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1 **Behavioural adjustment of fish to temporal variation in fishing**

2 **pressure affects catchability: an experiment with angled trout**

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12 ***Summary***

13 In passive fisheries, such as angling, the fishing success depends on the ultimate decision of a fish to

14 ingest the bait, based on an individual's internal state, previous experience and threat perception. Fish

15 surviving capture by anglers are known to be less vulnerable, and catch rates usually quickly decline with

16 increasing fishing effort. Previous theoretical models have thus suggested fishing closures as a means to

17 recover responsiveness of fish to angling gear and maintain catch rates, yet empirical support remains

18 limited. In a controlled replicated pond experiment, we evaluated the effects of temporal variation in

19 fishing pressure on catch rates of rainbow trout (*Oncorhynchus mykiss*) by simulating short term fishing

20 closures. Fishing closures increased catch rates and population-level catchability, by reducing threat

21 perception at the population level and allowing released individuals to return to a vulnerable state. Our

22 experimental results show that periodic fishing closures benefit catch-rates but at the risk of aggravating

23 the likelihood of overharvesting.

24

25 ***Keywords:*** angling vulnerability, avoidance behaviour, catchability, temporal fishing closure, risk

26 allocation

27

Introduction

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29

30   In increasingly human-dominated landscapes, wildlife is facing new threats. Unlike with natural

31   predators animals have co-evolved with and developed specific defense tactics against (Johnsson 2009),

32   prey species may not necessarily had the time to adapt to threats and risks associated with a range of

33   human-related activities. They therefore need to increasingly rely on their non-specific vigilance to sense

34   the environment, and on their behavioural flexibility to adjust to new human-induced challenges (Van

35   Buskirk 2012). In urban environments for instance, roe-deer (*Capreolus capreolus*) inhabiting agricultural

36   landscapes display an increased vigilance to general disturbances that permits them to benefit from rich

37   feeding resources associated with these landscapes, despite increased exposure to hunting (Padié et al.

38   2015). In marine systems, relative to fish from fished areas, fish inhabiting protected no-take zones

39   show reduced flight initiation distances when experimentally exposed to spearfishing (Januchowski-

40   Hartley et al. 2013) and are more vulnerable to angling (Alós et al. 2015), indicating that fish respond

41   differently to the same cues based on the habitat specific perceived risk. These examples highlight that

42   in addition to evolutionary adaptation of populations to harvest selection (Claireaux et al. 2018; Olsen

43   and Moland 2011), the plastic behavioural response of animals to perceived threats appears to be a

44   central component of importance to harvest regulations, wildlife conservation and management (e.g.

45   Arlinghaus et al. 2017a; Paton et al. 2017; Goetze et al. 2018).

46   In passive gear-type fisheries, such as recreational angling, fishing success depends on the

47   ultimate decision of a fish to approach and ingest the bait (Lennox et al. 2017), which is influenced by an

48   individual's internal state, previous experience and risk perception which vary over time. The idea that

49   fish vary over time in their vulnerability to predators, and fishing gear, has been conceptualized in the

50   foraging arena theory (Ahrens et al. 2012), according to which fish move from vulnerable to invulnerable

51   states over time, as they adjust their behaviour and space use to balance risks (e.g. predation) and gains

52   (e.g. fitness associated gains through access to resources, social- and mating behaviour) (Cox and

53   Walters 2002; Ahrens et al. 2012). Rates, at which fish move from a vulnerable to an invulnerable state,

54   and vice versa, have classically been regarded as a function of spatial overlap between fish and gear, i.e.

55   encounter rate (Cox and Walters 2002). However, and especially for passive fishing gear, encounter

56   between fish and gear is not sufficient to lead to a capture event (Monk and Arlinghaus 2017). In

57   addition to spatial overlap of fish and gear deployment, vulnerability of fish to fishing gear may also vary

58   over time as a function of a fishes internal state (e.g. satiation level, parasitic load) and in response to

59   the exposure to threats and disturbances (Andersen et al. 2016), related to fishing activity for instance

60   (e.g. boat noise, gear deployment, alarm cues released by conspecifics).

61   In recreational fisheries, the concept of vulnerable pool dynamics has been used to model the

62   observation that with increasing fishing effort, catchability (i.e. population level vulnerability of fish)

63   does tend to quickly decrease (Cox and Walters 2002), either because the pool of vulnerable fish

64   decreases as fish get captured (Askey et al. 2006) and/or because increased exposure to fishing

65   increases their vigilance and reduces their vulnerability to fishing gear (Beukema 1969; van Poorten and

66   Post 2005; Arlinghaus et al. 2017b). From a management perspective, fisheries exploitation models

67   assuming total catch-and-release fisheries have suggested that periodic harvest strategies or temporal

68   fishing closures would be a means to maintain a larger pool of vulnerable fish and therefore maintain

69   high catch rates (Camp et al. 2015). However no experiment has been completed to test this idea.

70   Although catch-rates are known to decrease with increasing fishing effort (e.g. angler-hours per unit of

71   surface; Beukema 1970; Kuparinen et al. 2010; Wegener et al. 2018), it is, to the best of our knowledge,

72   unknown to what extent the temporal variation in fishing pressure, affects the avoidance response of

73   individual fish and overall catch rates.

74   Using a salmonid model, we explored the effects of temporal variation in fishing pressure on

75   catch rates under controlled experimental conditions (i.e. known population sizes, individually

76   identifiable fish, and standardized fishing treatments in replicated systems). We simulated short term

77   fishing closures and experimentally manipulated threat perception by exposing naïve hatchery reared

78   rainbow trout (*Oncorhynchus mykiss*) to different angling frequency treatments, i.e. variable intervals

79   between angling events but standardized for total fishing effort. We expect longer intervals between

80   fishing events to reduce threat perception in rainbow trout, leading to the maintenance of a larger pool

81   of vulnerable fish and therefore to higher catch rates.

Material and Methods

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Mesocosm setup and experimental fish

83

84   Full-scale replicated angling experiments were carried out between 21st September and 20th

85   October 2015 in four semi-natural ponds (dimensions: 30 x 24 m, average depth: 2 m) belonging to the

86   Swedish anglers association *Sportfiskarna* in Gothenburg, Sweden (57.693°N, 12.037°E). Each pond was

87   supplied with unfiltered lake water (Lake *Delsjön*) and removed from vegetation to create comparable

88   conditions prior to the experiment. 150 rainbow trout (mean ± s.d: mass M = 382.2 ± 56.1 g; fork

89   length FL = 31.3 ± 1.6 cm) and 150 brown trout (*Salmo trutta*) (mean ± s.d: M = 392.9 ± 66.1 g; FL =

90   32.5 ± 1.7 cm) were stocked in equal densities in the ponds (25 of each species per replicated pond).

91   Both trout species originated from the same hatchery and were reared under comparable conditions

92   (*Källefalls Fiskodling*). The brown trout were F1 offspring from wild parents captured in the near-by Lake

93   *Vättern*. The rainbow trout were of a domesticated strain, now bred since 1997 within the hatchery and

94   used exclusively for stocking for angling in Swedish waters. Fish were supplied once a day with fish

95   pellets (Skretting T-2P Optiline ME SF; 1% of total body mass of fish in each pond), but could also feed

96   on naturally occurring prey, such as aquatic invertebrates and insects.

97   Prior to release to the ponds, fish were anesthetized (2-phenoxyethanol at 0.5 ml L^{-1}), measured

98   for initial body wet mass and FL, and a 23 mm passive integrated transponder (PIT-tag; HDX ISO

99   11784/11785, 0.6 g in air, Texas Instrument Inc.) was inserted into the coelomic cavity (using an 11-

100   blade scalpel) for individual identification during the angling trials. At the end of the experiment, fish

101   were anesthetized and final individual body wet mass and FL were measured to calculate specific growth

102   rates. Because of very low catch rates, likely induced by the presence of a large majority of mature

103   individuals (identified after draining the ponds at the end of the experiment), brown trout were

104   ultimately excluded from data analysis. Results on the relative catchability of rainbow trout and brown

105   trout are reported elsewhere in an independent experiment as part of the same project (Koeck et al.

106   2018). The present study thus focuses exclusively on catch rates of rainbow trout.

107 ***Fishing treatments***

108   The fishing experiments started after a 5 day period of acclimation in the experimental ponds and

109   consisted of three different duplicated angling intensity treatments, which were standardized for fishing

110   effort and only varied in terms of intervals between angling events. This way, effects related to

111   differences in fishing effort itself could be ruled out when investigating the response of fish to fishing.

112   Variable angling intensities were achieved by applying different intervals between fishing events

113   modulating angling frequencies. Treatment 1 corresponded to a 1 day interval, treatment 2 to a 4 days

114   interval and treatment 3 to a 7 days interval between successive fishing events (Fig. 1). Each replicate

115   received a total fishing effort E of 10 hours ($E = nb\ of\ anglers \times nb\ of\ hours \times nb\ of\ events$; Fig.

116   1). With four experimental ponds available, each treatment could be duplicated by repeating treatments

117   1 and 2 over time and rotating between ponds to avoid possible pond effects (Fig. 1).

118   Two common angling techniques were used simultaneously in the angling trials, natural baits and

119   artificial spinner lures (for more details on the angling methods, see Koeck et al. 2018). During each

120   angling event, two anglers were fishing for one hour while rotating every tenth minute within or

121   between ponds using alternatively natural bait or lure following a randomization schedule to control for

122   bias in fishing skills of anglers, site preference and gear effects. Landed fish were identified with a hand-

123   held PIT reader (BTS-ID, Helsingborg, Sweden) and kept in a holding tank until released to their initial

124   pond at the end of the fishing event. A fish could thus be captured only once per fishing event, but

125   recaptured at each new event.

126   *Data analysis*

127   Two semi-parametric Cox-proportional hazard regression models were used to compare the

128   capture rates between angling frequency treatments for right censored data, i.e. incorporating

129   information of caught and uncaught individuals. The first model included time until first capture of each

130   fish as response variable and was used to identify angling treatment effects on population level

131   vulnerability, i.e. to see if more or less individuals are at risk of capture for a given angling frequency

132   treatment. The second model allowed for repeated captures where all fish had the chance to be

133   captured at each angling event. This model was used to mimic a context of catch-and-release fishing,

134   accounting for recaptures in the assessment of total catch rates. The hazard function was of the form:

135    $h(t|z) = h_0(t) \exp(\beta),$

136   where h_0 is the baseline hazard and β is the hazard coefficient, estimated using a partial likelihood

137   function. Data analysis and graphical representations of survival curves were computed using the

138   package *survival* (Therneau 2014) and the package *survminer* (Kassambara and Kosinski 2018) for the *R*

139   statistical environment (R Core Team 2018).

140   **Results**

141   While in all treatments catch rates declined over time, strong differences were found between angling

142   frequency treatments in terms of number of captured fish and total catches (Table 1, Fig. 2). At the end

143   of the five angling events, 28, 40 and 46 fish were respectively captured in the 1-day, 4-days and 7-days

144   angling frequency treatments (respectively 56 %, 80 % and 92 %; Table 1). Additionally, the number of

145   recaptured individuals was also higher when angling was practiced at longer intervals between

146   successive angling events (Table 1, Fig. 3). Survival models accounting for time to first capture (Table 2,

147   Fig. 4) and accounting for time until capture including the possibility for recapture (Table 3) provided

148   similar model statistics (Tables 2, 3: similar hazard coefficient β between angling treatments). Both

149   models showed that the probability of survival was significantly lower when angling was practiced at 7-

150   days intervals and highest when it was practiced every day (Fig. 4), with a respective 57 % and 79 %

151   increase in hazard of being captured in the 4 days and 7 days angling frequency treatments compared to

152   when fishing was practiced daily (Table 2, 3).

153   ## *Discussion*

154   While it is known that fish that have experienced hooking display a reduced vulnerability to capture

155   (Young and Hayes 2004; Askey et al. 2006; Lennox et al. 2017; Wegener et al. 2018) and that catch rates

156   tend to quickly decline with increasing fishing effort (van Poorten and Post 2005; Kuparinen et al. 2010),

157   it is largely unexplored to what extent threat perception and temporal variation of fishing pressure plays

158   a role in the mechanism leading to observed hook avoidance and hyper depletion of catch. We found

159   that even short closures of just a few days had substantial impacts on catch rates. Catch rates of

160   rainbow trout were lower when angling in ponds was practiced at higher frequency (daily) as opposed to

161   a less frequent angling with either 4 or 7 day intervals, indicating that beyond total fishing effort, the

162   temporal variation in fishing pressure also affects avoidance behaviour of fish towards fishing gear. Our

163   results highlighted two mechanisms by which short term fishing closures affect catch rates: by increasing

164   the overall number of captured individuals (i.e., by increasing catchability), but also by increasing the

165   number of recaptures of previously captured and released fish (i.e., by increasing the rates at which fish

166   return to a vulnerable state).

167   While catch rates were generally declining with increasing frequency of fishing, indicative of

168   hook avoidance as reported elsewhere for salmonids (van Poorten and Post 2005; Askey et al. 2006), we

169   found an increase in number of recaptures in response to lower angling frequencies, indicating that

170   short-term fishing closures can allow captured individuals to recover from the acute physiological

171   hooking-related stress (reviewed in Cooke and Suski 2005) and return to vulnerable states within a few

172   days (as assumed in Camp et al. 2015). Rainbow trout, particularly of domesticated strain, is a relatively

173   fast recovering species (Ruane et al. 1999), which is confirmed by our results showing that recaptures

174   are significantly increased when allowing only a few days recovery between angling events. Similar fast

175   recovery times of just a few days have been reported for other freshwater and marine fish species in the

176   wild after catch and release angling when handled following best practice (Suski et al. 2003; Ferter et al.

177   2015). Recovery from capture related stressors is however not alone a sufficient condition for a fish to

178   return to a vulnerable state after catch and release. For example, although physiologically recovered

179   after just 12 hours (Rapp et al. 2014), prolonged periods of hook-avoidance was observed in carp

180   (*Cyprinus carpio*) for up to a year after an initial capture event (Beukema 1969; Raat 1985), indicating

181   species-specific differences in learning abilities (Coble et al. 1985) to affect the rates at which hooking

182   experienced fish return to a vulnerable state.

183   Importantly, under low angling frequency, in addition to higher rates of recapture, we also

184   observed an increase in the total number of captured fish, suggesting population-level decrease in

185   threat perception and vigilance level rendering a larger pool of fish vulnerable to capture. Previous

186   studies have shown that individual fish differ in their intrinsic vulnerability to capture and have

187   identified several drivers related to individual differences in risk-taking behaviour and stress resilience

188   (also termed coping styles; Louison et al. 2017; Koeck et al. 2018). In particular, it has been shown that

189   individual differences in the activation of the hypothalamic–pituitary–interrenal axis (HPI axis) were

190   related to individual differences in vulnerability to angling in rainbow trout (Koeck et al. 2018). Although

191   this remains to be tested, less frequent angling may possibly cause moderately stress resilient fish, that

192   are generally less vulnerable to angling (Louison et al. 2017; Koeck et al. 2018), to move into a

193   vulnerable state rendering them catchable and increasing population-level catchability.

194   While a number of studies have highlighted differences in wariness of fish from fished and

195   fishing free-habitats (e.g., Januchowski-Hartley et al. 2013; Alós et al. 2015), i.e. a behavioural

196   adjustment to spatial differences in threat perception, fewer studies have explored the effects of

197   temporal variation in fishing pressure. However, following the '*Predation Risk Allocation Hypothesis*'

198   (Lima and Bednekoff 1999), prey adopt and adjust the strength of anti-predator tactics also to the

199   temporal variation of the threat (Foam et al. 2005; Brown et al. 2006). Our results confirm that the

200   temporal dimension of threat perception is an important driver of behavioural adjustment and

201   responsiveness to angling gear. In terms of management implications, our experimental study is of

202   relevance to understanding the impacts of temporal fishing closures in a catch-and-release or put-and-

203   take fishing context and also extends to periodic or rotating harvest fishing contexts, including fisheries

204   with naturally temporal varying fishing intensities (e.g., where fishing is concentrated on weekends and

205   absent during weekdays). While these different management strategies aim at increasing fishing

206   efficiency and catch rates (Camp et al. 2015; Wegener et al. 2018; Abesamis et al. 2014; Goetze et al.

207   2016; Goetze et al. 2018; Chagaris et al. 2019), their effects on fish populations are substantially

208   different. In catch-and-release type fisheries, short term fishing closures are expected to reduce the

209   general threat perception of fish, thereby reducing the depletion of catch normally observed under

210   sustained fishing effort, which in turn can positively affect anglers' satisfaction (Camp et al. 2015;

211   Wegener et al. 2018). In periodically harvested areas however, the reduced wariness of fish in response

212   to fishing closures may accentuate the risks of overfishing (Goetze et al. 2016). Because of its

213   experimental nature, this study is limited in its' spatio-temporal scale, and even though realistically

214   representing pond and small-scale put-and take fisheries, the transferability of results to larger systems

215   need to be further evaluated. To fully appreciate the extend at which temporal variation in fishing effort

216   affects catchability of fish beyond the context of this study and for temporal fishing closures to be

217   effectively implemented, further investigations are required across fisheries context and for wild

218   populations.

219   Our results raise further questions regarding threat identification and avoidance learning

220   mechanisms in the context of fishing. While direct experience or private learning are obvious ways to

221   take informed decisions, animals in the wild usually do not have the opportunity for trial-and-error

222   when for instance escaping a predator or a fishing gear (Mathis et al. 1996). Fish may therefore, as also

223   demonstrated in many other taxa (Danchin et al. 2004), rely on social information use, i.e. on

224   information transmitted by conspecifics, to increase their performances in various contexts (Brown and

225   Laland 2003). In a context of threat, socially transmitted visual and chemical alarm cues produced by

226   injured skin of conspecifics (Wisenden 2000; Hall and Clark 2016) are most commonly used to inform

227   about risk-levels and adopt an adapted behavioural response. Only a couple of studies have so far

228   investigated the importance of social learning in a recreational fisheries context, showing no effect

229   (Wegener et al. 2018) or only a trend for the effect of social information use on hook avoidance (Lovén

230   Wallerius et al. in press). Because of known species-specific differences in learning abilities (Coble et al.

231   1985), it remains to be fully explored whether social information use affects the avoidance response of

232   individual fish and overall catch rates, which is of particular interest to catch-and-release fishing in the

233   context of periodic fishing closures.

234   *Conclusion.* Our results indicate that short term fishing closures have the potential to

235   substantially increase catch rates by altering the general threat perception, rendering less risk-taking

236   individuals more vulnerable, and by allowing the highly vulnerable fraction of the population to recover

237   and return to a vulnerable state after initial capture. Our work provides experimental evidence that, in

238   addition to evolutionary adaptation of populations to harvest selection, the behavioural flexibility of

239   animals to temporal variation of anthropogenic threats is of relevance to fish conservation and

240   management.

241

Ethical Statement

These experiments were approved by the Ethical Committee for Animal Research of the University of Gothenburg (license nr° 15.2014) and comply with Swedish and European law.

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384   *Tables*

385

386   **Table 1**. Number of captured fish (and number of recaptures) per replicated pond (R1, R2) and

387   treatment. Per treatment N=50 rainbow trout, i.e. 25 per replicated pond.

Treatment	Captured fish		Cumulated catch	Proportion of captured fish
	R1	R2		
1-day	12 (2)	16 (1)	31	56%
4-days	19 (5)	21 (7)	52	80%
7-days	25 (8)	21 (10)	64	92%

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389

390   **Table 2**. Cox-proportional hazards regression model examining the effect of angling frequency

391   treatments (1, 4 and 7 days of interval between successive angling days) on the hazard of being

392   captured by angling of rainbow trout. The response variable in this model is time until first capture,

393   assuming that fish are removed from the population. The 1-day angling treatment is coded as the

394   baseline level of the treatment factor of the model.

	β	e^{β}	$se(\beta)$	z	p-value
Treatment 4-days	0.580	1.786	0.247	2.35	0.019
Treatment 7-days	0.758	2.134	0.242	3.13	0.0017

n = 150, number of events = 114, Likelihood ratio test = 10.98 on 2 df, p = 0.004

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398   **Table 3**. Cox-proportional hazards regression model examining the effect of angling frequency

399   treatments (1, 4 and 7 days of interval between successive angling days) on the hazard of being

400   captured by angling. In addition to the model in Table 2, this model allows for repeated events, i.e.

401   individuals are released back to the population and can be recaptured at successive events. The 1-day

402   angling treatment is coded as the baseline level of the treatment factor of the model.

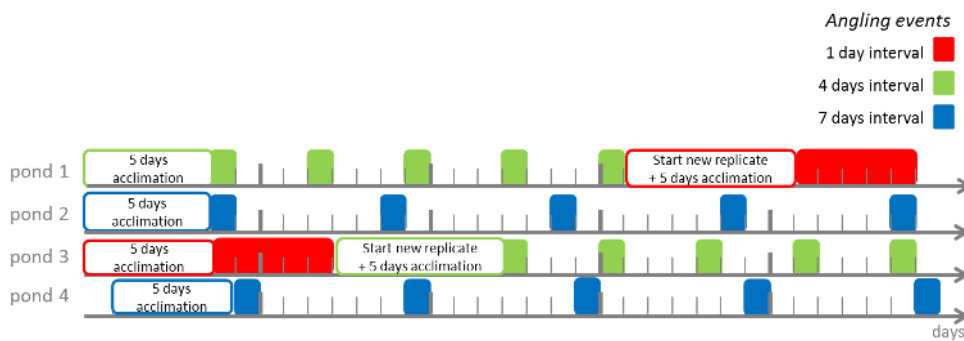|	β	e^{β}	$se(\beta)$	z	p-value
Treatment 4-days	0.574	1.776	0.227	2.53	0.0114
Treatment 7-days	0.790	2.204	0.219	3.61	0.0003
n = 750, number of events = 147, Likelihood ratio test = 14.4 on 2 df, p = 7e-04					

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Figures

Figure 1. Sampling design of the angling experiment: angling treatments were duplicated and differed only in the interval between successive angling days but corresponded to the same total fishing effort of 5 angling events.
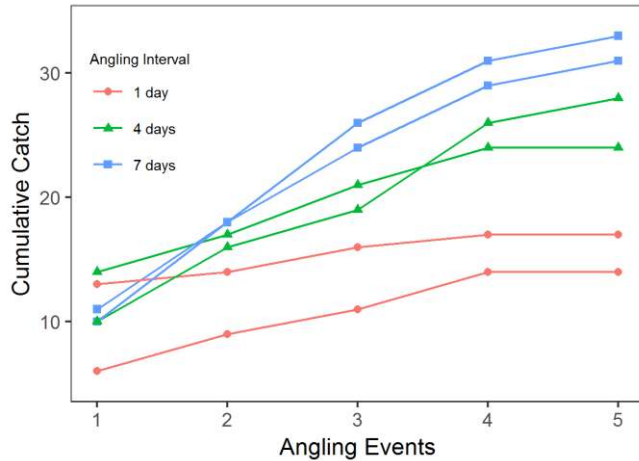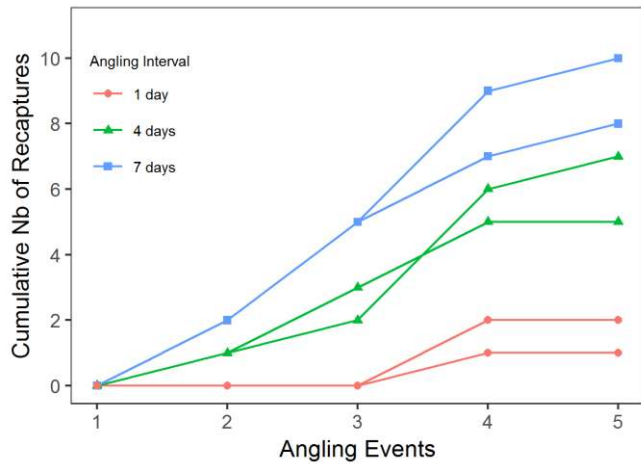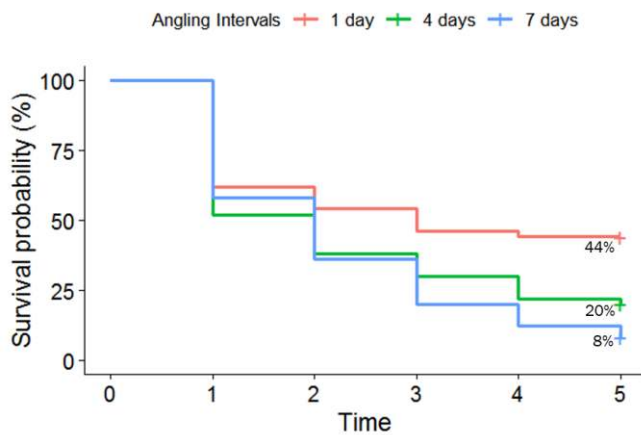

Figure 2. Cumulative catch in the two ponds per angling frequency treatment (1, 4 and 7 days intervals) over the successive angling events.

417

418 **Figure 3**. Cumulative recaptures in the two ponds per angling frequency treatment (1, 4 and 7 days

419 intervals) over the successive angling events.

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421

422 **Figure 4**. Survival plot representing the survival probability of rainbow trout at each successive angling

423 event (time 1 to 5) for the three angling frequency treatments (1, 4 and 7 days intervals), (i.e. the

424 response variable in the survival analysis corresponds to time until first capture only for each fish).