Guidance on optimal temperature regimes for protecting pike in catch and release activities

DRAFT REPORT

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1 Introduction

Pike is found in lowland rivers and still waters across most of England, and parts of Wales and southern Scotland. It is a popular angling species and the target of specialist anglers looking for trophy fish. Traditionally pike fishing occurs mostly in the cooler months of the year when the temperature is lower, but continues throughout the year depending on angler preferences and motive. To encourage good practice for catch and release angling, the Pike Angler's Club of Great Britain (PACGB) has provided guidance on fishing for pike (<u>https://pacgb.com/fishing-for-pike/</u>) and to address potential problems with fishing during the warmer periods of the year, it has provided guidance specifically for fishing in the summer (<u>https://pacgb.com/fishing-for-pike/summer-piking-guide/</u>).

More recently, concerns have been raised about fishing for pike during the very hot summer periods, especially those experienced in recent years when water temperatures have been in excess of 20 °C for prolonged periods (see **Error! Reference source not found.** for air temperature profile for Little P axton, in Cambridgeshire, in 2018). This seems to coincide with an increase in pike mortality, especially of larger individuals, possibly arising from catch and release fishing. Whilst the PACGB does not seek to recommend a national summer pike fishing close season, they feel that there is need for summer restrictions on fishing during these increasingly hot summer periods to protect the pike stocks. This document seeks to review the evidence that fishing for pike during higher summer temperatures may result in elevated stress conditions and potentially increase mortality, and offer guidance on best practice for catch and release pike angling during these potentially adverse conditions.

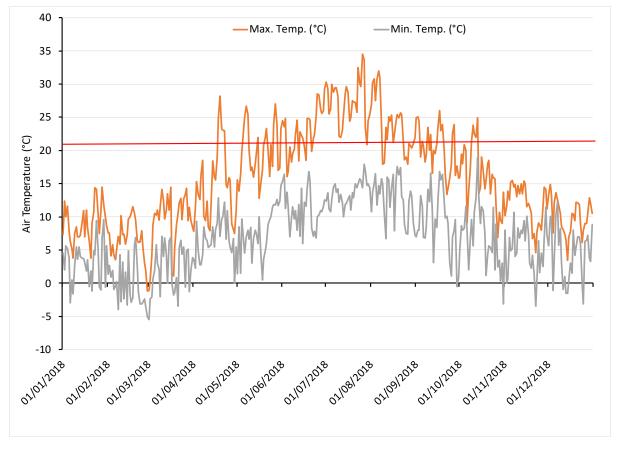


Figure 1. Maximum minimum air temperatures recorded at Little Paxton weather station in 2018 (Source http://www.paxtonweather.org/index/dwolinks.htm)

2 Ecology

2.1 Distribution and habitat

Pike (*Esox lucius*) has a circumpolar distribution across the northern hemisphere (Figure 2; Scott & Crossman, 1973; Craig 1996; Crossman 1996), with a range that has expanded into other northern areas as a result of introductions (Casselman & Lewis, 1996; Harvey, 2009). Pike are found throughout Europe, with the exception of Iceland, southern Italy and southern Balkans, although it is an introduced species in the Iberian Peninsula (Elvira 1995; Godinho et al., 1997). It is indigenous to the UK, and is widespread except in northern Scotland, where it is absent. These populations are one panmictic stock, although exhibits considerable genetic variability exists across the species distribution range (Pedreschi et al. 2014), particularly in Europe compared with North America and Siberia (Senanan & Kapuscinski 2000; Launey et al. 2006). This arises because of the possible existence of a single refuge area in North America compared with several such areas in Europe during the last period of glaciation.



Figure 2. Natural distribution of pike (Esox lucius) across the Northern Hemisphere

The biology of pike throughout its range has been reviewed by Craig (1996 & 2008), Harvey (2009), Raat (1988) and Skov and Nilsson 2018. Pike are typically found in lakes, slow-flowing rivers and canals with shallow to moderately deep waters and a high density of vegetation (Raat, 1988, Grimm, 1994). Young pike are usually associated with weed beds in shallow, sheltered areas (Bregazzi & Kennedy, 1980; Raat, 1988). By contrast, adult pike are often found in clear waters with a substrate of silt, clay, peat or sand (Frost & Kipling, 1967; Grimm, 1989). Those found inhabiting deeper, more turbid waters tend to be the larger individuals. Pike are non-territorial fish, with their distribution often related to that of their prey (Bregazzi & Kennedy, 1980; Casselman & Lewis, 1996; Minns, *et al.*, 1996; Eklov, 1997).

2.2 Feeding habits

Pike is a non-selective predator, and abundance and seasonal availability of food organisms determines food selection (Frost, 1954; Vostradovsky, 1981; Chapman *et al.*, 1989). Size-selectivity of

prey has been demonstrated (Frost, 1954; Mann, 1976): pike usually take food of about a third of their own length, although prey items of up to 70 per cent of body length have been recorded. When foraging, pike will remain concealed among vegetation or other available cover until prey is located. Initially this is by visual stimuli, followed by precise location using the lateral organ.

The feeding activity of pike follows a seasonal pattern and is related to several factors including temperature, prey abundance and the timing of the reproductive cycle (Frost, 1954; Lawler, 1965). Feeding activity is greatest during May, immediately after spawning, and remains high throughout the summer and early autumn (Bregazzi & Kennedy, 1980), but decreases over winter (Allen, 1939; Banks, 1970). In the River Stour, however, the proportion of empty stomachs was highest in the summer, despite this being the period of fastest growth (Mann, 1976). Higher temperatures, associated increased digestion rates and an increase in daylength, were suggested to be the cause of this apparent anomaly. Allen (1939) suggested that a high incidence of empty stomachs is a characteristic of piscivorous fish, as it is common in perch as well as pike. Pike also undergo a fast associated with the spawning period between March and April (Frost, 1954).

2.3 Growth

Pike often grow rapidly, although this varies greatly with location, and may be due to the differences in size and availability of prey fish species in different habitats. Diana (1979) suggested that faster growth occurs where pike are able to feed regularly on large prey items. Growth may also be dependent on the density of the population, i.e. poor growth being associated with high population (Kipling & Frost, 1969; Mann, 1975). Mann (1985) considered that density-dependent effects on 0+ pike were more important than the effect of temperature. By contrast, Frost & Kipling (1967) correlated high growth rates to higher temperatures (the number of degree days above 14°C). This may be a direct effect on metabolism, higher temperatures increasing digestion rates thereby allowing pike to feed more frequently (Mann, 1976). However, Lawler (1965) considered that high temperatures may inhibit growth. Mediocre growth of pike in Slapton Ley, Devon, was recorded despite high temperatures, with high productivity of the lake possibly reducing the ability of the pike to feed by sight (Bregazzi & Kennedy, 1980). A similar influence of light on the growth of pike was noted by Frost and Kipling (1967) and Banks (1970).

3 Environmental requirements

Temperature and dissolved oxygen are perhaps the most extensively studied environmental factors affecting fish growth and survival. Different fish can tolerate different water temperature ranges and can suffer or die if they are subject to temperatures outside of their range. They will also need a specific range of temperatures for successful spawning and will also have a specific preferred range of temperatures where they are most likely to be found and be most active.

According to Casselman (1975) pike is a cool-water species (mesothermic) with a temperature preference between those of typical cold water and warm water species. The optimal temperature tolerated by pike appears to decrease with increasing size of pike (Table 1; Souchon and Tissot 2012). This was confirmed by Vindenes et al. (2014) who suggested the growth and fitness of pike in Lake Windermere increased with increasing temperature but the sensitivity of pike to different temperatures was dependent on body size.

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Table 1. Preferred and upper temperature thresholds for pike (from Souchon and Tissot 2012)

The optimum temperature for the pike embryos ranges between 8 °C and 14 °C (Willemsen, 1959), with extremes tolerated in the laboratory of 4 °C and 23 °C (Lindroth, 1946; Lillelund, 1966; Ignatieva and Kostomarova, 1966). The minimum lethal temperature is 3 °C (Hassler, 1982), and the maximum lethal temperature for larvae was estimated at 28 °C (Hokanson *et al.* 1973 in Hokanson, 1977). The optimum is between 12 °C and 21 °C (Hokanson *et al.*, 1973; Teletchea *et al.*, 2009b).

The optimum temperature for growth of juvenile pike is between 19 °C and 21 °C. (Casselman 1978). Cvancara *et al.* (1977) recorded an upper lethal temperature of 29.4 °C in the Mississippi, while Scott (1964) found an upper lethal temperature of 33 °C in the laboratory.

The optimum temperature for the adult stage ranges between 10 °C and 24 °C (Mc Cauley & Casselman, 1981; Keith and Allardi, 2001; Hokanson, 1977; Casselman, 1978; Craig, 1996). Highest activity occurs in the period April-November. Growth of pike is related to temperatures above 12 °C (Mann, 1976). The physiological optimum temperature for pike is 19-21 °C. Pierce et al. (2013) found larger pike in deep lakes followed the thermocline to find cooler water of 16-21 °C during the summer, despite the majority of the lakes being considerably warmer. This suggests the preferred temperature is within this range.

The upper boundary temperature for pike in the River Rhône was reported as 27 °C (Ginot et al., 1996), while Huet (1962) reported an upper lethal temperature in Belgium of 29 °C. Scott (1964) recorded an upper lethal temperature of 34 °C in the laboratory, and Casselman (1978) found a lower lethal temperature of 0.1 °C in Ontario (Canada). Hokanson et al. (1973) and Casselman (1978) give an upper lethal temperature of around 29.4 °C, similar to the lethal temperature given by Huet (1962) in the natural environment. Temperatures approaching these thermal maxima can be extremely stressful (Beitinger et al. 2000), and the conditions are exacerbated when they interact with other factors such as low dissolved oxygen, typically found at higher water temperatures (Figure 2). Pike can tolerate low oxygen concentrations, particularly larval stages (Adelman & Smith 1970; Siefert et al. 1973). In winter they can survive at oxygen concentrations as low as 0.3 mg/L (Pierce et al. 2013). Within the preferred temperature range (10 - 24 °C), an oxygen concentration of 0.75 mg/L is lethal (Raat, 1988). Despite being tolerant of low oxygen levels, pike avoid levels below 3 mg/L and activity is reduced and feeding stops when concentrations are lower than 2 mg/L (Casselman & Lewis, 1996). Pierce et al. (2013) found that pike actively avoid the lowest oxygen concentrations, but in deep lakes with summer thermoclines and low oxygen concentrations around the hypolimnion, they trade off the two conditions and err towards the lower oxygen levels.

It is suggested that an oxygen content greater than 3 mg/L is the lower threshold for pike. However, dissolved oxygen concentrations do not have to drop to very low levels before physiological functions are affected. Sub-lethal hypoxia causes reduced feeding activity (Stickney 2000), reduced swimming performance, and reduced survival. Low DO levels have also been linked to immunosuppression in fish (Boyd and Tucker 1998; Stickney 2000), which has implications for increased risk of disease transmission. If this is coupled with potential increased stress when pike are caught and released during an angling event, it may affect the survival of the individual.

However, this is not simply the impact of lower oxygen levels on physiological characteristics. There is an exponentially increasing inverse relationship between temperature and the lowest oxygen concentrations tolerated (Casselman 1978), presumably linked to the lower oxygen concentrations found at higher temperatures (Figure 3). Oxygen solubility in water has an inverse relationship with water temperature; for example, water at 0°C holds about 14.6 mg O_2/L , but water at 25°C can only hold about 8.3 mg O_2/L (Kalff 2000). Because the aerobic metabolic rates of most aquatic poikliotherms increase with temperature, an increase in temperature both reduces the supply (through reduced saturation concentrations) and increases the biological oxygen demand (Kalff 2000). Fishes exposed to elevated water temperatures can face an "oxygen squeeze" where the decreased supply of oxygen cannot meet increased demand, i.e. environmental dissolved oxygen levels must be high enough to support aerobic metabolism in fishes (Moyle & Cech 1988).

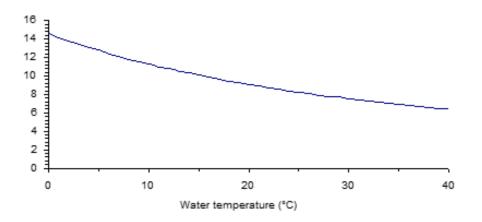


Figure 3. Effect of Temperature on dissolved oxygen saturation concentration

This relationship between oxygen and temperature was tested by Jin et al. (2010), who found oxygen consumption rates increased with increasing temperature, and asphyxiation occurred at high dissolved oxygen levels in warmer water. The suffocation point was reached at 1.68 mg/L for a water temperature of 13 °C, but was as low as 0.82 mg/L at 3 °C.

4 Physiological responses to stress

Wild fish are exposed to a variety of stressors in the natural environment, including biological (e.g. escape from a predator) or environmental (e.g. temperature extremities, low dissolved oxygen) stressors. These stresses result from both natural variability in environmental conditions or biological interactions, but can be exacerbated by extreme events, such as long, hot summers where the temperatures approach the maximum tolerated by the species or when exposed to greater predation pressure from fish-eating birds or other aquatic predators.

Fish are also exposed to angling-related stressors, typically when they are caught during angling or escape from the hook. Physiological changes occur in response to excessive exercise, which result from burst swimming during avoidance of capture or being played when hooked (Arlinghaus *et al.*, 2007). The effect can be particularly stressful if fish are handled badly during hooking, playing (especially during prolonged playing of fish) and being dehooked, and indeed these conditions can be exaggerated if coupled with adverse environmental conditions such as elevated temperatures (Wood *et al.*, 1983; Wilkie *et al.*, 1996). When fish are exposed to high water temperatures near their thermal maximum, they experience problems with osmoregulation (Boyd & Tucker 1998), possibly due to increased gill permeability at higher temperatures (Somero &Hofmann 1997).

Under normal conditions, these stressors produce physiological changes, via stress responses that can affect both short and long-term survival of the fish (Wendelaar Bonga, 1997). In fish, stressors tend to activate the sympathetic nervous system (and the release of catecholamines), which in turn stimulates the release of corticosteroid hormones (i.e. cortisol). The release of cortisol, which normally regulates energy metabolism and water/ mineral balance, frees energy resources (i.e. glucose) that allow the fish to cope with, and recover from, the stressor in the short term (Barton, 2002). Specifically, cortisol

release causes secondary responses such as increases in ion and water flux, metabolic rate, gluconeogenesis (increasing plasma glucose levels), respiratory rate, oxygen consumption and haematocrit, and a decrease in liver carbohydrate reserves (Mommsen *et al.*, 1999; Wendelaar Bonga, 1997). During these periods, the body responds with increasing levels of lactate in white muscle, decreases in muscle pH and reductions in white muscle concentrations of phosphocreatine (PCr), adenosine triphosphate (ATP) and glycogen (Booth *et al.*, 1995; Brobbel *et al.*, 1996; Arlinghaus *et al.*, 2007) that ultimately results in impaired swimming capacity. Sustained release of cortisol caused by chronic stressors also results in tertiary responses such as inhibition of growth, reduction of appetite suppression of the immune system and a negative effect on reproduction (reviewed in (Wendelaar Bonga, 1997). Similar acute stress can be caused by extreme temperatures or excessive exercise during catching and handling, and can affect survival and potentially result in death.

Associated with this stress is an increase in oxygen demand from the body tissues as oxygen consumption from the tissues will increase to keep up with cardiac output. These cardiac changes have been noted in several studies on C&R angling (Cooke *et al.*, 2002, 2003, 2004; Killen *et al.*, 2006). The oxygen levels in the environment will ultimately restrict the rate at which the body can take up oxygen, and with higher temperature waters holding less dissolved oxygen, can result in highly stressful conditions (Bartholomew & Bohnsack, 2005). Therefore, at lower water temperatures fish that are exhausted exhibit lower mortality rates, associated with lower metabolic rates and physical activity (Muoneke & Childress, 1994) and higher levels of dissolved oxygen in the water (Bartholomew and Bohnsack, 2005).

These physiological stress responses are an important adaptation that is crucial for fish to survive an acute challenge, whether extreme temperatures, low dissolved oxygen levels or being hooked and played. However, if the stressor is severe or sustained, this physiological response can have negative effects on the fish's well-being, behaviour and ultimate survival, as metabolic energy is redirected from growth and reproduction in an effort to maintain homeostasis (Barton, 2002). Under extreme conditions, often arising from exposure to elevated temperatures and/or low dissolved oxygen levels, the physiological conditions can result in death, perhaps not instantly, but after a few days. Larger individuals, which tend to be less tolerant to higher temperatures and lower oxygen levels, are inclined to be more vulnerable.

5 Catch and release angling

Catch-and-release (C&R) recreational angling is a popular angling method, conservation strategy and management tool used for an array of fish species and fisheries. The key aim of C&R angling is to ensure that the individual fish survive to grow on and contribute to the fishery and/ or to spawn. Implicit in C&R angling practices is the assumption that fish experience low mortality and minimal sublethal effects, and they swim away unharmed. Catch and release angling is, however, associated with stressors such as exhaustion, injury, capture and air exposure that induce a physiological stress response in the fish (Suski *et al.*, 2007). Although the fish may recover from the initial challenge, prolonged stress responses may have sub-lethal effects on fish behaviour, fitness and survival (Arlinghaus *et al.*, 2007; Cooke & Schramm, 2007; Donaldson *et al.*, 2008). Understanding recovery from such C&R exhaustive exercise and the stress responses is important as the rate at which an individual fish is able to restore homeostasis after angling will directly impact its ability to survive following release, and may ultimately have population-level effects.

The impacts of C&R angling on physiological stressors and behavioural impairment have been studied both under laboratory and field settings (Arlinghaus *et al.*, 2007; Arlinghaus *et al.*, 2009; Cooke & Suski,

2005), and specifically for pike (Robert Arlinghaus Laboratory in IGB, Berlin). Laboratory trails testing exhaustive exercise in pike (i.e. simulating a C&R angling event) were found to cause: increased levels of plasma glucose, increased plasma and muscle lactate, changes in plasma ionic status (increased potassium and sodium along with decreased chloride), decreases in energy resources (ATP and PCr) and decreases in blood pH (with associated decreased plasma HCO3- and increased PCO2) (Arlinghaus *et al.*, 2008 a,b, 2009; Kleforth et al. 2011; Schwalme & Mackay, 1985a,b). Recovery from these physiological disturbances were rapid, however, with all physiological variables, except plasma glucose, returning to baseline levels after 6 hours (Arlinghaus *et al.*, 2008 a). Similar responses were found in field experiments on pike, but with high blood lactate values following exhaustive exercise (Arlinghaus *et al.*, 2008b; Kleforth et al. 2011). This suggests these fish had experienced considerable exercise during the catch event. Interestingly, exposure of pike to air for between 0 s and 300 s associated with simulated C&R, had no additional impact on physiological stress indicators. However, pike exposed to air for more than 300 s were behaviourally impaired in the first hour post-release indicating that despite limited effects on physiological status, air exposure resulted in significant impairment of individual performance.

Although not tested, it is likely elevated temperatures during the air exposure / handling could exacerbate the stress responses. Close links have been found between water temperature and survival in C&R salmonid species, with elevated temperatures causing higher rates of delayed mortality (Anderson *et al.*, 1998; Dempson *et al.*, 2002; Boyd *et al.*, 2010; Havn, 2013; Havn *et al.*, 2015). For example, mortality rates of C&R Atlantic salmon tended to be less than 12 % when water temperatures were <18 °C (Brobbel *et al.*, 1996; Dempson *et al.*, 2002; Thorstad *et al.*, 2007; Havn *et al.*, 2015), but could be as high as 80 % when water temperature exceeds 18 °C (Wilkie *et al.*, 1996, 1997; Anderson *et al.*, 1998; Dempson *et al.*, 2002). Similar results have been reported in cutthroat trout (*Salmo clarki henshawi*) with 1.5 % mortality rates at water temperatures <16 °C, but rising to 60 % mortality at temperature increase physiological disturbances (Gustaveson *et al.*, 1991; Thompson *et al.*, 2002) and affect fish metabolism (Fry, 1971), cellular function (Prosser, 1991), protein structure (Somero & Hofmann, 1997), enzyme activity (Lehninger, 1982) and diffusion, as described previously.

Although most of the physiological disturbances that occur during C&R angling typically take 6-12 hours to fully resolve in the majority of fish species (Kieffer, 2000), studies on recovery rates in pike have varied (Arlinghaus *et al.*, 2009, 2017; Schwalme & Mackay, 1985a; Schwalme & Mackay, 1985b; Soivio & Oikari, 1976). This is possibly down to angling methods, which have the potential to differ in their impacts on fish survival following release, and especially so in pike (Arlinghaus et al. 2008a, b; Kleforth et al. 2011; Stålhammar et al. 2014). Angling methods, equipment and techniques can be selected to minimise physiological stress and physical injury, and maximise post-release survival (see Arlinghaus *et al.*, 2007, Cooke *et al.*, 2013 and Brownscombe *et al.*, 2016 for thorough reviews).

6 Conclusions and recommendations

Pike has a wide distribution across the northern hemisphere and exhibits similar ecological and physiological characteristics between regions (Raat 1988; Craig 1996 & 2008, Harvey 2009; Skov & Nilsson 2018). The species has an optimal temperature for growth between 10 °C and 24 °C (Mc Cauley & Casselman, 1981; Keith & Allardi, 2001; Hokanson, 1977; Craig, 1996), upper boundary temperature around 27 °C (Ginot *et al.*, 1996), and an upper lethal temperature of 29 °C. (Scott 1964; Hokanson *et al.* 1973; Casselman 1978). It should be noted larger adult pike are more vulnerable to the stresses of elevated temperatures than small juvenile fishes.

Pike can tolerate low oxygen concentrations, but tend to avoid levels below 3 mg/L, and activity is reduced and feeding stops when concentrations are lower than 2 mg/L (Casselman 1996).

As with other fish species, pike exhibit the physiological and behavioural characteristics of stress when environmental conditions are not optimal. They also exhibit characteristics of stress during catch and release fishing, although they appear to recover quickly from the latter (Arlinghaus *et al.*, 2008 a,b, 2009; Kleforth et al. 2011). Nevertheless, care must be taken when hooking, playing and handling fish during catch and release angling to ensure the individual pike does not experience excessive stress, which could perhaps affect their survival. This is particularly true when the water temperatures are high, above about 21°C. Under these conditions it is possible that the lower dissolved oxygen levels associated with higher water temperatures may combine with the high temperatures to put pike under undue stress. When this is coupled with the increased stresses associated with catch and release, it is possible pike, especially larger adult fish, will be subjected to higher stress factors that may adversely affect their physiological condition, and perhaps survival. This combination of conditions was likely experienced during periods of prolonged elevated water temperatures in the long, hot summer of 2018 (Figure 1), and are likely to be experienced on a regular basis in the future under predicted climate change scenarios.

This review demonstrates that water temperature needs to be considered when managing pike catch and release angling practices in the UK. Given the manifold influence of water temperature on fish physiological processes (Fry 1967), and the fact that temperatures approaching thermal maxima are stressful (Beitinger et al. 2000), there is a need to protect pike, and thus their associated populations, from the effects of thermal stress during warm summers. It is important to establish acceptable temperature criteria for surface waters that are protective of these fish and define thresholds above which angling should be controlled (advised that fishing for pike should be avoided). This is particularly important with the more prolonged and elevated temperatures being experienced during the summer in the UK in recent years. As a consequence, a wide range of water temperatures are experienced over the fishing season (from 0 °C to 26 °C) and temperatures above 21 °C for prolonged periods (days) may cause undue stress on the individual pike when coupled with being caught and released.

Moreover, water temperature can interact with other stressors (e.g. air exposure) and stressors that are not problematic at low temperatures, but can become multiplicative at higher temperatures (e.g. Gingerich et al. 2007). For that reason the adoption of fishing practices that reduce stress (and injury) to fish at all temperatures, but particularly at warmer temperatures are encouraged. Specifically, to reduce physiological disturbances and injury that could lead to delayed mortality, it is suggested anglers refrain from fishing during the summer when maximum air temperatures are consistently above 21 °C for extended periods of time (3-5 days). Such conditions may lead to elevated water temperatures throughout the day and cause inherent stress to individual fish. Adoption of these practices could be accomplished by the development of outreach and education materials (e.g. codes of practice) or through byelaws (e.g. seasonal closures). Regulating fishing activities around temperature thresholds is not a new principle. The Parks and Wildlife Commission of the State of Colorado USA prohibit fishing when the daily maximum water temperatures exceeds 74 °F (23.3 °C) or the daily average temperature exceeds 72 °F (22.2 °C) (Parks and Wildlife Commission of the State of Colorado 2018). The PACGB, already have codes of practices to moderate fishing activities during the summer (https://pacgb.com/fishing-for-pike/summer-piking-guide/), and these can be revised to account for this issue. However, there is also a need to target the general angling public who are not members of the PACGB and educate them about the consequences of fishing for pike during periods of high temperature.

All efforts to reduce stress and injury of fish that will be released after capture have the potential to reduce post-release mortality (i.e. catch and release mortality) and to improve the welfare status of pike populations. As indicated, fish caught by catch and release angling are subject to potential physiological stresses and damage at different phases of the angling event. Therefore, to explore opportunities to maximise survival of pike, it is best to assess the likely impacts in a sequential manner of the angling event from hooking to release (Figure 4: modified from Brownscombe *et al.*, 2017). This sequence also highlights opportunities where potentially stressful conditions can be reduced and should be considered in combination with any advice on avoiding fishing when water temperatures are high. In particular, anglers should be encouraged to use stronger-breaking gear during hot weather to land the fish quickly, minimise handling and avoiding holding fish in confined conditions. Such practices are well described in the PACGB codes of practices that can be downloaded from their website (https://pacgb.com/fishing-for-pike/) without being a member.

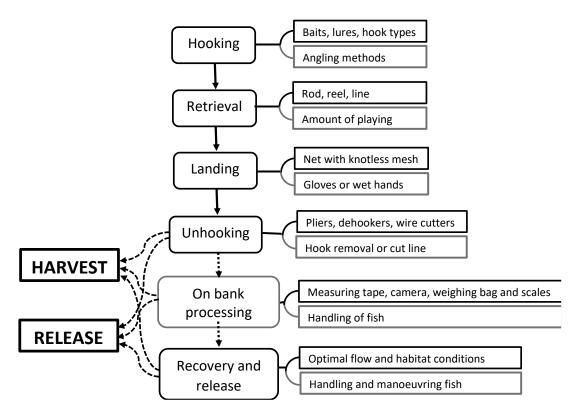


Figure 4. Conceptual diagram of potential stages of a catch and release angling event (from Hooking to Recovery) including considerations (angler choices) on angling tools (black boxes), and tactics (grey boxes), ultimately resulting in either the harvest or release of the captured fish. Solid connectors represent obligatory steps; dotted lines indicate potential steps dependent on angler choices (modified from Brownscombe et al., 2017)

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