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Behavioural and fitness consequences of direct and indirect non-lethal disturbances in a catch-and-release northern pike (*Esox lucius*) fishery

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ABSTRACT

Key-words: *angling, disturbance, fitness, telemetry, Esox lucius*

In a catch-and-release recreational fishery fish populations can be impacted by lethal and sub-lethal effects. In terms of sub-lethal effects anglers may directly (catch-and-release) and/or indirectly (angling-related disturbances, *e.g.* boating) influence the behaviour, growth and fitness of the fish. We quantified the long-term behavioural response of northern pike *Esox lucius* to angler-induced direct and indirect disturbances using radio-telemetry techniques. A whole lake experimental approach was conducted by dividing the study lake into an angling-disturbed and an angling-undisturbed lake side with 10 radio-tagged fish on each side, representing ~20% of the adult pike population. The impact of angling-caused disturbances on pike behaviour and growth as a proxy for fitness was assessed in a 7 month study period. Direct disturbances reduced swimming activities of pike and resulted in increased selection for structured (*i.e.*, safer) habitat, whereas indirect disturbances had no significant effect on pike behaviour. Growth rates of caught-and-released fish were significantly smaller than those of uncaught pike (44%). Because, fish that were not captured by angling during the study period showed similar growth rates on both sides of the lake, this indicated that only direct angler-induced disturbances influenced pike growth. Our findings call for minimization of angling-related stressors during the process of catch-and-release angling to avoid behavioural and fitness impairments of the released fish because these may ultimately have population-level effects.

RÉSUMÉ

Les conséquences des perturbations non-létales directes et indirectes sur le comportement et la fitness de brochets (*Esox lucius*) dans une pêcherie avec capture et relâcher

Mots-clés : *pêche, perturbation, fitness, télémétrie, Esox* lucius

Dans les pêcheries en capture-relâcher, les populations de poissons peuvent être impactées par des effets létaux et sub-létaux. En termes d'effets sub-létaux, les pêcheurs peuvent directement (capture-relâcher) et/ou indirectement (perturbations à lier à la pêche, la navigation, par exemple) influencer le comportement, la croissance et la forme du poisson. Nous avons quantifié la réponse à long terme du comportement du brochet *Esox Lucius* aux perturbations directes et indirectes induites par les pêcheurs en utilisant des techniques de radio-télémétrie. Une approche expérimentale globale du lac a été réalisée en divisant le lac étudié en un côté du lac perturbé par la pêche et un autre côté non perturbé avec 10 poissons

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radio-marqués de chaque côté, ce qui représente environ 20 % de la population des brochets adultes. L'impact des perturbations causées par la pêche sur le comportement des brochets et de leur croissance comme un proxy de la fitness a été évalué sur une période d'étude de 7 mois. Les perturbations directes réduisent les activités de déplacement du brochet et conduisent à la sélection accrue d'habitats structurés (*i.e.*, plus sûrs), alors que les perturbations indirectes n'ont aucun effet significatif sur le comportement des brochets. Les taux de croissance des poissons capturés-relâchés étaient significativement plus petits que ceux de brochets non capturés (d'un facteur 1,8). Toutefois, les poissons qui n'ont pas été capturés par la pêche pendant la période d'étude ont montré des taux de croissance similaires sur les deux côtés du lac indiquant que seules les perturbations directement induites par les pêcheurs influencent la croissance du brochet. Nos résultats incident à une réduction des facteurs de stress liés au processus de capture et relâcher pour éviter des déficiences comportementales et des baisses de forme des poissons relâchés parce qu'ils peuvent finalement avoir des effets au niveau de la population.

INTRODUCTION

Recreational angling constitutes the dominant use of freshwater fish stocks in all industrialized countries (Arlinghaus *et al.*, 2002). Across the entire industrialized world about 10.6% of the human population fishes for recreation (Arlinghaus and Cooke, 2009). Although recreational anglers often harvest their catch, voluntary and mandatory catch-and-release fishing is common (Arlinghaus *et al.*, 2007) involving about 60% of the fish that are captured (Cooke and Cowx, 2004). However, the behavioural and fitness consequences of this direct non-lethal interference of humans with fish in the wild are largely unknown (Cooke *et al.*, 2002; Arlinghaus *et al.*, 2007).

Catch-and-release mortality rates documented in the literature range widely between 0 and 89% (Muoneke and Childress, 1994) but are often fairly low if fish are captured from shallow depth (thus avoiding barotrauma) and are not substantially injured (Arlinghaus *et al.*, 2007, 2009; Wilde and Sawynok, 2009). Thus, catch-and-release is often not lethal for the individual fish. In any case, however, a non-lethal catch-and-release event inevitably constitutes a direct disturbance to the physiological homeostasis of the fish (Gustaveson *et al.*, 1991; Kieffer, 2000; Cooke *et al.*, 2002; Arlinghaus *et al.*, 2007, 2009). This, in turn, can affect the short-term behaviour post-release (Cooke *et al.*, 2000; Thompson *et al.*, 2008; Arlinghaus *et al.*, 2008a). Physiological responses of fish to catch-and-release are energetically costly (Meka and Margraf, 2007) potentially reducing the ability of fish to deal with basic ecological challenges such as foraging (Siepker *et al.*, 2006) and predator avoidance (Cooke and Philipp, 2004). They may also negatively affect the immune system (Pickering and Pottinger, 1989), growth (Siepker *et al.*, 2006), reproductive success (Ostrand *et al.*, 2004), and collectively reduce fitness post-release (Cooke *et al.*, 2002; Arlinghaus *et al.*, 2007; Siepker *et al.*, 2009). Whether direct disturbance of a fish through non-lethal catch-and-release angling over a long term period has behavioural and fitness consequences cumulatively affecting the population is currently not understood at the scale of field settings (Arlinghaus *et al.*, 2007).

Besides direct disturbance stimuli through catch-and-release angling, indirect disturbance effects of anglers on fish populations are also conceivable. It is known that terrestrial vertebrates and birds react physiologically and behaviourally to human-induced disturbances (Madsen and Fox, 1995; Beale and Monaghan, 2004). Similarly, anglers moving through an aquatic ecosystem (*e.g.* by boats) may signal their presence without catching or otherwise directly interfere with fish (Lewin *et al.*, 2006). It has been reported that anthropogenic sound elicits flight reactions and physiological stress responses in fish (Wysocki *et al.*, 2006; Graham and Cooke, 2008). The potential behavioural response to such indirect disturbance stimuli represents a trade-off decision between foraging activities and the avoidance of predation

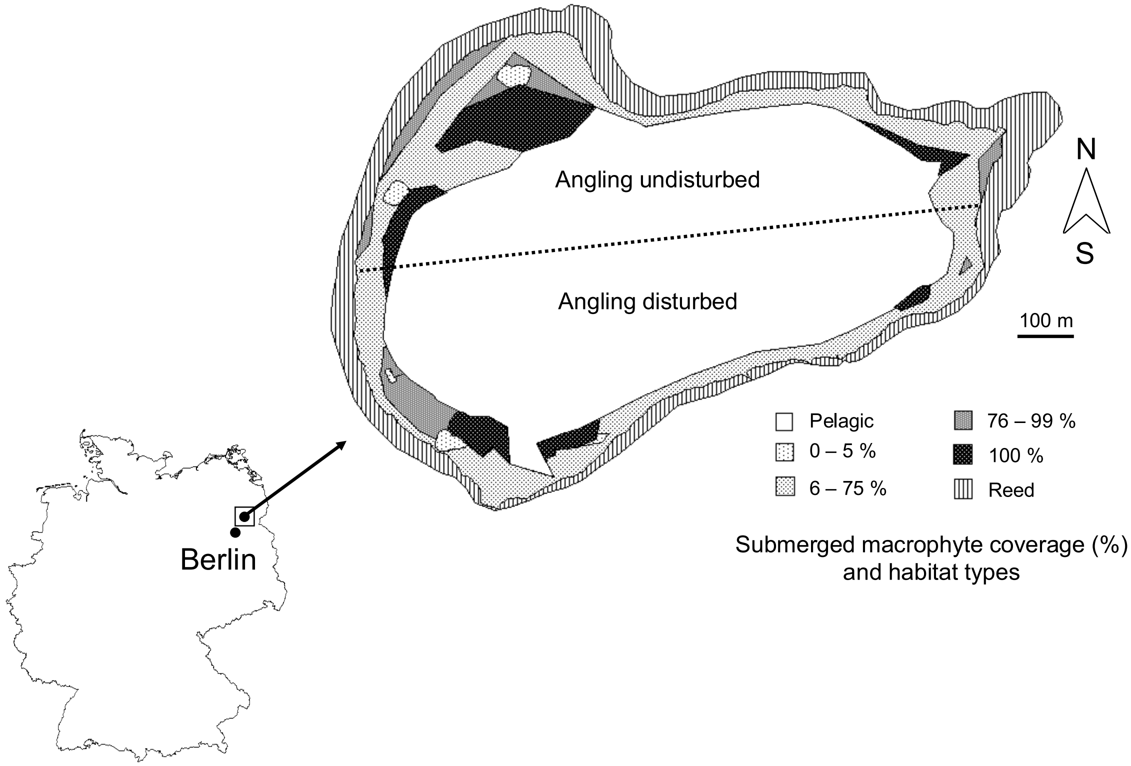

Figure 1
Map of Germany and Kleiner Döllnsee indicating the position of the angling-disturbed and angling-undisturbed side of the lake, the submerged macrophyte coverage (%) and other habitat types. Lake division was only visually not physically.

risk (Frid and Dill, 2002). This trade-off may result in altered habitat choice (Werner and Hall, 1988) and reduced swimming and feeding activities (Lima and Dill, 1990). Consequently, the behaviour and fitness of fish might be influenced through indirect angler-induced disturbance stimuli (hereafter called indirect disturbance), but no study exists testing for such indirect effects.

The objective of this study was to analyze the impact of direct and indirect disturbances from non-lethal recreational angling activities on the behaviour and growth of fish using northern pike (*Esox lucius*) as a model of an important target species for recreational fishing in North America and much of Europe (Paukert *et al.*, 2001; Arlinghaus and Mehner, 2004; Arlinghaus *et al.*, 2008a, 2008b). Using telemetry techniques we determined the extent of behavioural alterations in terms of habitat choice and swimming activity and how these alterations were reflected in growth rate depression as a correlate of fitness. We tested the hypotheses that (1) pike decrease their swimming activities; (2) alter their habitat choice; and (3) grow less when exposed to direct and indirect disturbance stimuli induced by recreational anglers.

MATERIAL AND METHODS

> STUDY SYSTEM

The study was conducted on the natural Kleiner Döllnsee, located 80 km northeast of Berlin (N 52° 59′ 32.1″, E 13° 34′ 46.5″) in the German lowlands (Figure 1). It is a 25 ha dimictic, shallow (mean depth 4.1 m, maximum depth 7.8 m) and slightly eutrophic lake (P concentration at spring overturn of 28 $\mu g \cdot L^{-1}$). The entire lake shoreline is surrounded by dense and wide (2–55 m) reed belts (*Phragmites communis, Typha latifolia*). In 2005, when our study took place, 14% of the lake was covered by emergent macrophytes, and 27% of the lake bottom was covered by submerged macrophytes (*Ceratophyllum demersum, Potamogeton crispus*, *Myriophyllum alterniflorum*, *Najas minor*) with varying degrees of cover and structural complexity depending on the season of the year (Figure 1). In 2005, the fish community comprised 12 different fish species (Kobler *et al.*, 2008a). Dominant top predators were northern pike and European perch (*Perca fluviatilis*). The lake has a natural, self-reproducing and unexploited pike population. No commercial or public recreational fishing was allowed on this private lake.

> EXPERIMENTAL DESIGN

To analyze the long-term impact of non-lethal recreational angling on the behaviour and fitness of pike, an *in situ* whole-lake experimental approach based on manual behavioural assessment of the fish by radio telemetry was chosen. Pike were randomly allocated to a treatment (*i.e.* fished) and a control (*i.e.* unfished) group ($N = 10$ each). To achieve a differential level of fishing intensity, Kleiner Döllnsee was divided into two similarly sized parts (fished and unfished; Figure 1). The division of the lake was not physical, but was indicated to experimental anglers by buoys and landmarks.

Similarity of both lake sides was assessed on the basis of the area, the habitat availability, the total length of radio-tagged pike (T_L) and the prey fish abundance and biomass. Prey fish abundance and biomass were estimated by monthly gill-netting (8, 12, 16 and 20 mm mesh size) in the littoral of both lake sides during two-hour surveys at both day and night between May and November, 2005. The mesh sizes used caught prey fish in a size range between 46 and 245 mm T_L, which is a size range preferentially and commonly consumed by adult pike $\geqslant$450 mm T_L (Raat, 1988; Kobler *et al.*, 2009). During each survey, three floating net fleets (each with all mesh sizes) were placed in the littoral zone of the disturbed and the undisturbed lake side (about 2 m deep) at the edge to the reed belts, each placed on the opposite sides of the lake along its greatest dimension. Species, total length (mm) and wet weight (WW, g) of catch were determined, and catch per unit effort (CPUE) calculated (number or g WW per m^2 gillnet and 2 h). Because diurnal differences in prey catch were low, averages from day- and night-time catches for prey fish abundances (NPUE, n fish per m^2 and 2 h) and biomasses (WPUE, g WW per m^2 and 2 h) were compared between both lake sides by repeated measures ANOVA.

> PIKE SAMPLING AND TAGGING

Twenty adult pike with a mean total length (T_L ± SD) of 577 ± 98 mm (range 450–755 mm) and an average weight ± SD of 1406 ± 779 g (range 580–2679 g) were caught by electrofishing (EFGI 4000, 4 kW Brettschneider Spezialelektronik, Chemnitz, Germany, 40 cm ring anode) between 21 April and 28 April, 2005 and radio-tagged on the same day of capture as described in Kobler *et al.* (2008a). SB-2 radio transmitters (Holohil Systems Ltd., Ontario, Canada; 20 × 9 mm, 5.2 g in air, 10 months battery life, 150.023 to 150.431 MHz) were used. The relative transmitter weight was $\leqslant$0.8% of pike's body mass, which has negligible influence on pike behaviour and growth post tagging (Jepsen and Aarestrup, 1999). An external sex determination was conducted following Casselman (1974), revealing that 18 out of the 20 pike were females. After tagging the recovered fish were released close to their individual capture point. Data collection started after a two week recovery period. Two fish died as a result of delayed hooking mortality after capture and release and another two fish died immediately after capture through lethal injury during the experimental angling period. One transmitter was found motionless in shallow water, and the fate of this fish remained unclear. Either this fish died without being captured or it simply lost its transmitter. The latter explanation was considered likely based on a missing carcass around the transmitter. These five transmitters were retrieved by diving and implanted into new fish, resulting in a total of 25 tagged individuals used for data analysis.

Besides those pike used for telemetry, every pike >250 mm T_L caught by electro-fishing surveys in spring and by angling (see below) during the experimental period was measured (nearest mm, T_L), weighed (nearest g), fin clipped and scale sampled. The scales (~10) were taken just above the lateral line and midway along the body length (Casselman, 1990). Fish captured on the northern lake side received a fin clip of the left pelvic fin and those on the southern lake side of the right pelvic fin. This procedure was also conducted during two additional electro-fishing events in September 2005. During all electro-fishing events, the entire shoreline was sampled by fishing the entire shoreline. Through analysis of mark-recapture data, abundance of pike was calculated using modified Schnabel abundance estimates (Ricker, 1975), revealing a spring population abundance estimate of 589 individual pike (95% CI: 498–706). The number of legal sized pike ($\geqslant 450$ mm T_L) in the beginning of the fishing season in spring was estimated as 91 (95% CI: 73–116). Thus, a substantial portion (17 to 27%, 95% confidence interval) of the adult pike population was radio-tagged. We assumed these fish were a representative sample of the pike population in Kleiner Döllnsee.

> *RADIO-TRACKING AND HABITAT MAPPING*

Radio tracking to assess pike behaviour and mortality was performed manually from boats powered by 12 V electric motors using a handheld receiver (SRX 400, Lotek, Ontario, Canada) and a three element Yagi antenna as described in detail in Kobler *et al.* (2008a). Once a fish was located, the position was taken by a GPS unit (etrex summit, Garmin, Olathe, KS, USA), corrected by a reference station (PFCBS Version 2.12, Trimble Navigation, Sunnyvale, CA, USA). Tracking error was ±6 m (Kobler *et al.*, 2008a). Each fish was tracked once a week for 24 h, with a 3 h interval between single locations. Hence, a total of eight positions per individual fish per tracking day were recorded, and these locations were used to determine a minimum displacement per day (MDPD) as an indicator of minimal swimming activity (Rogers and White, 2007). MDPD was defined as the sum of the straight line distances (m) between consecutive locations of the same fish, resulting in one value per fish per tracking day. If less than six positions of an individual were taken during a 24 h tracking session, the data for this individual on this tracking day were excluded. The first tracking day in each month was selected at random, afterwards each 7th day was chosen. Tracking took place from 18 May until 30 November, 2005.

A detailed map of the available habitats in Kleiner Döllnsee was created to relate positions of pike to the available habitats as described in detail in Kobler *et al.* (2008a). The following habitat categories were identified: emergent and submerged macrophytes, and a macrophyte-free pelagic area. Submerged macrophytes were divided into 4 categories (0–5%, 6–75%, 76–99% coverage of the lake bottom, and dense macrophyte beds with a coverage of 100%; Figure 1).

> *EXPERIMENTAL ANGLING*

Angling for pike took place on 101 days to induce a high level of angling-related direct and indirect disturbances. We simulated a total catch-and-release fishery from boats powered by 12 V electric motors. The gear used for fishing was intended to reflect common tackle used by pike anglers and is described in detail in Arlinghaus *et al.* (2008b). On the disturbed side, angling took place between 26 May and 31 August, 2005 and on both lake sides from 1 September to 28 October, 2005. During September and October, when both lake sides were fished, every part of the lake was fished simultaneously with the same fishing method and the same amount of rods. Experimental anglers rotated their fishing on the disturbed and undisturbed lake sides hourly to control for a potential angler skill effect.

Fishing took place unselective and selective for radio-tagged pike. During unselective fishing, tagged pike were captured by chance while fishing. For selective fishing, a fish was located and a bait was placed as close to the fish as possible. Selective fishing for radio tagged pike was done weekly by targeting every individual fish for 15 min. Selective fishing for previously undisturbed pike started at 1 September, 2005.

> GROWTH DETERMINATION

Measurement (T_L) of every captured pike and back-calculation of growth using scales were used to analyze the growth rate of pike within the experimental time and during the previous growing season during which the study lake was not fished by recreational angling. Magnification, digitalization and measurements of the scale annuli (anterior from the centre) were conducted with a vision measurement device (Quick Scope Manual, Mitutoyo, Japan). Three different readable scales were used to determine the age per fish. For growth back-calculation, the so called Fraser-Lee equation based on the scale-proportional hypothesis (reviewed in Francis, 1990) was used to back calculate the length of each fish at age *i*.

The main purpose of the growth rate analysis was to compare the growth of pike disturbed and undisturbed by angling. This was conducted in two ways. First, T_L measured after recapture of radio-tagged pike by angling in autumn was used to calculate relative growth rates (% d^{-1}) in the study year from the day of tagging in spring. Additionally, back-calculation of growth based on scale reading was used to compare the growth rate of radio-tagged pike the year before angling started, which represented a situation undisturbed from angling. Second, percent scale growth (the relationship between the scale growth of the current growth year to the scale radius from the centre to the last annuli before the experiment started) from every pike not captured by angling during the experimental time was used to assess individual growth rates of fish during the experimental period that only experienced indirect disturbances by anglers. These fish were captured by electro-fishing in September and percent scale growth was compared between pike from the disturbed and undisturbed lake side.

> STATISTICAL ANALYSIS

Hypothesis 1, *i.e.* the behavioural response of individual pike to angler induced long-term disturbance stimuli, was analyzed in terms of the movement activity metric MDPD (see above). Values for "minimum displacement per day" were transformed by the natural logarithm to reduce variances and to achieve normality of the data. A linear mixed model (including repeated measures of individual fish as a random effect) was used for analyses of MDPD in relation to direct and indirect angling-related disturbances and potentially confounding environmental variables. Environmental variables included as random effects were the mean daily water temperature (°C) continuously measured in 2 m water depth (YSI 6600, YSI Corporation, Ohio, USA), and a general weather factor consisting of the sum of mean daily values for wind speed ($m \cdot s^{-1}$), air pressure (hPa), daily sunshine duration (h) and amount of rain ($L \cdot m^{-2}$). To determine this, weather variable raw data were Z-transformed and included in a PCA to obtain a composite variable indicative of daily weather conditions. All 4 weather variables loaded on the same component (PCA loadings for wind speed, air pressure, daily sunshine duration, and amount of rain, 0.349, –0.343, –0.302, 0.324, respectively, together explaining 100% of the variance) and the resulting weather factor was not correlated with water temperature (Pearson‘s correlation coefficient = 0.092, P = 0.621). The mixed model consisted of predictor variables used as fixed effects that described direct and indirect disturbance stimuli as well as the T_L (LENGTH) of the pike. Direct disturbance stimuli were expressed through variables indicating short-term effects of a single capture event (Klefoth *et al.*, 2008) and long-term cumulative effects of multiple captures throughout the season (Barton *et al.*, 1986). Short-term effects were defined as a capture within the last tracking interval of one week (CAPTURED) and were based on the findings by Klefoth *et al.* (2008). Long-term effects were defined as the cumulative number of captures from the beginning of the study (RECAPTURES). Indirect disturbance stimuli were described by cumulative fishing intensities within the last three days prior to the tracking day (EFFORT). This time frame was chosen because preliminary models revealed the strongest effects on pike movement activity compared to all other possible time frames (tested from 1 to 7 days prior to the tracking day). The explanation rate of the model was calculated by comparison of predicted and estimated MDPD values using linear regression.

To test hypothesis 2, fish location maps were overlaid on a vegetation map in Arc View GIS 3.2 (ESRI, Redlands, CA, USA) (Kobler *et al.*, 2008a). With this method, the use and availability of the different habitat types was determined. To examine if fish used the available habitat in a non-random fashion, a log-likelihood test statistic was used following the procedures and analytic steps outlined by Manly *et al.* (1993). If selection for individual habitat was found, selection ratios and their associated Bonferroni-adjusted 95% confidence intervals (CI) were calculated to determine which types of habitat pike selected at the disturbed and the undisturbed lake sides. Positive selection was indicated with selection ratios (±95% CI) greater than one, while avoidance of a habitat was demonstrated with ratios less than one (Manly *et al.*, 1993).

To test hypothesis 3, the relative growth rate of radio tagged pike, a proxy for fitness of individual fish (Quattro and Vrijenhoek, 1989), based on actual length measurements (year of study) and in the previous year (back calculation), controlled for T_L at the start of the study, was compared between both lake sides. To disentangle the impact of direct and indirect disturbance on pike growth, scale growth of fish not captured by angling during the study period was also compared between both lake sides using ANCOVA with fish length in spring as the covariate to control for different T_L at the onset of the study.

To estimate total mortality $M_{(T)}$ in our catch-and-release fishery, immediate and delayed hooking mortalities of the radio-tagged fish, corrected by mortalities of all uncaught radio-tagged individuals serving as controls were used for calculation as recommended by Wilde *et al.* (2003). It was assumed that angling for radio-tagged pike resulted in similar mortalities as for the whole population exposed to similar fishing intensities. Total mortality during the whole study period was estimated as

$$\hat{M}_{(T)} = M_{I(T)} + \left[\left(\frac{n_{L(T)}}{N_{(T)}}\right) \times \hat{M}_{D(T)}\right],$$

where $M_{I(T)}$ is initial mortality of all captured fish (*i.e.*, dead within minutes after capture), $M_{D(T)}$ is delayed mortality of the fish captured by angling (i.e, death occurring some days or weeks after release), $n_{L(T)}$ is the number of fish successfully released after capture and $N_{(T)}$ is the total number of captures. The sampling variance for total mortality, Var($M_{(T)}$) was estimated as

$$\hat{Var}(M_{(T)}) = \left(\frac{n_{L(T)}}{N_{(T)}}\right)^2 \times \hat{Var}(M_{D(T)}),$$

where $\hat{\text{Var}}(M_{D(T)})$ is the sampling variance for delayed mortality (Wilde *et al.*, 2003). The standard error of $M_{(T)}$ was estimated as the square root of $\hat{\text{Var}}(M_{(T)})$ (Wilde *et al.*, 2003).

All statistical analyses were conducted with the SPSS software package version 14.0 (SPSS Inc., Chicago, IL, USA), at a type 1-error probability of $\alpha = 0.05$. The only exceptions were the analyses of selection ratios, which were calculated using Fishtel 1.4 (Rogers, 2002). Data are presented as means ±1 SD, unless otherwise noted.

RESULTS

> LAKE-SIDE SIMILARITY

Both lake sides were almost identical in size (Table I). However, there was a trend towards slightly more structured habitat on the angling-undisturbed lake side (Table I). No significant

Table I
Comparison of the angling-disturbed and angling-undisturbed lake sides of Kleiner Döllnsee. The disturbed and undisturbed sides were compared in terms of lake morphology, prey fish abundance and the total length of the radio-tagged fish. Variances are indicated as ±1 SD. mc = submerged macrophyte coverage of the lake bottom.

Characteristics	Disturbed	Undisturbed
Lake morphology		
Total area (ha)	12.6	12.4
0–5% mc (ha)	0.1	0.1
6–75% mc (ha)	2.0	2.4
76–99% mc (ha)	0.3	0.5
100% (ha)	0.4	1.0
Reed (ha)	1.3	2.3
Pelagic (ha)	8.5	6.1
Prey fish NPUE (*n* fish per m^2 and 2 h) littoral	0.30 ± 0.24	0.32 ± 0.33
Pike total length (mm)	565 ± 87	603 ± 112

differences were found in T_L of the pike from the disturbed and undisturbed sides (mean $T_L \pm$ SD of disturbed pike 565 ± 87 mm and undisturbed pike 603 ± 112 mm; T-Test, $T = 1.17$, DF = 18, $P = 0.257$).

Comparison of prey fish availability revealed no significant differences in the number and biomass per unit effort between the littoral of the disturbed side and the littoral of the undisturbed side (NPUE, rmANOVA, $DF_{Numerator} = 2$, $DF_{Denominator} = 21.5$, $F = 0.341$, $P = 0.565$; WPUE, rmANOVA, $DF_{Numerator} = 2$, $DF_{Denominator} = 5.5$, $F = 3.026$, $P = 0.137$; Table I).

> DESCRIPTIVE DATA ON ANGLER DISTURBANCE INTENSITY

From May to October, 2005, a total of 248 pike were caught, of which 139 were first captures and 109 recaptures. Radio-tagged pike were captured 27 times, *i.e.* there were 27 individual capture events. Seven pike were never caught, eleven individuals were caught once, five individuals twice and two individuals three times. Total catch-and-release mortality was estimated as 12.5 ± 9.1% (CI). With a 95% probability of confidence, 47–74% of the adult pike population ($T_L \geqslant 450$ mm) were caught by angling during the study period. The total recapture rate as an indicator of direct disturbances caused by angling was 44% of the adult pike population. On the disturbed side, the total fishing effort from May to August summed to 1968 h corresponding to 156 $h \cdot ha^{-1}$. In September and October, 2005, both lake sides were fished for 143 h each (12.9 $h \cdot ha^{-1}$). The average catch per unit effort (CPUE) over the whole study period was 0.18 ± 0.02 $pike \cdot h^{-1}$.

> IMPACT OF ANGLING-DISTURBANCES ON SWIMMING ACTIVITY (HYPOTHESIS 1)

Hypothesis 1 was partly supported by the mixed model predicting movement activity of pike. Fixed predictor variables representing measures of direct disturbances negatively affected movement rates of pike where the impact of the number of recaptures (RECAPTURES) was significant ($P = 0.002$) and a capture event within the last 7 days prior to the tracking day (captured) also negatively, though not statistically significant affected movement of pike ($P = 0.056$; Table II). Indirect disturbance stimuli caused by anglers as represented by the cumulative daily fishing effort three days prior to the tracking event (effort) had no significant affect on pike movement (Table II). In addition T_L (length) of the pike significantly influenced swimming activity with larger pike being more active (Table II). Swimming activity of radio-tagged pike in Kleiner Döllnsee was positively related to water temperature (°C) and the weather factor. Higher values of the weather factor correlated with increasing wind speeds,

Table II

Linear mixed model to explain long-term swimming activities of radio-tagged pike in Kleiner Döllnsee based on direct (captured, recaptures) and indirect (effort) disturbance stimuli over a seven month period. In addition, total length (length) of the fish was added as fixed effect due to small differences in size of the fish. The model contained the random effects water temperature (°C) and a combined weather factor consisting of the sum of z-scores of mean daily values for wind speed ($m \cdot s^{-1}$), air pressure ($h \cdot Pa$), daily sunshine duration (h) and amount of rain ($L \cdot m^{-2}$).

Fixed effects	Random effects	DF	*F*	Estimate	*P*	R^2
						0.45
Captured		1; 203.3	3.683	–0.296	0.056	
Recaptures		4; 286.1	4.462	–0.560	**0.002**	
Effort		1; 280.7	1.871	–0.001	0.172	
Length		1; 81.6	5.992	0.022	**0.017**	
	Water temp			0.001		
	Weather			0.013		

lower air pressure, reduced sunshine duration and increasing amounts of rain, *i.e.* increasingly "unpleasant" conditions from a human perspective. The overall explanatory power of the model explaining swimming activity of pike was 44.7%. Thus, angling-related direct disturbances induced by anglers negatively affected the swimming activity of pike over a seven month period in Kleiner Döllnsee, whereas indirect disturbances had no significant impact on movement of pike.

> INFLUENCE OF ANGLING-DISTURBANCES ON HABITAT CHOICE (HYPOTHESIS 2)

Hypothesis 2 received some support in our study. Selection ratios and their associated Bonferroni-adjusted 95% CI revealed that reed was selected by both disturbed and undisturbed pike over the study period, whereas macrophyte beds were positively selected by undisturbed pike only. Both groups avoided the pelagic and habitats with submerged macrophyte coverage of 0–5% (Figure 2a).

Impacts of angler-induced disturbance on habitat choice became apparent when inspecting seasonal dynamics of habitat choice. Pike from the disturbed and undisturbed side selected reed covered areas in May when fishing intensity was low. With increasing fishing intensity on the southern part of the lake, disturbed pike positively selected for reed in June, July and somewhat less pronounced also in August (Figure 2b). When both lake sides were fished simultaneously in September, also the undisturbed pike positively selected for reed, whereas reed selection of pike from the disturbed lake side was not significant anymore, suggesting a behavioural reaction to the reduced fishing intensity by selecting for less structurally rich habitat. Throughout October and November, fish from both lake sides behaved similarly in their selection for reed, corresponding with comparable disturbance intensities on both lake sides (Figure 2b).

> INFLUENCE OF ANGLING-DISTURBANCES ON GROWTH (HYPOTHESIS 3)

In terms of impact of angling-related direct and indirect disturbances on growth, 14 individual pike were recaptured by angling or electro-fishing in autumn (8 directly disturbed and 6 undisturbed pike). The time period between transmitter implantation and the last recapture event where the fish were measured was 128 ± 29 days for disturbed and 135 ± 45 days for undisturbed pike, and these differences were not significant (*T*-Test, $T = 0.386$, DF = 13, $P = 0.706$). The T_L of recaptured fish at the time of tagging did not differ between disturbed and undisturbed fish (537 ± 66 mm and 593 ± 95 mm, respectively; *T*-Test, $T = 1.290$, DF = 12, $P = 0.221$). Mean total growth of directly disturbed and undisturbed pike was 10.8 ± 10.5 and

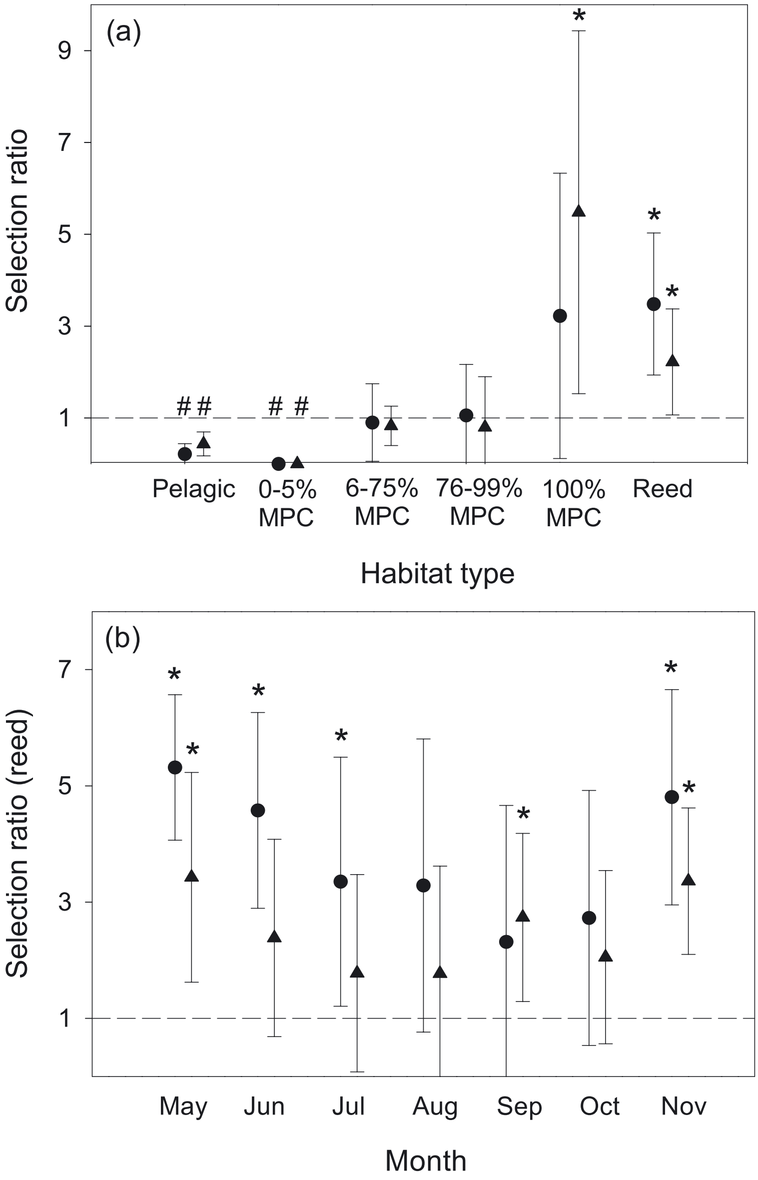

Figure 2

*Selection ratios and their associated Bonferroni adjusted 95% CI to show selection for (greater than one) or against (less than one) a given habitat type. (a) indicates selection of different habitat types by disturbed (circle) and undisturbed (triangle) pike in Kleiner Döllnsee during the whole study period; (b) indicates selection of reed for disturbed (circle) and undisturbed (triangle) pike from May to November. MPC macrophyte coverage; * positive selection; # negative selection of a given habitat type.*

19.3 ± 13.8 mm, respectively. Thus, on average, growth of undisturbed pike was higher by factor 1.8 than that of disturbed pike. Relative growth rates based on measured body length (% d^{-1}) of radio-tagged pike controlled for body length at the onset of the study were significantly smaller for captured pike on the disturbed lake side compared to undisturbed fish (ANCOVA, $F = 5.081$, DF = 1, $P = 0.048$; Figure 3). Comparisons of back-calculated growth rates in the previous unexploited year, using the same fish (except one individual with unreadable scales), revealed no difference between disturbed and undisturbed fish (ANCOVA, $F = 1.908$, DF = 1, $P = 0.172$; Figure 3).

In total 64 fish uncaught by angling during the study period were caught by electro-fishing in autumn (26 pike from the disturbed and 38 pike from the undisturbed side, mean T_L 328 ± 84 mm and 372 ± 116 mm, respectively). Scale growth during the experimental time

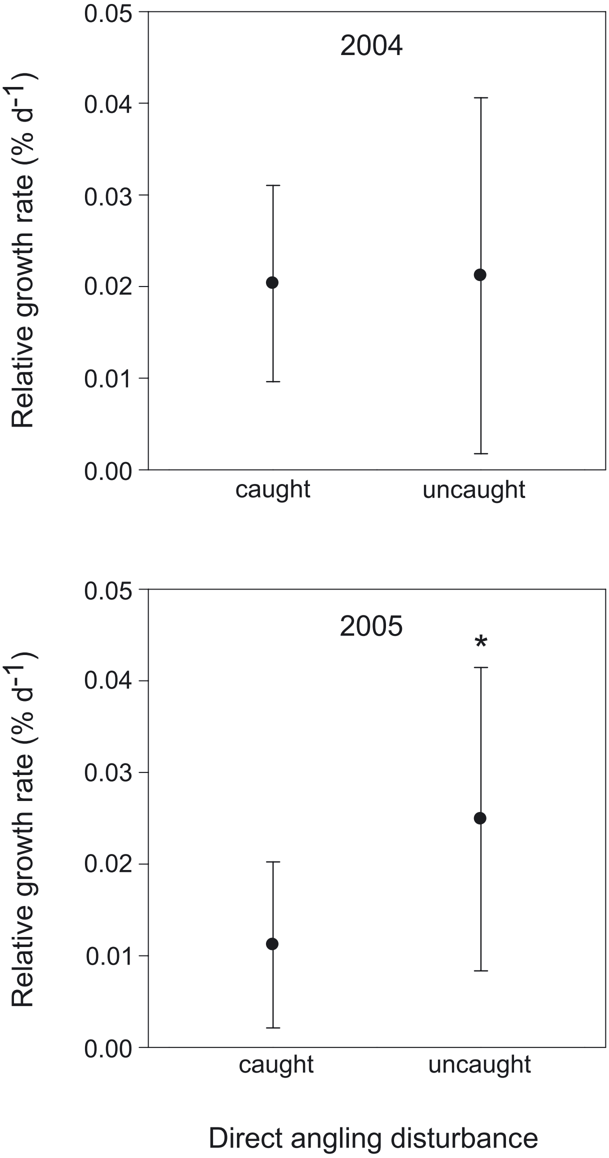

Figure 3
*Relative growth rate (% d^{-1}) of directly disturbed (caught; N = 7) and undisturbed (uncaught; N = 6) radio-tagged pike in Kleiner Döllnsee the year before the experiment started (2004) and after intensive catch-and-release angling (2005; N = 8 and N = 6, respectively). Calculated growth rates were corrected for individual fish length using ANCOVA. * indicates significant differences.*

since annulus formation in early spring did not differ between fish from the disturbed and undisturbed lake side (ANCOVA, $F = 0.996$, DF = 1, $P = 0.322$; Figure 4). Thus, indirect disturbances alone did not influence the growth rate of the pike in Kleiner Döllnsee.

DISCUSSION

We found support for all three hypotheses tested in a whole-lake experimental approach on the long-term impact of angling-related direct and indirect non-lethal disturbances on pike. Consistent with our hypotheses, we found that angling-related disturbances affected swimming activity, habitat choice and growth of pike. In terms of swimming activity, reductions were exclusively related to direct capture events whereas no significant effect was found for

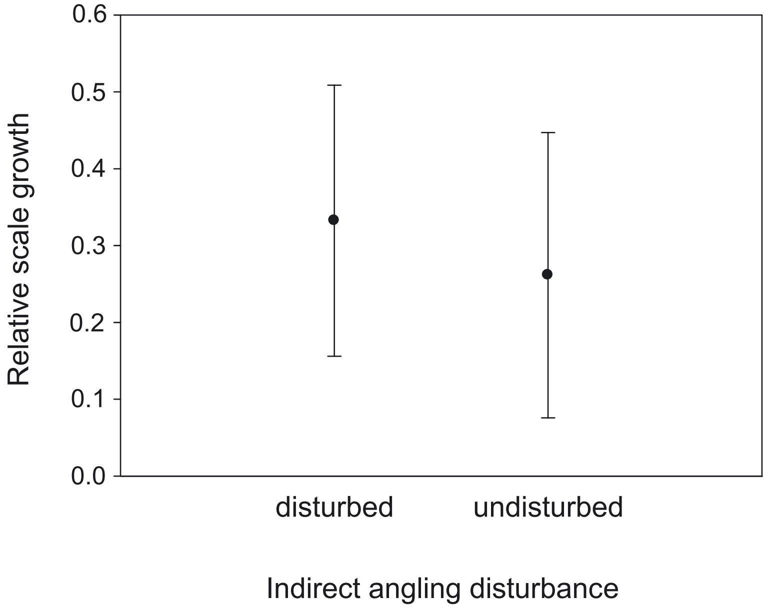

Figure 4
Relative scale growth (the relationship between the scale growth of the current growth year to the scale radius from the centre to the last annuli before the experiment started) of undisturbed (N = 38*) and only indirectly disturbed (N =* 26*) pike in Kleiner Döllnsee during the experimental period. Calculated growth rates were corrected for individual fish length using ANCOVA.*

indirect disturbance stimuli represented by cumulative angling efforts three days before the actual tracking event. In general, swimming activity of pike was found to be related to environmental variables, total length of the fish and two factors indicative of direct disturbance stimuli. While it is well-known that pike activity is positively related to water temperature and body length of fish (Kobler *et al.*, 2008a), the significant negative long-term impact of direct disturbances on movement activity of pike extends the preliminary finding by Klefoth *et al.* (2008) who found that pike reduced swimming activity to a single catch-and-release event but resumed normal swimming patterns within a week post-release. However, Klefoth *et al.* (2008) only analysed the behaviour of pike within a confined time frame (*i.e.*, two weeks) by comparing movement prior to, and directly after a catch-and-release event. In their study, individual pike served as their own "controls" and there was no attempt to control for confounding variables such as abiotic conditions, levels of angling effort or total length of fish. Most importantly, the work by Klefoth *et al.* (2008) did not answer the question on the relative importance of multiple capture events and the impact of indirect angling-caused disturbances through boating and trolling on the behaviour and growth of a pike population. Our study clearly indicates that pike in a natural water body reduce swimming and grow less after direct disturbance and we also showed negligible effects of indirect disturbance resulting for instance from boating or other angling-related underwater noise on behaviour and growth of the fish.

We found that a pike's swimming activity was reduced after capture and was particularly affected by multiple recaptures indicative of the cumulative nature of direct stressors. In the catch-and-release angling literature, sub-lethal behavioural effects after release have been previously reported (Donaldson *et al.*, 2008) but these effects were often generated in experimental settings in the laboratory or ponds in response to angling-related challenges such as air exposure and exhaustive exercise (Cooke *et al.*, 2000; White *et al.*, 2008). Specific for pike, Klefoth *et al.* (2008) reported reduced swimming activity in the short-term in response to a single catch-and-release event but resumption of normal behavioural patterns occurred within a week post-release. In the present study we verified this preliminary finding using an extended data set and multivariate analyses, and we observed reduced swimming activities of disturbed pike in the long-term over the whole fishing season. Such finding was impossible to be revealed by Klefoth *et al.* (2008) because these authors confined their analysis to three tracking points in terms of movement expressed by pike. Interestingly, pike are known to quickly recover physiologically from catch-and-release related stressors and recovery seems to be completed within a couple of hours (Schwalme and Mackay, 1985; Arlinghaus *et al.*, 2009). Therefore, the long-term decrease in swimming activity in response to non-lethal angling in the present study seems not only to be related to physiological disturbance but might also be resulting from evolved anti-predatory behavioural responses (Klefoth *et al.*, 2008). Swimming activity is known to be positively related to mortality risk, representing an important and general trade-off faced by animals (Werner, 1992). Reduced activity of pike following continuous direct disturbances by non-lethal catch-and-release angling might constitute a context-independent consistent behavioural response to stimuli perceived negatively by the fish, a phenomenon known as behavioural syndromes (Sih *et al.*, 2004). In general, animals under predation risk were observed to not only reduce their spontaneous activity levels, but in some cases reductions in activity resulted from increased use of refuges (Lima and Dill, 1990). In the present study similar patterns are likely as we found an increased use of reed habitat in response to non-lethal angling, which in turn might translate into a decreased propensity to move.

Activity of the pike in our study also slightly decreased with increasing fishing intensity, but the effect of indirect disturbances was low and not significant. Cumulative fishing intensity can be interpreted as a metric for angler-induced disturbances because all activities carried out by anglers (*i.e.*, boating, spin-fishing, shoreline access) are potential disturbance stimuli for the fish (Lewin *et al.*, 2006). Beukema (1970) found that pike altered foraging behaviour after exposure to artificial lures irrespective of previous capture suggesting learning without direct negative experiences. We, for the first time analysed pike behaviour in the wild in response to indirect non-lethal disturbances originating from angling activities. We assumed that anthropogenic noise (*i.e.*, shipping/boating) would evoke a physiological stress response in fish, as it was found in other species in response to commercial shipping noise (Smith *et al.*, 2004; Wysocki *et al.*, 2006; Graham and Cooke, 2008). Besides an endocrinological stress response like increasing cortisol levels after exposure to noise, behavioural reactions like fleeing and active avoidance of vessels have been reported (Vabø *et al.*, 2002; Mitson and Knudsen, 2003). These findings were not supported by our observations in a catch-and-release context. In a recreational fishing context indirect disturbance stimuli caused by anglers presumably cause lower ecological responses compared to direct stressors. This assumption is supported by the very low and insignificant pronounced behavioural reactions of pike to cumulative fishing effort relative to direct capture and recapture in the present study, and the similar growth rates exhibited by uncaptured and undisturbed fish and fish uncaptured but exposed to fishing pressure in our study.

Consistent with hypothesis 2 of our study, we found increased selection for reed by pike disturbed directly and indirectly by angling. The preferred use of reed under angler-exploited conditions might be related to the circumstance that angling was not possible within the dense reed stands. Thus, reed likely provided the highest amount of refuge in our study lake. The choice of safe habitat, independent of food supply, is an often-observed outcome of predator prey interactions in animals, including fish (Hugie and Dill, 1994). Results of the present study support the hypothesis that habitat choice of pike is affected by angling-induced disturbances but we were unable to distinguish the impact of direct and indirect disturbances on habitat choice of pike. Our study results nevertheless suggest that anglers and angling-related non-lethal disturbances are perceived by pike analogously to the way a prey fish perceives its piscine predator eliciting a behavioural response to seek more refuge (Frid and Dill, 2002).

As intriguing as they are, behavioural alterations as an adaptive response to human-induced disturbance are of most interest to biologists and fisheries managers if they affect mortality and reproductive success and therefore the fitness of the animals, and/or population size and dynamics (Gill *et al.*, 2001). The catch-and-release mortality rates of 12.5 ± 9.1% we observed were in agreement with other research on hooking mortality in pike (reviewed by Arlinghaus *et al.*, 2008b) and are of ecological relevance because they reduce the fitness of a fraction of the pike population to zero. In addition, we used growth rate as a surrogate for the fitness of pike. Indeed, absolute fecundity (Wright and Shoesmith, 1988; Edeline *et al.*, 2007) and relative reproductive success (Pagel *et al.*, unpublished data) scale positively with body size in pike such that reduced body size in response to angling-induced disturbances may affect reproductive output of pike. While absolute differences in growth between directly disturbed and undisturbed pike were less than 10 mm, relative differences in growth between the two groups of fish were comparably high (factor 1.8) and undisturbed pike grew significantly more than directly disturbed pike. Growth rates of pike in Kleiner Döllnsee can be considered to be generally low (Pagel *et al.*, unpublished data), but even small differences in growth can have severe impacts on fecundity (Edeline *et al.*, 2010). Based on a combined experimental and modelling approach, Edeline *et al.* (2010) found that small differences in pike growth (23% between two groups of fish) as a consequence of stress can cause a 37–56% decrease in vital rates of the fish. Thus, Edeline *et al.* (2010) concluded that small differences in growth, comparable to those found in our study, can have pervasive impacts on pike populations and that stress can be a primary driver of pike population dynamics. In our study, the level of stress caused by direct and indirect disturbance stimuli was not measured, but elevated indicators of physiological stress as a response to catch-and-release angling are well known in pike (Arlinghaus *et al.*, 2009). All together, growth differences within the observed magnitude between directly disturbed and undisturbed pike found in our study can be considered potentially relevant for dynamics of pike populations.

There are likely two major reasons for the decreased growth of pike in response to direct angling-related disturbances in our study. First, energy loss during the catch-and-release event might have led to a growth depression (Meka and Margraf, 2007). Second, we found that pike reduced their swimming activity and altered their habitat choice within their home range (*cf.* Kobler *et al.*, 2008b) in response to angling-related disturbances. Higher activity levels and habitat choice outside or at the edge to refuges would have increased the encounter probability of angling lures and the risk of being captured. In turn, the increased use of reed and reduced activity levels likely reduced prey intake and thus pike growth. Indeed, we found that angling effort levels two days prior to an angling event significantly reduced catch rates, which is indicative of altered foraging behaviour of pike (Kuparinen *et al.*, 2010). Unfortunately, due to the study design we are unable to provide unequivocal evidence about which of the two above-mentioned processes had affected growth rate depression in pike in our investigation, but we suspect both to play a role.

Our study design has the limitation that no full factorial design (control lake side, fishing-effort only, catch-and-release only, fishing effort and catch-and-release combined) was possible so we were unable to unambiguously disentangle the importance of direct and indirect disturbances on the behaviour and growth of pike. However, within the limits set by any whole-lake experimental approach our results were consistent with our initial hypotheses and withstood rigorous statistical analysis by accounting for potentially confounding environmental variables. The validity of our study findings depend on the assumption that the undisturbed lake side served as an appropriate control for the disturbed lake side. Even though in natural habitat a perfect control side never exists, only minor qualitative differences in the habitat features and prey abundance between the disturbed and undisturbed lake side were found (Table I). Additionally, substantial inter-side exchange of the pike was not recorded in Kleiner Döllnsee (Kobler *et al.*, 2008b) as only 378 of 4553 locations during the study period were recorded of pike residing on the opponent lake side, and all of these locations were only short-term for a couple of hours. We therefore are confident that the main differences between the two lake sides were angling activities rendering our experimental design useful with robust results. It would be advisable to replicate our approach across multiple lakes, with each lake serving as one treatment in a full factorial design. This approach, however, would demand substantial investment in stationary telemetry equipment because manual tracking of the intensity conducted in the present study would be fairly difficult to realize simultaneously across many lakes. Moreover, reliability of experimental anglers is an issue to be overcome if multiple lakes are included in one study simultaneously.

An important consideration for the generality of our findings is that we induced realistic angling patterns, for example concerning indirect (total fishing effort) and direct (capture rates) disturbance stimuli. The annual fishing effort in Kleiner Döllnsee was 167.5 $h \cdot ha^{-1}$. This is within a common range of pike fishing intensities (Kempinger and Carline, 1978; Pierce *et al.*, 1995). Moreover, the mean CPUE across fishing days in the present study was 0.18 $pike \cdot h^{-1}$, which is within common CPUE values reported for pike fisheries usually ranging between 0.03 and 0.66 $pike \cdot h^{-1}$ (Kempinger and Carline, 1978; Pierce *et al.*, 1995). The resulting hypothetical annual exploitation rate in the present study ranged between 47–74% of the adult population ($\geqslant$450 mm T_L) in spring. This can be considered high but is also within the range of reported values from other pike fisheries (8 to 46% of the population, Beyerle, 1978; Pierce *et al.*, 1995). It can be concluded that the fishing patterns in the present study resulted in effort densities and catch rates comparable to real life situations in other pike fisheries. Thus, we are confident that our findings are robust to be generalized but this necessitates further study in different systems.

To conclude, our study is the first jointly testing behavioural and growth impacts of non-lethal direct and indirect disturbances caused by recreational angling activities on fish on a field scale level. In contrast to other human-wildlife interactions, recreational fishing is characterized not only by indirect disturbances but also by direct disturbances that result for instance from the popular catch-and-release fishing. We found that particularly the direct disturbances of fish in the process of catch-and-release are affecting the fish influencing not only their behaviour but also reducing growth. Whether this growth depression has impacts on the population is currently unknown (Arlinghaus *et al.*, 2007), but recent studies support the assumption that even small differences in growth can have pervasive impacts on pike population dynamics (Edeline *et al.*, 2010). However, as our study showed, impacts of recreational angling on fish stocks exist, even in no-take fisheries, because of the responses of fish (in ecological time) to non-lethal angling-related disturbances. We recommend further studies to assess the long-term consequences of continuous disruption of habitats in total catch-and-release recreational angling fisheries and call for a minimization of direct and indirect angling-related stressors during the process of catch-and-release angling to avoid any population-level impacts of non-lethal angling from the perspective of an precautionary approach to sustainable recreational fisheries management.

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