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Explaining recreational angling catch rates of Eurasian perch, *Perca fluviatilis*: the role of natural and fishing-related environmental factors

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Abstract Angling catch records are frequently used to reveal fish population developments. It is therefore important to understand the determinants of angling catches. This study focused on angler-related, biotic and abiotic factors influencing catchability of Eurasian perch, *Perca fluviatilis* L. A multi-lake (21 lakes) study based on angling diaries collected in Mecklenburg-Vorpommern, Germany (2006/2007), found that angler-related factors such as fishing experience, species preference and bait/lure type had a large impact on perch catch rates. Additionally, environmental conditions (nutritional status and water transparency) affected either the size or the number of perch caught by anglers. Catch rates varied seasonally, which was confirmed by an experimental fishery on a gravel pit (2008). This portion of the study showed that altered food availabilities in the course of the year caused food limitation in perch, which in turn facilitated high catch rates and female-biased exploitation in autumn. It is concluded that both angler-related and abiotic factors interact affecting perch catch rates and size of perch captured in recreational angling.

KEYWORDS: catchability, diary, recreational fishing, sex-specific exploitation, starvation.

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Introduction

Recreational fishing is common throughout many freshwater ecosystems in temperate regions. It therefore represents a potentially valuable means to generate fishery-dependent data to infer insights about changes in fish populations (e.g. Lehtonen *et al.* 2009). Because a routine sampling protocol with scientific methods is often not possible in many recreational fisheries (Post *et al.* 2002; Daedlow *et al.* 2011), catch records from angler's diaries (e.g. collected by clubs) are often the only possibility to gather information on fish population developments (Cooke *et al.* 2000; Mosindy & Duffy 2007). This, however, demands that angler catch per unit effort (CPUE) is a reliable measure of fish population abundance, which is not necessarily the case (Erisman *et al.* 2011). Understanding how angling catch rates vary with abiotic and general limnological variables is important to interpret available angling records in the light of underlying population developments (Kuparinen *et al.* 2010).

Eurasian perch, *Perca fluviatilis* L. a widespread freshwater species in Europe, is a targeted angling species in many European countries such as Germany and Finland (e.g. Arlinghaus & Mehner 2004; Vainikka *et al.* 2012). Few studies on the catch aspects of Eurasian perch angling exist (Beardmore *et al.* 2011; Vainikka *et al.* 2012; but see e.g. Isermann *et al.* 2005; Irwin *et al.* 2008; Wilberg *et al.* 2008 for studies on yellow perch, *Perca flavescens* (Mitchill)), and there is no study that has investigated how environmental variables, such as lake morphometry, nutrient status and water transparency or season influence perch catch rates in perch recreational angling.

It is likely that catch rates of perch vary among lakes in relation to abundance of perch in line with prevailing ecological conditions. In general, high abundances of perch are found in relatively deep, vegetation-rich lakes with high water transparency and low to moderate nutrient concentrations (e.g. Persson *et al.* 1991; Jeppesen *et al.* 2000; Olin *et al.* 2002; Mehner *et al.* 2005). One would therefore expect catch rates of perch to peak under these environmental conditions. Vulnerability to angling is also related to individual behavioural traits (Uusi-Heikkilä *et al.* 2008) such as boldness (Mezzera & Largiadèr 2001). Perch activity correlates with nutritional status and hunger levels (e.g. Borcherding & Magnhagen 2008), predation risk (e.g. Bean & Winfield 1995) and temperature (Jacobsen *et al.* 2002). Thus, angling catchability of perch might not only depend on the lake's nutrient status, size and morphometry, but should also be influenced by other ecological factors, such as food availability or season.

In most recreational fisheries, positively size-selective exploitation is common (Lewin *et al.* 2006). This is the result of angler preference for large fish (Arlinghaus & Mehner 2003; Beardmore *et al.* 2011) and is further promoted by common management measures such as minimum length regulations (Arlinghaus *et al.* 2010). Moreover, morpho-physical aspects play an important role in the size selectivity as fish must be large enough to ingest a certain size of bait or lure. Moreover, individuals with higher growth potential and corresponding metabolic demands were shown to be more risk-prone and consume larger quantities of prey, and hence to be more vulnerable to capture in recreational fishing (Cooke *et al.* 2007; Redpath *et al.* 2010). In some freshwater top predators, such as pike, *Esox lucius* L., sex-specific differences in individual growth and associated behavioural differences were suggested to lead to a higher angling vulnerability of faster-growing female individuals resulting in sex-biased exploitation (Casselman 1975). Sex-specific growth differences also exist in Eurasian perch (Le Cren 1958) suggesting that perch vulnerability, but also the size of the perch angled, might be sex-dependent. The size of perch in the catch of anglers should also be connected to environmental variables because the size structure of perch populations strongly depends on competition and food availability connected to environmental limnological factors (e.g. Persson 1983, 1987; Claessen *et al.* 2000, 2002; Persson *et al.* 2004). A higher number of large-sized perch can be found in nutrient-poor lakes as the overall fish density and competition for food resources are low, such that individual perch can more easily reach the piscivorous stage (e.g. Jeppesen *et al.* 1997, 2000; Persson *et al.* 1998; Claessen *et al.* 2000) avoiding stunted growth (Ylikarjula *et al.* 1999).

In addition to natural factors, catchability of fish by anglers should also be correlated with a range of attributes of the angler, such as skill and fishing experience (e.g. McConnell *et al.* 1995; Arlinghaus & Mehner 2003), bait choice (Alós *et al.* 2009) or lure size (Wilde *et al.* 2003; Arlinghaus *et al.* 2008). While a clear effect of angler attributes on catchability and the size of fish captured has been reported in previous studies in different species (e.g. McConnell *et al.* 1995; Alós *et al.* 2009), limited information is currently available for perch (Beardmore *et al.* 2011).

The present study aimed at identifying factors influencing catch rates and size selectivity and sex selectivity of catches via angling for Eurasian perch focusing on: (1) angler-related factors (e.g. angling experience, angler's main target species or bait type); (2) environmental factors related to perch abundance and the size structure of perch populations (e.g. lake morphometry and nutritional status of the lake); and (3) factors related to the ecology of perch (e.g. feeding or sex). In a first step, data from angling diaries collected over a 1-year period in 21 natural lakes of Mecklenburg-Vorpommern (hereafter, multi-lake study), Germany, were analysed with respect to modelling variance in perch catch rates and mean maximum length of perch harvested. This part of the study mainly focused on angler-specific and environmental influences. In a second step, a single-lake study was conducted in a gravel pit in North-Rhine Westphalia, Germany, to understand physiological/ecological constrains related to sex-specific feeding, which could not be addressed in the multi-lake study but was also expected to influence angling success and size of perch captured with angling gear.

Materials & methods

Assessing perch catches – multi-lake study

Data on perch catches by recreational anglers fishing in natural lakes in Mecklenburg-Vorpommern (M-V) were generated in a 1-year angling diary study described in detail by Dorow and Arlinghaus (2011). Briefly, over a period from September 2006 to August 2007, randomly recruited anglers fishing regularly in M-V were asked to record detailed information on a fishing-trip level including location, targeted species, angling method, overall and method-specific and species-specific effort, species-specific catch and harvest and the size of the largest fish harvested of a given species. In this study, only lake fishing trips where perch was the targeted species for at least some fraction of the trip, including zero-perch catch days, were incorporated. The data set was confined to lakes that were fished by at least three anglers throughout the entire study period. Furthermore, all lakes selected were fished at least during three of four seasons (spring: March, April, May), summer (June, July, August), autumn (September, October, November) or winter (December, January, February). Catch rate and mean maximum length of perch landed by 143 anglers targeting perch in 21 natural lakes were analysed. An individual angler average perch catch per unit effort (CPUE; fish h^{-1}) for each lake and season was estimated as the ratio of means (sum of perch catches divided by the sum of targeted perch fishing effort in hours), which is the best measure for completed angling trips (Pollock *et al.* 1994). As a second metric of interest, an index of perch length in the catch was calculated. No information on mean length of perch catches was available so the mean maximum length (L_{max}) of perch harvested was used as a size metric instead. L_{max} was enumerated as the mean of individual angler means of perch maximum length retained to reduce possible effects of outliers of rare catches of extreme-sized perch and to keep the angler the sampling unit. Note that L_{max} was only recorded in the diary in cases where perch were harvested and where individuals were ≥ 15 cm in total length (15 cm was a minimum size limit in some of the study lakes).

Assessing perch catches – single-lake study

Further data on perch catches orginiated from the single-lake study performed by means of experimental fishing in a single gravel pit lake, Lake Speldrop, situated in North-Rhine Westphalia, Germany (51°46′50″N, 6°22′42″E). The Secchi depth of the eutrophic lake in summer reaching chlorophyll-*a* concentrations of 20–50 μg L^{-1} ranged between 1.1 and 8 m with a minimum at around the end of June. The lake has a surface area of about 7 ha, a mean depth of 7.4 m and is dominated by perch (for a more details, see Beeck *et al.* 2002; Borcher-ding *et al.* 2010). Gravel pit lakes differ structurally from natural lakes, by having steep banks, but quickly establish habitat features that are comparable to natural mesotrophic lakes. More than 20 000 gravel pits occur in Germany, of which over 1000 are situated in North-Rhine Westphalia (Berndt 1991). Therefore, such anthropogenically created ecosystems form water bodies typical for the landscape especially at the lower River Rhine (Berndt 1991). Former studies on perch populations in gravel pit lakes showed that the results are transferable to natural lakes (Beeck 2003).

Catch rates of perch were documented on one randomly chosen experimental angling sampling day per month from June to September 2008. On each sampling date, 4–6 experienced perch anglers distributed over 2–3 boats angled for 3–7 h using self-chosen sites. Anglers were spread over the whole lake but were angling mostly near the shore (15–20 m offshore). In each boat (staffed with 1–2 anglers), 3–4 fishing rods were used with either natural or artificial baits, where artificial baits were wobblers and spinners, and natural baits were mostly young-of-the-year (YOY) perch (about 60 mm) but sometimes also worms. In all but a few hours, both bait types were used simultaneously during the whole angling period, but anglers were free to choose the type of bait they used. Therefore, bait type was controlled, but size and type of natural or artificial bait were uncontrolled. As described earlier, catch rates of all perch caught with artificial and natural bait were expressed as CPUE (fish per rod-hour) including zero-catch values on a per boat basis. CPUE was calculated per boat and bait type; the resulting values were then averaged for each bait type and sampling day to compute the mean CPUE for each sampling date. Correspondingly, L_{max} of perch was calculated as the mean of the largest perch caught in a given boat for natural and artificial bait on each sampling date. To analyse sex-dependent catch rates, the percentage of female perch caught was calculated.

Environmental correlates of perch catch rates in the multi-lake study

Nine predictors were selected to model variation in perch angling CPUE and L_{max} across lakes in M-V (multi-lake study). Five environmental variables known from literature to be related to perch abundance and size structure (Sumari 1971; Jeppesen *et al.* 2000), namely lake size (area, ha), depth (mean and maximum depth, m) and nutrient status [average annual total phosphorus concentration (TP, mg L^{-1}), average annual secci depth, cm], were selected (Table 1).

Measurements of TP and secci depth in all 21 study lakes were taken according to standardised protocols by local environment authorities between 2005 and 2008 with a minimum of three samplings per year and lake. Angling skill and timing of angling-related potential predictors of perch rates as estimated from the diary study and accompanying telephone and mail surveys with the same anglers were added as predictors (Dorow & Arlinghaus 2011). First, fishing trips were partitioned according to season (categorial into four seasons) and bait type (natural or artificial). Information on bait size was not available. Bait type and seasonality (co-varying with water temperature) are known to affect catch rate in various fish species (e.g. Margenau *et al.* 2003; Scrogin *et al.* 2004; Alós *et al.* 2009; Kuparinen *et al.* 2010). Moreover, since a range of angling skill and angler types were generating data, each angler contributing catch rate information was characterised by a measure of angling skill related to perch in terms of absolute angling experience (years of fishing) and preferred target species (e.g. non-predatory or predatory fish). The latter classification was required because Wilde and Ditton (1994) showed that the self-reported target species by anglers is predictably related to a degree of specialisation and commitment such that one can assume that a person who classifies himself or herself as a predatory fish, angler will likely be more skilled in catching predatory fish such as large perch. Target species was classified as 1 = no preference for a certain species; 2 = preference for non-predatory fish [e.g. roach, *Rutilus rutilus* (L.) bream, *Abramis brama* (L.) carp, *Cyprinus carpio* L.]; 3 = other (e.g. salmonids, marine species); and 4 = preference for predatory fish [e.g. perch, pike, zander, *Sander lucioperca* (L.)].

Table 1. Characteristics of the lakes investigated in the multi-lake study including area, mean depth (Z_{mean}), maximum depth (Z_{max}), secci depth (SD) and total phosphorus concentration (TP). In addition, number of anglers, number of fishing trips, proportion of the angler types fishing at each lake and their average fishing experience [FE (years) + standard deviation (SD)] from a sample of anglers taking part in a diary study are shown. Angler type: 1 = no preference; 2 = non-predatory fish; 3 = other (salmonids, marine species); 4 = predatory fish

								Angler type (%)				
Lake	Area (ha)	Z_{mean} (m)	Z_{max} (m)	SD (cm)	TP (mg L^{-1})	*N* Anglers	*N* trips	1	2	3	4	FE (SD)
Dobbertiner See	374.2	11.8	5.0	140	0.073	5	13	40.0	60.0	0.0	0.0	27.6 (11.3)
Fleesensee	1077.5	26.3	6.1	230	0.124	5	22	40.0	0.0	0.0	60.0	28.8 (16.8)
Glammsee	61.6	17.6	7.8	154	0.077	6	7	83.3	16.7	0.0	0.0	24.5 (23.3)
Groß Labenzer See	230.4	34.9	10.2	200	0.064	3	5	33.3	0.0	0.0	66.6	11.7 (7.6)
Großer Wariner See	260.1	9.5	4.7	90	0.129	5	13	80.0	20.0	0.0	0.0	25.2 (27.6)
Inselsee	1507.1	28.9	7.3	240	0.020	7	14	85.7	0.0	0.0	14.3	18.4 (11.6)
Keezer See	122.5	17.9	8.1	146	0.079	3	6	100.0	0.0	0.0	0.0	10.0 (6.6)
Kritzower See	66.1	12.7	5.9	246	0.059	7	15	85.7	0.0	0.0	14.3	32.4 (14.2)
Kummerower See	3254.8	23.3	8.1	155	0.051	12	31	75.0	0.0	8.3	16.7	37.3 (16.6)
Malchiner See	1395.2	10.0	2.5	37	0.081	4	21	75.0	0.0	0.0	25.0	31.3 (13.1)
Müritz	10331.0	31.0	28.1	300	0.018	33	347	51.5	12.1	9.1	27.3	31.5 (15.1)
Neumühler See	171.5	17.1	7.9	362	0.020	4	5	75.0	25.0	0.0	0.0	15.0 (14.1)
Orthsee	52.2	1.8	5.4	130	0.120	4	42	75.0	0.0	0.0	25.0	19.3 (8.7)
Plauer See	3840.0	25.5	6.8	258	0.030	8	15	62.5	37.5	0.0	0.0	25.5 (11.9)
Schweriner See	6153.8	52.4	11.5	701	0.048	28	125	71.4	7.1	3.7	17.8	21.1 (16.0)
Teterower See	336.3	10.7	4.0	64	0.123	5	32	40.0	0.0	0.0	60.0	17.8 (9.4)
Tollensesee	1789.6	31.3	17.7	435	0.041	6	58	100.0	0.0	0.0	0.0	27.8 (17.5)
Torgelower See	351.0	6.9	3.3	163	0.097	6	71	83.3	0.0	16.6	0.0	26.5 (18.3)
Zahrener See	70.3	7.9	3.2	47	0.071	3	8	33.3	66.7	0.0	0.0	31.0 (28.5)
Ziegelsee	299.8	34.4	8.9	358	0.041	8	24	75.0	0.0	0.0	25.0	19.1 (20.4)
Zierker See	347.3	3.5	1.6	58	0.116	4	4	50.0	50.0	0.0	0.0	25.8 (15.7)

Assessing nutritional status of perch in the single-lake study

In Lake Speldrop, not only size of captured perch was estimated, but all perch were killed in line with German animal protection legislation and examined for nutritional status and sex. Perch were measured (total length TL, mm), weighed (g), intestines removed and preserved in ethanol (96%) for stomach content analysis, and the sex of each individual recorded. As the number of perch caught with artificial bait was too low to analyse a possible change of perch diet across season (in total n = 24 individuals, but only three and four, respectively, in August and September), stomach content analyses were restricted to perch caught with natural bait. In the laboratory, stomach content analysis of 17–58 individuals per sampling date (in total n = 167) was carried out by weighing (to the nearest 0.01 mg) the full and empty stomach. Stomach contents were identified to genus level, and the food spectrum of each perch was expressed as the percentage composition of food items by weight (see Borcherding *et al.* 2007). The index of stomach fullness (ISF) for each fish (caught with natural bait) was calculated to describe the wet weight of the prey as a percentage of the perch's wet weight including stomach and stomach content (Hyslop 1980). Fulton's condition factor (Bagenal & Tesch 1978) was computed to obtain a measurement of the physiological condition of perch (caught with natural bait) as $K = 10^5 \times M / TL^3$, where M is the wet weight (g) and TL the total length (mm).

Statistical analyses – multi-lake study

Boosted regression tree (BRT) analysis (De'ath 2007; Elith *et al.* 2008) was used to explain the variance in perch angling catches in the multi-lake study using broad limnological and angling-skill-related indicators. BRTs can simultaneously handle categorical and continuous data. Predictor variables do not need to be transformed, outliers need not be eliminated, and predictors can strongly correlate (Breiman *et al.* 1984; De'ath 2007). A Poisson error distribution was selected for perch CPUE and a Gaussian error distribution for L_{max}. Predictive performance of the BRT models was evaluated using 10-fold cross-validation following the study by Elith *et al.* (2008). Model predictions were compared to withhold proportions of the data by dividing the total data set into ten mutually exclusive subsets that were randomly selected during cross-validation process. Model selection was based on the optimal number of trees producing the lowest prediction error without model overfitting by testing learning rates from 0.05 to 0.001, tree complexities (tc) of 1–5 and using bag-fractions of 0.5 and 0.75. The learning rate determines the contribution of each tree when added to the model, and lower learning rates are generally recommended. According to Elith *et al.* (2008), the minimum number of trees for the selection of the final model with the smallest residual deviance was set to 1000. Interactions between the predictor variables were modelled using tc with no interactions being included, if tc was one, one-way interactions included, if the tc was two and so on. The bag-fraction determined the proportion of the data, which are selected at each step (50% or 75% here). This introduced stochasticity to the model and improved accuracy and reduced over-fitting (Friedman 2002).

Boosted regression tree analysis does not generate P-values, but the relative influence of each predictor to total variance explanation can be used to assess the importance of each predictor. The measure of relative influence is based on the frequency a predictor is selected for splitting the tree and it is related to its influence on model improvement. Partial dependence plots were used to visualise the functional effects of individual predictors in the model on the response variable CPUE and L_{max} after accounting for the average effects of all other predictors (Friedman 2002).

In addition, bait type used and zero-perch catches were tested for seasonal variation using multiple sample tests for equality of proportions with continuity correction to account for small sample sizes (see e.g. Newcombe 1998). The function prop.test in the R programming language was used. In case of significant differences, Bonferroni-corrected pair-wise comparisons were made.

To test whether perch catch rates were influenced by seasonal preferences among different angler types, that is, whether a certain angler type preferred a certain season, a generalised linear model (GLM, binomial distribution) was used with perch CPUE as the response variable and angler type and season as factors. Analyses were conducted using the R statistical software system version 2.8.0 (R Development Core Team 2009) including the gbm package (Ridgeway 2006) and the custom code provided by Elith *et al.* (2008) for BRT analysis.

Assessing perch catches – single-lake study

Similar to the multi-lake study, the distribution of bait type used in the single-lake study was tested for seasonal differences using chi-squared tests. The effect of bait type and season on CPUE in Lake Speldrop was graphically assessed because of low sample sizes (n June/July/August = 3, September = 2). The same was true for the influence of season and bait type on L_{max}. One-way ANOVA and pairwise Bonferroni tests were used to compare ISF of perch caught with natural bait across seasons. As Fulton's condition factor of perch caught is dependent on fish size (Froese 2006), ANCOVA with length as covariate and pairwise Bonferroni tests were used to test differences of condition of perch caught with natural bait across seasons. To understand whether the percentage of empty stomachs of perch caught with natural bait changed over the season, chi-squared tests were calculated. Chi-squared tests were also used to compare the percentage of females caught (with natural and artificial bait pooled) on each sampling date. Before calculating each ANOVA or ANCOVA, a Levene-test was computed to ensure homogeneity of variances ($P > 0.05$). Statistical analyses of Lake Speldrop data were conducted using SPSS, version 20 (SPSS IBM Corp., Armonk, New York, USA).

Results

Multi-lake study

In total, 8392 perch were reported caught during 878 fishing trips across the M-V lakes. Mean perch CPUE per angler ($n = 143$) averaged 2.4 [±2.5 standard deviation (SD)] fish h^{-1}. L_{max} of the largest perch harvested ($n = 119$ anglers) averaged 28.7 (±5.9 SD) cm with a maximum total length reported of an individual perch of 50 cm.

Final BRT models were run with learning rates of 0.005 (CPUE; $n = 2150$ trees) and 0.001 (L_{max}; $n = 2700$ trees). Interactions between the predictors were not included in the models (tc of 1) because they did not improve predictive performance substantially. Predictive performance was higher for the CPUE model (32.7%) compared with the L_{max} model (21.0%). The contribution of single predictors to variation in CPUE and L_{max} was highly variable and showed both linear and nonlinear patterns (Figs 1 & 2).

Highly influential variables on perch CPUE were angling-skill-related predictors (fishing experience, angler type) (Fig. 1). Furthermore, type of bait fished was important in affecting perch CPUE across the M-V lakes. In particular, fishing experience (years of fishing) had a large influence on angling success, with anglers having a long history of fishing (≥ 40 years) being the most successful. Furthermore, anglers who identified themeselves

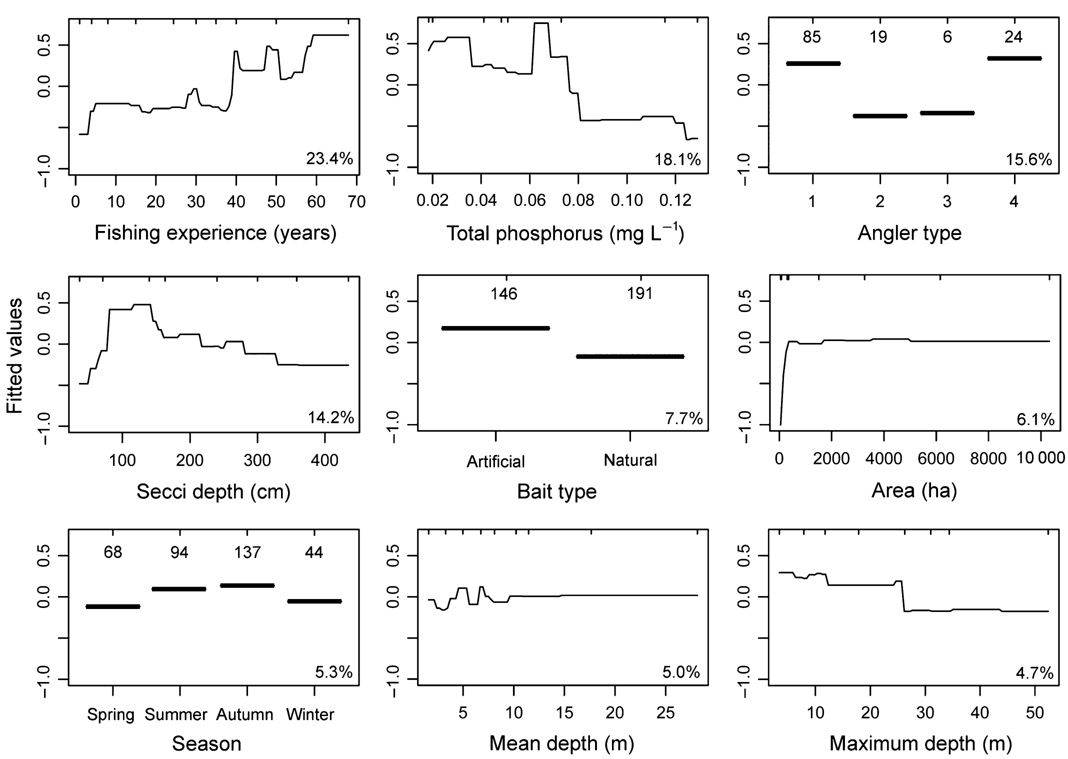

Figure 1. Partial effects of predictor variables on the angler catch per unit effort (CPUE, fish h^{-1}) of perch in lakes of Mecklenburg-Vorpommern (multi-lake study). Percentage values indicate the relative importance of the predictor variable in the boosted regression tree model. Rug plots on the top horizontal axes indicate the distribution of the predictor variables (*x*-axes), in deciles. In cases of categorical variables, sample size within each category is given on the top horizontal axes. Angler type: 1 = no preference; 2 = non-predatory fish; 3 = other (salmonids, marine species); 4 = predatory fish.

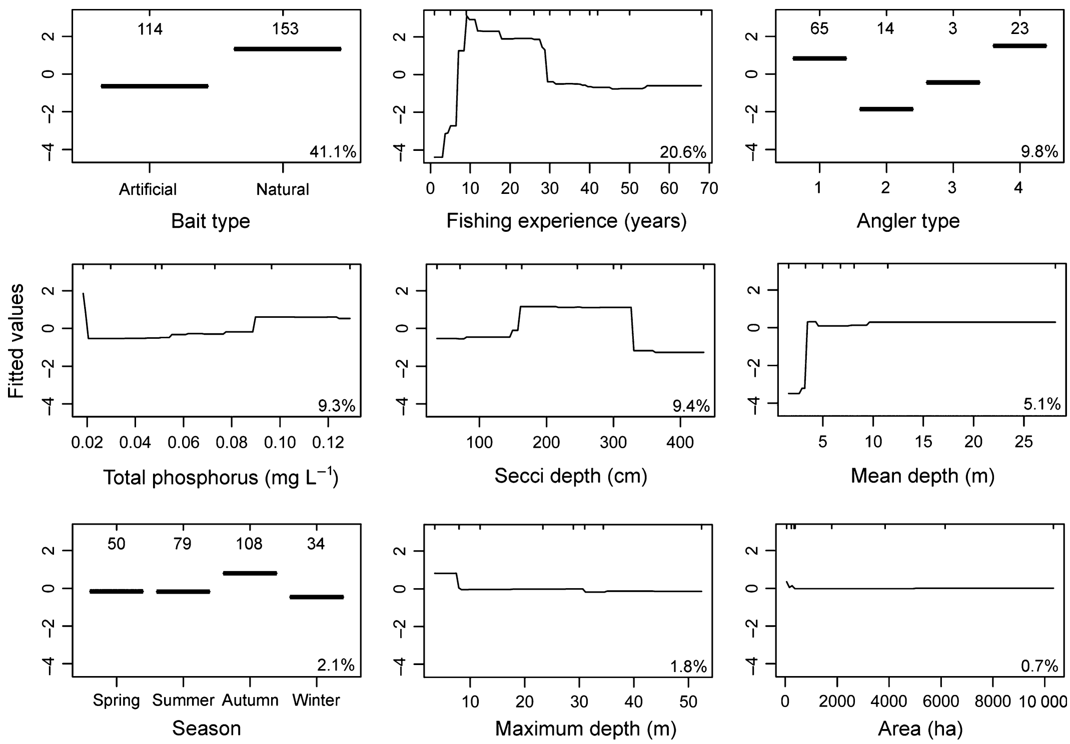

Figure 2. Partial effects of predictor variables on mean maximum length (L_{max}, cm) of perch caught by anglers in lakes of Mecklenburg-Vorpommern (multi-lake study). Percentage values indicate the relative importance of the predictor variable in the boosted regression tree model. Rug plots on the top horizontal axes indicate the distribution of the predictor variables (*x*-axes), in deciles. In cases of categorical variables, sample size within each category is given on the top horizontal axes. Angler type: 1 = no preference; 2 = non-predatory fish; 3 = other (salmonids, marine species); 4 = predatory fish.

as targeting predatory fish exhibited a higher perch CPUE, and in line with expectations, anglers identifying themselves as mainly targeting non-predatory fishes showed the lowest perch catch rates. However, anglers with no preference for a certain fish group had almost identical fishing success like anglers targeting predatory fish primarily. There was no seasonal preference of a certain angler type (GLM: interaction fishing type ~ season: $t = 0.35$, $P = 0.73$) indicating that the perch catch rates were not biased by different fishing intensities of the different angler types at certain seasons.

Anglers fishing with artificial lures caught more perch per hour of perch fishing than those engaged with natural bait (Fig. 1). In 56% of the fishing trips, anglers used natural baits with no significant seasonal change in the use of bait type ($\chi^2 = 1.5$, d.f. = 3, $P = 0.67$), suggesting that the results were not influenced by seasonal preferences of the anglers for a certain bait type.

Seasonal differences in perch CPUE were observed, with the highest perch catches observed during summer and autumn. However, the influcence of season on the total variation in perch CPUE was not strong. The proportion of zero catches differed significantly between the seasons ($\chi^2 = 10.5$, d.f. = 3, $P = 0.01$). A significantly higher ($P = 0.046$) proportion of trips with no perch caught was observed in spring (26.5%) than summer (15.2%). All other seasonal comparisons showed no significant differences ($P > 0.14$) in the proportion of zero-catch days (autumn: 17.1%; winter: 23.2%).

Predictors related to environmental conditions in lakes such as nutrient status (TP concentration) and water transparency also explained some of the variation in angler perch catches. Higher perch catch rates were obseved in oligotrophic and mesotrophic lakes (TP concentrations up to 75 μg L^{-1}) with water transparencies of 60–160 cm. Furthermore, perch CPUE was highest in lakes >400 ha, although the relative influence of lake area was weak (Fig. 2). Depth of the 21 lakes had no effect on the variation in angler's perch CPUE, but there were few shallow lakes with mean depth of <5 m in the data set (Table 1).

Bait type was the most influential predictor of size of perch landed in the BRT analysis (Fig. 2). Mean L_{max} of perch harvested by anglers using natural baits was higher than the anglers fishing with artificial lures. Furthermore, anglers with more than 8 years of fishing experience and those targeting predatory fishes or showing no preference for a certain fish group caught on average larger perch than anglers with less fishing experience or those targeting non-predatory fishes, salmonids or marine fishes. The largest perch were caught in the most oligotrophic lakes and in lakes with Secchi depths ranging between 160 and 320 cm. Predictors related to lake morphometry (area, depth) and timing of angling had only weak influence on the size of perch caught by anglers.

Single-lake study

Thirty hours of angling over 5 days (one per month) by 14 anglers was carried out on Lake Speldrop; 191 perch were landed, 167 caught with natural bait and 24 with artificial bait. Natural baits were used slightly more frequently than artificial baits (artificial/natural = 2:3), but there was no significant seasonal change in the use of bait type (χ^2-test: $P > 0.05$), suggesting that the results were not influenced by seasonal preferences of the anglers for a certain bait type. Most perch caught by standardised angling ranged between 12 and 25 cm in size, which corresponded to the age-1 and age-2 cohorts. However, in June and August, a few trophy individuals around 45 cm long were landed. The mean CPUE (fish fishing rod^{-1} h^{-1}) varied strongly over the season peaking in September with a fivefold increase compared with other months (Fig. 3, no statistical tests possible). There was a tendency for CPUE obtained with natural baits exceeding the CPUE values generated with artificial baits (Fig. 3).

L_{max} of the largest perch harvested in Lake Speldrop averaged 22.1 (±44.1 SD) cm with a maximum total length of 48 cm. As with the Mecklenburg-Vorpommern data, there was no trend across season or bait type (data not shown).

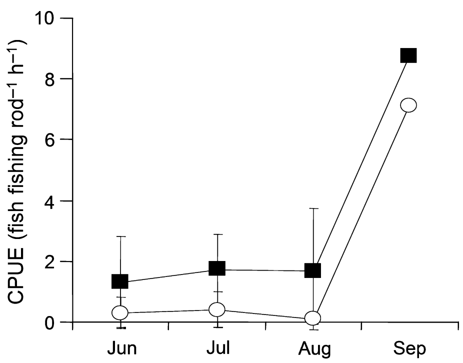

Figure 3. Angler catch per unit effort (CPUE, perch rod^{-1} h^{-1}) of perch caught with natural baits (black symbols) and artificial baits (white symbols) in Lake Speldrop (single-lake study) from June to September 2008. Error bars = standard deviation which was calculated if $n > 2$, n: June/July/August = 3, September = 2.

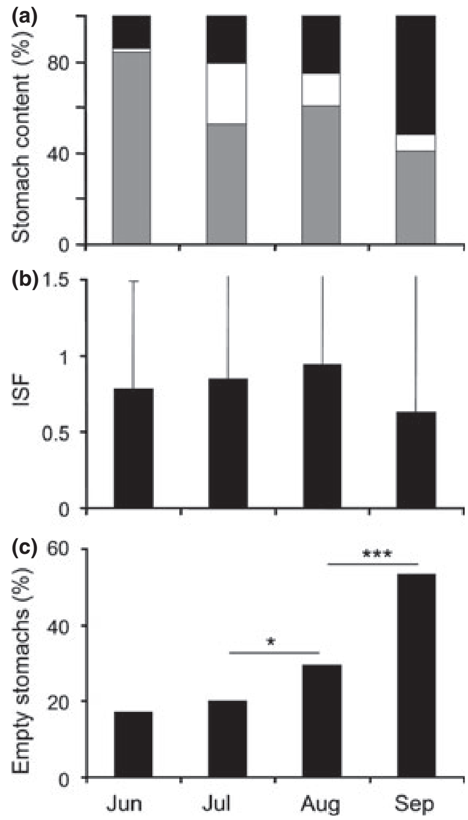

Figure 4. (a) Stomach content (%) of perch caught with natural baits in Lake Speldrop (single-lake study) from June to September 2008. Black bars = perch, white bars = macroinvertebrates, grey bars = zooplankton. (b) Index of stomach fullness (ISF) of perch caught with natural baits in Lake Speldrop (single-lake study) from June to September 2008. (c) Empty stomachs (%) of perch caught with natural baits in Lake Speldrop (single-lake study) from June to September 2008. Error bars = standard deviation, stars indicate level of significance of ANOVA (for ISF) or chi-squared tests (for empty stomachs): ***$P \leq 0.001$, *$P \leq 0.05$. n for all panels: June = 47, July = 45, August = 17, September = 58.

Stomach content analysis of perch captured with natural baits zooplankton was the predominant food consumed in early summer (June), (Fig. 4a), consisting mainly of *Daphnia* spp. and *Chaoborus* larvae. During the summer, piscivory increased, and perch cannibalised on their own young-of-the-year (YOY), and in September, about 50% of all food items consumed were YOY perch. Macroinvertebrates played a marginal role in the diet of perch. While there were no significant changes of the ISF over the season (ISF about 0.7 for all months; ANOVA: $F_{3,163} = 0.63$, $P = 0.94$) (Fig. 4b), the percentage of empty stomachs significantly increased from July onwards (χ^2-test: June/July $P > 0.05$, July/August $P < 0.05$, August/September $P < 0.001$), and in September, 50% of fish landed had empty stomachs (Fig. 4c).

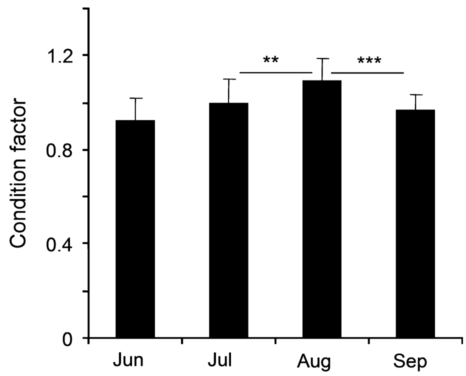

Figure 5. Condition factor of perch caught with natural baits in Lake Speldrop (single-lake study) from June to September 2008. Error bars = standard deviation, stars indicate level of significance of ANCOVA (length as covariate): $^{***}P \leq 0.001$, $^{**}P \leq 0.01$. *n*: June = 47, July = 45, August = 17, September = 58.

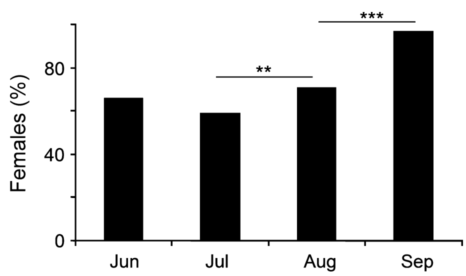

Figure 6. Proportion of females (%) of total catches of perch angled with natural baits in Lake Speldrop (single-lake study) from June to September 2008. Stars indicate level of significance of chi-squared tests: $^{***}P \leq 0.001$, $^{**}P \leq 0.01$. *n*: June = 47, July = 45, August = 17, September = 58.

The condition factor was the same in June and July (ANCOVA: $F_{3,235} = 34.4$, $P < 0.001$, Bonferroni tests: Jun/Jul $P = 0.32$) but increased from July to August (Fig. 5) (ANCOVA: $F_{3,235} = 34.4$, $P < 0.001$, Bonferroni tests: Jul/Aug $P < 0.01$). However, in September, the condition factor decreased (ANCOVA: $F_{3,235} = 34.4$, $P < 0.001$, Bonferroni tests: August/September $P < 0.001$).

In June and July, about 60% of perch caught were females (χ^2-test: June/July $P > 0.05$) (Fig. 6), increasing to 70% in August (χ^2-test: July/August $P = 0.01$) and almost all fish caught in September were females (97%, χ^2-test: August/September $P < 0.001$).

Discussion

Multi-lake study

This study found that perch catches by recreational angling are affected by angler-related factors, trophic lake characteristics and to lesser degree by lake morphometry and timing of angling. In the multi-lake study, angler-related attributes explained variance in catch rates, and to a lesser extent, size of perch harvested. Angling experience impacted both mean maximum length (L_{max}) of perch landed and catch rates of perch (CPUE). Both sharply increased after anglers passed a certain threshold of fishing experience (Figs 1 & 2). Only the very experienced anglers exhibited higher CPUE, while larger size of capture (L_{max}) occurred after only a few years of fishing experience. This, together with the lower predictive power of the length-based BRT model suggests that size of perch captured is less influenced by angler experience than CPUE, as found elsewhere (e.g. McConnell *et al.* 1995; Arlinghaus & Mehner 2003) and is interpreted as an increasing skill level positively affecting catch rates. It is, however, noteworthy that the peak size of perch captured occurred in younger age groups than the CPUE peak. This effect is possibly related to younger people using modern gear technology and fish finders to target trophy perch, while more experienced perch anglers seem to be better at achieving high catch rates because of their knowledge of the water body (cf. Eden & Bear 2011).

The self-rated target species preference (predatory or non-predatory fish) positively correlated with perch catch rates, with the highest CPUE achieved by anglers targeting predatory fish or anglers without any particular preference for a certain fish type. Both angler types are likely to be most committed (Wilde & Ditton 1994; Beardmore *et al.* 2011) and skilled in the capture of predatory fish such as perch, with the latter being more generic in their targeting behaviour, but also occasionally fishing for predators. By contrast, anglers identifying themselves as non-predatory fish anglers showed lower CPUE of the predatory fish perch. Similarly, the mean maximum length of perch harvested was highest for anglers targeting predatory fish or not targeting any specific species, which suggests greater skills in catching large perch.

Besides angler preferences for target species, bait type was another important variable affecting perch catch rates and size of fish caught, and similarly affected catch rates and size selectivity in other angling fisheries (e.g. Arlinghaus *et al.* 2008; Alós *et al.* 2009). Unfortunately, no data on bait size existed, so no effect of bait size on size of perch caught could be investigated. It is highly likely, however, that bait size will exert an effect on the size of perch captured (Wilde *et al.* 2003; Arlinghaus *et al.* 2008).

In angling in general, catching success is related to the motivation to ingest a bait, which can be connected to chemical components of the bait, its visual attractiveness and is moderated by bait size (reviewed in Løkkeborg & Bjordal 1992). Preferences of various fish species for certain types of lures were shown to be season specific, size specific and species specific but also dependent on the experience an individual gained concerning certain bait types (reviewed in Løkkeborg & Bjordal 1992; Stoner 2004). Moreover, catchability with certain baits types (e.g. artificial baits) might be strongly dependent on angling pressure and previous exposure of the lures to individual fish (Beukema 1970; Kuparinen *et al.* 2010). In the present study, catch rates of perch by artificial baits were higher than those by natural baits in the multi-lake study. However, although artificial bait was more successive in catching a high number of perch, the largest individuals were hooked with natural baits across M-V, as described earlier for pike (Arlinghaus *et al.* 2008).

Fishing success was also found to be dependent on the environmental variables characterising the fished lakes. Perch populations are known to be related to the lake's morphometry, nutrient status, vegetation coverage and turbidity, abundance being highest in deep, vegetation-rich lakes characterised by low nutrient concentrations and high water transparency (Persson *et al.* 1991; Jeppesen *et al.* 2000; Olin *et al.* 2002; Mehner *et al.* 2005; Radke & Gaupisch 2005). In line with this, trophic status and water clarity exhibited a strong effect on perch catch rates in the present study. In particular, oligo-mesotrophic with intermediate Secchi depth produced the greatest perch CPUE rates, likely reflecting larger underlying population sizes. The weak effect of water depth and area on perch CPUE was probably caused by little contrast in the data, as most lakes in the multi-lake study were relatively deep and large (Table 1).

Total phosphorus concentration and Secchi depth were also the environmental factors that significantly affected mean maximum size of perch caught by anglers in the multi-lake study. The overall lower explanatory power of the size model indicated greater degree of stochasticity in catching large fish compared with catching large numbers of perch. This agrees with Wilde and Pope (2004) who documented a very low probability of catching record size fish in recreational fisheries. In other words, anglers have less control over size of fish captured than number of fish. In the present study, the largest fish were caught in the most nutrient-poor lakes with higher water transparencies. Nutrient-poor lakes are generally inhabited by greater numbers of large-sized fish than nutrient rich lakes where perch densities and competition between individuals and species are often higher reducing the individual's growth potential and the ability of perch to grow to a size where they can become cannibals (Jeppesen *et al.* 1997, 2000; Claessen *et al.* 2000; Emmrich *et al.* 2011).

Single-lake study

Studies on fish species other than perch found temperature-influenced and season-influenced angling catch rates (e.g. Margenau *et al.* 2003; Damalas *et al.* 2007; Kuparinen *et al.* 2010). Results of the multi-lake study also showed an increased CPUE in summer and autumn, and drastically increasing CPUE for perch in September in the single-lake study where catch rates varied across the seasons. Seasonal changes of body composition (Craig 1977), metabolic rate (Karas 1990), allocation of energy to gonads (Treasurer & Holliday 1981), behaviour (Uusi-Heikkilä *et al.* 2008) and, in particular, shoaling behaviour (Vainikka *et al.* 2012 and references therein) may be the important factors affecting the variability of catches throughout the season intimately linked to food availability and possible starvation and hunger. While rising temperatures will increase metabolic demand, catchability of perch is expected to peak if moderate to warm water coincides with suitable environmental conditions (e.g. oxygen) and lack of natural food, which according to the single-lake study, was present in late summer and autumn.

Stomach content analysis showed perch consumed *Daphnia* and *Chaoborus* larvae in early summer, but shifted to a cannibalistic diet in late summer. This diet shift possibly illustrates the normal ontogenetic development, as perch are known to shift to piscivory while growing (Thorpe 1977), but also may reflect a decrease in *Daphnia* and *Chaoborus* larvae (Beeck *et al.* 2002), causing alteration in diet. Svanbäck and Bolnick (2007) showed that by decreasing preferred prey abundances, perch are forced to switch to alternative prey sources suggesting that perch in Lake Speldrop shifted to piscivory because of decreasing zooplankton biomass. By using alternative resources, perch were able to maintain the amount being consumed, which is illustrated by the ISF as a measure for relative fullness of stomachs that did not change across season. Contrasting to ISF, the percentage of empty stomachs of larger perch caught increased throughout the season with increasing consumption of fish prey (to 50% in September). This is most likely attributable to two factors. First, although piscivorous individuals benefit from the energy-richer resource, potentially leading to higher growth rates (Galarowicz & Wahl 2005; Borcherding *et al.* 2010), attack and capture efficiency of prey fish are reduced compared with zooplankton (Galarowicz & Wahl 2005). Second, piscivorous perch vulnerable to natural baits used by anglers usually face a diminishing number of prey fish (YOY perch) over the season because of natural mortality but also because of higher predation pressure by larger perch (Beeck *et al.* 2002). Hence, it appeared that satisfying the food demands became more difficult in late summer causing the shift to cannibalism. This food shortage existing in September in turn resulted in a drop in condition (see also Borcherding *et al.* 2007) likely elevating food demands, which in turn affected angling catch rates positively. Lack of food could then be the key explanation for higher catchability towards the end of summer in the present data.

Seasonal patterns in catch rates were accompanied by sex-biased exploitation patterns, which was most pronounced towards late summer. In June and July, about 60% of all perch landed were females. Although there are no data on the natural sex ratio for Lake Speldrop, previous studies showed that the ratio documented by angling in June and July in Lake Speldrop corresponded well to the natural sex ratio of other perch lakes (Jamet & Desmolles 1994; Rougeot *et al.* 2002). Surprisingly, perch caught in September were almost exclusively females (97%), suggesting that there were sex-specific reactions to food shortage in late summer (e.g. if females face greater energy intake they need to built up gonads) or the food shortage affected larger fish, which usually are females in perch, disproportionally. The sex-biased relative catchability might thus be explained by sex-dependent differences in growth (females grow up to 20% faster, Juell & Lekang 2001) and the elevated energy invested into gonads by females (Treasurer & Holliday 1981). This would result in higher energy demands by females, likely explaining the increased catch rates for female perch documented in the present study.

Conclusions

The results found that perch catch rates are strongly affected by angling-skill-related factors (fishing experience, angler type) and bait choice, but also reflected lake-specific limnological variables related to the trophic status of the lake (TP and Secchi depth). Because of the strong angler-type-related impacts on catch success the present results raise a cautionary note related to the use and interpretation of non-controlled angling diary data when used to infer population trends, as the reliability of the data will strongly depend on which angler type is reporting data. Another key finding related to seasonal patterns in perch catches is the female-biased exploitation coinciding with elevated hunger levels in late summer and autumn. Because (single-lake study) female perch were found to be particularly vulnerable to exploitation in periods other than winter time (see Vainikka *et al.* 2012 where no sex bias has been found in winter fishing for perch), autumn fishing activity in smaller water bodies could strongly bias sex-ratios and affect total fecundity, which in turn may affect recruitment, competition, predation control and subsequently population dynamics (Langangen *et al.* 2011). However, it has to be mentioned that further studies in multiple lakes should be conducted to clarify whether the patterns from the single-lake study are common across lakes.

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