2020), and as such help to improve the often poor or completely absent management of small lake fisheries (Cooke et al., 2016).

Boreal lakes are abundant throughout the Northern hemisphere. In Finland alone, there are 53,423 lakes of 1–100 ha in size (Raatikainen and Kuusisto, 1988), but most $<$ 50 ha lakes are not monitored for fish populations or water quality. Small ($<$ 50 ha) lakes can be locally important for recreational fisheries (Kaemingk et al., 2022), while they are also vulnerable to land-use driven changes in water quality and ecosystem functioning (Estlander et al., 2021; Holopainen and Lehikoinen, 2022). Browning, resulting from the increased concentration of dissolved organic matter (DOM), specifically dissolved organic carbon (DOC) and iron, is one of the strongest drivers of ecosystem functioning in small boreal waterbodies (Weyhenmeyer et al., 2014; Estlander et al., 2021; Blanchet et al., 2022). Changes in water colour can affect primary production (Jackson and Hecky, 1980), abundance of aquatic invertebrates (Arzel et al., 2020), structure and distribution of zooplankton and fish communities (Olin et al., 2010; Williamson et al., 2020) as well as Eurasian perch (*Perca fluviatilis*) growth (Estlander et al., 2010, 2012) and recruitment (Taipale et al., 2018). Hence, loading of DOC from drained peatlands and intensively managed forests (Nieminen et al., 2015; Aaltonen et al., 2021) could impose negative effects on fisheries.

Many of the seminal papers providing production estimates for freshwater fishes have focused on perch, the most common and abundant fish species in European boreal lakes (Viljanen and Holopainen, 1982; Rask and Arvola, 1985; Ranta and Lindström, 1989), and a popular fish for human consumption and recreational fishing through Europe (Lyach and Remr, 2019). Horppila et al. (2010) suggested that the density of perch populations would be a better predictor of production capacity than the individual growth rate of fish. Thus, a key requirement for attempts to optimize fisheries management is to be able to form a robust relationship between catch-per-unit-effort (CPUE) and fish population density. Population density of perch has been shown to predict CPUE in standard survey gill netting among a limited number of lakes (Linløkken and Haugen, 2006; Olin et al., 2016). However, the exponent function used by Olin et al. (2016) produces unrealistically high density estimates for a CPUE range beyond what was observed in the study (i.e. more than five perch per gillnet). Theoretically, standard Holling type I-III functional responses might be usable in describing catch rates in relation to population density. For example, Egglestone et al. (2008) showed that diver harvesting of lobsters follows type I functional response. While the need for robust abundance data is apparent, it is further necessary to assess the covariation between environmental factors, fish community size structure (Holmgren and Appelberg, 2005) and fish life-history traits, such as size at maturation and growth rate, to evaluate potential yields and optimal fisheries management measures (Höhne et al., 2020). Despite the difficulty of estimating natural mortalities and recruitment functions in any natural systems, size-structured population models offer a way to predict how population density and population-specific life-history traits translate to fisheries yields under various scenarios of harvesting (e.g. Vainikka and Hyvärinen, 2012; Vainikka et al., 2017).

Our aim in the present study is to provide tentative estimates for the potential sustainable yields of perch in small boreal lakes, create fisheries management recommendations, and link both yield estimates and management recommendations with hydro-morphological and chemical variables. Ultimately, we aim to find simple indicators that could provide robust predictors of perch yields for the use of local fisheries management and support the evaluation of the impacts of various environmental pressures on fisheries. We predict that shallow clear-water lakes with high primary nutrient concentrations would be the most productive environments for perch, while deep lakes with poor transparency, high levels of dissolved organic material and poor oxygen saturation levels would show the lowest yield estimates. Due to inherent difficulty of estimating potential fisheries yields of a single species as a part of a complex ecosystem with size-dependent interactions (Persson and De Roos, 2013; Persson et al., 2014; Trudeau et al., 2023), we assume that water quality and lake morphology can affect perch populations independently of the actual mechanisms (c.f. Kokkonen et al., 2019b) that are too complex to be explicitly accounted for in this study. We further assume that the obtained empirical data represent unfished conditions and calibrate the used size-structured model for each study lake using age-at-length, maturation size and population density data of perch. To further avoid inexplicable complexity arising from cannibalism between perch size-classes (Persson et al., 2000) and size-dependent diet variation (Persson and Greenberg, 1990b; Hjelm et al., 2000; Trudeau et al., 2023), we model the population dynamics without explicitly addressing intra- or interspecific predation and ontogenetic niche shifts.

2. Materials and methods

2.1. *Study design*

In total, 18 lakes in Lieksa area (North Karelia, Finland) and 8 lakes in Evo area (Tavastia, Finland) were sampled for water quality and test fished using Nordic survey nets (Appelberg et al., 1995; Tammi et al., 2006) during July-August 2020 and July 2021 ($N = 223$ gillnet nights, Table 1, Fig. 1). In addition, two Evo lakes, Lakes Majajärvi and Valkea-Kotinen were included in the estimation of sustainable perch yields based on published abundance data (Olin et al., 2016, Table 2) and analysed individual data (Table 1). Two additional lakes in Lieksa area, Lakes Iso-Piilo and Pieni Kangaslampi, were sampled only for water quality but included in the study to add generality. Four of the fully sampled lakes in Lieksa were fished using wire traps for mark recapture population estimates during summer 2021 (Table 1). Former abundance and Nordic survey net catch-per-unit-effort (CPUE) data (Olin et al., 2016) were combined with the CPUE data collected in this study to derive a predictive equation for the perch abundance by CPUE data (Table 2). Perch population in each lake was simulated using an age-, maturity- and size-structured population model (Vainikka and Hyvärinen, 2012), calibrated for each lake using data on 1) population density (either estimated or predicted), 2) age-at-lengths, and 3) maturation size to derive estimates of sustainable yields. Finally, the yield estimates were linked to principal component scores, reflecting the original environmental variables, using multivariate regression analysis. In addition, correlation analyses were performed to examine the potential effects of the relative photic bottom surface area and roach (*Rutilus rutilus*) CPUE since these variables could not be included in the

Table 1

List of the fished and/or water-sampled study lakes with the basic characteristics, the estimated relative surface area of bottom with capacity for photosynthesis, total phosphorus concentration as predicted for mid-July and the number of individual Eurasian perch (*Perca fluviatilis*) analysed for age and maturity.

Lake (E = Evo, L = Lieksa)	Coordinates (ETRS-TM35FIN)	Surface area (ha)	Shoreline length (m)	Maximum depth (m)	Altitude (m a.s.l.)	Secchi-depth (m)	Productive (euphotic) area %	Total P $\mu g\ L^{-1}$	*N* perch
Aitalampi (L)*	N = 7,017,121, E = 695,069	12.8	2288	1.7	173.9	1.3	100	11.5	58
Haukijärvi (E)	N = 6,789,042, E = 399,989	2.2	692	5	131.4	0.8	35	29.6	2
Hautjärvi (E)	N = 6,786,725, E = 400,264	7.7	1250	9	137.4	1.0	22	39.6	-
Hirsikankaan Rasku (L)*	N = 7,008,932, E = 683,093	5.5	1095	14.5	168	2.4	70	7.0	85
Horkkajärvi (E)	N = 6,788,049, E = 401,082	1.2	454	10	142.7	1.2	22	14.6	4
Hukkalampi (L)	N = 7,015,712, E = 697,799	12.7	1408	10	167.9	1.5	64	12.0	31
Iso Mustajärvi (E)	N = 678,7724, E = 398,484	2.6	819	8	129.6	1.1	42	20.6	28
Iso Piilo (L)§	N = 7,009,877, E = 692,959	43.8	4093	9.4	149.9	1.4	58	10.4	-
Iso Ruuhijärvi (E)	N = 6,789,560, E = 396,168	14.3	1840	6	149	1.1	46	52.6	5
Iso Saunajärvi (L)	N = 7,011,212, E = 685,493	24.9	3538	1.9	161.5	1.7	100	15.0	20
Iso Valkjärvi W (E)	N = 6,785,368, E = 398,295	3.9	758	8	126.3	2.6	100	14.6	23
Kaitalammi (E)	N = 6,786,233, E = 399,436	2.2	877	5	125.7	1.5	100	14.6	9
Kaivoslampi (L)	N = 7,012,241, E = 683,847	17.4	2007	3.7	162.4	1.6	100	20.0	55
Kalaton-Väärä (L)	N = 7,009,867, E = 690,553	12.2	1812	10.5	157.8	5.5	100	6.0	28
Kangas-Piilo (L)	N = 7,011,481, E = 693,716	26.3	3416	2	150.8	1.2	100	20.0	32
Litmonlampi (L)	N = 7,011,445, E = 684,016	14.3	1946	1.5	161.6	1.2	100	15.0	25
Majajärvi (E) *	N = 6,788,186, E = 400,012	3.4	1140	12	133.3	0.7	24	26.0||	51
Nikkilänlampi (L)	N = 7,011,115, E = 698,714	11.5	2120	10.1	171.2	2.0	79	10.5	20
Pieni Kangaslampi (L)§	N = 7,010,284, E = 684,921	3.5	1108	8.5	162.8	2.5	94	8.6	-
Pieni Saunajärvi (L)	N = 7,010,612, E = 685,396	12.3	2793	7.8	161.2	2.9	100	8.0	26
Pieni Venejärvi (L)	N = 7,011,970, E = 686,948	37.7	6549	1.8	159.3	1.4	100	16.0	20
Pieni-Piilo (L)	N = 7,010,242, E = 693,630	14.4	2226	5.2	149.9	0.8	93	19.6	26
Pikku-Hukka (L)	N = 6,999,960, E = 676,440	11.5	1438	4.6	167.3	0.9	67	13.5	25
Pitkänniemenjärvi (E)	N = 6,787,552, E = 399,485	14.0	2352	11	126.8	1.6	54	15.6	20
Raate (L)	N = 7,001,300, E = 676,390	19.9	2563	4.5	167.2	0.9	89	18.0	25
Synkkä-Rasku (L) *	N = 7,010,401, E = 681,988	4.9	1266	10	167.3	1.4	54	11.5	19
Valkea-Kotinen (E)‡	N = 6,791,264, E = 396081	3.6	1022	6	155.9	0.9	60	24.0||	53
Valkea Mäntyjärvi (L)†	N = 7,013,421, E = 681,901	53.9	6235	15	162.9	3.8	96	5.4	29
Valkealampi (L)*	N = 7,016,960, E = 695,576	10.2	1675	7.5	174.6	3.5	100	6.0	36
Valkea-Väärä (L)	N = 700,9151, E = 690,397	18.0	3200	2.4	157.2	2.1	100	9.5	30

*The lake was used for mark-recapture trapping of Eurasian perch and survey net fished again in 2021.
†The lake was fished with Nordic survey nets only in 2021.
‡No own sampling.
§Only water samples in 2020. ||Sampled and analysed separately in summer-autumn 2020.

single regression to avoid overfitting and inherent collinearities.

2.2. Ethics approval

All the fishing conducted in the project was performed under research licences from Parks & Wildlife Finland. The study procedures did not require an animal experimentation licence, but light benzocaine-induced sedation was used in the fin clipping of fish to avoid any unnecessary distress.

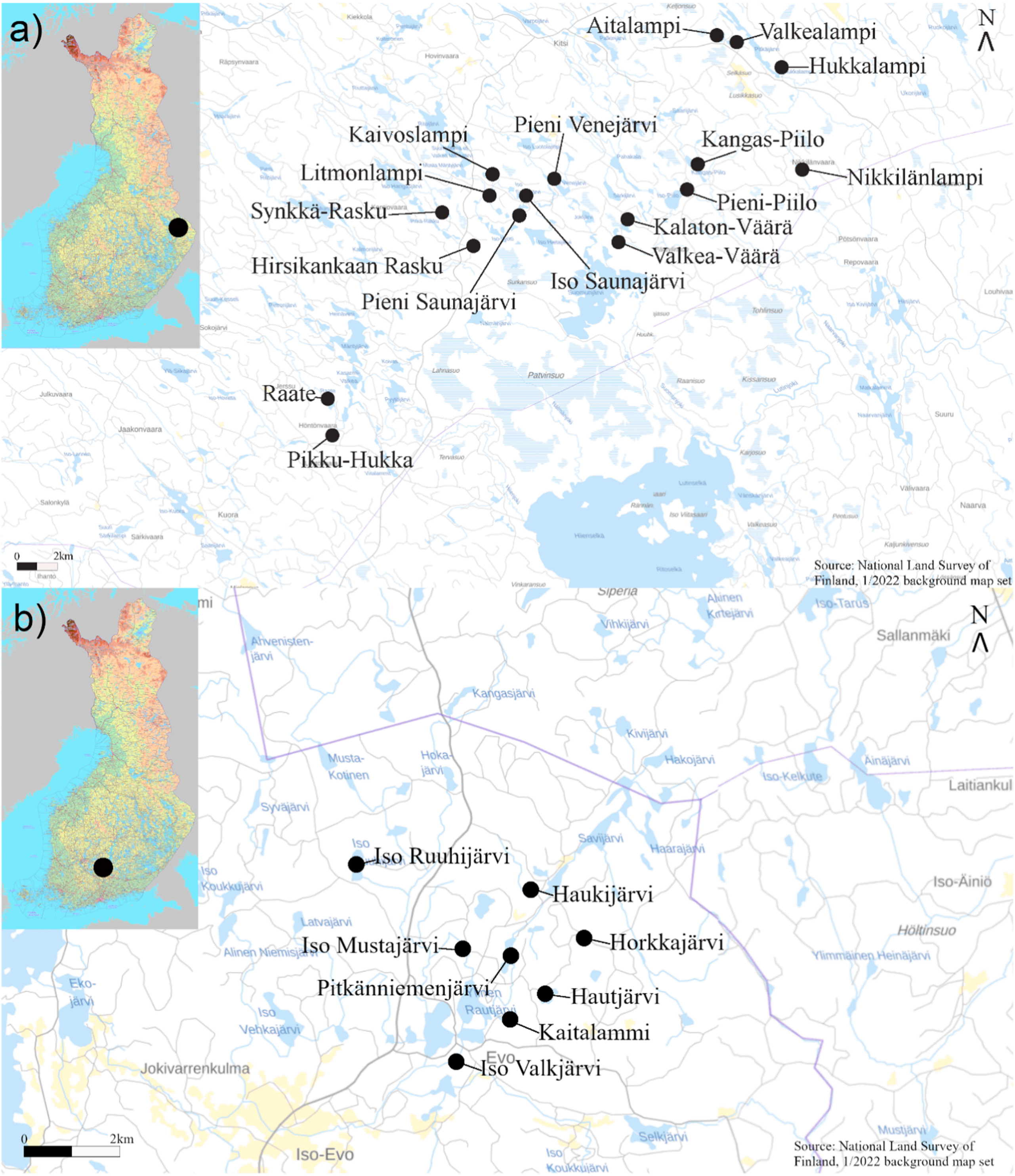

Fig. 1. Map of the study lakes in a) Lieksa area in Eastern Finland and b) Evo area in Southern Finland.

2.3. Lake characteristics

To capture the basic physical qualities of the lakes (Table 1), we obtained the total surface area, total shoreline length, maximum depth, and lake altitude from the Finnish National Topographic Database (fin Maastotietokanta) and public terrain maps (Karttapaikka, https://asiointi.maanmittauslaitos.fi/karttapaikka/) produced by the National Land Survey of Finland. We used geoinformatics (i.e. ArcGIS software, Esri Finland Oy, Finland) to extract the depth points and contour lines, in addition to the pond area polygons (further converted to lines) for the lakes in Lieksa from the database. We approximated the depth of the euphotic zone by multiplying the Secchi depth with 3 (Lee et al., 2018). The ratio between the true euphotic zone depth and Secchi depth generally increases with turbidity and decreases with humic colouration (Koenings and Edmundson, 1991) which implies that the selected constant multiplier (3) might have overestimated the true euphotic zone depth in the darkest lakes, yet it was robust for our comparative purpose. The relative proportion of the surface area shallower than the euphotic

Table 2
Relationship between mean catch per unit effort (CPUE) in Nordic survey gillnets versus estimated mean absolute population sizes of Eurasian perch (*Perca fluviatilis*) $\geq$ 90 mm in total length (for graphical presentation see Fig. A.1). The CPUE values are arithmetic means over the specified years as based on Olin et al. (2016) and our sampling in this study (years 2020–2021). Theoretical maximum was used as one data point to guide the CPUE $\sim$ abundance relationship to a generally feasible direction.

Lake	Sampling years	CPUE (n gillnet^{-1})	Estimate (n ha^{-1})	Source
Aitalampi	2020-2021	50.00	366	Primary data
Haarajärvi*	2006-2013	7.65	969	Olin et al. (2016)
Haukijärvi	2007-2013, 2020	4.18	847	Olin et al. (2016) + data
Hirsikankaan Rasku	2020-2021	5.36	136	Primary data
Hokajärvi*	2006-2013	5.82	487	Olin et al. (2016)
Iso Mustajärvi	2011, 2013, 2020	3.92	491	Olin et al. (2016) + data
Iso Valkjärvi E *	2007-2012	8.63	1046	Olin et al. (2016)
Iso Valkjärvi W	2007-2012, 2020	7.93	1154	Olin et al. (2016) + data
Majajärvi	2006-2013	8.36	2655	Olin et al. (2016) + data
Synkkä Rasku	2020-2021	1.42	561	Primary data
Valkea-Kotinen	2005-2013	8.97	1521	Olin et al. (2016)
Valkealampi	2020-2021	10.02	203	Primary data
Theoretical maximum		85	10,000	Database/ experiment

*The lake was sampled by Olin et al., (2016) and was not included in this study beyond the estimation of the equation predicting abundance by CPUE.

zone depth was calculated manually for the lakes in Evo for which there was no public digital depth contour data, but unpublished depth maps produced for research purposes. For the lakes in Lieksa, the bathymetry of each lake was interpolated based on the depth vector data in ArcGIS, and the interpolation results were cut with the pond polygon data. The interpolated lake data were reclassified based on the photic layer depths, i.e. the areas below and above the photic layer depth resulting in measures of the relative bottom surface area above the euphotic zone depth. The ratio of shoreline length to total surface area was calculated for all lakes as a measure of relative availability of littoral habitats.

2.4. Water quality

Water samples were collected using a Limnos-sampler (that allows sampling of certain water layer by remotely closable lids) from 1 m depth at the deepest point of the lake. The samples in Lieksa were collected on 29 June 2020 and 3 August 2020, and in Evo 5 August 2020. Handheld YSI Professional Plus QUATRO meter (Yellow Springs Instruments Inc., Yellow Springs, OH, USA) was used at each sampling occasion to record depth profiles for oxygen concentration, temperature, conductivity, and oxygen reduction potential. Secchi disk was used to determine water transparency. The air-free samples taken in 1 l bottles stored in cool boxes were transported to the laboratory at Lammi Biological Station of the University of Helsinki on the next day for immediate analyses (alkalinity, conductivity, pH, colour, total nitrogen, total phosphorus, phosphate phosphorus, dissolved organic carbon (DOC), chlorophyll *a*, and oxygen concentration) or stored for later determinations (Fe concentration). Conductivity was measured at 25 °C using YSI-3200, with cuvette YSI 3253). pH was measured with a pH meter along with the titration of alkalinity (Gran plot, detector DGI117-water) and oxygen concentration (Mettler, Toledo DL-53, detector DM-140SC). Water colour, absorbance and chlorophyll-*a* were measured using Shimatsu UV-1800 spectrophotometer. Water colour was determined with a spectrophotometer as absorption at 410 nm against Pt-Co standards (APHA 2000) after filtration through Millex-HA 0.45 µm membrane filter. Absorbance spectrum was measured at 200–750 nm with 0.5 nm steps. Water samples for chlorophyll-*a* measurements were filtered through GF/C glass fibre filters. After 5 min extraction in hot (75 °C) ethanol, absorption was measured at 665 and 750 nm wavelengths. Total nutrients (Tot-P and Tot-N) were analysed from nonfiltered samples by a spectrophotometer (Gallery™ Plus, Thermo Fisher Scientific, MA, USA). For phosphate-phosphorus (PO$_4$-P), the samples were filtered with pre-rinsed (deionized water MQ; Millipore, Billerica, MA, USA) 0.45 µm filters. DOC was analysed with a total carbon analyzer (TOC-V, Shimadzu, Tokyo, Japan). Iron (Fe) was determined by flame-AAS (Varian SpectrAAS 220, Varian, CA, USA).

2.5. Nordic survey net fishing

Nordic survey net fishing was executed according to the national standard (Olin et al., 2014). A standard Nordic gillnet is 30 m long and 1.5 m in height. It consists of twelve 2.5 m long panels with different mesh sizes (bar length): 5 mm, 6.25 mm, 8 mm, 10 mm, 12.5 mm, 15.5 mm, 19.5 mm, 24 mm, 29 mm, 35 mm, 43 mm and 55 mm (Olin et al., 2014). The lakes were divided into 50 m × 50 m squares for the randomization of the net locations. Each lake was fished twice on consecutive days, and two lakes were fished on the same days. The gillnets were set in the evening and lifted in the morning in the same order to ensure the approximate 12 h of fishing effort per net. Number of used nets in each lake was determined by lake size and number of depth zones (Olin et al., 2014). The randomized locations covered all habitat types (profundal, pelagic and littoral), but clearly anoxic deep areas were not fished. Total mass of fish in each mesh size was weighed by species and all fish individuals were measured for total length (to 10 mm classes). In addition to perch, roach abundance data (CPUE and biomass per gillnet, BPUE) were used in this study due to the potentially important role of roach in lake ecosystems (Persson and Greenberg, 1990a; Horppila et al., 2010). The fishing in Lieksa lakes took place between the 1 July and 22 July 2020, 6 July and 14 July 2021, and in Evo between the 4 August and 10 August 2020. We assumed that the fish populations would show temporally stable abundance (i.e. that lakes differ more from each other than years within lakes) since combined statistical and dynamic modelling of annual variations was beyond feasible options. Repeatability of annual Nordic net CPUE mean for perch was high when all data from Evo (years 2005–2020) and Lieksa (years 2020–2021) were combined (package ICC in R 4.0.2, $R = 0.613$, 95% C.I. 0.376 – 0.838) supporting this assumption.

A haphazard sample covering all perch sizes (all perch when very few were caught) of gill-netted perch from each lake ($N = 642$ in total) were frozen and later used for the determination of individual age from opercular bone under a light microscope and maturity status and sex of the adult fish by dissection of the fish. These data were amended with ($N = 143$) perch captured by ice-fishing in April 2021 (Turunen et al., 2023).

2.6. Mark-recapture population estimates

We conduced mark-recapture fishing in four of the Lieksa lakes (Table 1) in two periods to amend published data from Evo (Olin et al., 2016) (Table 2). In May-June 2021, ten wire traps operated from the lake shores were used. The traps consisting of bar length of 12 mm or 19 mm plastic-covered metal grids were moved between the lifting and marking events to cover as much of the lake shoreline as logistically feasible. The marking was performed by clipping a 3–4 mm long piece from the tip of the pelvic fin under light sedation by benzocaine (20 mg L^{-1}). In total, 377 perch were marked in Lake Aitalampi with 61 recaptures (16.2%), 221 perch in Lake Hirsikankaan Rasku with 83 recaptures (37.6%), 432 perch in Lake Synkkä-Rasku with 66 recaptures (15.3%) and 820 perch in Lake Valkealampi with 218 recaptures

(26.6%). Lakes Hirsikankaan Rasku and Synkkä-Rasku were connected to the same watercourse through small brooks, but no significant migration of perch was expected to occur. Lake Valkealampi discharges to Lake Aitalampi via a small ditch that is dry for most of the year. All fish were measured for total length using 10 mm length classes. The second fishing period occurred in July during the time when the lakes were fished with Nordic survey nets and angling. One Nordic gillnet experimental fishing night was used as a one mark-recapture event but with recording all captured fish as removed and not tagged. One angling day was considered as one mark-recapture event. The fin clipping was detectable throughout the study, but previous preliminary tagging in 2020 indicated that the fins had recovered within a year. The mark-recapture analysis was performed under assumptions of closed population, equal absence of selectivity between the fishing methods, no natural mortality or significant growth and complete mixing of the population between the fishing occasions. The population size estimates were derived for perch of ≥ 90 mm in total length using Schnabel's method (Schnabel, 1938) with Chapman's correction (Chapman, 1954) in R 4.1.0 (The R Foundation for Statistical Computing) using FSA package (Ogle et al., 2021).

2.7. Population estimates through Nordic survey net fishing

Theoretically, gillnets can be considered as predators: they saturate due to accumulation of fish, and some time is needed before a fish becomes entangled in the net (comparable to predator's handling time) (Olin et al., 2004). Thus, we used package *frair* in R 4.1.2 (Pritchard et al., 2017) to examine if the CPUE vs. abundance data would follow some type of functional response. Because the available data (Olin et al., 2016) came mostly from low-density lakes, the pilot analyses indicated that the analysis should be constrained to produce feasible (low enough) density estimates for high CPUE-lakes. For this purpose, one data point was created by using the maximum empirically observed perch density and the maximum CPUE value found in the survey gillnet fishing database maintained by the Natural Resources Institute Finland. The approximate maximum perch abundance (individuals $\geq$ 90 mm in length ha^{-1}) was derived from an experiment where Lake Koppelolampi (6.5 ha, N = 7,133,038.304, E = 641,581.609, Kuhmo, Finland), stocked with newly hatched Eurasian perch larvae ($N = 52{,}700$) in May 2015, was emptied by draining in August 2020 for density assessment. Function *frair_test* (Pritchard et al., 2017) was used to test statistical support for functional responses I-III with and without the maximum data point (Table 2, Fig. A.1) to ensure that the maximum data point did not affect the support for type II functional response ($P < 0.05$) or predictions for low-CPUE lakes. Finally, the function *frair_fit* with graphically determined starting values was used to fit the type II functional response equation based on maximum likelihood estimation to the data including the maximum data point. The estimated parameters were: $a = 0.0153 \pm 0.0020$ ($Z = 7.61$, $P < 0.001$), $b = 0.00786 \pm 0.00244$ ($Z = 3.21$, $P = 0.001$), and $t = 1$ (assumed time interval). Reversing the Holling's type II disc equation, the perch density d per ha for the lakes with no direct abundance estimates could be approximated from the CPUE (C) as (see Fig. A.1):

$$d = \frac{C/a}{(1 - bC)} \tag{1}$$

where a and b are estimable parameters (see above).

2.8. Model description and parameterization

An age, length and maturity structured discrete-time population model (Vainikka and Hyvärinen, 2012; Vainikka et al., 2017) was used in this study with modifications in the recruitment and growth processes, and improvements in the calculation of catches. The seasonal order of functions in the model follows the natural life cycle of perch: 1. Spawning and recruitment, 2. Maturation and growth, 3. Natural and fishing mortality. The population census occurs after mortality which corresponds to the situation prior to spawning in spring. All the model parameter values shared among all lakes are shown in Table 3 in the order of appearance in the text.

The age structure was used only for the calibration of growth, and the maturity classes share everything but the maturity status. Thus, the class indexing is not used in the notation. To determine the total fecundity, Ψ, of the population, individual size-dependent fecundities $\psi(l)$ (where l is the total length, mm) were calculated based on published data from Lake Suomunjärvi (Viljanen and Holopainen, 1982), located within the same watershed as the study lakes in Lieksa. The total number of spawned eggs (total fecundity of all females in a population), Ψ, assuming equal sex ratio was obtained using integral over all lengths l:

$$\Psi = \frac{1}{2}\int_0^\infty \psi(l) n_{mat}(l) \quad dl \tag{2}$$

where $n_{mat}(l)$ is the *number* of sexually mature individuals at size l (in mm), and fecundity $\psi(l)$ is calculated according to the empirical formula by Viljanen and Holopainen (1982) as:

$$\psi(l) = 10^{\left(0.199+2.904*\log_{10}\left(\frac{l}{10.0}\right)\right)} \tag{3}$$

The recruitment of the population, R, follows Beverton-Holt type recruitment:

$$R = \frac{\Psi}{1 + \eta\Psi} \tag{4}$$

where the parameter η sets the carrying capacity of the recruitment environment through assumption of finite suitable habitat for reproduction and scales the survival of eggs to 0-year-old recruits. A stabilizing, compensatory function was used, because there was no data to separate Ricker-type function from the simpler Beverton-Holt (*c.f.* Kokkonen et al., 2019a). The parameter η was found by automatic iteration refining the value until the simulated population size of individuals over a certain recruitment size (total length, mm) (N_{min}) of fish ($min = 90$ mm) matched the estimated population size of fish $\geq$ 90 mm

Table 3
Parameters shared by all populations for the size-structured model of the Eurasian perch (*Perca fluviatilis*) in the order of appearance in the text.

Parameter name	Symbol	Value	Unit	Source
Width of the maturation window	σ_m	10	mm	Adjusted from data-based 35 mm
Constant of maximum food intake	c_0	2	$g\ y^{-1}$	Fiogbé and Kestemont (2003)*
Unit conversion constant	c_1	1	g^{-1}	
Maximum food intake exponent	c_2	0.73	–	Fiogbé and Kestemont (2003)*
Unit conversion constant	υ_1	1	mm^{-1}	
S.D. in food availability	σ_e	30	–	Adjusted to yield realistic growth
Smoother of resource dynamics	β	5	–	Adjusted for feasible growth range
Size-independent mortality	d_0	0.18	y^{-1}	Based on Heibo et al. (2005)†
Size-dependent mortality	d_1	2.5	y^{-1}	Based on Heibo et al. (2005)†
Natural mortality decay size	l_0	75	mm	Based on Heermann et al. (2009)†
Variation over size limits	$\sigma_{f,min}$	30	mm	Knowledge on perch fisheries

*Allometry fitted using non-linear regression based on the reported optimum feeding ratios.

†There is no published length-based data, but natural mortality decreases strongly with age and size. Strong fishing pressure on the fish community likely replaces natural mortality with fishing mortality supporting lower values than found in non-fished or strongly predated populations.

in the lake at population dynamical equilibrium (Table 4) within the numerical precision of the model (< ca. 10 individuals):

$$N_{\min} = \int_{\min}^{\infty} n(l) \quad dl \tag{5}$$

Recruits are introduced to the simulated population at size l_r (Table 4). Thus, the size of the fish in the end of the first year corresponds the size l_r + annual growth. Individuals mature according to a logistic equation such that each individual at size l has a probability of entering the mature class of the population (spawn for the first time) $p(l)$,

$$p(l) = \left[1 + \exp\left(-\frac{l - l_{mat}}{\sigma_m}\right)\right]^{-1} \tag{6}$$

where σ_m defines the width of the range at which maturation occurs (Table 3), and l_{mat} is the length at 50% probability of maturing (Table 4). In the pooled individual data, the empirical σ_m was determined graphically to be ca. 35 mm but it was reduced to 10 mm in the simulations to provide stronger dependency of maturation on size, as is feasible within each population and sex. All fish mature in the beginning of the growing season so that the growth of maturing fish equals the growth of mature fish. The l_{mat} values (see published data) were iterated at 1 mm precision until the L_{50} derived from the simulated population using logistic regression matched the L_{50} derived from the empirical individual data (Table 4, see below).

The length-at-age L_a of perch was modelled using the biphasic growth model of Lester et al. (2004) that provides a mechanistic basis to model the effect of life-history on population dynamics (Wilson et al., 2017):

$$L_{a+1,t+1} = \left(\frac{3}{3+g}\right)L_{a,t} + \alpha\frac{3h}{3+g} \tag{7}$$

where g is the energetic GSI (zero for immature fish), h is the annual juvenile growth increment (i.e. measure of the somatic growth rate, Enberg et al., 2012) and α is the density-dependent scaler of growth rate (*omitted* in fitting, see below) (Dunlop et al., 2007; Arlinghaus et al., 2009). The growth model was fitted separately on each population (Fig. A.2) using age-at-length data (since age is conditional on size, see Mollet et al., 2013) and a custom C++ algorithm following principles of non-linear least squares regression (minimizing squared deviations between observed and predicted age-at-lengths) so that the algorithm iteratively tests pre-defined parameter spaces for the recruitment size l_r, juvenile growth rate h and energetic gonadosomatic index g (constrained between 0.05 – 0.5) (Lester et al., 2004) by using fixed empirically determined size at maturation l_{mat} (Table 4). Logistic regression was used to estimate the size at which 50% of the perch were sexually mature in each population. Due to the timing of sample collection, the samples included immature fish that would spawn for the first time on the next year. Because of this, the mean length increment of 35.76 mm between 0-year-old and 1-year-old perch was added to all L_{50}-estimates. This increased the L_{50}-estimates closer to 124.2 ± 19.4 mm reported for stunted perch populations (Heibo et al., 2005). For five lakes with no realistic estimates due to small sample size, the mean L_{50} was used. To ensure that the model correctly captured individual growth patterns, the realized length-at-ages were derived from the model at population dynamical equilibrium and plotted against empirical data and growth model fits (Fig. A.2). When needed, the constant ρ (Eq. 14) was adjusted to improve the alignment. It is known that female perch grow faster and mature later than male perch at the

Table 4

Population specific parameters of the Eurasian perch (*Perca fluviatilis*) populations used in the simulations. Densities, abundances and catch per unit effort (CPUE) are for perch ≥ 90 mm in total length. L_{50} refers to the size at which 50% of the population is sexually mature. υ_0 and υ_2 define the allometry between fish mass and length (see Eq. 9.). Recruit size (l_r in the text) refers to the total length of 0-year-old perch when they appear in the model, Lester h refers to the annual length increment of juvenile fish, Lester g to the energetic gonado-somatic index, and intercept υ_0 and exponent υ_2 are the parameters for regression explaining fish mass with fish total length.

	CPUE n^{-1}	Density ha^{-1}	Population size	L_{50} (mm)	Recruit size (mm)	Lester h	Lester g*	Intercept υ_0	Exponent υ_2
Aitalampi	50.0	366	4672	112	72.5	17.4	0.142	0.00000868	3.036
Haukijärvi†	4.18	847	1883	86	54.4	23.1	0.055	0.00000496	3.150
Hautjärvi†	0.12	8‡	59	86	54.4	23.1	0.055	0.00000496	3.150
Hirsikankaan Rasku	5.36	136	753	88	52.5	23.6	0.229	0.00000633	3.093
Horkkajärvi†	1.40	93‡	107	86	54.4	23.1	0.055	0.00000496	3.150
Hukkalampi	5.89	404‡	5149	149	45.1	24.0	0.050	0.00000273	3.269
Iso Mustajärvi	3.92	491	1297	86†	55.0	26.0	0.050	0.00001381	2.923
Iso Ruuhijärvi	0.50	33‡	470	138	38.8	44.2	0.140	0.00000589	3.116
Iso Saunajärvi	11.57	834‡	20,737	116	45.0	28.5	0.152	0.00000694	3.079
Iso Valkjärvi W	7.93	1154	2550	86†	63.8	22.2	0.142	0.00001841	2.885
Kaitalammi	1.40	93‡	200	128	50.4	27.6	0.380	0.00001290	2.942
Kaivoslampi	21.43	1688‡	29,443	109	61.5	20.2	0.075	0.00001090	2.977
Kalaton-Väärä	15.44	1151‡	14,081	136	74.6	22.1	0.050	0.00000342	3.219
Kangas-Piilo	60.80	7626‡	200,247	121	67.0	19.2	0.087	0.00000518	3.138
Litmonlampi	18.00	1373‡	19,593	126	65.8	21.5	0.050	0.00000742	3.077
Majajärvi	8.36	2655	8974	81	47.6	27.6	0.175	0.00000421	3.198
Nikkilänlampi	8.56	601‡	6923	120	62.8	22.1	0.050	0.00000269	3.272
Pieni Saunajärvi	10.80	773‡	9500	115	57.3	20.6	0.050	0.00000132	3.413
Pieni Venejärvi	12.67	921‡	34,696	139	58.0	21.4	0.129	0.00000379	3.195
Pieni-Piilo	6.13	421‡	6050	114	60.3	21.5	0.050	0.00000285	3.260
Pikku-Hukka	12.97	946‡	10,869	95	68.1	19.2	0.050	0.00000594	3.119
Pitkänniemenjärvi	3.17	213‡	2968	86†	60.0	22.6	0.175	0.00000561	3.117
Raate	13.86	1018‡	20,306	125	65.0	20.0	0.104	0.00001650	2.930
Synkkä-Rasku	1.42	561	2743	133	53.1	22.2	0.050	0.00000473	3.165
Valkea-Kotinen	8.97	1521	5462	108	48.1	31.3	0.164	0.00000392	3.207
Valkealampi	10.02	203	2077	110	7.5	53.0	0.442	0.00000418	3.187
Valkea Mäntyjärvi	16.22	1217‡	65,636	140	63.8	22.8	0.050	0.00000230	3.302
Valkea-Väärä	45.40	$4623^{\ddagger}$	83,085	83	45.0	36.2	0.371	0.00001115	2.978

*The g was constrained to the minimum of 0.05 to avoid unrealistically fast adult growth rates. Recruit size lr was used in the model as the size at which the fish were introduced to the population at age 0.

†Mean solution used due to the lack of lake-specific data (i.e. too few perch caught).

‡Predicted density used due to the lack of mark recapture based estimated density.

study latitudes (e.g. Estlander et al., 2017), but due to small number of fish, we could not take the sex difference into account and thus assume that both sexes contribute to the recruitment and biomass yields equally.

To implement density-dependence of individual growth rate, well documented for perch (Le Cren, 1958; Nyberg et al., 2010; Rask et al., 2014), we modelled the resource dynamics by assuming a constant unstructured annual resource E (g) input that is shared equally among the individuals according to their foraging needs. We assumed that individual perch have a maximal annual feeding capacity c (g yr^{-1}), which scales with body size (g) as

$$c(l) = c_0(c_1 m(l))^{c_2} \tag{8}$$

where *constants* c_0, c_1 and c_2 relate the maximal feeding capacity to body size. Body mass $m(l)$ was defined as:

$$m(l) = \upsilon_0(\upsilon_1 l)^{\upsilon_2} \tag{9}$$

where the *parameters* υ_0 and υ_2 were obtained using non-linear regression in MS Excel (Table 4). The resource available for each individual is inversely proportional to the total feeding pressure, Γ (g yr^{-1}):

$$\Gamma = \int_0^\infty c(l)n(l) \quad dl \tag{10}$$

where $n(l)$is the number of individuals at length l right after reproduction has occurred. To derive the variable α, we assumed dampened changes in per capita resource availability such that the mean individual share of resource $\bar{e}(l)$ at length l is given by

$$\bar{e}(l) = c(l)\frac{\frac{E}{\Gamma}}{\left((\beta - 1) + \frac{E}{\Gamma}\right)\Big/\beta} \tag{11}$$

where β is the damping coefficient (the smaller value, the stronger effect). For all the results with.

$\bar{e}(l) = c(l)\frac{E}{\Gamma}$, see Table A.4 and with constant $\bar{e}(l) = c(l)$, see Table A.5. The total resource availability was adjusted for each lake such that the $E/\ \Gamma$ -ratio was 1.5 corresponding the environment used by Vainikka and Hyvärinen (2012). Thus, the modelled numeric values and taxonomic composition of E or Γ in this paper are arbitrary and used to capture the density-dependence of growth in a mechanistic, yet equal, way in all lakes. To account for the inherent variation in the individual-level availability of prey, we assumed that the realized availability of resource, $e_r(l)$ varies according to a normal distribution among individuals of the same size. To scale the variance in food availability with absolute food availability, we assumed that the number of individuals at size l having realised share of energy $e_r(l)$(from here on e_r always includes this between-individual variation) was defined by the equation:

$$n\left(\frac{e_r}{c}, l\right) = n(l)\frac{1}{\sigma_e\sqrt{2\pi}}\exp\left(-\frac{\left(\frac{e_r(l)}{c(l)} - \frac{\bar{e}(l)}{c(l)}\right)^2}{2\sigma_e^2}\right) \tag{12}$$

where σ_e is the *standard* deviation of ecological resource availability. The parameter value of σ_e (Table 3) was found by comparing model-derived and observed population-specific standard deviations of length-at-ages and minimizing the difference by iteratively adjusting the σ_e value. This formulation simply means that $e_r(l)$ is normally distributed and translates into variance in individual growth rates. Individual fish cannot consume all available food due to behavioural restrictions, and we assumed that the Holling type II functional response describes the realized energy intake $i(l)$ at each level of individual energy share:

$$i(l) = \frac{e_r(l)}{1 + \frac{e_r(l)}{c(l)}} \tag{13}$$

Finally, the individual-level growth coefficient was calculated in relation to the individual food intake as:

$$\alpha(l) = \frac{\frac{i(l)}{c(l)}}{\rho} \tag{14}$$

where ρ is the *reference* resource level adjusted (precision 0.01) to yield population level length-at-ages that match the empirical data at population dynamical equilibrium (Fig. A.2). Holling type II functional response was chosen as it has often been determined as the best quantitative description of the empirically observed foraging responses of many predatory fish (e.g. Buckel and Stoner, 2000; Rindorf and Gislason, 2005).

Mortality arises from two components: 1) natural mortality and 2) fishing mortality. In biological reality, mortality is rather size- than age-specific (Post and Evans, 1989; Sogard, 1997; Heermann et al., 2009). Therefore, natural mortality M was defined as:

$$M = d_0 + d_1\exp\left(\frac{-l}{l_0}\right), \tag{15}$$

where d_0 defines the size-independent and d_1 the size-dependent mortality rate (Taborsky et al., 2003). The parameter l_0 defines the length at which the size-dependent mortality rate (d_1 exp($-l/l_0$)) decreases to $1/e$ = 36.8% relative to its value at size $l = 0$ (Taborsky et al., 2003). Fishing mortality was defined as the product of size-specific probability to be exposed to fishing $f(l)$ and instantaneous fishing mortality rate F. The probability to be exposed to fishing mortality $f(l)$ at length l was defined by a logistic curve as:

$$f(l) = \left[1 + \exp\left(-\frac{l - l_{\min}}{\sigma_{f,\ \min}}\right)\right]^{-1} \tag{16}$$

where $\sigma_{f,min}$ defines the width *of* the transition from zero probability of to be fished to full fishing mortality. The total mortality Z was thus length-dependent:

$$Z(l) = f(l)F + M(l) \tag{17}$$

that translates to individual survival s as

$$s(l) = 1 - e^{-Z(l)} \tag{18}$$

The annual fisheries catch (in numbers), Φ, for fish larger than l_y (mm) from the population after spawning and growth is calculated from Baranov's catch equation as:

$$\Phi = \int_{l_y}^\infty \frac{f(l)F}{Z(l)}\left(1 - e^{-Z(l)}\right)n(l)dl \tag{19}$$

In addition to real catches, theoretical catch for fish > 300 mm in length wase calculated by assuming $f(l) = 1$ for all fish > 300 mm in length (due to actual variation in f over sizes this implies that some of the theoretical catch would be catch and release catch). Similarly, the annual biomass fisheries yield (in grams), Y, for fish larger than l_y from the population after spawning was calculated as,

$$Y = \int_{l_y}^\infty \frac{f(l)F}{Z(l)}\left(1 - e^{-Z(l)}\right)n(l)m\left(\frac{l_t + l_{t-1}}{2}\right)dl \tag{20}$$

where t is the time (yr). The body mass of captured individuals was calculated based on the middle-of-the-*year* length to approximate the loss of potential yield due to fishing during growth season. Total population biomass B was calculated as

$$B = \int_0^\infty n(l)m(l)dl \tag{21}$$

Initial conditions in the model were defined for each lake so that the population dynamical equilibrium replicated the estimated fish density, growth and maturation in a situation without any fishing mortality.

There is some minor occasional recreational fishing in some of the lakes but taking this into account in the absence of data would have unnecessarily increased the uncertainty. Population dynamical equilibrium was defined as a stable zero population growth rate ($\ln(n_{t+1}/n_t)$) for at least 100 years. The model was implemented using Embarcadero C++ Builder XE3.

The model was used to simulate population dynamics with varying recruitment sizes to fishing (50- 250 mm in 10 mm steps) and varying fishing mortality rates (0–4 in 0.025 steps). As results for each population, 1) the highest possible yield (g), i.e. maximum sustainable yield (MSY), 2) MSY of fish ≥ 200 mm in length and 3) maximum theoretical catch of perch (numbers) > 300 mm in length, and the combination of recruitment size to fishing and fishing mortality rate producing these values were recorded. In addition, 4) the virgin biomass of the population and 5) yield of perch ≥ 150 mm with $F = 0.7$ were recorded. The yield of perch ≥ 150 mm with $F = 0.7$ was considered as a feasible catch, since perch of this size and above can be used as human food, and $F = 0.7$ represents a typical fishing mortality rate in Finnish inland fisheries (Vainikka and Hyvärinen, 2012).

For comparability, the modelling results are presented per hectare.

2.9. *Statistical analyses*

To account for the temporal changes during summer, lake-specific values (representing 15 July) for each original water chemistry variable were first predicted using a simple linear mixed effect (LME) model with sampling occasion and lake as fixed factors. Sampling occasion was modelled as a repeated term using *scaled identity* covariance type. Next, principal component analysis (PCA) with Varimax rotation was used to reduce the number of environmental variables: One PCA was conducted for physical-chemical variables, and another for absorbance values (200 nm – 750 nm with 0.5 nm steps) all characterizing water colour. The scores for rotated components having eigenvalues ≥ 1 were saved using regression method. Due to the very large number of absorption measures, the season correction for absorption spectra was done for the raw rotated components (RSRC1-RSRC3) using similar LME as for the other measures (we call the corrected components SRC1-SRC3). The simulation-derived yield estimates were Ln-transformed to account for their right-biased distribution and improve linearity of regression. Multivariate regression (GLM) was used to explain the yield estimates with the formed seven rotated components and second-order terms of RC1-RC4. The model was simplified by removing the least significant (highest P-value) term until the model had only statistically significant terms. The study region was not used as a factor to avoid over-fitting since we aimed to generalize the results on boreal lakes in Southern – Central Finland. Linear regression with backward F-test based elimination was used to explain fish growth rate (Lester h) and maturation size (L_{50}) with the component scores (RC1-RC4, SRC1-SRC3). Pearson's and Spearman's correlations (for non-normally distributed relative euphotic surface areas) and linear and non-linear regressions were used to describe the covariation in the data and to visualize the results. To avoid overfitting and problems in inferring causalities, the effect of roach CPUE and BPUE on yield estimates was studied using separate Pearson's correlation analyses. Independent samples t-test was used to compare lakes with differential optimal recruitment size to fishing. All statistical analyses were conducted in IBM SPSS Statistics 27.0.1.0 (IBM Corp., USA).

3. Results

3.1. *Water quality, CPUE and principal component analyses*

The study lakes varied from oligotrophic to eutrophic and had water colour varying from very clear to humic (Table 5, Table A.1). Perch dominated the Nordic survey net catches (mean ± S.D. CPUE 15.0 ± 21.9 fish per net, mean BPUE 481.2 g ± 629.4 g per net) while roach was the second most abundant species (CPUE 8.0 ± 12.9 fish per net, BPUE 244.7 g ± 338.2 g per net) (Table A.2, Table A.3).

Table 5
Physical and chemical characteristics of the study lakes as corrected for mid-July conditions. For lake-specific values see Table A.1.

	Mean	S.D.	Min	Max
Alkalinity (mmol l^{-1})	0.07	0.04	0.01	0.18
Altitude (m a.s.l.)	154.4	15.1	125.7	174.6
Chlorophyll *a* (µg l^{-1})	11.5	14.4	0.7	72.0
Colour (mg Pt l^{-1})	122.1	72.3	8.7	293.4
Conductivity (mS m^{-1})	1.97	1.00	0.83	4.59
Maximum depth (m)	7.3	3.9	1.5	15.0
DOC (mg C l^{-1})	12.3	5.8	3.5	26.1
Fe (mg l^{-1})*	0.66	0.66	0.03	3.15
O_2-saturation, bottom (%)	33.9	30.9	1.7	92.8
O_2-saturation, surface (%)	87.8	6.6	70.1	96.0
pH	6.2	0.5	5.3	7.6
Phosphate (µg l^{-1})	3.0	0.3	2.0	4.0
Secchi-depth (m)	1.8	1.0	0.8	5.5
Temperature, 1 m (°C)	19.6	1.0	17.3	21.0
Total N (µg l^{-1})	493.6	180.5	254.0	856.4
Total P (µg l^{-1})	15.9	10.1	5.4	52.6

*Detection limit was 0.1 mg l^{-1}.

PCA on the physical and chemical variables captured 81.65% of the total variance. The first rotated component, RC1, captured 28.36% of the variance (Table 6). The second, third and fourth rotated components explained 20.01%, 19.38% and 13.90% of the variance, respectively. The first component, RC1, reflected measures related to humic water colouration: high water colour, DOC, iron concentration and total nitrogen concentration, and low transparency, oxygen concentration in the surface water and summer water temperature (Table 6). The second component, RC2, reflected primary production, as it most clearly related positively to total phosphorus concentration, conductivity and chlorophyll-*a* concentration. The third component, RC3, reflected morphological basin complexity and low altitude, i.e. having higher order in a watercourse, and high alkalinity, conductivity and pH. The fourth component, RC4, reflected shallowness, high oxygen concentration close to the bottom, and high phosphate and iron concentrations.

PCA on all the 1101 absorbance wavelengths from 200 nm to 750 nm formed three principal components that explained 99.50% of the total variance in the original absorbances. 51.62% of the variance was captured by the first raw rotated component (RSRC1) that was strongly positively loaded by absorbances at all wavelengths (0.539 - 0.796) but decreasingly with increasing wavelength (i.e. strongest absorbance at UV and other short blueish wavelengths). The second component

Table 6
Varimax-rotated component matrix of the principal component analysis on physical-chemical characteristics of the study lakes. Loadings of rotated components (RC) with absolute value over 0.6 are in bold.

Variable	RC1	RC2	RC3	RC4
Shoreline: area	0.236	-0.198	**0.735**	-0.347
Max. depth	-0.145	-0.118	0.201	**-0.735**
Altitude	-0.071	-0.423	**-0.692**	0.145
Secchi-depth	**-0.647**	-0.456	-0.082	-0.224
O_2-% (bottom)	-0.115	-0.218	-0.459	**0.709**
O_2-% (surface)	**-0.922**	-0.108	-0.170	0.061
Water temperature	**-0.846**	0.126	-0.035	-0.099
Alkalinity	-0.004	0.139	**0.854**	0.346
Conductivity	0.328	0.457	**0.771**	-0.038
pH	**-0.615**	0.071	**0.658**	0.083
Colour	**0.896**	0.381	0.010	0.059
Total N	0.558	**0.751**	0.274	-0.052
Phosphate	-0.064	-0.008	0.255	**0.728**
Total P	0.267	**0.907**	0.118	0.102
DOC	**0.854**	0.474	0.063	-0.068
Chlorophyll *a*	-0.023	**0.946**	0.132	-0.038
Fe	0.578	0.040	0.237	**0.660**

(RSRC2) explained 47.33% of the variance and was positively loaded by absorbances of all wavelengths (0.604 – 0.822) but increasingly with increasing wavelength (i.e. strongest absorbance of red wavelengths). The third RC (RSRC3) explained only 0.55% of the variance and was very weakly positively loaded by absorbances at wavelengths from 200 nm to 378.5 nm and 671 nm to 732 nm (loadings from −0.114 to 0.127).

RC1 correlated positively with the SRC1 (Pearson's $R = 0.722$, $N = 28$, $P < 0.001$) and SRC2 (Pearson's $R = 0.567$, $N = 28$, $P = 0.002$). RC2 correlated positively with SRC1 (Pearson's $R = 0.457$, $N = 28$, $P = 0.014$). Due to standardization of the scores to a fixed date, the otherwise uncorrelated SRC2 and SRC3 showed a positive correlation (Pearson's $R = 0.493$, $N = 28$, $P = 0.008$).

3.2. Water quality, population density and fish life-history

Overall (average over the 26 lakes), perch juveniles grew (values of h) 26.1 ± 8.8 mm yr^{-1} (mean ± S.D.) and showed 50% maturity at length 109.9 ± 20.9 mm. Perch growth was not related to any of the environmental components (RC1-RC4, SRC1-SRC3) statistically significantly. According to the model selection procedure, size at maturation was negatively explained by SRC3 (slope = −9.0; $t_{25} = -1.770$; $P = 0.090$) and RC3 (slope = −7.0; $t_{25} = -1.862$; $P = 0.075$). In total, these component scores explained 21.4% of the variation in maturation size. Population density (number of perch ≥ 90 mm per ha) did not explain variation in growth rate (h) ($F_{1,\ 24} = 0.205$, $P = 0.655$) or in size at maturation ($F_{1,\ 24} = 0.001$, $P = 0.978$). Neither did summer water temperature explain variation in growth rate ($F_{1,\ 24} = 1.426$, $P = 0.244$) or in size at maturation ($F_{1,\ 24} = 0.145$, $P = 0.707$).

3.3. Estimates of sustainable yields

The estimated biomass of Eurasian perch of all sizes was 52.5 ± 51.2 kg ha^{-1}. The maximum sustainable yield (9.4 ± 12.1 kg ha^{-1} yr^{-1}) was reached, on mean with $F = 1.62 \pm 1.06$ yr^{-1} and with 66.8 ± 46.9 mm recruitment size to fishing, but so that in most cases the lowest considered size 50 mm produced the highest yield (Table 7, see Tables A3 and A4 for the effects of density-dependence). The mean yield with recruitment to fishing at 150 mm and $F = 0.7$ yr^{-1} was 4.4 ± 4.8 kg ha^{-1} yr^{-1} (Table 7). The highest yield of fish above 200 mm (mean 3.9 ± 4.0 kg ha^{-1} yr^{-1}) was most often observed by targeting the fishing to perch ≥ 200 mm with maximal mortality rate, except for in Lake Iso Ruuhijärvi (the most eutrophic lake where the perch growth rate was very fast, Table 4), where fishing perch with 250 mm limit and low effort would produce the highest yield of large perch. All the study lakes were poor in yielding large perch: the estimated theoretical catch of perch > 300 mm was only 1.6 ± 1.6 fish ha^{-1} yr^{-1}. The catch of large perch would be maximized by fishing only large (≥ 250 mm) perch with a low fishing mortality rate ($F = 0.21 \pm 0.10$ yr^{-1}) except in Lakes Kaitalammi and Valkealampi, where fishing should target perch above 50 mm (Table 7). Comparison of the lakes producing the highest yield with 50 mm vs. larger recruitment size to fishing revealed that the lakes producing larger perch had statistically significantly lower SRC2 scores ($t_{25} = 2.221$, $P = 0.036$: −0.81 vs. 0.07) and RC1 scores ($t_{25} = 2.156$, $P = 0.041$: −0.80 vs. 0.21).

3.4. Water quality components and estimated sustainable yields

Multivariate regression with all the seven rotated components and second-order terms of RC1-RC4 indicated no statistically significant terms in addition to the intercept (Wilks'$\Lambda \leq 0.936$, $F_{5,10} \leq 2.589$, $P \geq 0.094$). After eliminating the least significant terms one by one, the

Table 7
Estimates for absolute Eurasian perch (*Perca fluviatilis*) virgin (unfished) biomass, sustainable yields, and respective fisheries parameters producing the yields in the study lakes. Feasible yield refers to yield of perch over 150 mm in length with constant instantaneous fishing mortality rate of 0.7 yr^{-1}. MSY refers to maximum sustainable yield, and trophy catch is the number of potentially captured perch over 300 mm in length.

Lake	Biomass kg ha^{-1}	Feasible yield (kg ha^{-1} yr^{-1})	MSY (kg ha^{-1} yr^{-1}), and respective F (yr^{-1}) and recruitment size (mm)			MSY ≥ 200 mm* kg ha^{-1} yr^{-1}	Trophy catch of perch > 300 mm (no. ha^{-1} yr^{-1}) and F (yr^{-1})†	
Aitalampi	6.3	0.5	2.6	1.43	50	0.2	0.0	0.08
Haukijärvi	59.9	4.2	7.7	1.70	50	4.0	2.6	0.23
Hautjärvi	0.6	0.0	0.1	1.73	50	0.0	0.0	0.23
Hirsikankaan Rasku	3.5	0.2	1.4	1.55	50	0.1	0.0	0.08
Horkkajärvi	6.9	0.5	0.8	1.73	50	0.5	0.3	0.23
Hukkalampi	38.2	2.7	3.4	0.60	50	2.5	1.9	0.25
Iso Mustajärvi	43.9	2.9	4.1	1.83	50	3.0	3.5	0.28
Iso Ruuhijärvi	9.8	0.5	0.7	0.43	250	0.7 *	1.0	0.38
Iso Saunajärvi	53.0	5.0	7.7	1.00	50	4.8	2.3	0.20
Iso Valkjärvi W	32.6	2.7	10.5	4.00	90	2.0	0.3	0.13
Kaitalammi	2.7	0.3	0.9	0.95	50	0.1	0.0	0.63
Kaivoslampi	66.7	5.3	16.0	1.25	50	4.3	1.6	0.18
Kalaton-Väärä	73.8	5.5	7.9	1.23	50	5.1	3.5	0.23
Kangas-Piilo	212.3	18.2	51.7	1.05	50	13.8	2.9	0.15
Litmonlampi	68.0	5.4	10.2	1.13	50	4.9	2.8	0.23
Majajärvi	138.3	12.8	25.0	1.65	50	11.7	2.9	0.18
Nikkilänlampi	37.2	2.6	4.1	1.18	50	2.5	1.6	0.23
Pieni-Piilo	28.1	2.0	3.6	1.15	50	1.9	1.1	0.20
Pieni Saunajärvi	48.2	3.3	6.2	1.00	50	3.1	1.5	0.20
Pieni Venejärvi	36.8	3.8	8.0	0.80	50	2.9	0.4	0.15
Pikku-Hukka	32.7	2.5	6.7	1.98	50	2.1	0.8	0.18
Pitkäniemenjärvi	5.5	0.4	1.9	4.00	90	0.3	0.0	0.10
Raate	32.9	3.0	8.8	1.00	50	2.2	0.4	0.15
Synkkä Rasku	41.1	3.0	5.0	0.80	50	2.8	1.7	0.23
Valkea-Kotinen	133.0	11.6	14.2	1.25	50	11.9	6.8	0.23
Valkealampi	19.6	2.4	2.6	4.00	200	2.6	1.2	0.23
Valkea Mäntyjärvi	86.8	6.1	8.3	0.90	50	5.8	4.0	0.23
Valkea-Väärä	150.4	17.1	43.5	4.00	90	13.7	0.2	0.08

*The respective F is 4.0 yr^{-1} and recruitment size 200 mm for all the lakes except for Lake Iso Ruuhijärvi (F = 0.43 yr^{-1}, recruitment size = 250 mm).
†The recruitment size to fishing is 250 mm (i.e. the largest considered size) for all lakes except for Lakes Kaitalammi and Valkealampi for which it is 50 mm.

final model included four statistically significant terms (SRC3, Wilks'Λ $=0.545$, $F_{5,17} = 2.843$, $P = 0.048$, $\eta^2 = 0.455$; RC4, Wilks'Λ $=0.475$, $F_{5,17} = 3.752$, $P = 0.018$, $\eta^2 = 0.525$; RC2^2, Wilks'Λ $=0.191$, $F_{5,17} = 14.355$, $P < 0.001$, $\eta^2 = 0.809$; RC3^2, Wilks'Λ $=0.284$, $F_{5,17} = 8.585$, $P < 0.001$, $\eta^2 = 0.716$; Table 8). Accordingly, the RC4 showed the strongest positive effect on the maximum sustainable yield (MSY) of perch while high values of RC2 decreased yields non-linearly (Fig. 2). As the SRC3 and RC3^2 affected only the catch of perch > 300 mm in length, their effects were examined in more detail (Fig. A.3). Lake Kaitalammi with virtually no production of trophy-sized perch appeared an influential outlier, and by excluding this lake, only RC4 and RC2^2 remained statistically significant (RC4, Wilks'Λ $=0.478$, $F_{5,16} = 3.492$, $P = 0.025$, $\eta^2 = 0.522$; RC2^2, Wilks'Λ $=0.176$, $F_{5,16} = 15.932$, $P < 0.001$, $\eta^2 = 0.824$).

3.5. Correlation analyses

Spearman rank correlation indicated that the relative euphotic surface area was positively correlated with the MSY of perch (Spearman's $\rho = 0.570$, $N = 26$, $P = 0.002$, Fig. 2 h), yield of perch over 200 mm (Spearman's $\rho = 0.428$, $N = 26$, $P = 0.029$) and feasible yield (Spearman's $\rho = 0.472$, $N = 26$, $P = 0.015$) but not to the biomass or catch of large perch (Spearman's ρ, $N = 26$, $P \geq 0.067$). Roach CPUE did not correlate with any of the perch yield estimates, but roach BPUE showed a positive correlation with the perch MSY (Pearson's $R = 0.395$, $N = 26$, $P = 0.046$).

4. Discussion

Perch CPUE in Nordic survey gillnet fishing data followed type II functional response, which made it possible to derive rough estimates of fish abundance in the study lakes without mark recapture estimates of absolute abundance. Compared to simple yield estimates derived from CPUE and growth information (e.g. Karlsson et al., 2015; van Dorst et al., 2019), our approach allowed us to estimate the perch yields under feasible fishing scenarios, under resource-dependence in perch growth (Persson and De Roos, 2013), and by utilizing data on lake-specific growth and maturation patterns of perch yet we had to assume that the lakes shared a similar recruitment and growth environment. Naturally, size-dependent trophic interactions both within perch populations (e.g. Persson et al., 2000, 2003; Trudeau et al., 2023) and within fish communities (e.g. Persson et al., 2007) would add a whole new level of complexity for which explicit treatment through modelling would be beyond feasible options given the large number of lakes used in this study. As such, the presented theoretical MSY estimates must be interpreted with caution, and it is clear they are prone to error arising from multiple sources yet former predictions of pikeperch yields derived from the same model have proved surprisingly accurate in real fisheries (Vainikka and Hyvärinen, 2012; Marttunen et al., 2023). Independently of the unarguably high uncertainty, the MSY estimates varied greatly among lakes suggesting that the between-lake variation is yet more important for the interpretation of the results than inestimable within-lake error variation. Against our hypothesis, the yield estimates were not explained by water colour indicators as captured in RC1 (c.f. Karlsson et al., 2015). However, the concentrations of primary nutrients (RC2) showed a non-linear relationship with the perch MSY suggesting that there is an optimal level of primary production for perch (c.f. Ranta and Lindström, 1993; Finstad et al., 2014). Further, second-order term of RC3 and SCR3 explained variation in the predicted catches of trophy-sized perch yet these results were driven by a single lake with a very poor trophy catch estimate (see Fig. A.3). The positive effect of RC4 on perch yield estimates supports the idea that fish production in small lakes may be limited by depth and oxygen availability in addition to nutrient limitation (Karlsson et al., 2009; MacLeod et al., 2022). Consistent with the light-limitation hypothesis, the relative area of euphotic bottom surface area correlated positively with the estimated perch MSY (Seekell et al., 2018). This result likely reflected the contribution of primary production by periphyton (Vadeboncoeur et al., 2008) and secondary production of benthic food for perch (Nyberg et al., 2010; Arzel et al., 2020; Trudeau et al., 2023). Even though RC1 (largely indicative of water colour) did not explain variation in perch yields, the effects of water colour and especially the interaction between water colour and depth cannot be ruled out since colour-variables contributed also to RC2. As such, the correlation between the relative area of

Table 8
Between-subject *F*-test results and parameter estimates of multivariate linear regression for the environmental variables explaining the biomass (kg ha^{-1}), maximum sustainable yield (MSY, kg ha^{-1} yr^{-1}), maximum yield of fish above 200 mm in total length (kg ha^{-1} yr^{-1}), theoretical catch of Eurasian perch (*Perca fluviatilis*) above 300 mm (no. ha^{-1} yr^{-1}) and feasible yield of fish above 150 mm ($F = 0.7$, kg ha^{-1} yr^{-1}) among the 26 study lakes with all the data. All the dependent variables are Ln-transformed.

Dependent (Ln-transformed)	Variable	Estimate	s.e.	*F*	*d.f.*	Sig.	Partial η^2
Biomass	Intercept	3.566	0.287	154.38	1, 21	< 0.001	0.880
	SCR3	0.023	0.333	0.005	1, 21	0.946	< 0.001
	RC4	0.579	0.242	5.71	1, 21	0.026	0.214
	RC2^2	-0.145	0.090	2.61	1, 21	0.121	0.111
	RC3^2	-0.194	0.127	3.32	1, 21	0.143	0.099
MSY	Intercept	1.822	0.244	55.71	1, 21	< 0.001	0.726
	SCR3	0.136	0.283	0.23	1, 21	0.636	0.011
	RC4	0.615	0.268	10.65	1, 21	0.004	0.336
	RC2^2	-0.141	0.099	7.47	1, 21	0.012	0.262
	RC3^2	-0.221	0.141	2.74	1, 21	0.119	0.112
MSY of fish $\geq$ 200 mm	Intercept	0.873	0.317	7.58	1, 21	0.012	0.285
	SCR3	0.023	0.368	0.004	1, 21	0.951	< 0.001
	RC4	0.615	0.268	5.28	1, 21	0.032	0.201
	RC2^2	-0.141	0.099	2.02	1, 21	0.170	0.088
	RC3^2	-0.221	0.141	4.30	1, 21	0.132	0.105
Catch of fish > 300 mm	Intercept	0.0684	1.642	0.17	1, 21	0.681	0.008
	SCR3	4.159	1.904	4.77	1, 21	0.040	0.185
	RC4	0.763	1.386	0.30	1, 21	0.588	0.014
	RC2^2	0.066	0.513	0.016	1, 21	0.899	0.001
	RC3^2	-0.3662	0.279	1183.4	1, 21	< 0.001	0.546
Feasible yield	Intercept	1.047	0.281	13.88	1, 21	0.001	0.398
	SCR3	-0.012	0.326	0.001	1, 21	0.971	< 0.001
	RC4	0.637	0.237	7.20	1, 21	0.014	0.255
	RC2^2	-0.183	0.088	4.34	1, 21	0.050	0.171
	RC3^2	-0.177	0.125	2.76	1, 21	0.171	0.087

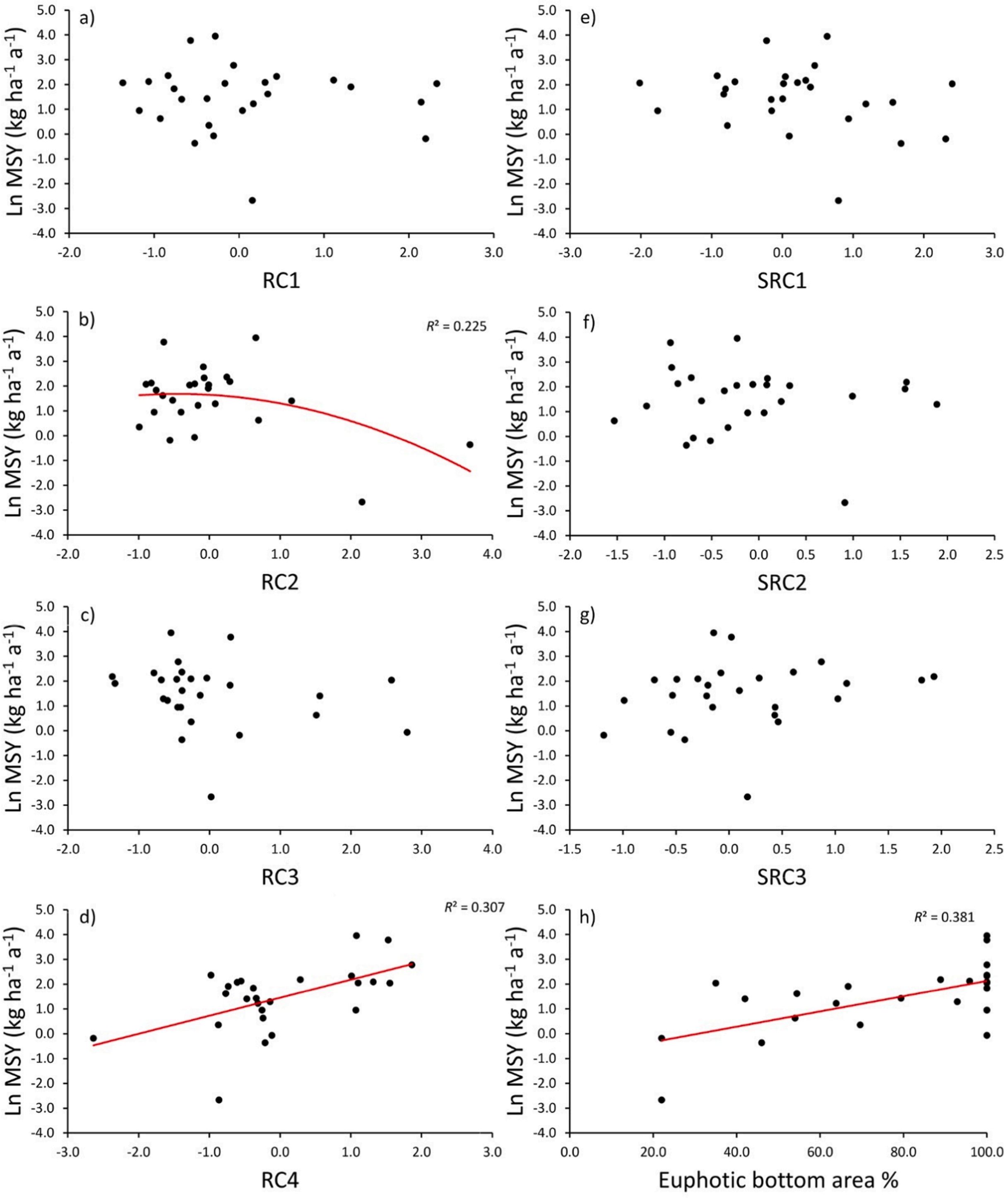

Fig. 2. Dependence of the (Ln-transformed) maximum sustainable yields of Eurasian perch (*Perca fluviatilis*) on the environmental components and proportion of euphotic surface area. The solid lines/curves represent statistically significant linear / polynomial regression fits for visualization purposes only (see Table 6 for component composition and Table 8 for statistics).

euphotic bottom surface area and perch yields was the clearest indication of the importance of light availability for fish production in this study.

Both fish populations and water quality metrics show pronounced temporal variation making it challenging to address their general relationships. To control for at least part of this variation, we combined water quality measures from two time points in the middle of the growing season and fish indicators from at least two separate experimental fishing occasions. Further, the perch CPUE estimates obtained on separate years showed significant repeatability indicating that most of the variation in perch CPUEs lies consistently among lakes and that our assumption of population dynamical equilibrium was feasible and within the realm of data availability. Physical and chemical variables formed logical rotated components in the principal component analysis (for similar approaches, see e.g. Dalal et al., 2010; Olsen et al., 2012). Variables related to humic water colouration formed a clear syndrome (RC1) characterized by low transparency, low surface water oxygen saturation, low water temperature, dark water colour, high dissolved organic carbon concentration and somewhat high iron and total nitrogen concentrations. These relationships were expected as resulting from material exports from managed peatland forests (Nieminen et al., 2015; Lepistö et al., 2021) and ditched catchments (Estlander et al., 2021; Finér et al., 2021) except for the negative relationship between water temperature (measured at 1 m depth) and water colour: in summer conditions, the surface water would be expected to be warmer in dark water absorbing more sunlight than clear water (Pilla et al., 2018). Increasing DOC concentration could also lead to anoxia in the bottom of the lakes due to strengthened thermal stratification (Brothers et al., 2014), but the oxygen saturation measured close to the bottom in the deepest part of the lakes was more clearly, yet weakly, related to the nutrient concentrations (RC2) than water colour or DOC in our data. The second component was dominated by chlorophyll-*a*, and total concentrations of nitrogen and phosphorus, but positively related also to DOC concentration and low transparency. As such the component could reflect a eutrophication syndrome. The third component was related to the position of the lake in the watercourse. With decreasing altitude, and as such, increasing length of the upstream watercourse, the relative length of shoreline, alkalinity, pH, and conductivity increased, while the oxygen saturation close to the bottom decreased. The fourth component was related to shallowness, high saturation of oxygen close to the bottom, and high concentrations of phosphate and iron. High phosphate and iron concentrations in shallow lakes may have been affected by wind-induced resuspension from sediments, seasonal dynamics in the vertical oxygen reduction potential in the sediment (Wildung et al., 1974; Søndergaard et al., 2003) or high run-off from terrestrial systems (Weyhenmeyer et al., 2014; Estlander et al., 2021).

Intensive peatland forestry produces high loading of DOC and nutrients (Laudon et al., 2009; Nieminen et al., 2015; Aaltonen et al., 2021; Lepistö et al., 2021), yet the effects can be mild when clearcuttings do not involve mechanical disturbance of the soils within the watershed (Deininger et al., 2019). To balance the societal benefits of forestry and draining activities with the costs in fisheries productivity, it is crucial to understand the effects of nutrients and dissolved organic substances on the function and structure of aquatic ecosystems. High water colour, as resulting from high concentrations of DOC and iron, may decrease individual perch growth rate due to several direct and indirect mechanisms including weakened foraging efficiency in dark water (Bergman, 1988; Horppila et al., 2010; Rask et al., 2014; Bartels et al., 2016; van Dorst et al., 2020). The lack of a negative relationship between DOC and perch growth or yield estimates in our study supports results obtained in an experimental DOC addition study with largemouth bass (*Micropterus salmoides*) (Koizumi et al., 2018). In yellow perch (*Perca flavescens*), DOC concentration did not affect the early growth rate in low-DOC Quebec lakes, although increasing DOC decreased CPUE (Benoît et al., 2016). However, the absence of a negative relationship between the RC1 and perch yield estimates does not necessarily mean that the overall fish production would be unimpacted by changes in water colour (Jarvis et al., 2020). It may be too simplistic to assume that colour-related environmental metrics would dominate differences in potential fisheries yields among lakes when several important variables such as total nutrient concentrations or water temperature covary with DOC levels (Nürnberg and Shaw, 1999; Huser et al., 2018; van Dorst et al., 2019). Solomon et al. (2015) reviewed the effects of dissolved organic material in lakes and showed that many of the effects are non-linear and interact with other environmental variables. For example, the negative effect of water colour on fish biomass may be stronger in deep lakes than in shallow lakes (Seekell et al., 2018). Since our study lakes were generally shallow, an increase in primary nutrients with a decrease in transparency thus likely enhanced rather than decreased total primary and secondary production that eventually support perch yields as well. Combined increase of DOC and decrease of phosphorus concentrations could impose the strongest decline on the production of boreal lakes (Huser et al., 2018). The supressing effect of DOC on zoobenthos biomass (Arzel et al., 2020) and production may result from correlated hypolimnetic anoxia (Knoll et al., 2018) rather than light-driven reduction in benthic algal production (Craig et al., 2015). This mechanism was supported by our finding that RC4 (indicative of oxygen concentration in the deepest part of the lake) had a positive effect on the yield estimates. Further, the effect of DOC on the primary production may be strongly dependent on the quality of the DOC: bioavailable DOC may increase production by supporting heterotrophic plankton while certain less bioavailable DOC components can decrease production by inhibiting light penetration (e.g. Forsström et al., 2013). A true ecosystem approach should account also for the presence of semi-aquatic ecosystem engineers such as beavers due to their strong effects on DOC dynamics and fish assemblages (Schlosser and Kallemeyn, 2000; Nummi et al., 2018).

In the present study, yield estimates for shallow lakes were higher than for deeper lakes supporting earlier comparative findings (Rawson, 1952; Chu et al., 2016; Seekell et al., 2018). Also, the relative area of bottom shallower than the euphotic zone depth was related to the perch MSY estimates confirming earlier results (Seekell et al., 2018). While the variation in RC1 did not explain variation in perch yield estimates, clear-water lakes produced the highest yield with larger recruitment size to fishing in comparison to humic lakes. This result is in line with the observation that bluegill (*Lepomis macrochirus*) reach smaller asymptotic sizes in high-DOC lakes compared to low-DOC lakes (Craig et al., 2017) and that perch may face stronger intraspecific competition for different food resources in dark-water lakes (Bartels et al., 2016). This suggests that perch fisheries should be guided to target larger perch in clear-water lakes than in humic lakes (c.f. Craig et al., 2017), which alone is a significant message for management. However, the potential catch of large perch, i.e. fish over 300 mm, was explained only by the SCR3 that explained very little of the overall variation in water colour spectra and the second-order term of RC3 that was mostly related to pH, alkalinity, conductivity, high shoreline: surface area relationship and low altitude. Bearing in mind the strong effect of a single lake on these results, this suggests that the capacity of lakes to produce large perch may not be directly related to environmental metrics but could depend on structural differences such as presence of certain prey species in the food web, highly size-structured population dynamics and strong density-dependence (Persson et al., 2003; Persson et al., 2014; Trudeau et al., 2023). For example, presence of the large planktonic microalga, *Gonyostomum semen*, may significantly shape fish production (Trigal et al., 2011). We pooled the Evo and Lieksa regions for statistical power and generality, but environmental differences between these regions could explain part of the variances in this study calling for further comparative studies with large number of lakes.

Nordic survey gillnet CPUE has been shown to reflect absolute abundances of perch according to an exponential function (Olin et al., 2016) that produced unrealistically high abundance estimates for the present study lakes showing generally high CPUEs. We derived rough CPUE-based fish abundance estimates by applying a better fitting Holling type II functional response curve that accounts for the decreasing catchability with the accumulation of the fish in the net (Olin et al., 2004), comparable to predator saturation, and incorporates the fact that zero population abundance must yield zero CPUE. The obtained fish density estimates were in line with the published literature (e.g. Linløkken and Haugen, 2006; Horppila et al., 2010). Viljanen and Holopainen (1982) used scuba diving to produce an estimate of 312 ≥ 3 years-old perch individuals per hectare in Lake Suomunjärvi located very close to the Lieksa area study lakes. Rask and Arvola (1985) estimated that the total biomasses of perch in two Finnish small boreal lakes were 37.0 kg ha^{-1} and 21.0 kg ha^{-1}, with respective production rates of 15.9 kg ha yr^{-1} and 5.3 kg ha yr^{-1} (0.3–0.4 from the standing biomass) being likely related to light and oxygen availability as observed in this study. Horppila et al. (2010) calculated that the lakes in Evo area had perch biomass from 13.1 kg ha^{-1} to 45.6 kg ha^{-1} with production varying from 6.0 to 16.5 kg ha^{-1} yr^{-1}. The estimated mean perch biomass in our study lakes was 52.5 kg ha^{-1}. The highest estimated biomass was 212.3 kg ha^{-1} in a shallow eutrophic lake (Lake Kangas-Piilo) that was connected to a river. As such, the very high biomass estimate might not entirely reflect production within the lake, but higher production in the adjacent river system (Randall et al., 1995) and temporary migration of fish to this lake. This lake was not used for mark-recapture estimates excluding potential bias on our results in general. While recreational fishing could have affected the density or size-structure of perch populations in some of the study lakes, it has been shown that ecological factors generally affect fish indicators more strongly than metrics on fishing (Chu et al., 2016). However, any CPUE-based estimation method involves the inherent problem of separating the effect of environmental variables on the catchability of fish from their effects on the abundance of fish (Olin et al., 2016). In this study, we prioritized the comparability of the lakes by conducting the experimental fishing during a period that was kept as short as possible. Two lakes were always fished in equal conditions, which likely also reduced the environmental impact present overall in the data. However, to further develop CPUE-based yield estimation methods, the effects of the key variables affecting catchability should be better known and controlled for by including their effects directly in the functional response. Further, the precision of the CPUE determination is highly dependent on the number of gillnets used, different habitat types covered and the temporal weather conditions (Olin et al., 2016). Thus, CPUE-data from several years, as we had for Evo region lakes, would generally be advisable for the estimation of long-term mean fisheries yield potential. Further, size-based indicators could be used to better standardize the influence of population size structure on the total density of fish above certain size, because total fish biomass and individual size are often negatively correlated (Randall et al., 1995).

We used a size-structured population model (Vainikka and Hyvärinen, 2012; Vainikka et al., 2017) to derive the estimates of potential yields. This model has appeared accurate in predicting pikeperch catches in Lake Oulujärvi (Marttunen et al., 2023). A relatively complex model was used due to the need to consider the effect of individual life-history, density-dependence of growth and different scenarios for fishing. The model was parametrized equally for all lakes in environmental terms, which means that we implicitly assumed that all the differences in perch populations were intrinsic, i.e. decoupled from the factors we used to explain variation in the predicted yields. Individual growth of perch is density- and temperature-dependent (Le Cren, 1958; Nyberg et al., 2010), and affected by the presence of other fishes such as roach (Estlander et al., 2010). Optimally, the growth and maturation patterns in each lake could be modelled as environmentally driven by including various environmental factors in the model. However, this would require very detailed information about the abundance of various and variously sized food items and the strength of both intra- and interspecific competition (Persson and Greenberg, 1990b; Persson et al., 2014). Further, correlative datasets may hide potential negative relationships, for example, between perch and roach (Persson and Greenberg, 1990a; b), as in our study, roach BPUE showed a positive correlation with perch MSY suggesting that both species benefit from same environmental variables within the observed ranges. Even though our model captured size- and density-dependence, it did not include cannibalism that is shown to be highly important for perch population dynamics and the effects of perch on the whole ecosystems (Claessen et al., 2002; Persson et al., 2003). However, it would be nearly impossible to parametrize a model with cannibalism to such a large set of lakes, because the prevalence of cannibalism is dependent on the annual recruitment variations and growth rate differences among individuals, and a cannibalistic perch population would show temporally stable dynamics only in very special circumstances (Claessen et al., 2000; Persson et al., 2000; Claessen et al., 2002). Nordic survey gillnet fishing revealed that some of the lakes were able to produce perch over 300 mm against the model predictions. Thus, cannibalism and related variations in size at which individuals undergo ontogenetic niche shifts (Persson and Greenberg, 1990b; Hjelm et al., 2000; Trudeau et al., 2023) may partially explain why some of the generally low-productive lakes still produce a few large perch (e.g. Persson et al., 2003).

Our study has some important managerial implications. First, high relative euphotic bottom area and good oxygen saturation close to the lake bottom appeared important in predicting perch yields suggesting that watershed scale management should ensure these qualities to maintain good perch fisheries. Second, the estimated yields, and as such the yield to biomass -ratios (c.f. Table 7), were strongly dependent on the size of the perch captured and the yield estimates for reasonable large perch were significantly smaller than for perch in total. As a rough average estimate, the maximum yield of perch over 200 mm in total length was 3.9 kg ha^{-1} yr^{-1} and it was obtained by applying a 200 mm minimum size limit except for in one lake with fast-growing perch. Reasonable fishing mortality rate combined with a 150 mm minimum size limit produced a yield average of 4.4 kg ha^{-1} yr^{-1}. Minimum size limits are very rarely applied in real perch fisheries (e.g. Lyach and Remr, 2019), they are legally problematic for example in Finland, and they might induce strong density-dependence among fish smaller than the minimum size limit (or any technical recruitment size to fishing gear) and that rely mainly on invertebrate prey (Estlander et al., 2010). Thus, boreal perch fisheries aiming to yield fish of value for human consumption could be scaled according to the 5 kg ha^{-1} yr^{-1} catch target as a first guess and as a basis for further lake quality based and empirical adjustments without strict minimum and maximum sizes for the landed fish beyond the avoidance of harvesting immature fish and recommendations to release the largest fish (Olin et al., 2012, 2017). While quota-based management is usually beyond feasible options in recreational fisheries, it could often produce the best outcome (e.g. Johnson et al., 1992), and other measures such as effort limitations can be taken to target certain levels of catch. Due to the efficient reproduction of perch that mature at very young age and small size in small boreal lakes compared to larger systems (Heibo et al., 2005; Vainikka et al., 2012), these populations can tolerate high annual fishing mortalities such as 50% of the biomass (Olin et al., 2017). However, under heavy mortality the average size of captured perch could be less than 100 mm, i.e. very small compared to most perch fisheries (Lyach and Remr, 2019), and as such of very little importance for human consumption (Olin et al., 2017). Further, single-species MSY targets (such as the 9.4 kg ha^{-1} yr^{-1} estimate for perch) could induce significant ecosystem-level alterations with overall negative outcomes (Lee et al., 2021). Whether fisheries in small lakes with early maturing perch could be managed to utilize perch piscivory to transform the abundant small fish (both perch and other fishes) into larger individuals requires long-term empirical attempts with carefully designed maximum size and daily bag limits (Persson et al., 2000, 2007; Olin et al., 2017). To maximize the catch of large “trophy” sized fish, the lakes should also be fished very differently compared to the simple aim of maximizing biomass yield. Most often, the catch of perch over 300 mm would be maximized by targeting large fish with a low fishing mortality rate.

5. Conclusions

In conclusion, our study provides methodological advancements to further evaluate fisheries yields in small lakes and develop fisheries management measures needed to ensure optimal management of freshwater fish stocks in lakes differing in their limnological qualities. Our study challenges the use of simple production to biomass ratios and encourages incorporation of information on how the environmental variables affect fish life-history and fisheries management measures needed to realize potential sustainable yields. We did not find direct evidence for water-colour associated limitation of fisheries productivity, but correlatively the shallow lakes with the most relative euphotic bottom surface area and good oxygen saturation showed the highest yield estimates. Thus, covariation of water colour and nutrient concentrations may have hidden some of the potentially existing links in among-lakes comparisons due to the lack of controls. Our study also demonstrates that while most of the boreal lakes are rather unproductive, certain shallow lakes may support levels of yields that have practical fisheries relevance and should thus be valued against other more detrimental nature exploitation such as intensive forestry that may affect fisheries through water quality.

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CRediT authorship contribution statement

Lotsari Eliisa: Investigation, Methodology, Writing – review & editing. **Salgado-Ismodes Andrés:** Data curation, Investigation. **Ruuhijärvi Jukka:** Data curation, Supervision, Writing – review & editing. **Olin Mikko:** Data curation, Methodology, Supervision, Writing – review & editing. **Arzel Céline:** Methodology, Supervision, Writing – review & editing. **Huuskonen Hannu:** Methodology, Resources, Supervision, Writing – review & editing. **Kahilainen Kimmo K.:** Conceptualization, Methodology, Resources, Writing – review & editing. **Nummi Petri:** Methodology, Supervision, Writing – review & editing. **Vainikka Anssi:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Turunen Aatu:** Data curation, Funding acquisition, Investigation.

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

Data and model are available at https://doi.org/10.23729/24986d9b-fff1–4cb7–87b5–467d1873369d.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2023.106922.

References

Aaltonen, H., Tuukkanen, T., Palviainen, M., Laurén, A., Tattari, S., Piirainen, S., Mattson, T., Ojala, A., Launiainen, S., Finér, L., 2021. Controls of organic carbon and nutrient export from unmanaged and managed boreal forested catchments. Water 13, 2363. https://doi.org/10.3390/w13172363.

Appelberg, M., Berger, H.-M., Hesthagen, T., Kleiven, E., Ruuhilahti, M., Raitaniemi, J., Rask, M., 1995. Development and intercalibration of methods in nordic freshwater fish monitoring. Water Air Soil Pollut. 85, 401–406. https://doi.org/10.1007/BF00476862.

Arlinghaus, R., Matsumura, S., Dieckmann, U., 2009. Quantifying selection differentials caused by recreational fishing: development of modeling framework and application to reproductive investment in pike (*Esox lucius*). Evol. Appl. 2, 335–355. https://doi.org/10.1111/j.1752-4571.2009.00081.x.

Arzel, C., Nummi, P., Arvola, L., Pöysä, Davranche, A., Rask, M., Olin, M., Holopainen, S., Viitala, R., Einola, E., Manninen-Johansen, S., 2020. Invertebrates are declining in boreal aquatic habitat: the effect of brownification? Sci. Tot. Environ. 724, 138199 https://doi.org/10.1016/j.scitototenv.2020.138199.

Bartels, P., Hirsch, P.E., Svanbäck, R., Eklöv, P., 2016. Dissolved organic carbon reduces habitat coupling by top predations in lake ecosystems. Ecosystems 19, 955–967. https://doi.org/10.1007/s10021-016-9978-x.

Benoît, P.-O., Beisner, B.E., Solomon, C.T., 2016. Growth rate and abundance of common fishes is negatively related to dissolved organic carbon in lakes. Can. J. Fish. Aquat. Sci. 73, 1230–1236. https://doi.org/10.1139/cjfas-2015-0340.

Bergman, E., 1988. Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernua*, under different environmental conditions. J. Anim. Ecol. 57, 443–453. https://doi.org/10.2307/4916.

Blanchet, C.C., Arzel, C., Davranche, A., Kahilainen, K.K., Secondi, J., Taipale, S., Lindberg, H., Loehr, J., Manninen-Johansen, S., Sundell, J., Maanan, M., Nummi, P., 2022. Ecology and extent of freshwater browning - What we know and what should be studied next in the context of global change? Sci. Tot. Environ. 812, 152420 https://doi.org/10.1016/j.scitotenv.2021.152420.

Brothers, S., Köhler, J., Attermeyer, K., Grossart, H.P., Mehner, T., Meyer, N., Scharnweber, K., Hilt, S., 2014. A feedback loop links brownification and anoxia in a temperate, shallow lake. Limnol. Oceanogr. 59, 1388–1398. https://doi.org/10.4319/.lo.2014.59.4.1388.

Buckel, J.A., Stoner, A.E., 2000. Functional response and switching behavior of young-of-the-year piscivorous bluefish. J. Exp. Mar. Biol. Ecol. 245, 25–41.

Chapman, D.G., 1954. The Estimation of Biological Populations. Ann. Math. Stat. 25, 1–15. https://doi.org/10.1214/aoms/1177728844.

Chu, C., Lester, N.P., Giacomini, H.C., Shuter, B.J., Jackson, D.A., 2016. Catch-per-unit-effort and size spectra of lake fish assemblages reflect underlying patterns in ecological conditions and anthropogenic activities across regional and local scales. Can. J. Fish. Aquat. Sci. 73, 535–546. https://doi.org/10.1139/cjfas-2015-0150.

Claessen, D., de Roos, A.M., Persson, L., 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. Am. Nat. 155, 219–237. https://doi.org/10.1086/303315.

Claessen, D., Van Oss, C., de Roos, A.M., Persson, L., 2002. The impact of size-dependent predation on population dynamics and individual life history. Ecology 83, 1660–1675. https://doi.org/10.1890/0012-9658(2002)083[1660:TIOSDP]2.0.CO;2.

Cooke, S.J., Allison, E.H., Beard Jr., T.D., Arlinghaus, R., Arthington, A.H., Bartley, D.M., Cowx, I.G., Fuentevilla, C., Leonard, N.J., Lorenzen, K., Lynch, A.J., Nguyen, V.M., Youn, S.-J., Taylor, W.W., Welcomme, R.L., 2016. On the sustainability of inland fisheries: Finding a future for the forgotten. Ambio 45, 753–764. https://doi.org/10.1007/s13280-016-0787-4.

Craig, N., Jones, S.E., Weidel, B.C., Solomon, C.T., 2015. Habitat, not resource availability, limits consumer production in lake ecosystems. Limnol. Oceanogr. 60, 2079–2089 https://doi.org/10.1002./lno.10153.

Craig, N., Jones, S.E., Weidel, B.C., Solomon, C.T., 2017. Life history constraints explain negative relationship between fish productivity and dissolved organic carbon in lakes. Ecol. Evol. 7, 6201–6209. https://doi.org/10.1002/ece3.3108.

Dalal, S.G., Shirodkar, P.V., Jagtap, T.G., Naik, B.G., Rao, G.S., 2010. Evaluation of significant sources influencing the variation of water quality of Kandla creek, Gulf of Katchchh, using PCA. Env. Mon. Ass 163, 49–56. https://doi.org/10.1007/s10661-009-0815-y.

Deininger, A., Jonsson, A., Karlsson, J., Bergström, A.K., 2019. Pelagic food webs of humic lakes show low short-term response to forest harvesting. Ecol. Appl. 29, e01813 https://doi.org/10.1002/eap.1813.

Downing, J.A., Plante, C., Lalonde, S., 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Can. J. Fish. Aquat. Sci. 47, 1929–1936.

Dunlop, E.S., Shuter, B.J., Dieckmann, U., 2007. Demographic and evolutionary consequences of selective mortality: predictions from an eco-genetic model for smallmouth bass. Trans. Am. Fish. Soc. 136, 749–765. https://doi.org/10.1577/T06-126.1.

Egglestone, D.B., Parsons, D.M., Kellison, G.T., Plaia, G.R., Johnson, E.G., 2008. Functional response of sport divers to lobsters with application to fisheries management. Ecol. Appl. 18, 258–272. https://doi.org/10.1890/06-1409.1.

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S., Heino, M., 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Mar. Ecol. 33, 1–25. https://doi.org/10.1111/j.1439-0485.2011.00460.x.

Estlander, S., Nurminen, L., Olin, M., Vinni, M., Immonen, S., Rask, M., Ruuhijärvi, J., Horppila, J., Lehtonen, H., 2010. Diet shifts and food selection of perch *Perca fluviatilis* and roach *Rutilus rutilus* in humic lakes of varying water colour. J. Fish. Biol. 77, 241–256. https://doi.org/10.1111/j.1095-8649.2010.02682.x.

Estlander, S., Horppila, J., Olin, M., Vinni, M., Lehtonen, H., Rask, M., Nurminen, L., 2012. Troubled by the humics – effect of water colour and interspecific competition on the feeding efficiency of planktivorous perch. Boreal Environ. Res. 17, 305–312.

Estlander, S., Kahilainen, K., Horppila, J., Olin, M., Rask, M., Kubečka, J., Peterka, J., Říha, M., Huuskonen, H., Nurminen, L., 2017. Latitudinal variation in sexual dimorphism in life- history traits of a freshwater fish. Ecol. Evol. 7, 665–673. https://doi.org/10.1002/ece3.2658.

Estlander, S., Pippingsköld, E., Horppila, J., 2021. Artificial ditching of catchments and brownification-connected water quality parameters of lakes. Water Res 205, 117674. https://doi.org/10.1016/j.watres.2021.117674.

Finér, L., Lepistö, A., Karlsson, K., Räike, A., Härkönen, L., Huttunen, M., Joensuu, S., Kortelainen, P., Mattson, T., Piirainen, S., Sallantaus, T., Sarkkola, S., Tattari, S., Ukonmaanaho, L., 2021. Drainage for forestry increases N, P and TOC export to boreal surface waters. Sci. Tot. Environ. 762, 144098 https://doi.org/10.1016/j.scitotenv.2020.144098.

Finstad, A.G., Helland, I.P., Ugedal, O., Hesthagen, T., Hessen, D.O., 2014. Unimodal response of fish yield to dissolved organic carbon. Ecol. Lett. 17, 36–43. https://doi.org/10.1111/ele.12201.

Fiogbé, E.D., Kestemont, P., 2003. Optimum daily ration for Eurasian perch *Perca fluviatilis* L. reared at its optimum growing temperature. Aquaculture 216, 243–252. https://doi.org/10.1016/S0044-8486(02)00409-X.

Forsström, L., Roiha, T., Rautio, M., 2013. Responses of microbial food web to increased allochtonous DOM in an oligotrophic subarctic lake. Aquat. Microbiol. Ecol. 68, 171–184. https://doi.org/10.3354/ame01614.

Heermann, L., Eriksson, L.-O., Magnhagen, C., Borcherding, J., 2009. Size-dependent energy storage and winter mortality of perch. Ecol. Freshw. Fish. 18, 560–571. https://doi.org/10.1111/j.1600-0633.2009.00371.x.

Heibo, E., Magnhagen, C., Vøllestad, L.A., 2005. Latitudinal variation in life-history traits in Eurasian perch. Ecology 86, 2277–3386. https://doi.org/10.1890/04-1620.

Hjelm, J., Persson, L., Christensen, B., 2000. Growth, morphological variation and ontogenetic niche shifts in perch (*Perca fluviatilis*) in relation to resource availability. Oecologia 122, 190–199. https://doi.org/10.1007/PL00008846.

Höhne, L., Palmer, M., Monk, C.T., Matern, S., Nikolaus, R., Trudeau, A., Arlinghaus, R., 2020. Environmental determinants of perch (*Perca fluviatilis*) growth in gravel pit lakes and the relative performance of simple versus complex ecological predictors. Ecol. Freshw. Fish. 29, 557–573. https://doi.org/10.1111/eff.12532.

Holmgren, K., Appelberg, M., 2005. Size structure of benthic freshwater fish communities in relation to environmental gradients. J. Fish. Biol. 57, 1312–1330. https://doi.org/10.1111/j.1095-8649.2000.tb00489.x.

Holopainen, S., Lehikoinen, A., 2022. Role of forest ditching and agriculture on water quality: Connecting the long-term physico-chemical subsurface state of lakes with landscape and habitat structure information. Sci. Tot. Environ. 806, 151477 https://doi.org/10.1016/j.scitotenv.2021.151477.

Horppila, J., Olin, M., Vinni, M., Estlander, S., Nurminen, L., Rask, M., Ruuhijärvi, J., Lehtonen, H., 2010. Perch production in forest lakes: the contribution of abiotic and biotic factors. Ecol. Freshw. Fish. 19, 257–266. https://doi.org/10.1111/j.1600-0633.2010.00410.x.

Huser, B.J., Futter, M.N., Wang, R., Fölster, J., 2018. Persistent and widespread long-term phosphorus declines in Boreal lakes in Sweden. Sci. Tot. Environ. 613-614, 240–249. https://doi.org/10.1016/j.scitotenv.2017.09.067.

Jackson, T.A., Hecky, R.E., 1980. Depression of primary productivity by humic matter in lake and reservoir waters of the boreal forest zone. Can. J. Fish. Aquat. Sci. 37, 2300–2317. https://doi.org/10.1139/f80-277.

Jarvis, L.A., McMeans, B.C., Corrêa Giacomini, H., Chu, C., 2020. Species-specific preferences drive the differential effects of lake factors on fish production. Can. J. Fish. Aquat. Sci. 77, 1615–1638. https://doi.org/10.1139/cjfas-2020-0105.

Johnson, B.L., Milliman, S.R., Bishop, R.C., Kitchell, J.F., 1992. Evaluating fishery rehabilitation under uncertainty: a bioeconomic analysis of quota management for the Green Bay yellow perch fishery. North Am. J. Fish. Man. 12, 703–720.

Jones, J.R., Hoyer, M.V., 1982. Sportfish harvest predicted by summer chlorophyll-α concentration in midwestern lakes and reservoirs. Trans. Am. Fish. Soc. 111, 176–179.

Kaemingk, M.A., Arlinghaus, R., Birdsong, M.H., Chizinski, C.J., Lyach, R., Wilson, K.L., Pope, K.L., 2022. Matching of resource use and investment according to waterbody size in recreational fisheries. Fish. Res. 254, 106388 https://doi.org/10.1016/j.fishres.2022.106388.

Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., Jansson, M., 2009. Light limitation of nutrient-poor lake ecosystems. Nature 460, 506–510. https://doi.org/10.1038/nature08179.

Karlsson, J., Bergström, A.-K., Byström, P., Gudasz, C., Rodríguez, P., Hein, C., 2015. Terrestrial organic matter input suppresses biomass production in lake ecosystems. Ecology 96, 2870–2876. https://doi.org/10.1890/15-0515.1.

Knoll, L.B., Williamson, C.E., Pilla, R.M., Leach, T.H., Brentrup, J.A., Fisher, T.J., 2018. Browning-related oxygen depletion in an oligotrophic lake. Inland Wat 8, 255–263. https://doi.org/10.1080/20442041.2018.1452355.

Koenings, J.P., Edmundson, J.A., 1991. Secchi disk and photometer estimates of light regimes in Alaskan lakes: effect of yellow color and turbidity. Limnol. Ocean. 36, 91–105. https://doi.org/10.4319/lo.1991.36.1.0091.

Koizumi, S., Craig, N., Zwart, J.A., Kelly, P.T., Ziegler, J.P., Weidel, B.C., Jones, S.E., Solomon, C.T., 2018. Experimental whole-lake dissolved organic carbon increase alters fish diet and density but not growth or productivity. Can. J. Fish. Aquat. Sci. 75, 1859–1867. https://doi.org/10.1139/cjfas-2017-0283.

Kokkonen, E., Heikinheimo, O., Pekcan-Hekim, Z., Vainikka, A., 2019a. Effects of water temperature and pikeperch (Sander lucioperca) abundance on the stock–recruitment relationship of Eurasian perch (Perca fluviatilis) in the northern Baltic Sea. Hydrobiologia 841, 79–94. https://doi.org/10.1007/s10750-019-04008-z.

Kokkonen, E., Mitikka, S., Huuskonen, H., Olin, M., Ruuhijärvi, J., Vainikka, A., 2019b. Structural equation models suggest that bottom-up processes override top-down processes in boreal pikeperch (Sander lucioperca) lakes. Freshw. Biol. 64, 1054–1063. https://doi.org/10.1111/fwb.13285.

Laudon, H., Hedtjärn, J., Schelker, J., Bishop, K., Sørensen, R., Ågren, A., 2009. Response of dissolved organic carbon following forest harvesting in a boreal forest. Ambio 38, 381–386. https://doi.org/10.1579/0044-7447-38.7.381.

Le Cren, E.D., 1958. Observations on the growth of perch (*Perca fluviatilis* L.) over twenty-two years with special reference to the effects of temperature and changes in population density. J. Anim. Ecol. 27, 287–334.

Leach, J.H., Dickie, L.M., Shuter, B.J., Borgmann, U., Hyman, J., Lysack, W., 1987. A review of methods for prediction of potential fish production with application to the Great Lakes and Lake Winnipeg. Can. J. Fish. Aquat. Sci. 44, 471–485.

Lee, K., Apriesnig, J., Zhang, H., 2021. Socio-ecological outcomes of single-species fisheries management: The case of yellow perch in Lake Erie. Front. Ecol. Evol. 9, 703813 https://doi.org/10.3389/fevo.2021.703813.

Lee, Z., Shang, S., Du, K., Wei, J., 2018. Resolving the long-standing puzzles about the observed Secchi depth relationships. Limnol. Oceanogr. 63, 2321–2336. https://doi.org/10.1002/lno.10940.

Lepistö, A., Räike, A., Sallantaus, T., Finér, L., 2021. Increases in organic carbon and nitrogen concentrations in boreal forested catchments — Changes driven by climate and deposition. Sci. Tot. Environ. 780, 146627 https://doi.org/10.1016/j.scitotenv.2021.146627.

Lester, N.P., Shuter, B.J., Abrams, P.A., 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. Proc. R. Soc. Lond. B 271, 1625–1631. https://doi.org/10.1098/rspb.2004.2778.

Linløkken, A., Haugen, T.O., 2006. Density and temperature dependence of gill net catch per unit effort for perch, *Perca fluviatilis*, and roach, *Rutilus rutilus*. Fish. Manag. Ecol. 13, 261–269. https://doi.org/10.1111/j.1365-2400.2006.00502.x.

Lyach, R., Remr, J., 2019. The effects of environmental factors and fisheries management on recreational catches of perch *Perca fluviatilis* in the Czech Republic. Aquat. Living Resour. 32, 15. https://doi.org/10.1051/alr/2019013.

MacLeod, H.A., Shuter, B.J., Minns, C.K., Rennie, M.D., 2022. Productivity of fish populations: environmental and ecological drivers. In: Mehner, T., Tockner, K. (Eds.), Encyclopedia of Inland Waters, 2nd edition.,. Elsevier, pp. 207–224. https://doi.org/10.1016/B978-0-12-819166-8.00198-5.

Marttunen, M., Turunen, J., Kukkonen, M., Vilmi, A., Mustajoki, J., Huuki, H., Härkönen, L., Hyvärinen, P., Louhi, P., Räsänen, S., Kopsakangas-Savolainen, M., Hellsten, S. 2023. Oulujoen vesistöalueen vesistövisio – ARVOVESI-hankkeen tulokset. Suomen ympäristökeskus, raportteja 8/2023. ⟨http://urn.fi/URN:ISBN:978–952-11–5568-0⟩.

Mollet, F.M., Engelhard, G.H., Vainikka, A., Laugen, A.T., Rijnsdrop, A.J., Ernande, B., 2013. Spatial variation in growth, maturation schedules and reproductive investment of female sole Solea solea in the Northeast Atlantic. J. Sea Res 84, 109–121. https://doi.org/10.1016/j.seares.2012.12.005.

Mosindy, T.E., Momot, W.T., Colby, P.J., 1987. Impact of angling on the production and yield of mature walleyes and northern pike in a small boreal lake in Ontario. N. Am. J. Fish. Manag. 7, 493–501.

Nieminen, M., Koskinen, M., Sarkkola, S., Láuren, A., Kaila, A., Kiikkilä, O., Nieminen, T. M., Ukonmaanaho, L., 2015. Dissolved organic carbon export from harvested peatland forests with differing site characteristics. Water Air Soil Pollut. 226, 181. https://doi.org/10.1007/s11270-015-2444-0.

Nummi, P., Vehkaoja, M., Pumpanen, J., Ojala, A., 2018. Beavers affect carbon biogeochemistry: both short-term and long-term processes are involved. Mamm. Rev. 48, 298–311. https://doi.org/10.1111/mam.12134.

Nürnberg, G.K., Shaw, M., 1999. Productivity of clear and humic lakes: nutrients, phytoplankton, bacteria. Hydrobiologia 382, 97–112. https://doi.org/10.1023/A:1003445406964.

Nyberg, K., Vuorenmaan, J., Tammi, J., Nummi, P., Väänänen, V.-M., Mannio, J., Rask, M., 2010. Re-establishment of perch in three lakes recovering from acidification: rapid growth associated with abundant food resources. Bor. Environ. Res. 15, 480–490.

Ogle, D.H., Doll, J.C., Wheeler, P., Dinno, A. 2021. FSA: Fisheries Stock Analysis. R package version 0.9.1.9000, ⟨https://github.com/droglenc/FSA⟩.

Olin, M., Kurkilahti, M., Peitola, P., Ruuhijärvi, J., 2004. The effects of fish accumulation on the catchability of multimesh gillnet. Fish. Res. 68, 135–147. https://doi.org/10.1016/j.fishres.2004.01.005.

Olin, M., Vinni, M., Lehtonen, H., Rask, M., Ruuhijärvi, J., Saulamo, K., Ala-Opas, P., 2010. Environmental factors regulate the effects of roach *Rutilus rutilus* and pike *Esox lucius* on perch *Perca fluviatilis* populations in small boreal forest lakes. J. Fish. Biol. 76, 1277–1293. https://doi.org/10.1111/j.1095-8649.2010.02559.x.

Olin, M., Jutila, J., Lehtonen, H., Vinni, M., Ruuhijärvi, J., Estlander, S., Rask, M., Kuparinen, A., Lappalainen, J., 2012. Importance of maternal size on the reproductive success of perch, *Perca fluviatilis*, in small forest lakes: implications for fisheries management. Fish. Man. Ecol. 19, 363–374. https://doi.org/10.1111/j.1365-2400.2012.00845.x.

Olin, M., Lappalainen, A., Sutela, T., Vehanen, T., Ruuhijärvi, J., Saura, A., Sairanen, S., 2014. Ohjeet standardinmukaisiin koekalastuksiin. RKTL:n työraportteja 21/2 014. ⟨https://jukuri.luke.fi/handle/10024/519927⟩.

Olin, M., Tiainen, J., Kurkilahti, M., Rask, M., Lehtonen, H., 2016. An evaluation of gillnet CPUE as an index of perch density in small forest lakes. Fish. Res. 173, 20–25. https://doi.org/10.1016/j.fishres.2015.05.018.

Olin, M., Tiainen, J., Rask, M., Vinni, M., Nyberg, K., Lehtonen, H., 2017. Effects of non-selective and size-selective fishing on perch populations in a small lake. Boreal Env. Res 22, 137–155.

Olsen, R.L., Chappell, R.W., Loftis, J.C., 2012. Water quality sample collection, data treatment and results presentation for principal components analysis – literature review and Illinois River watershed case study. Water Res 46, 3110–3122. https://doi.org/10.1016/j.watres.2012.03.028.

Persson, L., De Roos, A.M., 2013. Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults. Ecology 94, 1487–1498. https://doi.org/10.1890/12-1883.1.

Persson, L., Greenberg, L.A., 1990a. Juvenile competitive bottlenecks: the perch (Perca fluviatilis)-roach (Rutilus rutilus) interaction. Ecology 71, 44–56.

Persson, L., Greenberg, L.A., 1990b. Optimal foraging and habitat shift in perch (Perca fluviatilis) in a resource gradient. Ecology 71, 1699–1713.

Persson, L., Byström, P., Wahlström, E., 2000. Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. Ecology 81, 1058–1071. https://doi.org/10.2307/177178.

Persson, L., De Roos, A.M., Claessen, D., Byström, P., Lövgren, J., Sjögren, S., Svanbäck, R., Wahlström, E., Westman, E., 2003. Gigantic cannibals driving a whole-lake trophic cascade. Proc. Natl. Acad. Sci. 100, 4035–4039. https://doi.org/10.1073/pnas.0636404100.

Persson, L., Amundsen, P.-A., De Roos, A.M., Klemetsen, A., Knudsen, R., Primicerio, R., 2007. Culling prey promotes predator recovery — alternative states in a whole-lake experiment. Science 316, 1743–1746. https://doi.org/10.1126/science.1141412.

Persson, L., Van Leeuwen, A., De Roos, A.M., 2014. The ecological foundation for ecosystem-based management of fisheries: mechanistic linkages between the individual-, population-, and community-level dynamics. ICES J. Mar. Sci. 71, 2268–2280. https://doi.org/10.1093/icesjms/fst231.

Pilla, R.M., Williamson, C.E., Zhang, J., Smyth, R.L., Lenters, J.D., Brentrup, J.A., Knoll, L.B., Fisher, T.J., 2018. Browning-related decreases in water transparency lead to long-term increases in surface water temperature and thermal stratification in two small lakes. J. Geophys. Res. Biogeosci 123, 1651–1665. https://doi.org/10.1029/2017JG004321.

Post, J.R., Evans, D.O., 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Can. J. Fish. Aquat. Sci. 46, 1958–1968. https://doi.org/10.1139/f89-246.

Pritchard, D.W., Paterson, R.A., Bovy, H.C., Barrios-O'Neil, D., 2017. FRAIR: an R package for fitting and comparing consumer functional responses. Methods Ecol. Evol. 8, 1528–1534. https://doi.org/10.1111/2041-210X.12784.

Raatikainen, M., Kuusisto, E., 1988. Suomen järvien lukumäärä ja pinta-ala. Terra 102, 97–110.

Randall, R.G., Kelso, J.R.M., Minns, C.K., 1995. Fish production in freshwaters: are rivers more productive than lakes? Can. J. Fish. Aquat. Sci. 52, 631–643. https://doi.org/10.1139/f95-063.

Ranta, E., Lindström, K., 1989. Prediction of lake-specific yield. Fish. Res. 8, 113–128. https://doi.org/10.1016/0165-7836(89)90026-X.

Ranta, E., Lindström, K., 1993. Theory of fish yield versus water quality in lakes. Ann. Zool. Fenn. 30, 71–75.

Rask, M., Arvola, L., 1985. The biomass and production of pike, perch and whitefish in two small lakes in Southern Finland. Ann. Zool. Fenn. 22, 129–135.

Rask, M., Sairanen, S., Vesala, S., Arvola, L., Estlander, S., Olin, M., 2014. Population dynamics and growth of perch in a small, humic lake over a 20-year period — importance of abiotic and biotic factors. Bor. Environ. Res 19 (suppl. A), 112–123.

Rawson, D.S., 1952. Mean depth and the fish production of large lakes. Ecology 33, 513–521.

Rindorf, A., Gislason, H., 2005. Functional and aggregative response of North Sea. whiting. J. Exp. Mar. Biol. Ecol. 324, 1–19.

Ryder, R.A., 1965. A method for estimating the potential fish production of north-temperate lakes. Trans. Am. Fish. Soc. 94, 214–218.

Schindler, D.W., Beaty, K.G., Fee, J., Cruikshank, D.R., DeBruyn, E.R., Findlay, D.L., Linsey, G.A., Shearer, J.A., Stainton, M.P., Turner, M.A., 1990. Effects of climatic warming on lakes of the Central Boreal. For. Sci. 250, 967–970.

Schlosser, I.J., Kallemeyn, L.W., 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. Ecology 81, 1371–1382. https://doi.org/10.1890/0012-9658(2000)081[1371:SVIFAA]2.0.CO;2.

Schnabel, Z.E., 1938. The estimation of the total fish population of a lake. Am. Math. Mothl 45, 348–352. https://doi.org/10.1080/00029890.1938.11990818.

Seekell, D.A., Byström, P., Karlsson, J., 2018. Lake morphometry moderates the relationship between water color and fish biomass in small boreal lakes. Limnol. Oceanogr. 63, 2171–2178. https://doi.org/10.1002/lno.10931.

Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bull. Mar. Sci. 60, 1129–1157.

Solomon, C.T., Jones, S.E., Weidel, B.C., Buffam, I., Fork, M.L., Karlsson, J., Larsen, S., Lennon, J.T., Read, J.S., Sadro, S., Saros, J.E., 2015. Ecosystem consequences of changing inputs of terrestrial dissolved organic matter to lakes: current knowledge and future challenges. Ecosystems 18, 376–389. https://doi.org/10.1007/s10021-015-9848-y.

Søndergaard, M., Jensen, J.P., Jeppesen, E., 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506-509, 135–145. https://doi.org/10.1023/B:HYDR.0000008611.12704.dd.

Taborsky, B., Dieckmann, U., Heino, M., 2003. Unexpected discontinuities in life–history evolution under size–dependent mortality. Proc. R. Soc. Lond. B 270, 713–721. https://doi.org/10.1098/rspb.2002.2255.

Tammi, J., Rask, M., Ala-Opas, P., 2006. Ecological classification of Finnish lakes using a multimetric fish index. Verh. Intern. Ver. Limnol. 29, 2276–2278. https://doi.org/10.1080/03680770.2006.11903098.

Trigal, C., Goedkoop, W., Johnson, R.K., 2011. Changes in phytoplankton, benthic invertebrate and fish assemblages of boreal lakes following invasion by Gonyostomum semen. Freshw. Biol. 56, 1937–1948. https://doi.org/10.1111/j.1365-2427.2011.02615.x.

Trudeau, A., Mehner, T., Klefoth, T., Matern, S., Nikolaus, R., Arlinghaus, R., 2023. Lake depth alters the trajectory of ontogenetic niche shifts in Eurasian perch (*Perca fluviatilis*) in small lakes. Ecol. Freshw. Fish. 33, e12738 https://doi.org/10.1111/eff.12738.

Turunen, A., Salgado-Ismodes, A., Huuskonen, H., Kahilainen, K.K., Olin, M., Ruuhijärvi, J., Vainikka, A., 2023. Ice fishing reveals size structure but not abundance of Eurasian perch in small boreal lakes. Fish. Man. Ecol. 30, 99–108. https://doi.org/10.1111/fme.12603.

Vadeboncoeur, Y., Peterson, G., Zanden, M.J.V., Kalff, J., 2008. Benthic algal production across lake size gradients: interactions among morphometry, nutrients, and light. Ecology 89, 2542–2552. https://doi.org/10.1890/07-1058.1.

Vainikka, A., Hyvärinen, P., 2012. Ecologically and evolutionarily sustainable fishing of the pikeperch *Sander lucioperca*: lake Oulujärvi as an example. Fish. Res. 113, 8–20. https://doi.org/10.1016/j.fishres.2011.09.004.

Vainikka, A., Koskimäki, J., Niemelä, P.T., Kortet, R., 2012. Composition of the Eurasian perch (*Perca fluviatilis*) catches in ice fishing: does capture order predict body size? Fish. Res. 115-116, 24–30. https://doi.org/10.1016/j.fishres.2011.11.004.

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. Bor. Environ. Res. 22, 187–212.

van Dorst, R.M., Gårdmark, A., Svanbäck, R., Beier, U., Weyhenmeyer, G.A., Huss, M., 2019. Warmer and browner waters decrease fish biomass production. Glob. Change Biol. 25, 1395–1408. https://doi.org/10.1111/gcb.14551.

van Dorst, R.M., Gårdmark, A., Svanbäck, R., Huss, M., 2020. Does browning-induced light limitation reduce fish body growth through shifts in prey composition or reduced foraging rates? Freshw. Biol. 65, 947–959. https://doi.org/10.1111/fwb.13481.

Viljanen, M., Holopainen, I.J., 1982. Population density of perch (*Perca fluviatilis* L.) at egg, larval and adult stages in the dys-oligotrophic Lake Suomunjärvi, Finland. Ann. Zool. Fenn. 19, 39–46.

Weyhenmeyer, G.A., Prairie, Y.T., Tranvik, L.J., 2014. Browning of boreal freshwaters coupled to carbon-iron interaction along the aquatic continuum. PLOS One 9, e88104 https://doi.org/19.1371/journal.pone.0088104.

Wildung, R.E., Schmidt, R.L., Gahler, A.R., 1974. The phosphorus status of eutrophic lake sediments as related to changes in limnological conditions–total, inorganic, and organic phosphorus. J. Environ. Qual. 3, 133–138. https://doi.org/10.2134/jeq1974.00472425000300020009x.

Williamson, C.E., Overholt, E.P., Pilla, R.M., Wilkins, K.W., 2020. Habitat-mediated responses of zooplankton to decreasing light in two temperate lakes undergoing long-term browning. Front. Environ. Sci. 8, 73. https://doi.org/10.3389/fenvs.2020.00073.

Wilson, K.L., Honsey, A.E., Moe, B., Venturelli, P., 2017. Growing the biphasic framework: techniques and recommendations for fitting emergent growth models. Methods Ecol. Evol. 9, 822–833. https://doi.org/10.1111/2041-210X.12931.