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ARTICLE

Behavioural adjustment of fish to temporal variation in fishing pressure affects catchability: an experiment with angled trout

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Abstract: In passive fisheries, such as angling, the fishing success depends on the ultimate decision of a fish to ingest the bait, based on an individual's internal state, previous experience, and threat perception. Fish surviving capture by anglers are known to be less vulnerable, and catch rates usually quickly decline with increasing fishing effort. Previous theoretical models have thus suggested fishing closures as a means to recover responsiveness of fish to angling gear and maintain catch rates, yet empirical support remains limited. In a controlled replicated pond experiment, we evaluated the effects of temporal variation in fishing pressure on catch rates of rainbow trout (*Oncorhynchus mykiss*) by simulating short-term fishing closures. Fishing closures increased catch rates and population-level catchability by reducing threat perception at the population level and allowing released individuals to return to a vulnerable state. Our experimental results show that periodic fishing closures benefit catch rates but at the risk of aggravating the likelihood of overharvesting.

Résumé : Dans les pêches passives, comme la pêche à la ligne, le succès de la pêche dépend de la décision d'un poisson d'ingérer l'appât, prise à la lumière de son état interne, son expérience antérieure et sa perception de la menace. Il est établi que les poissons ayant survécu à une prise par des pêcheurs à la ligne sont moins vulnérables, et les taux de prise baissent en général rapidement quand l'effort de pêche augmente. Si des modèles théoriques antérieurs ont suggéré que des fermetures de la pêche seraient un moyen de rétablir la susceptibilité des poissons aux engins de pêche à la ligne et de maintenir les taux de prise, l'information empirique appuyant cette hypothèse demeure limitée. Dans le cadre d'une expérience contrôlée en étangs répétés, nous avons évalué les effets des variations temporelles de la pression de la pêche sur les taux de prise de truites arc-en-ciel (*Oncorhynchus mykiss*) en simulant des fermetures de courte durée de la pêche. Ces fermetures font augmenter les taux de prise et la capturabilité à l'échelle de la population en réduisant la perception de la menace à cette échelle et en permettant aux spécimens relâchés de retourner à un état vulnérable. Nos résultats expérimentaux montrent que des fermetures périodiques de la pêche ont un effet bénéfique sur les taux de prise, mais risquent d'accroître la probabilité de surpêche. [Traduit par la Rédaction]

Introduction

In increasingly human-dominated landscapes, wildlife is facing new threats. Unlike with natural predators that animals have co-evolved with and developed specific defense tactics against (Johnsson 2009), prey species may not necessarily had the time to adapt to threats and risks associated with a range of human-related activities. They therefore need to increasingly rely on their nonspecific vigilance to sense the environment and on their behavioural flexibility to adjust to new human-induced challenges (Van Buskirk 2012). In urban environments for instance, roe deer (*Capreolus capreolus*) inhabiting agricultural landscapes display an increased vigilance to general disturbances that permits them to benefit from rich feeding resources associated with these landscapes, despite increased exposure to hunting (Padié et al. 2015). In marine systems, relative to fish from fished areas, fish inhabiting protected no-take zones show reduced flight initiation distances when experimentally exposed to spearfishing (Januchowski-Hartley et al. 2013) and are more vulnerable to angling (Alós et al. 2015), indicating that fish respond differently to the same cues based on the habitat-specific perceived risk. These examples highlight that in addition to evolutionary adaptation of populations to harvest selection (Claireaux et al. 2018; Olsen and Moland 2011), the plastic

behavioural response of animals to perceived threats appears to be a central component of importance to harvest regulations, wildlife conservation, and management (e.g., Arlinghaus et al. 2017a; Paton et al. 2017; Goetze et al. 2018).

In passive gear fisheries, such as recreational angling, fishing success depends on the ultimate decision of a fish to approach and ingest the bait (Lennox et al. 2017), which is influenced by an individual's internal state, previous experience, and risk perception, which vary over time. The idea that fish vary over time in their vulnerability to predators and fishing gear has been conceptualized in the foraging arena theory (Ahrens et al. 2012), according to which fish move from vulnerable to invulnerable states over time as they adjust their behaviour and space use to balance risks (e.g., predation) and gains (e.g., fitness-associated gains through access to resources, social and mating behaviour; Cox and Walters 2002; Ahrens et al. 2012). Rates, at which fish move from a vulnerable to an invulnerable state, and vice versa, have classically been regarded as a function of spatial overlap between fish and gear (i.e., encounter rate; Cox and Walters 2002). However, and especially for passive fishing gear, encounter between fish and gear is not sufficient to lead to a capture event (Monk and Arlinghaus 2017). In addition to spatial overlap of fish and gear

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Fig. 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 five angling events. [Colour online.]
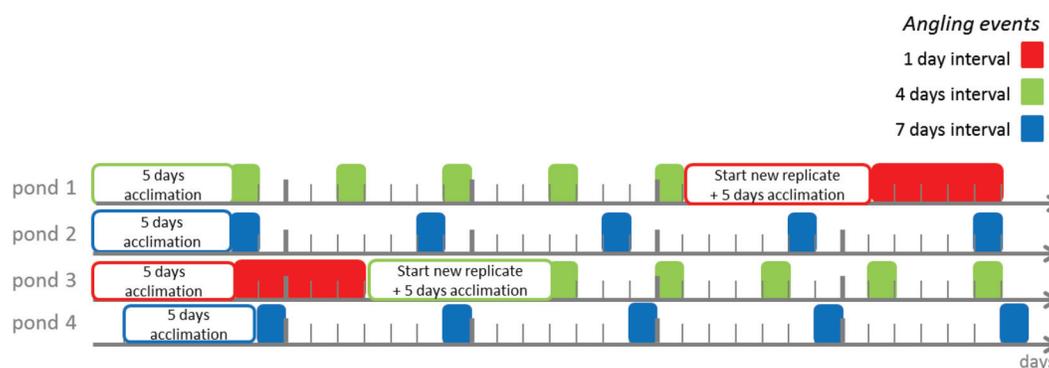
deployment, vulnerability of fish to fishing gear may also vary over time as a function of a fish's internal state (e.g., satiation level, parasitic load) and in response to the exposure to threats and disturbances (Andersen et al. 2016), related to fishing activity for instance (e.g., boat noise, gear deployment, alarm cues released by conspecifics).

In recreational fisheries, the concept of vulnerable pool dynamics has been used to model the observation that with increasing fishing effort, catchability (i.e., population-level vulnerability of fish) does tend to quickly decrease (Cox and Walters 2002), either because the pool of vulnerable fish decreases as fish get captured (Askey et al. 2006) and (or) because increased exposure to fishing increases their vigilance and reduces their vulnerability to fishing gear (Beukema 1969; van Poorten and Post 2005; Arlinghaus et al. 2017b). From a management perspective, fisheries exploitation models assuming total catch-and-release fisheries have suggested that periodic harvest strategies or temporal fishing closures would be a means to maintain a larger pool of vulnerable fish and therefore maintain high catch rates (Camp et al. 2015). However, no experiment has been completed to test this idea. Although catch rates are known to decrease with increasing fishing effort (e.g., angler hours per unit of surface; Beukema 1970; Kuparinen et al. 2010; Wegener et al. 2018), it is, to the best of our knowledge, unknown to what extent the temporal variation in fishing pressure affects the avoidance response of individual fish and overall catch rates.

Using a salmonid model, we explored the effects of temporal variation in fishing pressure on catch rates under controlled experimental conditions (i.e., known population sizes, individually identifiable fish, and standardized fishing treatments in replicated systems). We simulated short-term fishing closures and experimentally manipulated threat perception by exposing naïve hatchery-reared rainbow trout (*Oncorhynchus mykiss*) to different angling frequency treatments (i.e., variable intervals between angling events but standardized for total fishing effort). We expect longer intervals between fishing events to reduce threat perception in rainbow trout, leading to the maintenance of a larger pool of vulnerable fish and therefore to higher catch rates.

Materials and methods

Mesocosm setup and experimental fish

Full-scale replicated angling experiments were carried out between 21 September and 20 October 2015 in four seminatural ponds (dimensions: 30 m × 24 m, mean depth: 2 m) belonging to the Swedish anglers association Sportfiskarna in Gothenburg, Sweden (57.693°N, 12.037°E). Each pond was supplied with unfiltered lake water (Lake Delsjön), and vegetation was removed to create comparable conditions prior to the experiment. 150 rainbow trout (mean ± SD: mass (M) = 382.2 ± 56.1 g; fork length (FL) = 31.3 ± 1.6 cm) and 150 brown trout (*Salmo trutta*) (mean ± SD:

M = 392.9 ± 66.1 g; FL = 32.5 ± 1.7 cm) were stocked in equal densities in the ponds (25 of each species per replicated pond). Both trout species originated from the same hatchery and were reared under comparable conditions (Källefalls Fiskodling). The brown trout were F1 offspring from wild parents captured in the nearby Lake Vättern. The rainbow trout were of a domesticated strain, now bred since 1997 within the hatchery and used exclusively for stocking for angling in Swedish waters. Fish were supplied once a day with fish pellets (Skretting T-2P Optiline ME SF; 1% of total body mass of fish in each pond), but could also feed on naturally occurring prey, such as aquatic invertebrates and insects.

Prior to release to the ponds, fish were anesthetized (2-phenoxyethanol at 0.5 mL·L⁻¹), measured for initial body wet mass and FL, and a 23 mm passive integrated transponder (PIT tag; HDX ISO 11784/11785, 0.6 g in air, Texas Instrument Inc.) was inserted into the coelomic cavity (using an 11-blade scalpel) for individual identification during the angling trials. At the end of the experiment, fish were anesthetized and final individual body wet mass and FL were measured to calculate specific growth rates. Because of very low catch rates, likely induced by the presence of a large majority of mature individuals (identified after draining the ponds at the end of the experiment), brown trout were ultimately excluded from data analysis. Results on the relative catchability of rainbow trout and brown trout are reported elsewhere in an independent experiment as part of the same project (Koeck et al. 2019). The present study thus focuses exclusively on catch rates of rainbow trout.
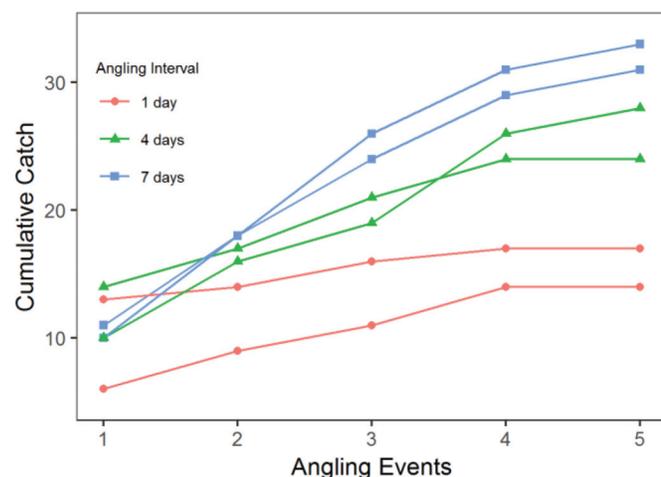
Fishing treatments

The fishing experiments started after a 5-day period of acclimation in the experimental ponds and consisted of three different duplicated angling intensity treatments, which were standardized for fishing effort and only varied in terms of intervals between angling events. This way, effects related to differences in fishing effort itself could be ruled out when investigating the response of fish to fishing. Variable angling intensities were achieved by applying different intervals between fishing events modulating angling frequencies. Treatment 1 corresponded to a 1-day interval, treatment 2 to a 4-day interval, and treatment 3 to a 7-day interval between successive fishing events (Fig. 1). Each replicate received a total fishing effort E of 10 h (E = number of anglers × number of hours × number of events; Fig. 1). With four experimental ponds available, each treatment could be duplicated by repeating treatments 1 and 2 over time and rotating among ponds to avoid possible pond effects (Fig. 1).

Two common angling techniques were used simultaneously in the angling trials, natural baits, and artificial spinner lures (for more details on the angling methods, see Koeck et al. 2019). During each angling event, two anglers fished for 1 h while rotating

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

Treatment	Captured fish		Cumulated catch	Percentage 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%

Note: Per treatment: $n = 50$ rainbow trout (i.e. 25 per replicated pond).

Fig. 2. Cumulative catch in the two ponds per angling frequency treatment (1-, 4-, and 7-day intervals) over the successive angling events. [Colour online.]

Fig. 3. Cumulative recaptures in the two ponds per angling frequency treatment (1-, 4-, and 7-day intervals) over the successive angling events. [Colour online.]

Table 2. Cox-proportional hazards regression model examining the effect of angling frequency treatments (1-, 4-, and 7-day intervals between successive angling days) on the hazard of being captured by angling of rainbow trout.

Treatment	β	$\exp(\beta)$	SE (β)	z	p
4 days	0.580	1.786	0.247	2.35	0.019
7 days	0.758	2.134	0.242	3.13	0.0017

Note: $n = 150$, number of events = 114, likelihood ratio test = 10.98, df = 2, $p = 0.004$. The response variable in this model is time until first capture, assuming that fish are removed from the population. The 1-day angling treatment is coded as the baseline level of the treatment factor of the model.

every tenth minute within or among ponds using alternatively natural bait or lure following a randomization schedule to control for bias in fishing skills of anglers, site preference, and gear effects. Landed fish were identified with a hand-held PIT reader (BTS-ID, Helsingborg, Sweden) and kept in a holding tank until released to their initial pond at the end of the fishing event. A fish could thus be captured only once per fishing event, but recaptured at each new event.
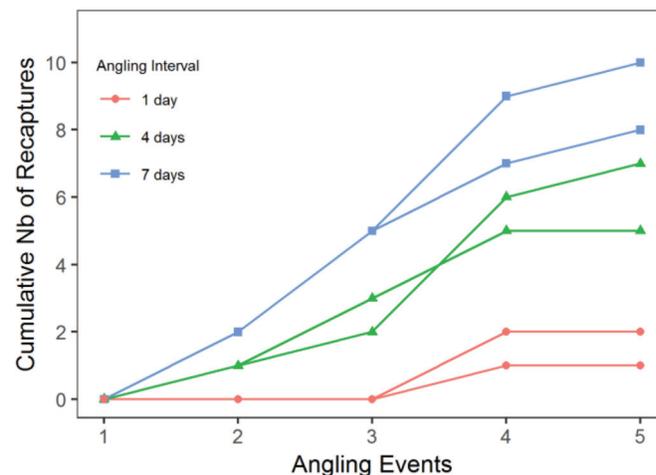
These experiments were approved by the Ethical Committee for Animal Research of the University of Gothenburg (license No. 15.2014) and comply with Swedish and European law.

Data analysis

Two semiparametric Cox-proportional hazard regression models were used to compare the capture rates between angling frequency treatments for right-censored data (i.e., incorporating information of caught and uncaught individuals). The first model included time until first capture of each fish as response variable and was used to identify angling treatment effects on population-level vulnerability (i.e., to see if more or less individuals are at risk of capture for a given angling frequency treatment). The second model allowed for repeated captures where all fish had the chance to be captured at each angling event. This model was used to mimic a context of catch-and-release fishing, accounting for recaptures in the assessment of total catch rates. The hazard function was of the following form:

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

where h_0 is the baseline hazard and β is the hazard coefficient, estimated using a partial likelihood function. Data analysis and graphical representations of survival curves were computed using the package "survival" (Therneau 2015) and the package "survminer"

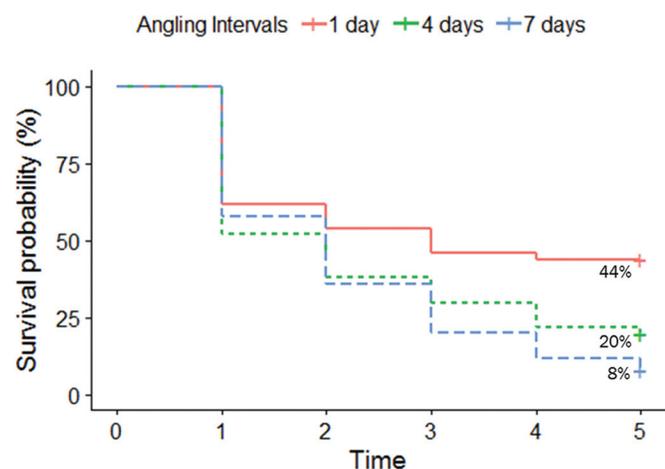(Kassambara and Kosinski 2018) for the R statistical environment (R Core Team 2015).

Results

While in all treatments catch rates declined over time, strong differences were found between angling frequency treatments in terms of number of captured fish and total catches (Table 1; Fig. 2). At the end of the five angling events, 28, 40, and 46 fish were respectively captured in the 1-day, 4-day, and 7-day angling frequency treatments (respectively 56%, 80%, and 92%; Table 1). Additionally, the number of recaptured individuals was also higher when angling was practiced at longer intervals between successive angling events (Table 1; Fig. 3). Survival models accounting for time to first capture (Table 2; Fig. 4) and accounting for time until capture including the possibility for recapture (Table 3) provided similar model statistics (Tables 2 and 3: similar hazard coefficient β between angling treatments). Both models showed that the probability of survival was significantly lower when angling was practiced at 7-day intervals and highest when it was practiced every day (Fig. 4), with a respective 57% and 79% increase in hazard of being captured in the 4-day and 7-day angling frequency treatments compared with when fishing was practiced daily (Tables 2 and 3).

Discussion

It is known that fish that have experienced hooking display a reduced vulnerability to capture (Young and Hayes 2004; Askey et al. 2006; Lennox et al. 2017; Wegener et al. 2018) and that catch rates tend to quickly decline with increasing fishing effort (van Poorten and Post 2005; Kuparinen et al. 2010). However, the extent to which threat perception and temporal variation of fishing pressure plays in the mechanism leading to observed hook

Fig. 4. Survival plot representing the survival probability of rainbow trout at each successive angling event (time 1 to 5) for the three angling frequency treatments (1-, 4-, and 7-day intervals; i.e., the response variable in the survival analysis corresponds to time until first capture only for each fish). [Colour online.]

Table 3. Cox-proportional hazards regression model examining the effect of angling frequency treatments (1-, 4-, and 7-day intervals between successive angling days) on the hazard of being captured by angling.

Treatment	β	exp(β)	SE (β)	z	P
4 days	0.574	1.776	0.227	2.53	0.0114
7 days	0.790	2.204	0.219	3.61	0.0003

Note: n = 750, number of events = 147, likelihood ratio test = 14.4, df = 2, $p = 7e^{-04}$. In addition to the model in Table 2, this model allows for repeated events (i.e. individuals are released back to the population and can be recaptured at successive events). The 1-day angling treatment is coded as the baseline level of the treatment factor of the model.

avoidance and hyper depletion of catch is largely unexplored. We found that even short closures of just a few days had substantial impacts on catch rates. Catch rates of rainbow trout were lower when angling in ponds was practiced at higher frequency (daily) as opposed to a less frequent angling with either 4- or 7-day intervals, indicating that beyond total fishing effort, the temporal variation in fishing pressure also affects avoidance behaviour of fish towards fishing gear. Our results highlighted two mechanisms by which short-term fishing closures affect catch rates: by increasing the overall number of captured individuals (i.e., by increasing catchability), but also by increasing the number of recaptures of previously captured and released fish (i.e., by increasing the rates at which fish return to a vulnerable state).

While catch rates were generally declining with increasing frequency of fishing, indicative of hook avoidance as reported elsewhere for salmonids (van Poorten and Post 2005; Askey et al. 2006), we found an increase in number of recaptures in response to lower angling frequencies, indicating that short-term fishing closures can allow captured individuals to recover from the acute physiological hooking-related stress (reviewed in Cooke and Suski 2005) and return to vulnerable states within a few days (as assumed in Camp et al. 2015). Rainbow trout, particularly of domesticated strain, is a relatively fast-recovering species (Ruane et al. 1999), which is confirmed by our results showing that recaptures are significantly increased when allowing only a few days recovery between angling events. Similar fast recovery times of just a few days have been reported for other freshwater and marine fish species in the wild after catch-and-release angling when handled following best practice (Suski et al. 2003; Ferter et al. 2015). Recovery from capture-related stressors is, however, not alone a sufficient condition for a fish to return to a vulnerable state after catch and release. For example, although physiologically recovered after just 12 h (Rapp et al. 2014), prolonged periods of hook avoidance was observed in carp (*Cyprinus carpio*) for up to a year after an initial capture event (Beukema 1969; Raat 1985), indicating species-specific differences in learning abilities (Coble et al. 1985) to affect the rates at which hooking-experienced fish return to a vulnerable state.

Importantly, under low angling frequency, in addition to higher rates of recapture, we also observed an increase in the total number of captured fish, suggesting population-level decrease in threat perception and vigilance, rendering a larger pool of fish vulnerable to capture. Previous studies have shown that individual fish differ in their intrinsic vulnerability to capture and have identified several

drivers related to individual differences in risk-taking behaviour and stress resilience (also termed coping styles; Louison et al. 2017; Koeck et al. 2019). In particular, it has been shown that individual differences in the activation of the hypothalamic–pituitary–interrenal axis (HPI axis) were related to individual differences in vulnerability to angling in rainbow trout (Koeck et al. 2019). Although this remains to be tested, less frequent angling may possibly cause moderately stress resilient fish, which are generally less vulnerable to angling (Louison et al. 2017; Koeck et al. 2019), to move into a vulnerable state rendering them catchable and increasing population-level catchability.

While a number of studies have highlighted differences in wariness of fish from fished and fishing-free habitats (e.g., Januchowski-Hartley et al. 2013; Alós et al. 2015) (i.e., a behavioural adjustment to spatial differences in threat perception), fewer studies have explored the effects of temporal variation in fishing pressure. However, following the "Predation Risk Allocation Hypothesis" (Lima and Bednekoff 1999), prey adopt and adjust the strength of antipredator tactics also to the temporal variation of the threat (Foam et al. 2005; Brown et al. 2006). Our results confirm that the temporal dimension of threat perception is an important driver of behavioural adjustment and responsiveness to angling gear.

In terms of management implications, our experimental study is of relevance to understanding the impacts of temporal fishing closures in a catch-and-release or put-and-take fishing context and also extends to periodic or rotating harvest fishing contexts, including fisheries with naturally temporal varying fishing intensities (e.g., where fishing is concentrated on weekends and absent during weekdays). While these different management strategies aim at increasing fishing efficiency and catch rates (Camp et al. 2015; Wegener et al. 2018; Abesamis et al. 2014; Goetze et al. 2016, 2018; Chagaris et al. 2019), their effects on fish populations are substantially different. In catch-and-release type fisheries, short-term fishing closures are expected to reduce the general threat perception of fish, thereby reducing the depletion of catch normally observed under sustained fishing effort, which in turn can positively affect anglers' satisfaction (Camp et al. 2015; Wegener et al. 2018). In periodically harvested areas, however, the reduced wariness of fish in response to fishing closures may accentuate the risks of overfishing (Goetze et al. 2016).

Because of its experimental nature, this study is limited in its spatiotemporal scale, and even though realistically representing pond and small-scale put-and-take fisheries, the transferability of results to larger systems need to be further evaluated. To fully appreciate the extent at which temporal variation in fishing effort affects catchability of fish beyond the context of this study and for temporal fishing closures to be effectively implemented, further investigations are required across fisheries context and for wild populations.

Our results raise further questions regarding threat identification and avoidance learning mechanisms in the context of fishing. While direct experience or private learning are obvious ways to make informed decisions, animals in the wild usually do not have

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the opportunity for trial-and-error when, for instance, escaping a predator or a fishing gear (Mathis et al. 1996). Fish may therefore, as also demonstrated in many other taxa (Danchin et al. 2004), rely on social information use (i.e., on information transmitted by conspecifics) to increase their performances in various contexts (Brown and Laland 2003). In a context of threat, socially transmitted visual and chemical alarm cues produced by injured skin of conspecifics (Wisenden 2000; Hall and Clark 2016) are most commonly used to inform about risk levels and adopt abehavioural response. Only a couple of studies have so far investigated the importance of social learning in a recreational fisheries context, showing no effect (Wegener et al. 2018) or only a trend for the effect of social information use on hook avoidance (Lovén Wallerius et al. In press). Because of known species-specific differences in learning abilities (Coble et al. 1985), it remains to be fully explored whether social information use affects the avoidance response of individual fish and overall catch rates, which is of particular interest to catch-and-release fishing in the context of periodic fishing closures.

Conclusion

Our results indicate that short-term fishing closures have the potential to substantially increase catch rates by altering the general threat perception, rendering less risk-taking individuals more vulnerable, and by allowing the highly vulnerable fraction of the population to recover and return to a vulnerable state after initial capture. Our work provides experimental evidence that, in addition to evolutionary adaptation of populations to harvest selection, the behavioural flexibility of animals to temporal variation of anthropogenic threats is of relevance to fish conservation and management.

Acknowledgements

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