The impact of catch-and-release on the foraging behaviour of pike (Esox lucius) when released alone or into groups

Martin Stålhammar a, *, Rasmus Linderfalk a, Christer Brönmark a, Robert Arlinghaus b, c, P. Anders Nilsson a

a Department of Biology, Aquatic Ecology, Lund University, Ecology Building, 223 62 Lund, Sweden
b Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany
b Inland Fisheries Management Laboratory, Department for Crop and Animal Sciences, Faculty of Agriculture and Horticulture, Humboldt-Universität zu Berlin, Philippstrasse 13, Haus 7, 10115 Berlin, Germany

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A commonly practiced method intended to reduce mortality from recreational fisheries is mandatory (e.g., small fish protected by minimum-size limits) or voluntary catch-and-release (C&R), where fish are caught with hook and line and released alive on the assumption that fish survive unharmed. C&R can, however, have both lethal and sub-lethal consequences for fish, with altered behaviour serving as a useful indicator of sub-lethal effects. We here present a mesocosm study on the short-term effects on foraging-behaviour in response to C&R in pike (Esox lucius), when being released alone or into conspecific groups. Due to the potential of cannibalistic attacks or agonistic interactions post-release, we expected that foraging behaviour would be affected by social environment at release. We found that the time to first interest in and attack on prey was significantly delayed in caught and released pike individuals, but these delays were less pronounced in pike released into groups of conspecifics. We also found that the caught and released pike expressed agonistic behaviours in comparable frequencies to unfished group conspecifics. We conclude that the short-term effects of C&R involve altered foraging behaviours, partly depending on the social context at release. Altered feeding, even if only in the short-term, may reduce body growth post-release, which may affect individual fitness and also have effects at the fish community level as a result of changes in pike predation pressure.

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1. Introduction

Recreational angling is a globally common form of fish population exploitation that contributes to human quality of life and also generates a substantial contribution to national and rural economies (Arlinghaus et al., 2002; Parkkila et al., 2010). These socioeconomic benefits justify the further development of recreational angling opportunities, ideally with a view towards sustainable recreational fisheries that maximize human benefits whilst minimizing biological impacts on stocks or aquatic ecosystems (Cowx et al., 2010). Recreational angling has the potential to overharvest fish stocks (Post et al., 2002; Lewin et al., 2006). To minimize the negative impacts on stocks targeted by recreational anglers, harvest regulations are commonly introduced, such as daily or annual bag limits, size-based harvest limits, no-take zones, protected areas, and restricted fishing periods that for example prohibit fishing during the spawning season. Protected fish species or sizes must be released back into the water, resulting in mandatory catch-and-release (C&R). Moreover, many anglers voluntarily engage in C&R of legally harvestable fish species or sizes (Cooke and Suski, 2005; Arlinghaus et al., 2007) and there is a trend for increasing voluntary C&R in some specialized fisheries (Allen et al., 2008). C&R in one form or another is expected to reduce fishing mortality relative to catch-and-keep angling (Pollock and Pine, 2007), and thereby has the potential to promote recreational angling with minimal depleting effects on fish stocks (Arlinghaus, 2007). For this to happen, fishing effort and hooking mortality must be low (Coggins et al., 2007), and other sub-lethal impacts on released fish must not affect fitness substantially (Arlinghaus et al., 2007).

To further our understanding of the impact of C&R on fish, both lethal and short- and long-term sublethal effects on individuals have to be studied. The lethal effects of C&R, known as ‘hooking mortality’, have been a major focus in C&R research (Bartholomew and Bohnsack, 2005; Hünn and Arlinghaus, 2011). However, non-lethal indirect effects are also vital for understanding the effects of C&R on fish stocks (Cooke and Suski, 2005; Gingerich et al., 2007). For instance, exposure to C&R can affect physiological states (Cooke...
et al., 2002b), such as increased heart rate (Anderson et al., 1998) and reduced gas exchange due to gill lamellae collapse after air exposure (Ferguson and Tufts, 1992). Fish may also respond to C&R by altering behaviours post release that affect food intake and exposure to predators, with potential effects on growth rate (Siepker et al., 2006; Arlinghaus and Hallermann, 2007; Klefoth et al., 2008, 2011) and survival (Cooke and Philipp, 2004). If so, C&R may impact fish stocks even if it does not have direct numerical effects on fish densities through fisheries mortality (Cooke et al., 2002a).

The pike (Esox lucius) is a popular species amongst anglers (Paukert et al., 2001; Arlinghaus and Mehner, 2004), and voluntary C&R is an increasingly important component of pike recreational angling in some countries. The pike is also an important top predator in temperate freshwater food webs, constituting a structuring force in many lake ecosystems (Raat, 1988; Findlay et al., 2005; Byström et al., 2007; Craig, 2008). Collectively, the predation pressure by pike on other components of food webs together with its high value for anglers renders pike an important model species for evaluations of short-term behavioural responses to C&R angling.

Earlier results indicate that hooking mortality is relatively low in pike (<1%) (Burkholder, 1992; Arlinghaus et al., 2008a), whilst the hooking mortality of other species may be substantially higher (up to 88%) (Hühn and Arlinghaus, 2011). It has been suggested that pike are relatively robust to C&R overall, including injuries related to capture and to handling-induced stressors (Arlinghaus et al., 2008b, 2009). Using telemetry in the wild, it has, however, previously been shown that pike reduce movement activity in response to the C&R event, whilst showing recovery of normal behavioural patterns after a couple of days (Arlinghaus et al., 2008a, 2009; Klefoth et al., 2008, 2011). Decreased activity following release could be caused by the C&R-induced stress response in pike (Arlinghaus et al., 2009), but it is unclear if the activity reduction also includes a decreased foraging propensity. If pike alter foraging behaviours after C&R, this angling practice could cause negative effects on both individual growth (Klefoth et al., 2011) and pike predation rates, potentially causing cascades through the food web due to altered behavioural and size-structured interactions with prey (Nilsson, 2001). The present laboratory study focuses on the effects of C&R on foraging behaviours in pike. We predict that we will document a decreased foraging propensity after experiencing a C&R event due to the need to recover from C&R-induced physiological disturbances.

Pike foraging and top-down trophic effects from pike predation depend partly on pike intraspecific interactions (Nilsson, 2001). Pike are cannibalistic and kleptoparasitic (Grimm, 1981b; Nilsson and Brönnmark, 1999), and individuals avoid these risks by reducing foraging activity and altering spatial distribution patterns in the presence of potentially agonistic conspecics (Nilsson, 2006; Nilsson et al., 2006). Hence, it is reasonable to expect that pike exposed to C&R will reduce foraging propensity comparably more if released in the presence of conspecics than if released alone. Furthermore, pike released into groups of unfished conspecics should be more exposed to agonistic interactions if the C&R procedure impairs behavioural performance. We here present a mesocosm study evaluating pike individual foraging behaviours before and after experiencing C&R, and when being released alone or into conspecific groups.

2. Materials and methods

Pike were caught by electrofishing, and the main prey of pike, roach (Rutilus rutilus), by cast nets in Lake Krankesjön (N55° 42', E13° 28') in southern Sweden. Fish were transported and acclimated to laboratory conditions at Lund University. All fish were acclimatized to the experimental light and temperature conditions for three weeks prior to participating in experiments. Pike were fed with roach to satiation every third day and roach fed with chironomids to satiation every second day.

Two circular wading pools (3 m diameter, water depth 40 cm) with no structural complexity were used in the experiments. The pools were situated in a greenhouse (natural photo period in October–February, water temperature 18.2 ± 1.4 °C, mean ± SD) and were encircled with tarps lined with the ceiling to minimize disturbance on fish. A video camera was mounted above each pool to record behaviours without disturbing the fish.

At the start of each trial, individual focal pike (N = 16, total length, TL = 36.8 ± 2.3 cm, mean ± SD); body mass (BM = 258.5 ± 56.8 g) were placed in the pools and given one roach (TL = 11.2 ± 1.4 cm; BM = 10.8 ± 2.6 g). Three days after the pike had eaten the roach, five new roach were added, and the pool was video recorded until the pike had eaten one roach, after which the remaining roach were removed. The pike was angled three days later, using roach as bait. Roach were sacrificed with an overdose of benzocaine and rinsed with regular tap water. Baited roach were rigged with Owner hooks (size 10), Strike Wire Extreme™ 0.13 line with a breaking strength of 9 kg, and a float. One hook was attached in the mouth and one in the back of the roach. After hooking and an approximately 30 s “fight”/angling duration, the pike was landed by hand with a grip over the neck and exposed to air for 1 min. The hooks were carefully detached using forceps, and each caught pike was released into a pool containing either no or two conspecics (N = 16, TL = 36.1 ± 11.4 cm; BM = 244.8 ± 34.0 g), as well as five new roach, and was video recorded for another 3 h. Of the 16 focal pike, eight were released alone and eight released with conspecics. In the trials where pike were released into the pool without conspecics, both pike and roach were left over night to record if individuals that had not eaten during the three video-recorded hours had done so the following day. The focal pike and the conspecics were individually marked with alcin blue using a pan-jet injector for identification. Between the trials pike were held in separate aquaria with the same temperature and light conditions as the pools. Roach individuals and focal pike were not reused. Experiments were performed under ethical permission from the Malmö/Lund Ethical Committee (M165-07).

The video recordings were analysed using Inter Video WIN DVD for individual pike foraging behaviours before and after the angling event. The focal behavioural parameters examined were (1) time elapsed to first interest in prey turning towards or following prey (s), (2) time to first attack (s), (3) capture success (number of attacks per successful capture), and (4) distance to nearest prey when becoming interested (cm). The dependent behavioural variables were evaluated in SPSS (version 19 for Mac) and compared between before and after C&R at the individual pike level, using a nested randomized block ANOVA (Quinn and Keough, 2002). The blocking factor ‘pike individual’ was nested within factor alone/group, as focal pike participated in either of these treatments. The statistical model considered potential differences in behavioural expression amongst pike individuals, compensated the degrees of freedom according to repeated observations of pike behaviours, and also focused on the relative individual change in behavioural expressions between before and after the C&R event. Furthermore, agonistic behavioural interactions post release in pike groups (i.e. the frequency of approaches, chases, attacks, and bites aimed at conspecics) were compared between focal pike and the average of the two non-focal pike in each group by paired t-tests.

3. Results

The ANOVA revealed significant Alone/Group x Before/After interaction-term effects on time to first interest in prey and on time to first attack (Table 1). Time to first interest in prey was longer...
after pike had experienced a C&R event (Table 1), but pike released into groups of conspecifics became interested in prey sooner after C&R compared to pike released alone (Table 1, Fig. 1A). Similarly, time to first attack was delayed after C&R, but pike released into groups attacked prey relatively sooner than pike released alone (Table 1, Fig. 1B). Only three out of eight pike released alone attacked prey within 3 h post C&R, compared to six out of eight pike released into conspecific groups (Fig. 1B). Neither capture success, nor distance to prey at interest was significantly affected by the treatments (Table 1, Fig. 1C and D). The factor pike individual had no significant effect on the dependent variables (Table 1). Finally, the frequency of agonistic behaviours (i.e. approaches, chases,
attacks and biting) did not differ between focal and non-focal pike ($f_0 \leq 0.917, p \geq 0.395$, Fig. 2).

4. Discussion

In line with expectations, pike showed short-term changes in foraging behaviours as a response to experiencing a C&R event. As predicted, time to first interest in and attack on prey were delayed after being caught and released, but these delays were unexpectedly less pronounced for pike released into groups of conspecifics. The delays in interest and attack propensities are most likely a consequence of an altered physiological status of the fish. Exposure to stressors like air exposure and extreme physical exercise will result in accumulation of lactate due to anaerobic metabolism and other physiological disturbances, which has been reported in pike and other species (Cook and Suski, 2005; Gingerich et al., 2007; Klefoth et al., 2008; Arlinghaus et al., 2009). A further reason could be a learning effect to become more cautious after a potentially negative experience, as previously demonstrated in pike by Beukema (1970) in pond studies. Similarly, Kuparinne et al. (2010) reported that pike catchability decreased after repeated fishing in a natural lake, suggesting a potential for learning to avoid capture. In the present experiments, the reason why the behavioural impairment in foraging was reduced in the presence of conspecifics is less clear because these fish should have been as physiologically affected as the fish released alone after capture. In our study, neither capture success nor distances to prey at interest were affected by the treatments. Pike are sit-and-wait predators that attack prey from a short distance with generally high capture success (Webb and Skadsen, 1980; Nilsson et al., 2006), and this specialised foraging mode seems not to be affected by C&R once initiated.

It has previously been shown that pike foraging in groups of conspecifics reduce their attack and consumption rates compared to when foraging alone, presumably to avoid risk of agonistic interactions (Nilsson et al., 2006). This led us to expect that conspecific presence would have a further negative effect on foraging propensity post C&R, compared to when pike were released alone. This prediction was also guided by the previous finding that pike should minimize movements to decrease risk of attacks from conspecifics (Nilsson and Brönmark, 1999). However, we did not find a greater reduction of movement and foraging after catch and release back into groups. A possible suggestion is that the presence of uncaptured conspecifics, presumably showing more natural foraging behaviours, triggered an earlier recovery from the C&R-induced stress in terms of resuming normal foraging behaviours. This implies that physiological effects are not the sole reason for the decreased foraging propensity in pike after C&R. A qualitative observation from the experiments suggests that movement in any other pike elicited movement in focal pike, and such conspecific-induced movement may include the triggering of foraging behaviour. This potential triggering effect should however not be viewed as social facilitation, as can be the case in Eurasian perch (Perca fluviatilis) (Eklov, 1992; Nilsson et al., 2006), but rather as an effect of caught and released pike acting like surrounding conspecifics, which indirectly facilitated the resumption of foraging behaviour. It has moreover been shown than juvenile lake sturgeon (Acipenser fulvescens) exhibits shortened stress responses in the presence of conspecifics (Allen et al., 2009). More studies are needed to address the mechanism behind the effects of conspecific presence on fish recovery from stress situations.

According to our results, pike suffer comparably smaller negative effects from C&R on foraging propensity when released into waters or sites containing conspecifics. However, pike are also cannibalistic and if caught pike are released into waters containing larger pike, and not only similar-sized pike as in our experiments, released pike would probably run an increased risk of cannibalism from disoriented re-entry into habitats containing potentially cannibalistic conspecifics. A similar effect has been reported by Cooke and Philipp (2004) and Danyliuk et al. (2007) for caught and released bonefish (Albula vulpes) that were consumed by larger-sized predators (Lemon sharks, Negaprion brevirostris) after release. It is therefore possible that the relatively small behavioural responses to C&R in our study could still have numerical effects on pike populations through C&R-induced elevated risk of cannibalism. This could be especially true for smaller pike, as in this study, whilst larger pike should be less vulnerable to cannibalism (Grimm, 1981a). However, although pike are solitary foragers, they aggregate size assortedly in natural habitats (Hawkins et al., 2005; Nilsson, 2006), suggesting a higher probability of being caught and released amongst similar-sized rather than larger conspecifics. Nevertheless, similar-sized conspecifics pose a threat in the form of kleptoparasitic and agonistic behaviours (Nilsson and Brönmark, 1999, 2000; Nilsson et al., 2006). Thus, in early stages post C&R pike may be more vulnerable to attacks from also similar-sized conspecifics, unless they seek refuge during recovery as suggested by telemetry studies in larger pike (Klefoth et al., 2008). Interestingly and unexpectedly, our focal pike expressed agonistic behaviours in comparable frequencies to their group conspecifics. This suggests that agonistic behaviours are not affected by the C&R experience, further reducing the likelihood of individual pike experiencing negative effects when released into groups of similar-sized conspecifics.

Klefoth et al. (2008, 2011) suggested only limited and mainly sublethal behavioural and growth effects of C&R on pike, and Arlinghaus et al. (2009) emphasized that pike recover within hours from angling-induced stress. This body of knowledge and the present experiment cumulatively suggest that pike are fairly resilient to C&R related stressors. However, even if pike are resilient to and readily survive many C&R events, sublethal effects on released fish will occur in terms of behaviour, which may incur unknown effects on populations and communities. Our experimental C&R procedure indeed prolonged the time to first interest in prey, as well as the time to first attack, in accordance with studies on caught and released largemouth bass (Micropterus salmoides, Siepker et al., 2007). This reduced foraging, even if short term, could explain the empirical findings of reduced pike growth rates following C&R in the wild (Klefoth et al., 2011). When pike reduce foraging and growth as a response to C&R, they would also reduce predation rates on their prey, at least short-term. The pike released alone in our study were left overnight with prey, and had all eaten the following day, indicating a relatively short
delay before resuming foraging. Even small decreases in foraging propensity will however affect consumption rates, and thereby not only individual growth but also the effect of predation on community and trophic processes (Carpenter and Kilchell, 1993; Fryxell and Lundberg, 1998). Such effects are however only likely where substantial C&R activity takes place, which is locally the case in for instance coastal areas of the Baltic sea. Given the important top-predator role of pike in aquatic food webs, altered pike predation rates and behaviour may then have consequences for prey population density and composition (Nilsson and Brömholm, 2000; Nilsson, 2001). Although our study is a mesocosm experiment and we cannot exclude the possibility of laboratory-induced effects on pike behaviours, we suggest that intense C&R fisheries, and perhaps especially repeated C&R of individual pike, may affect pike behaviour and overall predation and growth rates also in the wild (Klefoth et al., 2008, 2011). The possible ecological consequences of C&R-induced behavioural changes in pike should thus not be neglected, but deserve attention in future work.

We conclude that the short-term effects on foraging behaviour of pike we found may be one of the mechanisms explaining previously observed growth depression after C&R in this species. Whilst we assume that the change in foraging rate is not strong enough to cause mortality, the altered feeding can potentially have effects at the fish community level as a result of altered pike predation pressure, if, for instance, fishing intensity is high and individuals are repeatedly caught and released. Moreover, any growth depression will affect individual fitness of pike and cumulatively the population as shown in the study by Edeline et al. (2010). Our study further underscores the novel, and unexpected, finding that the social environment around pike improves their propensity to recover behaviourally from catch-and-release. It should further be noted that the results from the present study reflect a standardized C&R procedure, whilst, for instance, flight time and angling duration (Gustavson et al., 1991; Schreer et al., 2001), air exposure (Cooke et al., 2001; Gingerich et al., 2007), water temperature (Willie et al., 1996), equipment used (Arlinghaus et al., 2008b) and angler knowledge about fish handling (Dunnall et al., 2001) can affect the consequences of C&R for fish. Further understanding of species-specific responses and consequences of such stressors is therefore required to assist conservation, management and development issues of recreational fisheries (Cooke and Suski, 2005; Pelletier et al., 2007; EIFAC, 2008; Arlinghaus et al., 2010).

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