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Abiotic and fishing-related correlates of angling catch rates in pike (*Esox lucius*)

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ABSTRACT

Understanding how angling catch rates vary between environments is of interest from ecological and fisheries management perspectives, but this has rarely been investigated in detail. Using experimental catch-and-release angling records for northern pike (*Esox lucius*) from a small natural lake in Germany and a generalized linear model we investigated how abiotic and fishing-related environmental variables as well as time of day affect pike catch per unit effort (CPUE; fish per hour). Catch rates of pike were significantly increased at low temperatures, high wind speeds and around full and new moon as well as during dusk. Large fishing effort during the past two days reduced catch rates significantly, indicating the combined influence of abiotic and human-induced variables on the catch rates of pike with angling gear. Of all the significant covariates, fishing effort had the most pronounced effect on catch rates. Our results indicate that anglers can increase catch rates by choosing appropriate weather conditions and lunar phases, but that continuously intensive fishing negatively affects future catch rates even in the absence of harvest. This has implications for the choice of sampling effort using angling gear when attempting to assess fish stocks.

1. Introduction

Angling is a popular recreational and commercial fishing method. While angling methods usually involve rod-and-reel in recreational fisheries, long-lining is the most important angling technique in commercial fisheries. Understanding how angling catch rates vary with environmental variables is of interest from ecological and fisheries management's perspectives. Angling requires fish to attack/ingest the bait or the artificial lure, so that angling catch rates provide insights into the activity and feeding patterns in fish and potentially level of aggressive attacks in predatory fish. In particular, catch rates in angling fisheries should depend on the foraging activity and hunger level of fish as well as their ability to locate or avoid the bait or lure (Uusi-Heikkilä et al., 2008). These processes, in turn, are likely affected by environmental cues correlated with activity and metabolism such as water temperature (Stoner, 2004). Therefore, quantifying the vulnerability of fish to angling gear necessitates identifying environmental variation in angling catch rates, but this has rarely been investigated in detail using rod-and-reel-type angling. Moreover, as stock assessments are sometimes conducted using angling methods (e.g., Myers and Worm, 2003; Pierce and Tomcko, 2003; Hansen et al., 2005; Lehtonen et al., 2009), distinguishing environmental variations in angling catch per unit effort (CPUE; an index of relative abundance) from variation arising from differences in population density is vital for obtaining reliable information about the population size (Stoner, 2004).

Out of the potential abiotic factors affecting angling catch rates water temperature appears to be the variable most commonly reported in the literature (e.g., Bigelow et al., 1999; Stoner, 2004; Stoner et al., 2006; Damalas et al., 2007; Ortega-Garcia et al., 2008). This is presumably due to its pervasive influence on movement activity, metabolism, and foraging activity in all poikilothermic aquatic animals (Brown et al., 2004). Other abiotic environmental variables such as wind speed, light, barometric air pressure, day length, time of day and air temperature have also been shown to affect catch rates in angling fisheries (e.g., Millar et al., 1997; Bigelow et al., 1999; Margenau et al., 2003; Stoner, 2004; Wall et al., 2009). However, particularly in recreational fisheries, analyses of such relationships are sparse, presumably due to the lack of datasets providing high resolution measurements of abiotic environmental variables along catch records (Stoner, 2004). This lack of knowledge contrasts with a wealth of anecdotal information about correlations between abiotic environmental variables and angling catch rates, culminating in fishing 'calendars' that are commonly applied by anglers to predict future fishing success.

A particularly intriguing aspect related to abiotic environmental variations in catch per unit effort (CPUE) is the potential role of lunar cycles. Namely, it is a common belief among professional and recreational anglers that catch rates depend on the moon

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phase, with catches being highest around full and new moon (e.g., http://www.solunarforecast.com/). In the context of baited fishing gears, this hypothesis has rarely been investigated and the available evidence is mixed. In some longline fisheries for marine species, catches have been seen to peak around full or new moon (Bigelow et al., 1999; Lowry et al., 2007; Damalas et al., 2007), while other studies have reported lack of correlations between lunar phases and catch rates (Millar et al., 1997; Ortega-Garcia et al., 2008). Overall, the extent to which lunar cycles might affect CPUE in angling is still largely unknown and may be species-specific. Moreover, as pointed out by deBruyn and Meeuwig (2001), weak lunar cycles in catch rates easily remain undetected if the statistical methods that are applied are not appropriate.

In addition to abiotic environmental variables, it is undisputed that a number of biotic features affect catch rates of angling gears. For example, food abundance and the density of conspecifics generally increase competition for food or induce social stress in cannibalistic species (Edeline et al., in press), which may affect food intake rates, foraging activity and hunger levels. Not surprisingly, density-dependent factors have been reported to substantially affect catchability in angling fisheries (Raat, 1986, 1991; Hansen et al., 2005). In some species, angling catchability also depends on learning to avoid capture, particularly if catch-and-release fishing is widespread (Raat, 1985; van Poorten and Post, 2005; Askey et al., 2006), but the same pattern can also emerge as a result of high angling effort with easily-identifiable lures as was demonstrated by Beukema (1970). In his catch-and-release experiment conducted in ponds, northern pike (*Esox lucius*) learned to avoid future capture by artificial lures regardless of whether individuals were hooked previously, but similar learning effect did not occur for natural baits (Beukema, 1970). This finding along with other studies in freshwater fisheries conducted with artificial lures (van Poorten and Post, 2005; Askey et al., 2006) suggests that fishing effort might affect angling catch rates negatively (Cox and Walters, 2002; Young and Hayes, 2004). Thus, fishing effort must be accounted for when investigating the impact of environmental factors on catch rates in angling fisheries.

The objective of this study was to investigate the impacts of a wide range of abiotic and fishing-related environmental variables including lunar cycles and fishing effort on CPUE in northern pike (hereafter termed pike) rod-and-reel angling. Pike is a fast growing, early maturing and strongly cannibalistic top piscivore in freshwater and brackish ecosystems; it was chosen as the model species for the present study because it has great value for both commercial and recreational fisheries throughout its circumpolar natural range in the northern hemisphere (Paukert et al., 2001; Arlinghaus and Mehner, 2004). Field data were collected by experimental catch-and-release fishing in a natural lake. The study site was protected from any other forms of fishing and was confined to a short period of intensive sampling within one season. Therefore, variations in CPUE were likely not associated with large changes in population density, which would otherwise confine the analyses of abiotic and fishing-related variations in catch rates (Hansen et al., 2005; VanDeValk et al., 2005).

2. Materials and methods

2.1. Data

Experimental pike angling took place in the Kleiner Döllnsee during the spring to autumn of 2005. This small (25 ha), dimictic, shallow (mean depth 4.1 m, maximum depth 7.8 m) natural lake is located in north-east Germany (N52°59′, E13°34′). Kleiner Döllnsee is mesotrophic to slightly eutrophic (P concentration at string overturn 28 $\mu g\,l^{-1}$) sustaining a natural pike population protected from

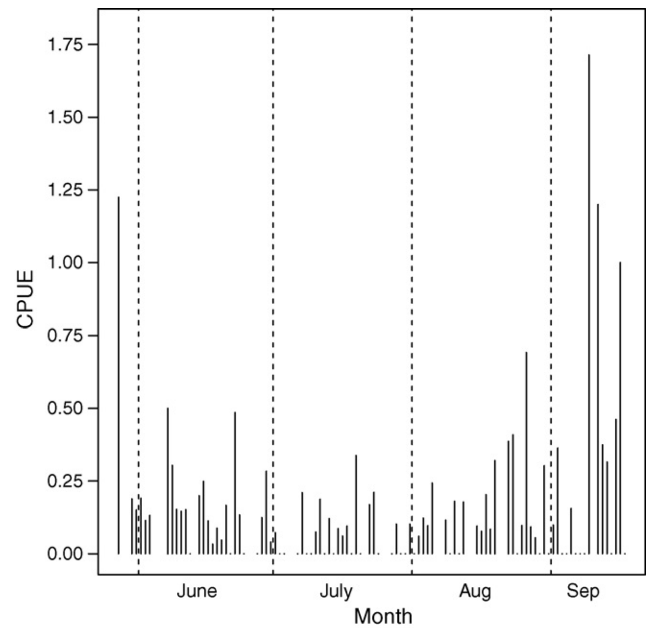

Fig. 1. Pike catch per unit effort (CPUE; fish per hour) at daily intervals over the study period from 27th May to 17th September 2005.

any form of commercial or public recreational fishing (Klefoth et al., 2008; Kobler et al., 2008a). In spring of 2005, abundance of age 1 year and older pike was estimated as 544 individuals (95% CI: 194–1088) (Kobler et al., 2008a,b). Within the study period from 27th May to 17th September 2005 pike were angled on a total catch-and-release basis using 25 skilled anglers (3 fishing regularly on each sampling day, occasionally supplemented by in total 22 additional experimental anglers). Most the anglers were part of the research team and all employed standard recreational pike angling fishing techniques described in detail in Arlinghaus et al. (2008a). Briefly, each angler was instructed to use a personal choice of artificial lures using medium-action rods for spinning or trolling and, when occasionally using organic bait, to set the hook quickly to avoid deep hooking (Arlinghaus et al., 2008a). Anglers were asked to fish all habitats during a fishing day, but for logistical reasons and to add realism anglers were not assigned to randomly selected fishing sites. Due to the small size of the lake all available habitats were sampled on a given angling day, but some more productive fishing sites (e.g. dense macrophyte patches) known by anglers to host particularly high abundances of pike (see Kobler et al., 2008a,b, 2009) might have been more intensively fished on particular days. However, this is typical for any recreational fishing sites and, hence, managers would normally have aggregated daily catches over a sample of anglers. Once a pike was landed, it was quickly de-hooked, checked for any signs of marks or tags, and its length and weight were measured after which the individual was released. Immediate hooking mortality was low and estimated as 3.9% (see Arlinghaus et al., 2008a for details). For each angling day, the cumulative number of pike caught and the cumulative duration of fishing over all anglers was recorded, separately for daytime and the hours of dusk, yielding 169 observations in total (93 during daytime and 76 during dusk spread over 94 fishing days; Fig. 1). For more ecological details about the study system, see Klefoth et al. (2008) and Kobler et al. (2008a,b, 2009).

Abiotic environmental conditions were measured on a daily basis. Variables measured (and their ranges) were water temperature (14.7–24.1 °C), wind speed (0.7–6.9 $m\,s^{-1}$), wind direction [categories (frequencies of observation): east (14), south (38), west (40), north (2)], air humidity (58–98%), rain

Table 1
Pearson's correlation coefficients (*r*) among the continuous environmental variables.

	Air pressure	Future air pressure	Humidity	Hours of sunshine	Rain	Water temperature	Wind speed
Air pressure	1	−0.319	−0.393	0.450	−0.314	−0.125	−0.312
Future air pressure		1	0.373	−0.320	0.149	−0.074	0.200
Humidity			1	−0.762	0.480	−0.267	0.139
Hours of sunshine				1	−0.412	0.318	−0.346
Rain					1	−0.062	0.094
Water temperature						1	−0.206
Wind speed							1

Table 2
Effects of the significant covariates on the number of pike caught per hour, as estimated through a generalized linear model with a log link and Poisson errors[a] (N = 169).

Model term	Coefficient (SE)	Deviance[b]	p-Value
Intercept (time of the day: daytime)	0.477 (0.828)		
Past two day fishing effort	−0.019 (0.005)	17.83 (df = 1)	<0.001
Time of the day: dusk	0.556 (0.181)	8.58 (df = 1)	0.003
Water temperature	−0.095 (0.037)	6.40 (df = 1)	0.011
Wind speed	0.160 (0.061)	6.66 (df = 1)	0.010
cos(2θ)	0.238 (0.114)	4.52 (df = 1)	0.034

[a] Null deviance 209.01 (df = 169), residual deviance 168.82 (df = 163).
[b] Marginal increase in residual deviance upon deletion of the term.

(0.0–14.3 l m^{-2}), hours of sunshine (0–15 h day^{-1}), and air pressure (997.8–1024.6 hPa) and change in air pressure within the following 24 h (−11.4–12.8 hPa). Generally, the measured variables did not show strong correlations (Table 1), except humidity and the hours of sunshine for which Pearson's correlation coefficient was <−0.5. The daily moon phase at the geographic location of the study site was obtained from the Naval Oceanography Portal (http://aa.usno.navy.mil/data/docs/MoonFraction.php), and was expressed in terms of the fraction of moon disk illuminated and whether the moon was waxing or waning. As an index of angling pressure on the ecosystem, fishing effort (hours of angling) was calculated jointly for the first two days prior to the sampling day (i.e., total hours of fishing over the two days), and separately for the third and fourth day prior to the sampling day (hours of fishing over the respective day).

2.2. Statistical analyses

Our aim was to investigate whether daily abiotic and fishing-related environmental variables affected pike catch rates with typical recreational angling gear during day and dusk. To this end, the number of pike caught (daily catch split into two categories for the time of the day) was modelled with a generalized linear model (GLM) with a log link function and Poisson errors, and corresponding angling hours as an offset variable. Being constructed in this way, the model predicts the pike catch rate in fish per hour. As explanatory variables we considered the recorded environmental variables (see above) and time of the day (daytime or dusk) as a categorical variable. Fishing effort during the previous two days, and during the third and the fourth day prior to the sampling day were used as explanatory variables to account for the known behavioural responses of pike to angling activity-induced habitat disturbance (Klefoth et al., unpublished data), which may translate into reduced catch rates. Lunar cycles in the pike catch were investigated by converting the fraction of moon disk illuminated into radians (θ), so that one lunar cycle corresponded to a gradual increase from 0 to 2π radians (e.g., 0 and 2π radians corresponded with full moon and π radians with new moon). Transformations cos(θ), sin(θ), cos(2θ), and sin(2θ) were then included in the model as explanatory variables to investigate possible lunar effects around full/new moon (cosine), around half moon (sine) and for lunar effects peaking twice within one lunar cycle (cosine and sine transformations of 2θ). For more details of this method, see deBruyn and Meeuwig (2001).

Because of the large number of investigated covariate candidates in relation to the number of observations, interaction terms could not be readily included to the model. Analyses were therefore carried out in two consecutive steps: First we fitted a model with the additive main effects of all the covariate candidates. After having identified the significant covariates, we then fitted a model with both the main effects and two-way interactions of the significant environmental covariates. Significance of the covariate candidates was investigated by stepwise reduction of the full model and Chi-squared test of deviance. Possible non-linearity in the effects of the significant covariates was investigated with a generalized additive model (GAM). The impact of potential outliers was investigated by excluding those from the data and repeating the analyses.

Because environmental variables were measured on a daily basis, a potential day effect was not included in the model as it could easily sweep variation in the catch rate assigned to variations in the other explanatory variables. However, to investigate possible daily variations that were not encompassed by the considered explanatory variables and to detect seasonal trends in pike catch rates (Margenau et al., 2003), residuals of the fitted model were further analysed. Relative magnitudes of within and between day variations in catch rates were estimated by modelling the residuals with a linear mixed effect model with a fixed intercept and date as a random effect. A possible temporal trend in catch rates over the study period was investigated by fitting a GAM model to the residuals in which the potential day effect was described though a non-parametric smoothing term. All the statistical analyses were performed in R 2.10.0 (R Development Core Team, 2009).

3. Results

Catch rates of pike fluctuated widely during the study period with no obvious pattern visible from the time series (Fig. 1). The catch rate of pike by angling gear was found to be significantly affected by the past two days' fishing effort, time of the day, and average daily water temperature, wind speed and moon phase (Table 2). Catch rates were significantly increased during dusk, at high wind speeds and around full and new moon, and decreased significantly with increasing water temperatures and when large amounts of fishing took place during the previous two days (Fig. 2). The effects of other explanatory variables were non-significant (in the order of deletion from the model, hours of sunshine: $\chi^2 < 0.0001$, df = 1, $p = 0.998$; fishing

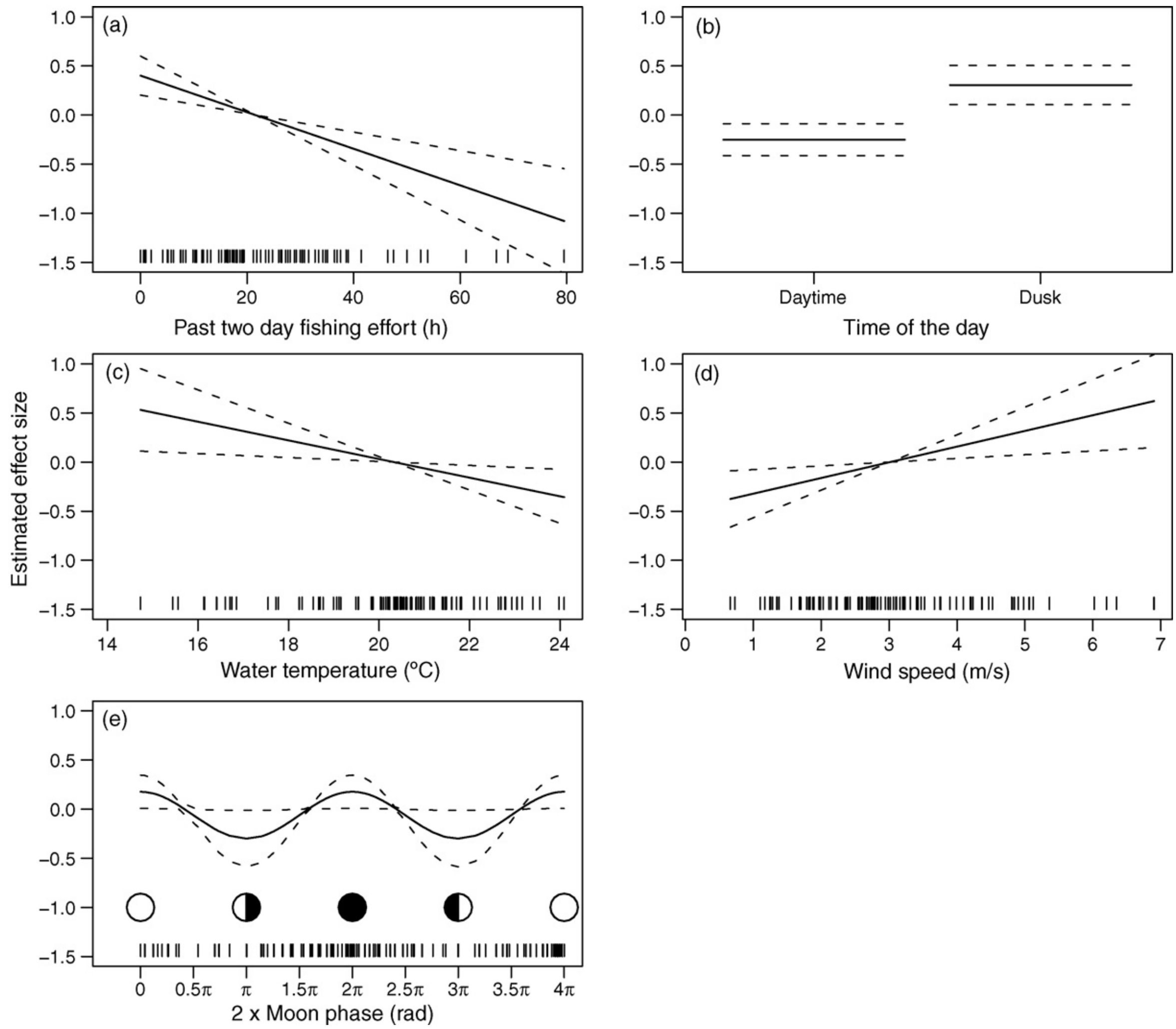

Fig. 2. Partial effects (solid line) of past two day fishing effort (a), time of the day (b), water temperature (c), wind speed (d), and cosine of double the moon phase (e) on the log transformed pike catch rate (fish per hour) predicted by the generalized linear model in Table 2. Standard error ranges are indicated with dashed lines and densities of observations are illustrated with rugs. In case of time of the day categories, there were 93 observations during daytime and 76 during dusk.

effort during the fourth day prior the sampling day: $\chi^2 = 0.0004$, df = 1, $p = 0.985$; air pressure: $\chi^2 = 0.008$, df = 1, $p = 0.960$; wind direction: $\chi^2 = 2.902$, df = 3, $p = 0.407$; fishing effort during the third day prior the sampling day: $\chi^2 = 0.490$, df = 1, $p = 0.484$; sin(θ): $\chi^2 = 0.625$, df = 1, $p = 0.429$; air pressure change: $\chi^2 = 1.4$, df = 1, $p = 0.237$; rain amount: $\chi^2 = 1.610$, df = 1, $p = 0.205$; humidity: $\chi^2 = 1.914$, df = 1, $p = 0.167$; sin(2θ): $\chi^2 = 2.006$, df = 1, $p = 0.157$; cos(θ): $\chi^2 = 3.720$, df = 1, $p = 0.054$). The overall explanatory power of the significant covariates on pike catch rates remained modest, with the reduced model explaining 19.2% of the null deviance and its Nagelkerke's R^2 (Nagelkerke, 1991) being 21.4%. Generally, the model fit was acceptable and there was no evidence of overdispersion, as indicated by the goodness-of-fit test based on deviance ($\chi^2 = 168.82$, df = 163, $p = 0.361$). No interactions were found between the significant covariates on pike catch rates (in the order of deletion, water temperature × cos(2θ): $\chi^2 = 0.345$, df = 1, $p = 0.557$; wind speed × cos(2θ): $\chi^2 = 0.880$, df = 1, $p = 0.348$; wind speed × time of the day: $\chi^2 = 0.813$, df = 1, 0.367; water temperature × time of the day: $\chi^2 = 0.828$, df = 1, $p = 0.363$; time of the day × cos(2θ): $\chi^2 = 1.814$, df = 1, $p = 0.178$; water temperature × wind speed: $\chi^2 = 2.346$, df = 1, $p = 0.126$). GAM analyses did not reveal deviations from linearity in the effects of fishing effort, water temperature, and wind speed on catch rate (judged visually). Residuals, leverages and Cook's distances pointed out four possible outliers but excluding those from the data had no effect on the outcome of the analyses. Variation in residuals could not be encompassed by daily random effects (the variance component was 6.8×10^{-7} and thus virtually zero), and no significant temporal patterns in residuals were detected by a smoothed day effect ($F_{2.541,169} = 1.867$, $p = 0.147$).

4. Discussion

Our results illustrate how angling catch rates of a common predatory freshwater fish vary within and between days due to variation in abiotic and fishing-related environmental variables. From a wide range of potential covariates pike catch rates were found significantly correlated with averages daily water temperature, wind speed, and moon phase, as well as with the timing of fishing within the day and the previous two day fishing intensity levels (Fig. 2), together inducing one order of magnitude variation in the predicted catch rates (0.05–0.44 fish per hour). However, despite the distinguished role of these covariates, a large amount of variation in the observed catch rates remained unexplained (Table 2). This suggests that a good deal of stochasticity remained associated with fishing success. This could have arisen from differences in bait or lure types employed by experimental anglers across sampling days (Arlinghaus et al., 2008a; Alós et al., 2009), angler's skills (Alós et al., 2009) or varying spatial distribution of fishing across sites in the study lake (Alós et al., 2009). These variables could not be accounted for in our analyses, but they are not expected to bias the results of our analyses for two reasons. First, variation arising from anglers and sites should not be large as data were averaged over these variables and the negligible variance component of the day effect suggests that no variation was associated with daily combinations of anglers. Second, anglers and sampling of sites within the lake were generally independent of the considered environmental covariates, so that they would only add to the residual variation of the model but not affect our inference on significant environmental covariates of the pike catch rate. Additional variation in catches might also have arisen from within-day variations in environmental conditions (e.g., temperature or oxygen fluctuations), from variation in the size of pike population vulnerable to angling in the course of the study resulting from recruitment or natural mortality, from unaccounted environmental drivers such as prey fish distribution, or from deviations from model assumptions. Nevertheless, the presence of unexplained variation in catch rates does not affect the robustness of our findings, which show that abiotic environmental variables as well as fishing effort significantly affected catch rates in pike angling. Moreover, it should be noted that all the mentioned sources of uncertainty are typically present in recreational angling catch data, thus increasing the realism of our angling experiment from the perspective of practical fisheries management. In other words, the environmental patterns seen in our catch rates are likely to be present in pike angling catch rate records typically available unless there are substantial differences in environmental covariates of pike catch rates across lakes or rivers. This is currently unknown and warrants future research and replication.

The previous two days of fishing effort at the study lake turned out to be a much more important predictor of the pike catch rate than any meteorological or lake-specific abiotic variable (Table 2). This result is in line with previous observations that fish, including pike (Beukema, 1970; Klefoth et al., unpublished data), temporarily alter their behaviour in response to human-induced disturbances such as catch-and-release events, habitat disturbance through boating, or presence of anglers and associated sound originating from the fishing activity (e.g., Raat, 1985; Young and Hayes, 2004; Askey et al., 2006). However, this effect has been found to be rather short term in pike, lasting a couple of days (Klefoth et al., 2008) or just some hours (Arlinghaus et al., 2008b, 2009). In our study, a potential 'memory' of pike to avoid future capture appeared to extend only up to two days back as reflected by the non-significant effects of the daily fishing effort three and four days prior to the sampling day. This is also indicated by the observation that after the start of intensive angling on this otherwise unexploited pike population there was no sudden and consistent drop in catch rates as has been shown for other freshwater fish species (Raat, 1985; van Poorten and Post, 2005; Askey et al., 2006) suggesting comparatively low levels of learning to avoid future capture by pike. However, extrapolations to other systems should be done cautiously because fishing effort more intensive than that in our study might have longer term effects (compare Beukema, 1970). Moreover, in fish habitat size and complexity can affect sensitivity to remembering negative stimuli (Pollock and Chivers, 2003) as well as the development of brain and sense organs (Pollen et al., 2007), and this might explain the contrasting findings by Beukema (1970) from pond-angled pike that showed rapid learning to avoid capture by lures, but not by natural bait, in this low complexity environment. Therefore, we speculate that the negative impact of fishing effort on angling catch rates might be less pronounced in larger and more complex ecosystems than the one we sampled. An alternative reason for our findings unrelated to a short-term memory hypothesis might be that in a given point in time pike populations might cluster into individuals temporarily vulnerable and invulnerable to fishing, e.g. due to short-term elevated hunger levels or habitat choice (Cox and Walters, 2002). If this is the case heavy fishing pressure in a short time period of two days might temporarily remove a great fraction of the vulnerable pool leaving behind more invulnerable fish, which, in turn, reduces catch rates. Irrespective of the exact mechanism responsible for declining catch rates with short-term elevated fishing effort, several practical implications can emerge from our observations. First, to ensure high catch rates it might be worthwhile to distribute fishing effort equally in time and allow the population to 'recover' between pulses of intensive fishing (cf. van Poorten and Post, 2005). Secondly, if catch rates in angling are applied as a proxy for population density (e.g., Pierce and Tomcko, 2003; Lehtonen et al., 2009), fishing effort over the previous days should be kept constant because it influences catch rates and might therefore influence the abundance index derived using angling gear.

We found that increasing water temperature from about 14 °C to the maximum observed temperature of about 24 °C was associated with decreasing pike catch rate. This temperature range coincides well with earlier studies on catch rates of pike with stationary gill nets in lakes: outside spawning time catch rates were found to be highest at temperatures between 15 and 17 °C and lowest at the maximum temperatures between 20 and 24 °C (Casselman, 1978). Although active swimming may not necessarily be expected for successful foraging for a predator such as pike regularly engaging in a sit-and-wait hunting strategy, direct correlations exist between the rate of food consumption, swimming activity and water temperature in this species (Casselman, 1978). Casselman (1978) also reported that for adult pike rapid somatic growth commences at about 14 °C after spawning in spring because appetite to restore lost energy resources is stimulated and pike actively seek food. With further increasing temperature, instantaneous growth and activity of juvenile pike have been shown to increase in laboratory experiments but after reaching a threshold value of about 19–20 °C both growth and activity of pike decline (Casselman, 1978). Because in pike the optimum temperature for growth and activity decrease with age, and food supply is often limited under natural conditions, Casselman (1978) concluded that maximum activity of pike in natural environments should occur at low temperature ranges <20 °C. This would match with the inverse relation between temperature and pike catch rates by angling found in the present study. Presumably, in this mesothermal or 'coolwater' fish species (Casselman, 1978) overly high water temperature during summer may pose physiological stress, particularly if food supply is limited, because for metabolic reasons it would be more efficient (Bevelhimer et al., 1985) if swimming activity and feeding is reduced (Casselman, 1978). However, also an alternative reason might help to explain the inverse relation between water temperature and pike catch rates found in the present study. Elevated temperature during the warming spring and summer period coincides with high movement activity (Jacobsen et al., 2004) and abundance of prey fish such as roach (*Rutilus rutilus*) (Kobler et al., 2009). Because the encounter probability with naturally more active prey is increased at high water temperature, the angler's lure and bait might face a 'competitive disadvantage' reducing catch rates. Along the same lines, we can suspect that the higher catch rates of pike at colder water temperatures (see also Margenau et al., 2003) could be associated with parallel declines in prey movement activity (Jacobsen et al., 2004) coupled with the tendency of pike to keep being associated with underwater structure as refuge and shelter even at low water temperature (Kobler et al., 2008a). This facilitates the identification of pike habitat by anglers (Post et al., 2002), which at lower temperature coincides with reduced prey encounters and presumably higher hunger levels of pike, jointly increasing the pike catch rates by angling.

In our study, we also found pike to be more vulnerable to angling during twilight periods. During these periods pike are usually more active in terms of swimming (Kobler et al., 2008a,b) and feeding (Casselman, 1978) because prey fish start to emerge from shelter and disperse in the open water (Jacobsen et al., 2004) and because pike are able to approach their prey closer and therefore the chances of successful attacks are increased (Pitcher and Turner, 1986). However, greater fishing success at twilight conditions might also be explained because during the dusk period a visual predator such as a pike might have greater difficulties in identifying (and consequently avoiding) an artificial lure than during day time. Similarly, we suspect that the positive effect of high wind speeds on catch rates of pike might be associated with the fact that strong winds tends to induce turbidity (e.g., Cózar et al., 2005), which is known to affect foraging and feeding activity of pike (Nilsson et al., 2009) and distribution of prey like roach (Jacobsen et al., 2004) and small perch (*Perca fluviatilis*) (Skov et al., 2007). Thus, increased wind speeds can alter the reactivity of pike to the fishing gear by reducing water transparency (e.g., Stoner, 2004) and/or altering prey encounters, thus jointly affecting the susceptibility of individual pike to lures. This speculation of the catch rates being enhanced by reduced water transparency as a result of wind speed is in agreement with the observation made by Casselman (1978) that pike feed more actively on cloudy, overcast days than on bright, sunny days.

One of the most intriguing and novel finding of our study is the clear relationship between moon phase and catch rates in pike angling. Interestingly, the shape of the moon effect detected in pike catch rates with catch rates peaking around full and new moon matches well with that predicted by anecdotally supported fishing calendars. Our study therefore adds scientific weight to the usefulness of fishing calendars that are based on moon phases. What our analysis does not reveal, however, are the mechanisms underlying the observed pattern. Typical secondary moon effects arising from tidal formations or illumination (Kuparinen et al., 2009) may be thought of as not playing an important role in pike as the lake environment was free from tides and fishing took place during daytime and dusk, so that the potential effect of moonlight can be excluded. However, it is possible that shifts in illumination along lunar cycles are associated to periodic changes in zooplankton and prey fish distribution, leading to changes in predator foraging activities that transcend the night phases (Hernández-León, 2008). Thus, it might also be conceivable that predators such as pike respond to signals of the moon that correlate in a predictable and repeatable way with altered distributions of both zooplankton and prey fish. Direct lunar gravitational patterns might offer one possible explanation as a biological trigger of a behavioural response by predators because those have previously been found to induce behavioural reactions in fish, e.g. inducing migration of smolts in salmonid species (DeVries et al., 2004). However, mechanisms through which pike might sense gravitational cues, and the biological role these might have in motivating feeding and, thus, vulnerability to angling remains unknown providing a challenge for future research.

To conclude, our study sheds light onto some important correlates of catch rates in angling by rod-and-reel for pike. Although a substantial amount of variation in catch rates remained unexplained, we found daily averages of abiotic variables (water temperature, wind speed, lunar phase), time of the day, and fishing variables (angling effort) to significantly affect catch rates. Our study is useful in directing future attempts to assess the size and structure of pike stocks based on angling catches by emphasizing the importance to account for environmental variables significantly influencing catch rates. This can be most easily achieved by randomly selecting sampling days and avoiding temporal clustering, so that a large environmental gradient is sampled. Moreover, our study confirmed some of the anecdotal evidence by anglers about the seasonality and diurnal dynamics of pike catch rates that seem to be also mediated by lunar cycles. This information is important for anglers interested in maximizing their catches by allocating scarce fishing time to the most productive periods within a season and throughout the day.

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