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ARTICLE

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Thunderstorms have species and gear-specific indirect effects on the catchability of Mongolian salmonids

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Abstract

Climate change is predicted to cause increasingly frequent and intense storms. Northern Mongolia is already warming at a rate twice the global average, and thunderstorms, defined as intense, short, patchy rains associated with thunder, lightning and high precipitation rates, are becoming more frequent. Because Mongolia's fish populations are lightly exploited, Mongolia provides a model system in which to study the effects of storms on fish behaviour and fishing vulnerability. The impacts of thunderstorm-related hydrological changes on fishes' vulnerability to two fishing gears were evaluated. Two thunderstorm-related factors, turbidity and river stage, reduced catch rates of the salmonids lenok *Brachymystax lenok* (Pallas) and Baikal grayling *Thymallus baicalensis* Dybowski. Fly-fishing gear was more effective than spinning gear in this fishery and retained higher catch rates in extreme conditions. These gear-specific effects suggest that turbidity and rising river stage affect fishing vulnerability by influencing feeding behaviour.

KEYWORDS
climate change, drift feeding salmonids, fishing vulnerability, gear selectivity, Mongolia, turbidity

1 | INTRODUCTION

Climate change is altering the freshwater ecosystems that support inland recreational fisheries by increasing surface temperatures, changing precipitation patterns and increasing the frequency of extreme storm events (Hartmann et al., 2013). The state of knowledge on the ways in which climate change might affect inland recreational fisheries is growing but uneven. For instance, a large body of research has investigated how warming waters will change fish population abundance and shift species distributions over the long term (Ficke et al., 2007; Kovach et al., 2016). Much less well understood are the more abrupt, short-term hydrological changes associated with storm events (Hartmann et al., 2013), which can also have significant effects on fish populations and human communities (Santos et al., 2016). In addition, several studies have predicted how fish and anglers will each respond to new temperature regimes and weather patterns (Kerr et al., 2009; Townhill et al., 2019), but few investigate how climate change might alter fishes' vulnerability to fishing gear.

One way that climate change could affect these fishery interactions in the immediate future is through storm events, which are expected to become more frequent and severe as climate change intensifies (Hartmann et al., 2013). Extreme storm events like thunderstorms can be expected to change salmonids' behaviour, and therefore their interactions with fishing gear, in a number of ways.

Turbidity resulting from sediment loading increases reaction distance to prey (Mazur & Beauchamp, 2003; Vogel & Beauchamp, 1999) and lowers feeding rates (Rowe et al., 2003) in visually foraging fish. Pulses of high river flow, such as those produced by precipitation runoff, reduce fish activity and swimming speed (Larranaga et al., 2018). Increased river stage following thunderstorms also increases the volume of water within which a fish must search for prey. Unless there is a corresponding increase in prey available (e.g. from terrestrial prey washed into the river), then prey density and encounter rates will decrease.

A number of confounding environmental factors can also affect fish behaviour and catchability, making it hard to isolate the effects of storm-related factors. Catch rates change with season (van Poorten & Post, 2005) and diel cycles, with many fish species more active and therefore more vulnerable to fishing gear at dawn and dusk (Arlinghaus et al., 2017; Kuparinen et al., 2010). Factors relating to anglers' behaviour and gear choices can also affect catchability, because fishermen's skill influences their catch rates (Arlinghaus et al., 2017), and different types of angling gear vary in their efficiency in catching fish, and in their selectivity for different species and sizes of gear.

For several reasons, Mongolia is a valuable model system to study interactions between fish and angling gear under climate change. First, air temperature records show that Mongolia has warmed by almost 2°C since 1940 (Nandintsetseg et al., 2007), a rate about double the global average (Hartmann et al., 2013). Along with warming, Mongolia is also experiencing new precipitation patterns: the gentle, long-lasting rains typical of summer precipitation in northern Mongolia are being replaced with thunderstorms, defined by Goulden et al., (2016) in a Mongolian context as "intense, short, patchy rains with large drops…associated with thunder, lightning, and precipitation rates greater than 7.6 mm/hr." These thunderstorms produce sudden pulses of runoff and sediment erosion into rivers, dramatically altering the habitat in which Mongolian fishes move, forage and interact with fishing gear. Second, Mongolia's rivers are relatively untouched by other disturbances that are expected to confound the effects of climate change, such as stocking, flow control and invasive species (Hunt et al., 2016; Kovach et al., 2016). Finally, Mongolia's Eg-Selenge watershed contains healthy populations of the coldwater salmonids lenok *Brachymystax lenok* (Pallas) and Baikal grayling *Thymallus baicalensis* Dybowski (Mercado-Silva et al., 2008). These two species are already experiencing temperatures near their upper limits for growth in the summer in Northern Mongolia (Hartman & Jensen, 2017).

Because active angling gears, like fly and spinning gears, imitate prey items, changes in fishes' feeding behaviour caused by thunderstorms should also control their encounter rate with spinning and fly gear (Lennox et al., 2017). Although lenok and Baikal grayling are both drift feeders, lenok has a higher proportion of benthic invertebrates and fish in its diet than grayling (Olson et al., 2016). This means that compared to grayling, it should be more vulnerable to lures that imitate prey fish, such as spinners. Since spinners may attract fish using sound as well as a visual cue, these lures may remain effective even in highly turbid water, while catch rates on purely visual lures, like the majority of artificial flies used in fly fishing, should be much more sensitive to turbidity. In Mongolia, these gear-specific interactions with river conditions could result in different levels of fishing success for different angler populations, creating winners and losers among Mongolia's recreational anglers.

This study evaluates how the thunderstorm-associated factors turbidity and river stage affected Mongolian salmonids' vulnerability to fishing on two different angling gears. A standardised experimental fishing approach that rotated spinning and fly gears equally among a team of anglers, following Arlinghaus et al. (2017), was used to estimate how thunderstorms affect catch rates on different gears. Three predictions were made: (1) that increased turbidity and increased river stage both reduce catch rates of lenok and grayling; (2) that turbidity has a greater effect on catch rates with fly than with spinning gear, while the effect of stage does not depend on gear; and (3) that lenok remain more vulnerable to capture on spinning gear than grayling during turbid conditions, while the two species are equally likely to be caught on fly gear during the same conditions.

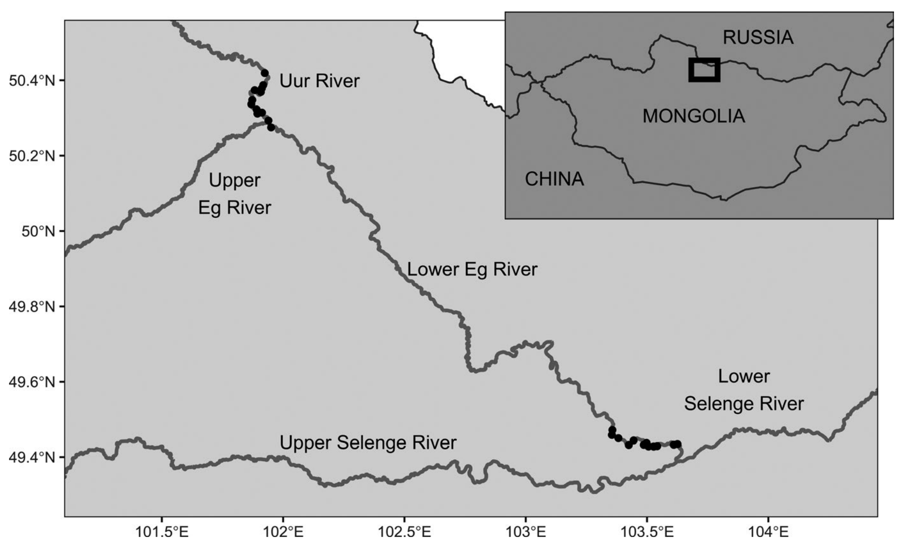

FIGURE 1 Experimental fishing was conducted in north-central Mongolia (inset) at 24 sites spanning a total of 60 km of river distance. The Eg-Uur site is located in the upper left area, and the Eg-Selenge site is located in the bottom right area of the map

2 | METHODS

2.1 | Materials and methods

Standardised fishing was conducted on 30 km of the Uur River directly above its confluence with the Upper Eg River and on 30 km of the Lower Eg River above its confluence with the Selenge (Figure 1). The two fishing areas are located 251 river kilometres apart in the Hovsgol and Bulgan provinces of north-central Mongolia, which occupy the ecotone between Mongolian steppe and Siberian taiga forest. The Uur is predominantly fed by groundwater and precipitation runoff and is characterised by a mixed riparian habitat and large meanders in a wide floodplain valley. Below their confluence, the combined Eg and Uur rivers are known as the Lower Eg and have a similar riparian habitat but with increased width and reaches with large boulders (Gilroy et al., 2010). Mongolia's summer rainy season lasts from late June to late August (Goulden et al., 2016). Therefore, fishing on the Uur River was conducted throughout the 10-day period from 21 July to 30 July 2019 and on the Lower Eg from 2 August to 14 August 2019.

Twelve fishing sites were selected on each river, equally divided between three, 10-km segments to ensure uniform fishing effort throughout the 30-km stretch. The fishing sites were selected by a local fishing guide with more than a decade of experience fishing on the two rivers. Good lenok and grayling habitat was generally considered riffles or runs. Compared with unselected sites, they tended to have coarser substrate (gravel or cobble rather than silt or sand) and sparser riparian vegetation. One 10-km segment was selected randomly for fishing each day, and three or four sites within the segment were fished depending on time constraints. To avoid confounding site effects with time of day, the order in which sites were fished (starting either downstream or upstream) was determined using a coin toss.

Spin fishing was conducted with standardised medium-fast action rods (6½ foot Shakespeare UglyStik and Abu Garcia Vendetta) and standard reels (Abu Garcia, Silvermax 40 and Blackmax 20). Spinning lures were restricted to #1 and #2 dressed Mepps aglia treble hook spinners in silver and gold, with two hooks removed and the remaining barb crimped to comply with Mongolian law, which requires single barbless hooks. Anglers used Trilene 8-lb test monofilament line, and a barrel swivel was fixed 50 cm above the lure. Fly fishing was conducted with an 8.5 foot 5-wt Orvis fly rod and a Clearwater Classic III fly reel with 5X tippet (Rio Powerflex brand). Dry flies were restricted to size 14 and 16 Parachute Adams and Royal Wulff patterns, and nymphs were restricted to a beadhead Prince Nymph and a non-beadhead Hare's Ear pattern of the same size (Figure S1). For both species, there were minimal differences in catch rates (Figure S2) and size selectivity (Figure S3) between the dry fly and nymph patterns.

Fishing events consisted of 40 min of active angling by two fishermen at a single site, equally divided between spinning and fly fishing. Time spent processing captured fish and changing lures and gear was not included in the total fishing time to avoid artificially creating hyperstable catch rates due to handling time limitations (Korman & Yard, 2017). Fishing was carried out by four skilled recreational anglers with an average of 31 years of experience fishing on spinning gear and 25 years of experience fly fishing. This is similar to the median of 30 years of overall fishing experience and 18 years of fly-fishing experience observed in international ecotourist anglers in Mongolia (Golden et al., 2019). For each fishing event, two anglers fished the site simultaneously such that both gear types were presented to the fish at the same time, rotating rods after 20 min to control for angler skill with each gear following Arlinghaus et al., (2017). The angler using fly-fishing gear changed between a nymph and a dry fly halfway through each 20-min period. The gear each angler started with, and the type of fly (dry fly vs nymph) used by the fly fishers in the initial 10-min period, were randomised with a coin flip to control for the possibility that catch rates decreased over the course of a fishing event, regardless of gear type and angler skill. Anglers were instructed to fish as they normally would within the constraints imposed by the study to maximise their fishing success in terms of total length of fish caught per fishing event.

Each fish caught was landed, measured (total length, mm), and the anal fin was clipped to permit identification of previously captured fish. Time of capture, site, angler identity, gear used, species and the number of casts from the beginning of the 10-min period using that gear type were recorded by dedicated note takers. As in most recreational angling, some fish were lost before they could be landed, and these were recorded and the loss noted. The recreational fishing protocol was approved by Rutgers University's Institutional Animal Care and Use Committee (Protocol # PROTO201900052).

Environmental variables were measured immediately before each fishing event. Water and air temperature (°C), barometric pressure (mm Hg), dissolved oxygen (mg/l and % saturation), conductivity (µS/cm) and total dissolved solids (mg/l) were measured using a YSI Professional Series probe. Water turbidity was measured in formazin nephelometric units (FNU) using a Hach 2100Qis portable turbidimeter. YSI measurements and turbidity samples were taken in midstream adjacent to each fishing site. Weather (sunny, partly cloudy, cloudy, rain) was recorded from visual observation before each fishing event. River stage (cm) was recorded at the beginning and end of each fishing day.

2.2 | Statistical analyses

Generalised linear mixed effects models (GLMMs) were fit to the catch data to explain variation in overall catch rates and species-specific catch rates for lenok and grayling. Because they were in the form of count data, catch rates were modelled using a Poisson distribution. For all models, the response variable was in the form of landed fish per angler per 20-min interval, to account for angler-specific variation as a random effect and gear type as a fixed effect. All models were fit in R version 3.6.0 using the "lme4" package version 1.1–21 (Bates et al., 2015; R Core Team, 2019). Principal component analysis (PCA) was conducted on the environmental covariates, and the first principal component was extracted and used as a candidate explanatory variable in the model selection process described below (see Appendix). River stage was included as a candidate explanatory variable in the form of the standardised difference in stage from the previous day (referred to throughout as "change in river stage") to capture the known importance of changes in river level on fish movement and foraging.

After determining the best random effect structure using AIC_C (corrected Akaike Information Criterion; Hurvich & Tsai, 1989), maximal models were fit that included standardised turbidity, change in river stage, time of day, weather, Julian day, gear type and the first principal component of the PCA. For overall catch rate and lenok catch rates, interactions between turbidity and change in river stage with gear type were also incorporated into candidate models, reflecting the *a priori* hypothesis that the effect of these environmental factors depends on fishing gear. However, gear interactions were not tested for grayling catch rates because the majority (90.9%) of grayling were caught by fly fishing. Nested candidate models that represented different hypotheses about the importance of key variables turbidity, change in river stage, and gear and the interaction between them were competed using AIC_C following Betini et al. (2017). Model fit was assessed using marginal and conditional coefficients of determination calculated with the trigamma method (R^2; Nakagawa & Schielzeth, 2013) and the "DHARMa" package version 0.2.6 in R (Hartig, 2019). The partial effects of each parameter included in the best-fit model were calculated and plotted using the "effects" package version 4.1–3 in R (Fox, 2003; Fox & Weisberg, 2019).

3 | RESULTS

3.1 | Overall catch rates

Eighty, 40-min fishing events were conducted across 24 sites for a total of 320 observations (two 20-min observations per angler in each fishing event). 398 total fish were landed across 5 species, with grayling and lenok accounting for 27% and 32% of the total catch, respectively (Table S1). The majority of captures were on fly-fishing gear (n = 305), with about a quarter of fish caught on spinning gear (n = 93) (Figure 2). Captures on fly-fishing gear were relatively evenly distributed between dace *Leuciscus leuciscus* (L.) (n = 139, a non-target species), grayling (n = 100) and lenok (n = 66). In contrast, 70% of spinning gear captures were lenok (n = 65), with ten or fewer captures each of grayling, dace, perch *Perca fluviatilis* L. and taimen *Hucho taimen* Pallas. Of the 398 fish landed, only two grayling and one perch were previously captured during the study, as indicated by the presence of a fin clip. An additional 97 fish were hooked but not landed. Since most of these could not be identified to species, they were excluded from the analysis.

The model that best explained patterns of variation in overall catch rates of landed fish included main effects for turbidity, change in river stage, gear and interaction terms between turbidity and gear

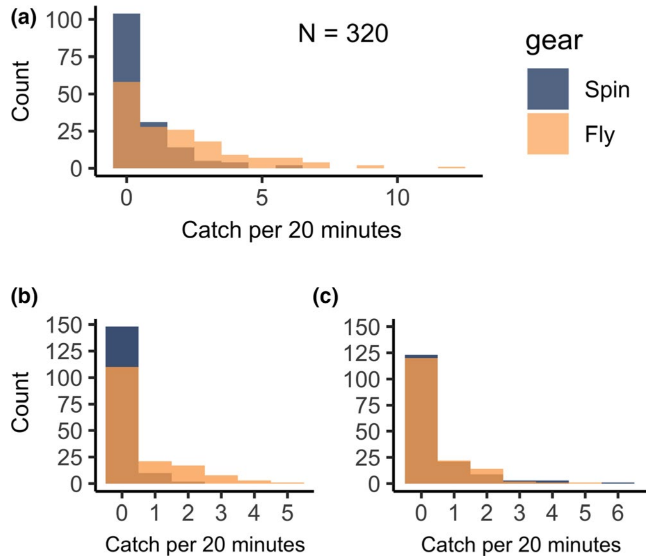

FIGURE 2 Histogram of (a) overall catch rates per 20 min of experimental fishing, (b) catch rates of grayling and (c) catch rates of lenok. All plots are divided into catches on spinning gear (dark blue) and fly gear (orange)

and between change in river stage and gear (Table S2). It included an angler random effect and a random effect for fishing site nested within sampling location (Eg-Uur or Eg-Selenge). A candidate model that included all of these variables and a fixed effect for time of day was similarly supported by AIC_C (ΔAIC_C = 1.90), but it included an additional parameter that did not improve model likelihood, so this model was rejected (following Arnold, 2010). All other candidate models had ΔAIC_C >2 (Table S2). All fixed effects in the best-fit model were significant at the p < 0.01 level except for change in river stage (p = 0.27), which was retained because its interaction with gear type was significant (p = 0.009) (Table 1).

The effect of both turbidity (p = 0.005) and change in river stage (p = 0.009) depended on gear type. Specifically, increased turbidity and positive change in river stage reduced catch rates on fly-fishing gear, while for spinning gear, catch rates declined exponentially with increased turbidity, but were unaffected by increases in river stage from the previous day (Figure 3). For an increase in turbidity from 5 to 35 FNU and an increase in river stage from −10 to 15 cm from the previous day, such as occurred during the study period following three days of continual rain, the model predicted a decrease in fly-fishing captures from 1.7 to 0.8 fish per 20 min for an average angler at an average site. For spinning gear, the model predicted a decrease from 0.9 to 0.3 fish per 20 min for the same change in conditions. Overall, the random effects, which represented variability among anglers and fishing locations, explained about the same amount of variation in catch rates as the variables of interest did. Specifically, the fixed effects of turbidity, change in river stage and fishing gear explained 28% of the variation in catch rates (marginal adjusted R^2), while the model as a whole (fixed and random effects; conditional adjusted R^2) explained 59% of the variation (Table 1).

TABLE 1 Fixed and random effects of the model that best explained variation in log-transformed catch rates of all fish

Fixed effects		β (*SE*)
Intercept		−1.11 (0.46)*
Standardised turbidity		−0.94 (0.25)***
Standardised difference in stage from previous day		0.19 (0.17)
Gear (fly)		1.22 (0.15)***
Turbidity * Gear (fly)		0.66 (0.24)**
Difference in stage * Gear (fly)		−0.41 (0.16)**
Random effects	**Num. obs.**	**Variance**
Event:camp	76	0.35
Angler	4	0.22
Camp	2	0.25
n = 304		
Marginal Adj R^2 = 0.27		
Conditional Adj R^2 = 0.57		

Note: Coefficient estimates (β) and standard errors (*SE*) of fixed effects are shown, and number of observations and variance of random effects is shown. Marginal and conditional adjusted R^2 values were calculated using the trigamma function.

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

3.2 | Species-specific catch rates

Grayling were much more vulnerable to fly-fishing gear than to spinning gear, with 91% of grayling captures occurring on fly gear ($n = 110$) and only 9% on spinning gear ($n = 10$) (Table S1). For this reason, a model explaining grayling catch rates was only fitted to captures on fly-fishing gear. Four candidate models to explain grayling catch rates were similarly supported by AIC_C <2. All of these models included a highly significant turbidity term ($p < 0.001$), with some also including non-significant terms for the first principal component of the environmental variables, time of day and change in river stage from previous day (Table S3). Since the coefficient estimates for turbidity were similar across all supported models, and the additional parameters improved the model likelihoods only marginally, only the parameter estimates from the most parsimonious model are reported (following Arnold, 2010). This model included a turbidity fixed effect and random effects for angler and for fishing event nested within fishing site (Table 2). Grayling catch rates on fly-fishing gear decreased exponentially as turbidity increased ($p = 0.001$) (Figure 4a). An increase in turbidity from 5 FNU to 35 FNU decreased catch rates from 0.8 to 0.2 fish per 20 min. The model's fixed effects explained 17% of the variation in grayling catch rates, and the model as a whole explained 41% of the variation.

Lenok were caught equally often on spinning gear and fly gear (49.6% and 50.4%, respectively) (Table S1). Variation in lenok catch rates was best explained by a model that included fixed effects for turbidity, gear type, change in river stage, an interaction between turbidity and gear, and random effects for angler and fishing event (Table S4). The effects of turbidity ($p = 0.003$) and the turbidity/gear interaction ($p = 0.004$) were significant, while the main effect of change in river stage was marginally non-significant ($p = 0.06$) (Table 3). Increased turbidity reduced catch rates on spinning gear exponentially, with the greatest effect occurring at low values of turbidity. Catch rates on fly were stable across the range of observed values for turbidity (Figure 4b). Increased river stage from the previous day decreased catch rates slightly, and this effect did not depend on gear type (Figure 4c). On spinning gear, the model predicted catch rates of 0.5 fish per 20 min when turbidity was 5 FNU and river stage had dropped by 10 cm from the previous day. When turbidity was 35 FNU and river stage had increased 15 cm from the previous day, such as occurred after three days of rain during the study period, the model predicted catching only 0.1 lenok per 20 min. By contrast, the model predicted fly catch rates of 0.2 and 0.1 fish per 20 min for the same interval. Overall, the fixed effects explained only 5.3% of the variation in lenok catch rates, while the model as a whole explained 23% of the variation.

4 | DISCUSSION

Standardised experimental fishing observations showed that, as predicted, both increased turbidity and increased river stage reduced catch rates for lenok and grayling by both gear types. Across the board, turbidity had a greater effect on catch rates than changes in river stage. The influence of turbidity was greatest in relatively clear water, with the greatest declines in catch rates occurring when turbidity increased from near zero to about 40 FNU. Contrary to expectations, fly-fishing gear outperformed spinning gear in this fishery, retaining higher catch rates than spinning gear across a range of environmental conditions (Figure 3). For example, the overall catch rates model predicted that catch rates of all fish would decline 86% on spinning gear and only 44% on fly-fishing gear with an increase in turbidity from 0 to 40 FNU. For lenok, spinning gear was more effective under normal water conditions, but above a low threshold of turbidity, fly-fishing gear was more effective (Figure 4b). Fly fishing was even more effective for grayling than for lenok, accounting for 91% of grayling captures in this study, regardless of environmental conditions. The most parsimonious model fit to grayling catch rates, which had fewer observations, only included a single fixed effect for turbidity. This suggests that changing river stage had a weaker influence on catch rates that could only be detected with greater statistical power. For all models, the random effects for angler and fishing location explained a greater proportion of the variation in catch rates than the fixed effects did. The degree of variability explained by the fixed effects (marginal adjusted R^2) and the model as a whole (conditional adjusted R^2) varied greatly among models. The model fit to overall catch rates had the most explanatory power, with the fixed effects explaining 27% of the variation (marginal adjusted R^2). The model fit to lenok catch rates alone had the least, with the model as a whole only accounting for 23% of the variation in catch rates and the fixed effects explaining 5%. None of the covariates that might have

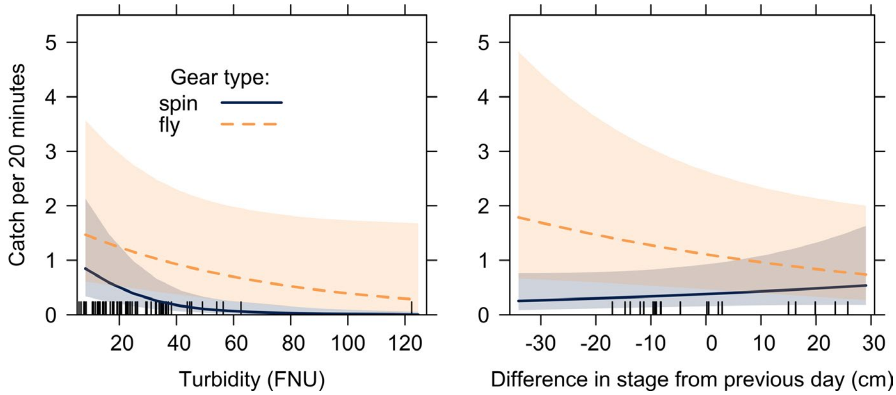

FIGURE 3 The partial effects of both turbidity (formazin nephelometric units, FNU) and change in river stage from the previous day (centimetres) on overall catch rates per angler per 20 min of experimental fishing. Partial effects for fly-fishing gear are indicated with an orange dashed line, and spinning gear is indicated with a solid dark blue line. 95% confidence intervals are indicated with shaded bands. The distribution of observations is indicated with a rug at the bottom of each plot

TABLE 2 Fixed and random effects of the model that best explained variation in log-transformed catch rates of grayling on fly-fishing gear

Fixed effects	β (*SE*)	
Intercept	−1.47 (0.38)***	
Standardised turbidity	−1.04 (0.32)***	
Random effects	**Num. obs.**	**Variance**
Event:site	76	0.52
Site	24	0.66
Angler	4	0.14
$n = 152$		
Marginal Adj $R^2 = 0.16$		
Conditional Adj $R^2 = 0.41$		

Note: Coefficient estimates (β) and standard errors (*SE*) of fixed effects are shown, along with number of observations and the variance of random effects.

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

confounded the variables of interest, such as Julian day, time of day, barometric pressure and weather, significantly improved model fit.

The importance of turbidity in explaining catch rates matched previous experimental evidence that turbid water reduces many fishes' feeding rates and reaction distance to prey (Chapman et al., 2014). Because the angling gears used here passively imitate fish and invertebrate prey items moving on the surface and in the water column, fishes' encounter rate with these gears depends on the distance from which they can identify and react to prey. Mazur and Beauchamp (2003) found that some piscivorous salmonids' reaction distance declined almost 20% when turbidity was increased from 0.08 to 1.5 nephelometric turbidity units (NTU) in controlled experiments; note that the turbidity units NTU and FNU are considered equivalent (World Health Organization, 2017). Across a wider range of observed values, Harvey and White (2008) found that salmonid feeding success on benthic invertebrate prey declined by nearly 60% when turbidity increased from 0 to 100 NTU in an experimental setting. In the present study, catch rates declined exponentially with increasing turbidity, which matches the well-established experimental finding that turbidity and reaction distance are exponentially related (Hansen et al., 2013; Vogel & Beauchamp, 1999). Declines in reaction distance are likely to have outsized impacts on encounter rates with prey as reaction distance is a squared term in most foraging models (e.g. Jensen et al., 2006), that is a decline in reaction distance of 50% would yield a decline in prey encounter rates of 75%.

Lenok were more vulnerable to fly fishing than spinning gear under extreme water conditions, although lenok catch rates on spinning gear were higher under normal conditions. This contradicted the hypothesis that lenok would remain more vulnerable to spin fishing at high turbidities because of spinning lures' auditory/vibratory component, which was hypothesised to remain effective regardless of water clarity. One possible explanation for this unexpected result is provided by contrast degradation theory, which predicts that turbidity should reduce the visibility of distant objects more than that of objects that are nearby. Therefore, a given increase in turbidity should reduce the visibility of large prey items like fish, which can be observed from a distance, more than small prey items like invertebrates or plankton that are only visible within a small visual range (Utne-Palm, 2002). Consistent with this theory, De Robertis et al., (2003) found that turbidity had a greater effect on feeding rates of piscivorous fish than planktivorous fish in a controlled experiment. This theory can be extended to lure types that imitate differently sized prey items and hypothesise that spinning lures, which imitate larger prey, should be more sensitive to turbidity than the smaller fly-fishing lures used here. This suggests that the visual component of spinning lures may be more important than originally assumed or that lenok forage primarily using visual cues.

Although its effect was smaller and less consistent than that of turbidity, change in river stage also affected catch rates. Change in river stage from the previous day, the metric used here, provided a proxy for river flow, which has well-established effects on fish activity levels and movement patterns. Many

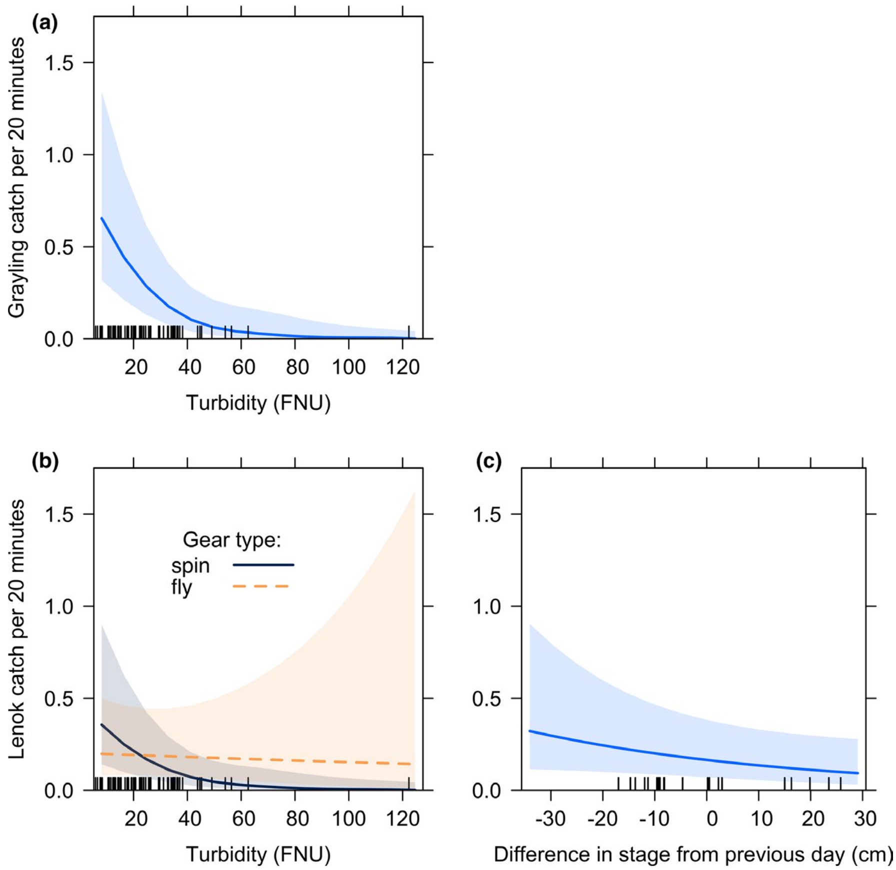

FIGURE 4 The partial effects of turbidity (formazin nephelometric units, FNU) and change in river stage from the previous day (centimetres) on catch rates of (a) grayling and (b,c) lenok per angler per 20 min of experimental fishing. Partial effects for fly-fishing gear are indicated with an orange dashed line, and spinning gear is indicated with a solid dark blue line. 95% confidence intervals are indicated with shaded bands. Partial effects plots with a single blue line do not depend on an interaction with fishing gear

TABLE 3 Fixed and random effects of the model that best explained variation in log-transformed catch rates of lenok on fly and spinning gear

Fixed effects		β (s.e.)
Intercept		−1.95 (0.45)***
Standardised turbidity		−0.92 (0.31)**
Standardised difference in stage from previous day		−0.31 (0.17)
Gear (fly)		0.28 (0.21)
Turbidity * Gear (fly)		0.86 (0.30)**
Random effects	**Num. obs.**	**Variance**
Event	76	0.95
Angler	4	0.53
$n = 304$		
Marginal Adj $R^2 = 0.05$		
Conditional Adj $R^2 = 0.23$		

Note: Coefficient estimates (β) and standard errors (*SE*) of fixed effects are shown, along with number of observations and the variance of random effects.
***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

studies of fish movement patterns in artificially manipulated waterways, like the tailraces of hydropower dams, have established that pulses of flow increase variability in fish movement and feeding behaviour (Larranaga et al., 2018; Rocaspana et al., 2019). For example, Larranaga et al., (2018) found that juvenile Arctic charr *Salvelinus alpinus* L. increased their activity rate, swam more quickly and attacked prey at longer distances in low-flow conditions and that they stopped moving entirely in high flow. This pattern could be explained by opportunistic feeding on the increased drift of invertebrates produced by high-flow events and could underlie the increased catch rates observed in the present study on days when river stage had dropped from the previous day. Supporting this explanation, the estimated effect of changes in river stage was greatest for overall catch rates on fly-fishing gear (Figure 3), which imitate drifting invertebrate prey. These results suggest that thunderstorms could make Mongolian salmonids' feeding behaviour more varied, producing more uncertain catch rates for anglers, and that periods after thunderstorms when water levels drop may be hotspots of fish feeding activity and susceptibility to fishing gear. These findings are relevant in the context of the proposed Egiin Gol Hydropower Project (EGHPP), which would construct an 82 m high hydropower dam immediately downstream of the Eg-Selenge fishing site (Figure 1). Artificially manipulated flow, along with the obvious stressor of habitat fragmentation produced by dam construction, could intensify the stressors of climate change-induced extreme water conditions for these fish.

The two gear types evaluated here are strongly associated with two distinct demographic groups of anglers in this fishery. Gear effectiveness under extreme water conditions could influence these two groups future fishing success as climate change intensifies. The demographic that most often uses fly-fishing gear in Mongolia is international ecotourist anglers (Golden et al., 2019), who primarily target taimen but also occasionally fish for lenok and grayling when taimen is not available. Taimen is listed as vulnerable on the IUCN Red List of Endangered Species (Hogan & Jensen, 2013), and as threats against the species intensify, international taimen anglers may rely more heavily on the fallback option of lenok and grayling. Less is known about the spin fishermen who target these species. However, fishing is becoming a more popular hobby among Mongolians, and most of the Mongolians observed fishing in the Eg-Selenge Watershed between 2016 and 2019 used spinning gear (A.S. Golden, unpubl. data). In this fishery, fly fishing by international ecotourists is generally associated with catch and release, and spin fishing by Mongolian anglers is associated with fishing for harvest. Therefore, this division between gears may also represent a tipping point between sustainable and unsustainable fishing (Jensen et al., 2009). However, some Mongolian activists are trying to promote the combination of fly fishing and catch and release practices to Mongolian fishermen (B. Baatar, pers. comm.). The results reported here suggest that fly fishing is a more effective technique for fishing in these rivers in adverse conditions, which in theory could help accelerate a transition towards more sustainable practices among Mongolia anglers.

This study is somewhat limited by the nature of the standardised observations. The catch rates observed here are likely lower than true recreational anglers would experience, because fishing was conducted in a randomised manner and was continued for a set duration regardless of fishing success. Additionally, the data included one extreme outlier, a fishing event conducted on a day when river stage had increased by 36 cm from the previous day and the turbidity was 122 FNU, twice the magnitude of the next highest turbidity observation (see Figure 3). Only one experimental fishing event was possible that day because of logistical challenges associated with the high water event. However, rerunning the analysis without this outlier did not change the outcome of the model selection process or the pattern of results (Figure S4).

As storm events become more frequent globally (Hartmann et al., 2013), the results presented here suggest that they could have significant and complex impacts on the interactions between fish and fishing gear. In the focal ecosystem of northern Mongolia, turbidity and increased river stage reduced catch rates for both lenok and grayling, regardless of gear type. Turbidity had the greatest effect on catch rates, suggesting that other sources of sediment loading, like bank erosion caused by overgrazing, could also impact fish catchability. The number of grazing animals in Mongolia has increased dramatically in the last 30 years, and cashmere goats, whose browsing behaviours can cause severe overgrazing, represent the greatest increase (Lkhagvadorj et al., 2013). The effects of turbidity on Mongolian salmonids are therefore relevant beyond the context of thunderstorms. Additionally, the gear-specific outcomes observed here could translate into divergent outcomes for two distinct angler demographic groups, or potentially into the adoption of new gears. Along with the more well-known threat of rising temperatures, climate change-induced increases in thunderstorm frequency and severity will have nuanced effects whose net results will depend on interactions between environmental change and social change.

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DATA AVAILABILITY STATEMENT

Data are available upon request.

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SUPPORTING INFORMATION

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