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Review

The physiological consequences of catch-and-release angling: perspectives on experimental design, interpretation, extrapolation and relevance to stakeholders

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Abstract Over the past 20 years, there has been a dramatic increase in the use of physiological tools and experimental approaches for the study of the biological consequences of catch-and-release angling practices for fishes. Beyond simply documenting problems, physiological data are also being used to test and refine different strategies for handling fish such that stress is minimised and survival probability maximised, and in some cases, even for assessing and facilitating recovery post-release. The inherent sensitivity of physiological processes means that nearly every study conducted has found some level of – unavoidable – physiological disturbance arising from recreational capture and subsequent release. An underlying tenet of catch-and-release studies that incorporate physiological tools is that a link exists between physiological status and fitness. In reality, finding such relationships has been elusive, with further extensions of individual-level impacts to fish populations even more dubious. A focus of this article is to describe some of the challenges related to experimental design and interpretation that arise when using physiological tools for the study of the biological consequences of catch-and-release angling. Means of overcoming these challenges and the extrapolation of physiological data from individuals to the population level are discussed. The argument is presented that even if it is difficult to demonstrate strong links to mortality or other fitness measures, let alone population-level impacts of catch-and-release, there remains merit in using physiological tools as objective indicators of fish welfare, which is an increasing concern in recreational fisheries. The overarching objective of this paper is to provide a balanced critique of the use of physiological approaches in catch-and-release science and of their role in providing meaningful information for anglers and managers.

KEYWORDS: bycatch, conservation physiology, discards, recreational fisheries, stress.

Introduction

Catch-and-release (C&R) is a common practice whereby recreational anglers either release fish voluntarily or to remain compliant with fishing regulations when fish sizes or species are captured that are protected by regulations. One of the assumptions associated with C&R is that fish survive with negligible long-term impact on their fitness (Wydoski 1977); an assumption that is not met in at least some instances (reviewed in Muoneke & Childress 1994; Arlinghaus *et al.* 2007a). Attributes of C&R events, such as fight time, water temperature at capture and air exposure have been shown to induce a physiological stress response from which fish may or may not recover unharmed (reviewed in Cooke & Suski 2005; Arlinghaus *et al.* 2007a). These and other aspects of a C&R event (e.g. level of injury affected by gear choice) are generally under direct control of the angler. However, anglers differ greatly in their handling skill level and C&R behaviour (e.g. differences in landing and de-hooking times between experienced and novice anglers; Diodati & Richards 1996; Dunmall *et al.* 2001; Meka 2004), making the physiological consequences of C&R for fish highly context dependent. To predict and manage for the lethal and sublethal impacts of C&R adequately, it is necessary to understand further how the full range of angler behaviours (e.g. extended handling times, imposition of injury during de-hooking), biotic factors (e.g. interspecific and intersexual variation, fish size) and environmental conditions (e.g. water temperature, dissolved oxygen) influence the short and long-term physiological and behavioural consequences for angled fish and how this contributes to mortality or other components of fitness (Arlinghaus *et al.* 2007a). Indeed, advances in knowledge of the physiological stress response experienced by fish during angling and release is a fundamental first step towards the development of scientifically defensible best practices that are disseminated to, and hopefully employed by, anglers to reduce their impact on individual fish and cumulatively on fish stocks (see EIFAC 2008 for an example).

Although sublethal physiological endpoints are increasingly being used in studies of C&R (Arlinghaus *et al.* 2007a), there remain a number of challenges with relying exclusively on such metrics. Moreover, the interpretation of physiological data is to some degree subjective (e.g. a physiological stress response may be judged detrimental or not depending on personal values), and there are opposing implications drawn from physiological indicators of stress response in caught and released fish (Rapp *et al.* 2012). All of the authors on this paper routinely use such physiological metrics in studies of C&R and have become familiar with the challenges through their own work on a diversity of fish species and in the literature. Although there are a number of previous reviews on C&R, including some that summarise data arising from physiological endpoints (e.g. Cooke & Suski 2005; Arlinghaus *et al.* 2007a,b), there are no papers that provide a critical assessment of physiological tools and knowledge relative to C&R in terms of both the challenges and opportunities. To that end, this paper begins with an outline of the physiological tools used in the study of C&R, followed by a discussion of the challenges in using physiological tools for the study of C&R related to experimental design and interpretation, and commentary on means of overcoming these challenges. Additionally, responsible dissemination and use of physiological knowledge in the context of stakeholder interaction is discussed. Finally, commentary is provided on the extrapolation of physiological data from individuals to the population-level, the fundamental unit of most contemporary fisheries management. The general objective of this article is to provide a balanced critique of what physiological tools and knowledge can and cannot do to address biological or social C&R angling issues and to generate meaningful information for managers and anglers.

Overview of common physiological tools

By far, the most common physiological method used in C&R science is the collection and analysis of blood prior, during and after the C&R event. Blood samples can either be collected from live animals [either by a 'grab and stab' approach (e.g. Thompson *et al.* 2008; Clark *et al.* 2011), through cannulation (e.g. Ferguson & Tufts 1992)], or via lethal sampling (e.g. Suski *et al.* 2007a). Once collected, blood is typically analysed for ionic status (e.g. osmolality, Cl^-, K^+, Ca^{++}, Na^+), metabolites (e.g. glucose, lactate), stress hormones (e.g. cortisol), haematological characteristics [e.g. haematocrit (HCT), haemoglobin (HB)] and acid-base status [e.g. pH, bicarbonate and blood gases such as partial pressure of O_2 (PO_2) and CO_2 (PCO_2)]. The most common measures used in C&R studies are cortisol, glucose and lactate, which are useful for evaluating the extent of physiological disturbance related to a primary (cortisol) or secondary stress responses (glucose, lactate). On occasion, more specialised assays have been used to examine tissue damage to heart, liver or other key organs (e.g. intracellular enzymes such as lactate dehydrogenase [LDH] or aspartate transaminase [AST] are released into the plasma if tissue is damaged (Wells *et al.* 1986; Morrissey *et al.* 2005; Butcher *et al.* 2011; Rapp *et al.* 2012) or growth consequences (e.g. IGF II; Galima 2004). Several studies have measured reproductive hormone titres to examine the potential reproductive consequences of C&R (e.g. Pankhurst & Dedual 1994) or catecholamines (e.g. noradrenaline, adrenaline) to examine the primary stress response in further detail (Lowe & Wells 1996). White muscle sampling has also been used in studies of C&R (e.g. Booth *et al.* 1995; Kieffer *et al.* 1995; Suski *et al.* 2004) to examine tissue energy status [e.g. adenosine triphosphate (ATP), phosphocreatine (PCr), glycogen] and metabolites (e.g. lactate), although unless the fish is sufficiently large to enable a suitably sized muscle biopsy this approach requires lethal sampling (Suski *et al.* 2007a). Collectively, analyses of blood and muscle physiology are the most commonly used physiological tools in C&R science.

Another suite of tools has been used to examine the cardio-respiratory aspects of C&R. In the laboratory, fish have been outfitted with probes to measure blood flow (e.g. Cooke *et al.* 2001; Schreer *et al.* 2001) and thus determine heart rate, stroke volume and cardiac output, an approach that has yet to be used reliably in the field largely owing to technical limitations. Heart rate transmitters (Anderson *et al.* 1998; Cooke *et al.* 2004) and loggers (Donaldson *et al.* 2010a) have been used on free-swimming fish, but never on animals that were at total liberty (i.e. fish were held in large tanks, raceways, or an experimental stream channel). Biotelemetry devices capable of measuring locomotor activity (e.g. electromyogram telemetry; Cooke *et al.* 2000; accelerometers, Landsman *et al.* 2011) have been used to evaluate muscle and swimming activity of fish before, during and after real or simulated angling. Respirometry and swimming tunnels have been used to evaluate the metabolic costs of angling practices (Schultz *et al.* 2011; Clark *et al.* 2012) and to evaluate performance impairments (Schreer *et al.* 2005), respectively. Ventilation frequency has also been used on occasion as an indicator of physiological disturbance (White *et al.* 2008; Gale *et al.* 2011), but must be used with caution as it does not always reflect the severity of a stressor (Barreto & Volpato 2004). A more recent development is the use of reflex impairment assessments, which include evaluating the ability of a fish to regain equilibrium or the response to stimulus from the handler (e.g. touching the caudal fin; Davis 2010), although these responses have only occasionally been applied to C&R (see Thompson *et al.* 2008; Diamond & Campbell 2009; Campbell *et al.* 2010; Gale *et al.* 2011). There are certainly other tools that exist for physiological research, but to our knowledge, the examples presented previously represent the full suite of those that have been applied in a C&R context.

How have physiological indices been used?

In a review of C&R science, Arlinghaus *et al.* (2007a) revealed that nearly 25% of the 209 C&R studies published used a physiological indicator of stress when assessing C&R. The first published C&R study that included a physiological component was in 1976 (i.e. Wydoski *et al.* 1976) where the blood chemistry of hatchery and wild rainbow trout, *Oncorhynchus mykiss* (Walbaum), was compared after angling. Since this pioneering study, physiological tools have been used for four primary purposes: (1) to characterise the stress associated with different angling-related stressors; (2) to characterise recovery profiles following different angling-related stressors; (3) to evaluate various strategies for facilitating recovery and enhancing survival; or (4) to develop predictors of mortality (i.e. physiological thresholds that result in mortality once they are exceeded) for released fish. An over-riding theme is that the research tends to be done to provide a mechanistic basis for previously observed mortality and to identify practices (or factors) that reduce stress and enhance recovery. In other words, the body of C&R science with a physiological component is almost always ‘solutions-based’ rather than simply using those tools to identify problems. Moreover, given that pragmatic functions-based definitions of fish welfare consider physiological endpoints to be objective measures of welfare status (Davie & Kopf 2006; Cooke & Sneddon 2007; Iwama 2007; Arlinghaus *et al.* 2009b), all of these studies also have the potential to contribute to identifying practices that minimise welfare consequences for individual fish (Arlinghaus *et al.* 2007b, 2009a,b) – an issue that is increasingly discussed at least in some countries (Huntingford *et al.* 2006). Following is a brief discussion with examples of the four primary applications of physiology to C&R science.

Characterise the stress associated with different angling-related stressors

The physiological changes that occur in fish during an angling event are primarily the result of burst exercise during the capture event, which has been thoroughly studied and well characterised but not always in the context of C&R (e.g. Wood *et al.* 1983; Wood 1991; Wang *et al.* 1994; Kieffer 2000). In essence, burst exercise results in an energetic expenditure in white muscle that exceeds the ability of the tissue to respire aerobically, resulting in anaerobic respiration to fuel activity. As a result of anaerobic respiration, stores of fuels such as PCr, adenosine triphosphate (ATP) and glycogen in white muscle are consumed, and lactate is concomitantly produced (Wood 1991; Wang *et al.* 1994). Often coupled with this burst exercise is the activation of the primary stress response, which can release the stress hormones adrenaline, noradrenaline and cortisol into the bloodstream (Barton 2002). The release of stress hormones induces a suite of changes to physiological properties of fish that include the release of glucose to fuel aerobic tissues such as the heart or gill, splenic contraction to release red blood cells, elevated cardiac output to increase oxygen delivery to tissues, and a recruitment of gill lamellae to enhance oxygen uptake (Wood 1991; Wang *et al.* 1994; Barton 2002).

To understand how fish respond to angling events, studies have examined the impact of different stressors and factors on a variety of stress responses or performance metrics in C&R contexts. The magnitude of physiological disturbance related to angling has been shown to correlate positively with angling duration; largemouth bass, *Micropterus salmoides* (Lacepède), showed blood lactate levels that were almost twofold greater after 5 min of angling compared with 1 min of angling (Gustaveson *et al.* 1991; but see below for discussion of the timing of sample collection). Similarly, both the magnitude of cardiac disturbance and the magnitude of blood-based disturbances correlate positively with duration of air exposure that typically occurs during hook removal or photography (Cooke *et al.* 2001; Suski *et al.* 2007b; for a counter example, see Arlinghaus *et al.* 2009a). The magnitude of angling-related physiological disturbances can increase at sub- or supraoptimal water temperatures (Gustaveson *et al.* 1991), can be greater for large fish relative to smaller fish (Gingerich & Suski 2012; Clark *et al.* 2012) and can be greater for fish that have not been feeding relative to well-fed individuals (Gingerich *et al.* 2010). Such studies have served to characterise the stress associated with different components of the angling event and have revealed that gear choices (e.g. use of gear that extends fight duration, Meka & McCormick 2005; or retention gear, Rapp *et al.* 2012), and thus, angler behaviour can influence the level of physiological stress experienced by fish. Although there are fewer examples in the literature, severe injury that leads to blood loss or enables development of opportunistic pathogens also would have physiological consequences.

Characterise recovery profiles following different angling-related stressors

Most knowledge on recovery and response to angling has been developed from comparative physiology studies on exercise stress (Wood 1991). Angling-related stress is often described as being analogous to exercise stress, providing a ‘real world’ example of intense burst exercise (Milligan 1996; Kieffer 2000). The ability to recover from angling-related stressors has ecological outcomes, because swimming performance can be limited during the time required to clear metabolites from the blood and restore muscle energy stores such as glycogen, PCr and ATP (Milligan 1996). Failure to recover homoeostasis efficiently can result in mortality either directly as a result of metabolic collapse (Wood *et al.* 1983), or indirectly via post-release predation (Danylchuk *et al.* 2007). It had generally been thought that the recovery of plasma and muscle metabolites was prolonged, taking *c.* 24 h to return to pre-stress conditions (Black 1957; Turner *et al.* 1983), but it can also be much quicker within hours post-release (Arlinghaus *et al.* 2009a,b; Rapp *et al.* 2012). Many of the recovery studies were laboratory-based placing fish in recovery environments with static (i.e. non-flowing) water, where fish were unable to swim at routine speeds. The work of Milligan *et al.* (2000) and Suski *et al.* (2006) highlighted the importance of recovery environment (i.e. water velocity, dissolved oxygen content and temperature) to the rate of physiological recovery. While much of the research on recovery has focused on salmonids, interspecific differences in recovery from exercise and fisheries-related stress are known to occur, likely as a consequence of different life histories and physiological requirements (Turner *et al.* 1983; Milligan & McDonald 1988; Suski *et al.* 2007a; Arlinghaus *et al.* 2009a,b). Studies on free-swimming fish in large tanks or raceways supplied with fresh, flowing water suggest that while plasma metabolites and other indices of stress may begin to recover rapidly, heart rate and other cardiac variables can remain elevated for up to 18 h after the stressor (Anderson *et al.* 1998; Donaldson *et al.* 2010a). Indeed, recovery duration can scale proportionately with the duration and the magnitude of the stressor (Schreer *et al.* 2001). Quantification of recovery duration is useful to identify the potential latent effects of fisheries stressors (e.g. how long physiological and behavioural impairments may last if the fish was to encounter a predator), as well as to compare how different components of the angling event influence recovery time. For example, Suski *et al.* (2006) sampled fish after a 2-h recovery period to compare fish exposed to different recovery environments. Studies that use technological solutions such as cardiac monitoring (e.g. Clark *et al.* 2010; Donaldson *et al.* 2010a) enable continuous data collection and thus determination of exact recovery times relative to studies that use discrete time points for blood sampling such as 1, 2, 4 and 24 h. Studies that evaluate recovery require the generation of a temporal sequence of physiological profiles, ideally from the same, undisturbed individual. In addition to the data logging and telemetry technology detailed previously, measurements of oxygen consumption rates may be useful because they can be done without touching the fish. Nonetheless, animals still do have to be handled to be introduced to the chambers and not all animals cope well with confinement. This is of particular concern in wild fish, while using hatchery fish in C&R studies risks that the stress response is less intensive compared with wild conspecifics owing to habituation or selection effects.

Evaluate various strategies for facilitating recovery and enhancing survival

Following angling or exhaustive exercise, a number of strategies have been attempted to enhance the survival of released fish through facilitated recovery. Physiological knowledge and research is useful for identifying potential recovery strategies and evaluating their success. One of the precursors to facilitation of recovery is the use of physiological tools to determine first the most detrimental aspects of the angling/handling event to identify opportunities where efforts would be best directed. To date, recovery strategies have met with mixed success, both within and across species. An effective strategy for salmonids has been the use of low-velocity swimming, as opposed to recovery in static (non-flowing) water (see Milligan *et al.* 2000; Farrell *et al.* 2001). When examined in largemouth bass, however, recovery was accelerated following 1 h of swimming, but by 4 h after exercise recovery in low-velocity water resulted in additional physiological disturbances (Suski *et al.* 2007a). The failure of low-velocity swimming to accelerate recovery in largemouth bass is likely due to largemouth bass being largely sit-and-wait predators that do not regularly perform large swimming episodes. Donaldson *et al.* (2011) held upriver migrating sockeye salmon, *Oncorhynchus nerka* (Walbaum) in a net pen for 24 h to enable fish to recover from an angling event, but holding itself led to elevated cortisol and glucose, and following release all but one fish (3%) held in the net pen failed to complete the migration to spawning areas. Conversely, fish that were beach seined or angled and immediately released had 52 and 36% migration success, respectively. This suggests that although facilitating recovery can be beneficial, recovery environment and duration are important considerations, and extended durations may lead to chronic holding stress and high mortality (Portz *et al.* 2006). This raises some methodological concerns as to the relevance of some recovery studies that may induce high levels of confinement stress on experimental animals.

For many years, salt (NaCl) has been added to tanks of freshwater fishes to reduce the physiological impacts of fish hauling by elevating ambient concentrations of ions such as sodium and chloride that can be lost by fishes through the gills in fresh water during prolonged stressors (Carmichael *et al.* 1984; Barton *et al.* 2003). When this practice has been examined in the context of recovery from exercise or angling-related stressors, results have been less clear. Davis *et al.* (1982) reported that simple exposure of striped bass, *Morone saxatilis* (Walbaum) to a 1% salt solution independent of angling induced a significant stress response. Similarly, VanLandeghem *et al.* (2010) showed that sudden increases or decreases in water temperature can induce significant physiological disturbances for largemouth bass, while work by Suski *et al.* (2006) showed that variation in water temperature that was either above or below ambient impaired recovery from exercise in largemouth bass relative to individuals that were recovered at ambient temperature. In addition, Cooke *et al.* (2002) showed that cardiac disturbances during simulated livewell confinement of largemouth bass recovered most quickly in water without any form of salt or commercially available water conditioner, and recovery was delayed by nearly 50% when a 0.5% salt solution was used in livewells. Experimental results of physiological examinations suggest an increased stress response for freshwater fishes recovered in water with salt, commercially available conditioners or water temperatures that vary from ambient, but field tests in angling tournament scenarios would suggest improved survival owing to use of combinations of salt and ice.

Develop predictors of mortality

A long-standing goal for much of the C&R research has been to develop physiological biomarkers to predict mortality of released fish (Cooke & Schramm 2007), an outcome that would enable rapid assessment of mortality potential in different fisheries given that it is often expensive and time-consuming to conduct mortality studies in the natural environment. To date there have been a few studies that have attempted to do so in the context of C&R (Arlinghaus *et al.* 2008; Thompson *et al.* 2008; Gale *et al.* 2011), but this work is not without challenges and limitations (see Davis *et al.* 2001). Studies have released fish with telemetry devices and attempted to link physiological status to fate (e.g. Thompson *et al.* 2008; Arlinghaus *et al.* 2009a; Rapp *et al.* 2012) or held fish in tanks and evaluated the physiological correlates of mortality (e.g. Gale *et al.* 2011). In some cases, links between release physiology and delayed mortality were not identified maybe because mortality rates were low or negligible despite substantial physiological changes (Arlinghaus *et al.* 2009a; Rapp *et al.* 2012). However, even relating physiological state and subsequent behaviour post-release has not resulted in many significant findings (Arlinghaus *et al.* 2009a; Rapp *et al.* 2012). Many fish species have high thresholds for coping with physiological stress (i.e. able to resolve even highly disturbed blood chemical profiles), which constrains the ability to develop predictive relationships of physiological variables and mortality. In other words: linking physiological measures and behaviour and mortality is much less straightforward than initially believed.

Some of the challenges associated with using physiological measures as indicators of whole-organism impacts cannot be easily resolved. Traditional blood measures used to assess physiological state offer limited utility as mortality predictors because they cannot be easily used by anglers or managers, and typically not in real time (i.e. a field setting). Lately, there has been a growing interest in the use of reflex impairment assessments (Davis 2010), which have the capacity to both predict delayed mortality (Diamond & Campbell 2009; Campbell *et al.* 2010) and be used by anglers. Assessments of reflex impairment or other macroscopic indicators of fish condition (e.g. ventilation rate; see Gale *et al.* 2011) are simple enough to be used by anglers to quantify fish condition. Gingerich *et al.* (2007) used ventilation rate and equilibrium status (i.e. physical orientation of the fish) to evaluate thresholds of air exposure and water temperature for angled bluegill, *Lepomis macrochirus* Rafinesque that can result in mortality. On the whole, efforts to validate and implement applications of physiological predictors of mortality are in their infancy, particularly in the context of recreational fisheries. To date, it appears macroscopic indicators of fish condition and injury (e.g. blood loss) offer more promise for predicting mortality (Arlinghaus *et al.* 2008) than traditional physiological measures in blood or muscle, but more work is required to clarify this observation.

Limitations with existing C&R physiology studies

In an effort to identify opportunities for improving the science of C&R, a critical discussion of some of the limitations with many of the existing C&R studies is presented herein. Some of the limitations are truly difficult to overcome and will require creativity and technological innovations, but the benefits of doing so will be immense, and hopefully this transparent and critical assessment will stimulate attempts to elevate the application of physiological techniques to C&R science. Ten limitations are identified, each discussed below. Each section is concluded with recommendations for how these limitations could be addressed.

Confounded mortality estimates

It can be problematic when angling studies that are designed primarily to assess physiological consequences are also used to generate mortality estimates. For example, Ferguson and Tufts (1992) cannulated rainbow trout and then exposed some of them to exercise and some to exercise plus air exposure while also maintaining a control group. While the physiological data were compelling, the authors also reported mortality rates in the different treatments that were remarkably high for the air exposed fish (i.e. 72% mortality within 12 h following exercise and 60 s of air). Future studies on air exposure have shown that exposure to air only kills fish in situations where unrealistically large exposure times are employed (Gingerich *et al.* 2007) and in very sensitive species (e.g. pike-perch, *Sander lucioperca* L.; Arlinghaus & Hallerman 2007), while zero mortality of air exposed fish was reported in many other studies (e.g. Thompson *et al.* 2008; Arlinghaus *et al.* 2009a; Rapp *et al.* 2012). Cannulation itself is a difficult procedure that can result in death, particularly if fish thrash about and dislodge the cannula, which could easily happen during a real or simulated angling event. The levels of mortality mentioned (Ferguson & Tufts 1992) are routinely cited by researchers, the angling media, and NGOs as being 'real' but the presence of the cannula and the differential risk of pulling out the cannula make the survival data highly problematic. There are only a few other studies, even in the presence of extreme water temperatures, that have documented similarly high levels of mortality in salmonids that are not cannulated (reviewed in Muoneke & Childress 1994; Arlinghaus & Hallerman 2007; Donaldson *et al.* 2011). Another example is that of Beggs *et al.* (1980) where adult muskellunge, *Esox masquinongy* Mitchell, were captured at a field site, transported several hours to a laboratory, anesthetised, cannulated, exposed to repeated blood sampling and then mortality rates reported (*c.* 30%). This high level of mortality for muskellunge was assumed for wild caught fish until a recent study using micro radio transmitters in the field (i.e. Landsman *et al.* 2011) revealed no mortality during a 2-week post-release monitoring period for two different angling protocols at temperatures similar to those used by Beggs *et al.* (1980). Therefore, caution should be taken by those doing physiological studies that involve rather extensive interventions (e.g. cannulation, transport and repeated handling) or holding of fish in non-realistic conditions (e.g. sensory deprivation chambers) to only report mortality with extreme transparency about the limitations.

Some studies have also withdrawn small amounts of blood from angled fish and then released them with telemetry tags (e.g. Thompson *et al.* 2008; Rapp *et al.* 2012). That approach has potential to elucidate correlates of mortality, but it is also possible physiological sampling impairs fish and promotes mortality so there is need for validation studies (e.g. Cooke *et al.* 2005) and/or use of controls that are tagged but not physiologically sampled, or parallel physiological sampling on non-tagged fish (e.g. see Donaldson *et al.* 2011). Probably the best study design, however, would consist of tagging and releasing fish followed by recapture of a subset after a sufficiently long recovery period. Such research would be suitable if one can discount a moderating effect of the tag itself on the fitness of fish. It is also ideal to have paired laboratory and field studies that use identical approaches and populations/species such that mechanisms can be assessed in the laboratory with knowledge that they are grounded in field realism (see below and Arlinghaus *et al.* 2009a; Rapp *et al.* 2012 for examples).

Lack of appropriate controls

Appropriate baseline physiological controls for C&R studies to compare values from capture and handling treatments can be difficult to obtain and the best type of control will vary according to the question that is being asked (Pollock & Pine 2007). In C&R studies on wild fish, the most common controls are wild fish that are quickly captured by angling and blood sampled quickly (e.g. Pankhurst & Dedual 1994; Meka & McCormick 2005; Rapp *et al.* 2012), wild fish that have been quickly captured using other methods (e.g. electric fishing, Landsman *et al.* 2011), or wild fish that have been captured and held in sensory deprivation chambers (e.g. Suski *et al.* 2004; Morrissey *et al.* 2005). All of these methods are problematic to some degree: capturing wild animals will always cause some level of physiological disturbance; confinement and holding wild fish in a laboratory can elicit a stress response; and capturing fish by alternate methods (e.g. electric fishing) can potentially result in more physiological disturbance than angling. This is particularly challenging for large fish that cannot be landed quickly and that are difficult to hold in laboratory facilities (e.g. big game species; Wells *et al.* 1986). Obtaining accurate control estimates of mortality can be similarly challenging (Pollock & Pine 2007). Acknowledging these issues, the most appropriate method to date has been to capture wild fish as quickly as possible and sample the animals before physiological parameters typically measured in C&R can change (i.e. minutes) in response to the capture and handling event (see Clark *et al.* 2011). Physiological parameters that respond on faster timescales (e.g. catecholamines, which respond within seconds) will remain inappropriate as C&R tools.

In some cases, values from fish captured and immediately sampled can be lower than those obtained from fish held in black boxes or net pens (e.g. Suski *et al.* 2004) and are therefore thought to be more indicative of a wild fish's resting state, although this typically requires inferences to be made if true reference values are unavailable. In some studies, the challenges associated with the field site or study species mean that controls cannot be obtained, and values can only be compared among different treatment groups (e.g. O'Toole *et al.* 2010). It may be helpful in such cases to develop extensive reference values for some of the common study species of interest. However, this is challenging because reference values are highly context dependent, and factors such as environmental conditions (e.g. temperature, dissolved oxygen), life stage (e.g. juvenile vs adult), level of reproductive development (e.g. non-mature vs mature adult), pre-capture condition (e.g. diseased vs healthy), hatchery vs wild, sex and in some cases even population would need to be taken into consideration. The challenging lack of true replicates in any wild fish is difficult to overcome (no wild individual is identical to another, e.g. parasite load will differ), and probably can only be overcome by increasing the number of replicates. Moreover, assay types and analytical tools also vary study-to-study and laboratory-to-laboratory, further confounding the ability to establish reference values.

Failure to develop predictors of post-release fate

As noted previously, a long-standing goal in C&R science is to be able to use physiological or behavioural metrics to predict long-term survival of teleost (Cooke & Schramm 2007; Skomal 2007) and elasmobranch (Skomal *et al.* 2007; Renshaw *et al.* 2012) fishes. To do so in a field setting requires obtaining a non-lethal physiological sample (usually blood) and an associated assessment of fate (Donaldson *et al.* 2008). Such an approach has been used to develop relationships between gene expression and various physiological metrics (e.g. hormone profiles, lactate) and the fate of Pacific salmon, *Oncorhynchus* spp. during an arduous migration (Cooke *et al.* 2006a,b; Donaldson *et al.* 2010b; Miller *et al.* 2011). The few examples of applying this technique in a C&R context have been limited by the low statistical power to test such relationships because the overall sample sizes and mortality rates have been relatively small (Arlinghaus *et al.* 2009a; Rapp *et al.* 2012). One of the first examples involved blood sampling largemouth bass and then releasing them with radio transmitters to examine post-release behaviour and survival (Thompson *et al.* 2008). Despite using lengthy air exposure periods, neither mortality nor significant behavioural impairments were reported. A similar outcome was noted for a study of northern pike, *Esox lucius* L. (Arlinghaus *et al.* 2009a) and muskellunge (Landsman *et al.* 2011). Studies of marine species have also failed to establish concordance between plasma measures and delayed mortality (Davis *et al.* 2001; Skomal 2007). Beyond the problems noted previously, there is mounting evidence that, taken alone, conventional blood chemistry measures may not be definitive enough to forecast long-term survival following fisheries-related injuries and stressors (see Skomal & Bernal 2010; Pankhurst 2011; Renshaw *et al.* 2012), although another possible explanation is that researchers are failing to use the appropriate physiological indices (Renshaw *et al.* 2012; see section below on use of a limited set of metrics). Although now technically feasible to attempt to link physiological condition to fate, it has thus far failed to enhance C&R science with respect to long-term outcomes. However, with shorter-term outcomes (e.g. behavioural endpoints) and when used for conducting mechanistic laboratory studies to complement field studies, physiology has yielded valuable insight.

Unlike traditional physiological tools, there has been considerable success in using a simple reflex impairment index [reflex assessment mortality predictors (RAMP) score] to predict delayed mortality for fish released from commercial fishing gears and subsequently monitored in large tanks (summarised in Davis 2010) or released into the wild with telemetry tags (Raby *et al.* 2012). The success of RAMP for predicting mortality is likely attributed to its holistic nature: underlying physiological impairments are integrated into whole-animal responses that can easily be assessed in a quantitative way. In the context of C&R, Campbell *et al.* (2010) developed a condition index for red snapper, *Lutjanus campechanus* Poey, that combined reflex impairment with indicators of barotrauma and was associated with immediate mortality and proxy indicators of post-release predation risk (post-release mortality was not assessed directly). Ventilation rate, an indirect measure of respiration, also may have relevance. For example, Gale *et al.* (2011) reported that in sockeye salmon exhaustively exercised and air exposed for 1 min, individuals with ventilation rates of 60 per min were three times more likely to suffer mortality within 24 h than fish with ventilation rates of 90 per min. Additional research is needed to develop predictors of fate in C&R science and the logical focus should be on fisheries for which significant mortality is observed that seems to be independent of physical injury (e.g. deep hooking). Reflex assessment mortality predictors will not replace traditional physiological metrics, but it is a valid and inexpensive complement and could be incorporated into any study of C&R mortality even if the project team has little or no experience in physiological research.

Reliance on hatchery fish

Many popular freshwater and saltwater game fish species are extensively cultured throughout the world as part of stocking and mitigation efforts in various jurisdictions (e.g. Heidinger 1999). As hatchery fish are readily available on demand without the need for costly field collections, researchers have used these fish in physiological studies of C&R (Wydoski *et al.* 1976; Ferguson & Tufts 1992; Milligan *et al.* 2000; Rapp *et al.* 2012) as surrogates for wild fish with the implicit assumption that hatchery and wild origin fish are similar. However, the use of hatchery fish as a surrogate for wild fish is called into question by the many genotypic and phenotypic differences between hatchery and wild fish stocks (Lorenzen *et al.* 2012). Cumulatively, differences in the hatchery environment have the potential to lead to differences in behaviour (Symons 1969; Hill *et al.* 2006; Roberts *et al.* 2011), physiology (Folmar & Dickhoff 1980; Shrimpton *et al.* 1994; Congleton *et al.* 2000), stress response (Pottinger 2006), health and nutritional condition (Wood *et al.* 1957; Ludwig 1982; Powell *et al.* 2010) and ultimately, survival (Kennedy *et al.* 2007) relative to wild conspecifics. In particular, cultured fish are often subjected to disturbance and handling stress in the form of crowding and transfer between tanks, grading and culling, anaesthesia (e.g. via high CO_2 exposure), treatment for disease and disturbance owing to facility maintenance activities (Piper *et al.* 1982; Barton & Iwama 1991). Because hatchery fish are often genotypically and phenotypically different from wild fish, and usually more resistant to stress, conclusions derived from C&R studies using hatchery fish must be regarded with caution and may need to be corroborated with studies on wild fish and vice versa (e.g. Rapp *et al.* 2012). Although unrelated to the issue of using hatchery fish in research, theoretically, it would also be possible to select experimentally for individual fish with low stress responsiveness (as has been done for aquaculture purposes; Overli *et al.* 2005), such that fish are less likely to experience deleterious effects of the physiological aspects of angling, although the authors do not advocate for such an endeavour for conservation reasons of genetically pure wild fish stocks.

Failure to take physiological tools to the field

Historically, physiological research was restricted to laboratory environments, but of late there has been increased interest in field physiology (Costa & Sinervo 2004) and the expansion of the field physiology toolbox. For example, innovations in biotelemetry and biologging (reviewed in Donaldson *et al.* 2008) as well as validation of portable diagnostic meters (e.g. for lactate, haemoglobin, blood gases, glucose, ions; e.g. Mandelman & Farrington 2007; Clark *et al.* 2008; Cooke *et al.* 2008; Gallagher *et al.* 2010) has improved the ability to study C&R in field-relevant situations (e.g. on fishing boats; Arlinghaus *et al.* 2008) including remote fisheries (Cooke *et al.* 2008). Generating physiological data in the field using portable diagnostics (for a limited suite of metrics) can inform in-season research efforts to refine study design or management models (e.g. for Pacific salmon fisheries interactions relative to river temperature; Cooke *et al.* 2012). If samples are collected and stored for later analyses, data are not available until laboratory analysis is completed weeks or months after sample collection. Use of portable analytical tools is a promising development but there remains much opportunity for application of physiological tools in the field, thus increasing realism and incorporating physiology into field studies that have traditionally focused solely on injury and mortality with no mechanistic component. Given the inherent complexities of conducting physiological experiments in the field, it is first necessary to refine and validate techniques to ensure reliable data (e.g. Clark *et al.* 2011).

Reliance on simulated angling events

Logistical and time constraints, and at times acrimonious relationships, can impede researchers from working directly with recreational anglers for the collection of physiology data from fish exposed to authentic angling events, despite the advantages of doing so (Danylchuk *et al.* 2011). Nonetheless, there are a number of examples where this has been successful (e.g. Suski *et al.* 2003; Donaldson *et al.* 2011; Landsman *et al.* 2011). In a desire to control residual variance caused by uncontrolled angler effects, researchers often depends on simulated angling events that may ultimately result in a mismatch between study results and the physiological stress response experienced by fish caught by recreational anglers in field settings. While this often enables a better understanding of how fish respond to fisheries-related stress under controlled conditions, the results should be taken with caution by fisheries managers. For example, it is unclear whether the fight times used during simulated angling actually reflect fight times consistent with what occurs in a fishery composed of heterogeneous participants with different levels of expertise. It is not unreasonable for novice anglers, for instance, to play fish to exhaustion because of their inexperience or interest in getting the most out of the experience, yet extreme treatments are often excluded from study designs (Wedemeyer & Wydoski 2008). Alternatively, researchers may add extreme treatments to see effects, which may be unrealistic in nature (e.g. extended air exposure in Gingerich *et al.* 2007).

Without exploring the full range of fight times or other stressors such as air exposure, no general conclusions about the physiological impacts of C&R can be drawn because there is a lack of benchmarks or turning points that are of particular value for the angling constituency to guide angling behaviour (Schreer *et al.* 2005). Nevertheless, angling simulations can indeed play an important role in C&R studies, especially when attempting to control for interangler variation (Anderson *et al.* 1998; Cooke *et al.* 2008). For instance, Cooke *et al.* (2008) used simulated angling to regulate fight times of bonefish, *Albula vulpes* (L.) so that the duration of the angling event reflected the physical capacity of the fish and not the varying abilities of different anglers. The duration of the angling used by Cooke *et al.* (2008) reflected that imposed on fish during authentic angling events (Danylchuk *et al.* 2007), thus making the results of their study applicable for the development of best practices for bonefish. If working directly with recreational anglers to sample angled fish is not feasible, it is prudent to first quantify the elements of authentic angling events (e.g. duration of fight) and then use that information to increase the authenticity of simulated angling used for research. Researchers should be conscious of the possibility that anglers may alter their behaviour in the presence of researchers, which could result in biased data. Relatedly, anglers chosen or that volunteer to participate in C&R studies may not represent the heterogeneity of the sector. For example, members of fishing clubs/angling organisations or professional guides and anglers seem to be targeted frequently for participating in C&R studies (e.g. Cooke *et al.* 2001; Landsman *et al.* 2011). It is important to compare the characteristics of those participating in C&R studies relative to those of the broader angling community to understand the representativeness of their behaviours.

Failure to understand how physiological disturbance can influence population-level processes

A common criticism of C&R studies that have found individual-level effects is that they fail to provide links to population-level processes (see below for link to management implications). These links can be difficult to obtain owing to the challenges associated with following wild animals and their recruitment for extended periods of time, and with challenges inherent in linking any individual metric to population processes. Individual-level processes such as compensation (e.g. compensatory growth following a period of growth suppression; Ali *et al.* 2003; Cline *et al.* 2012) and population-level processes such as population growth rate as moderated by density-dependent competition can modulate how individual-level effects translate to population dynamics (Edeline *et al.* 2010; O'Connor *et al.* 2011). Thus far, C&R studies have shown individual effects at multiple levels, from cellular processes to whole-animal parameters (e.g. growth depression), although this is strongly species and context dependent and cannot be generalised across species. Growth depression and other whole-organism effects can indeed have population-level consequences (Edeline *et al.* 2010), but there are few studies of population-level effects of C&R other than those focusing on the mortality effects of C&R (Coggins *et al.* 2007). Some of these whole-animal effects likely influence population dynamics; for example, deep hooking (Aalbers *et al.* 2004) or the act of C&R in a high density population has been shown to cause growth suppression in some fish such as pike (Klefoth *et al.* 2011), and suppressed growth rate has in turn been shown to reduce population growth rate in this species (Edeline *et al.* 2010). However, the links remain theoretical, indirect (as demonstrated previously), or are made through potentially oversimplified mathematical modelling exercises (e.g. O'Connor *et al.* 2011). Population-level monitoring (e.g. whole-lake monitoring) may be the logistically difficult but necessary step required to demonstrate population-level C&R angling effects (Cline *et al.* 2012). If simple physiological predictors (e.g. reflex impairment) of post-release mortality are developed and validated, they could be used to monitor the impact of C&R fishing on tagged individuals that, in turn, feed back to population-level processes, although the tracking of individual fate and individual reproductive success may ultimately be needed to understand such processes in full detail. An alternative might be to use whole-lake experimental designs, where some lakes are exposed to total C&R fishing and others are not in a before-after-impact design.

Failure to consider physiological time course when developing sampling strategies

A continued challenge for both laboratory and field studies is the timing of sample collection, particularly when measuring indices of acute response that begin changing immediately upon contact with fishing gear. To measure the stress associated with angling, fish are often sampled immediately upon landing (e.g. Donaldson *et al.* 2011), which misses the peak response of many of the more commonly measured variables (e.g. plasma cortisol typically peaks 1–2 h post-stressor; Barton 2002) but captures the physiological condition immediately following the capture event. The acute stress response is on a fixed time course, where most parameters that are commonly measured, such as metabolites and stress hormones, increase from the time of capture, towards a peak, plateau and recovery (Skomal & Bernal 2010; see Fig. 1). Immediate sampling is problematic when wishing to compare physiological condition among treatment groups that vary based on fight time, air exposure time or other time-based criteria, because the timing of sample collection will greatly influence the values obtained for each group. Conversely, researchers may wish to measure the peak changes in values to reduce the variation associated with comparing between groups immediately following capture. However, an issue with trying to capture the peak change is that fish need to be transferred to a holding area until the time of sampling (e.g. often up to 1–2 h for commonly measured parameters), such as a net pen or livewell, which may inadvertently stress the fish additionally to the capture event itself, even in the short term (Portz *et al.* 2006). Clearly, there is no ideal way to collect samples from fish without researchers themselves posing additional stress, a problem inherent to all studies measuring acute animal stress responses (Langkilde & Shine 2005), which can have dramatic and undesirable outcomes in some cases (Voss *et al.* 2010).

To minimise researcher effects when sampling fish, several methods should be considered. Researchers need to be cognisant that any disturbance such as netting, handling and even observer presence in the laboratory can influence the physiological condition of fish. In the laboratory, methods such as dorsal aorta cannulation to collect blood can be used, but this typically requires fish be confined to small tanks or enclosures, and there is likely to be substantial stress associated with anaesthetising individuals, surgically implanting cannula and potential problems with wound healing and stress associated with cannula burden (see previous sections). Field researchers should have a well-organised sampling schedule and standard operating procedure. It is recommended that all researchers and teams of technicians have the opportunity to practice fish handling and sampling prior to the study to ensure that each fish is sampled rapidly, efficiently and consistently. If necessary, it is possible to statistically control for variation in time between cessation of the capture stressor and collection of the sample (Raby *et al.* 2012). An appropriate sampling setup should be established, ensuring the best possible practices and water conditions be used (e.g. troughs equipped with fresh, flowing water; Cooke *et al.* 2005). If researchers are trying to capture true peak values for the variables they are measuring, appropriate holding conditions must be established and ideally these values should be compared back to laboratory-based values from cannulated fish under control conditions (either from previously published work or from a companion study, where possible). Comparing variables that respond on different time courses can be valuable (e.g. one could measure plasma cortisol, plasma lactate, muscle lactate and use physiological data loggers to track the continuous

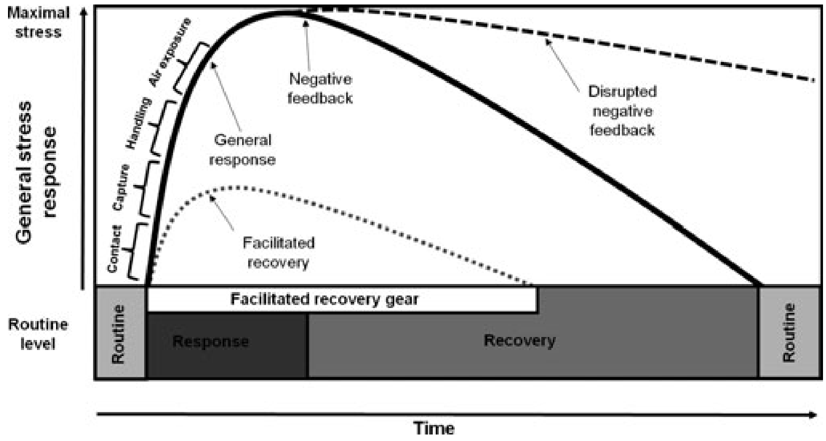

Figure 1. Schematic of the general stress response to fisheries capture. The thick black solid line labelled 'general response' provides an example of a typical response of a physiological indicator of stress, such as plasma cortisol, to a fisheries capture event. Following the initial response, a negative feedback occurs and recovery is initiated. The stressors connected by a bracket to the general response line exemplify the multiple, interactive and potentially cumulative stressors involved in a fisheries capture event, all of which contribute to the general stress response and are dependent on environmental conditions and the initial condition of the individual fish. The thick black broken line represents a disrupted recovery pattern, where recovery to routine physiological condition does not occur and there are life history consequences. The grey broken line represents an example recovery profile for individuals held in facilitated recovery gear, where the general physiological response is muted and recovery to routine condition is accelerated.

response of heart rate) for telling a more complete story of the stress response and recovery of angled fish. Regardless, there are no perfect methods for measuring acute stress responses in the laboratory or field. Although precautions can be put in place to ensure the best possible procedures are used to collect data, researchers should use caution when making inferences based on absolute physiological values and instead focus on comparing treatment groups (e.g. Donaldson *et al.* 2011).

Failure to study interactions and synergistic effects

Most work examining the aspects of the C&R angling event such as fight time, air exposure or angler experience look at these effects in isolation. However, Gingerich *et al.* (2007) demonstrated that air exposure and water temperature interact to raise mortality sharply when air exposure is long and water temperatures are high. Interactive, additive and synergistic effects are well-known aspects of stress physiology in other contexts (Barton 2002), and such effects need to be considered for a complete knowledge of C&R effects. What is the influence of environmental conditions such as elevated water temperature or even contaminants on how fish respond to a C&R event? What influences do repeated angling events have on the animal's physiology and do repeated capture and water temperature interact? Or is there habituation to being caught multiple times, or do animals face interactive and additive stress effects associated with multiple captures that may not have been apparent with single capture? Because of the potential for interactive effects on the physiology, behaviour and mortality of caught and released fish, there is a wide range of possible outcomes for C&R in different contexts. Developing rapid, simple, and inexpensive ways to assess fish condition and predict mortality (see section How have physiological indices been used? above and What is needed to make physiology more relevant to managers and anglers? below) could help more efficiently assess synergistic effects of the numerous possible combinations of environmental, biotic and anthropogenic factors associated with C&R. The notion that physiological effects arising from fishing interactions can vary and interact with other stressors, environmental conditions, season, etc. is difficult to communicate with managers and the public and remains a priority research topic in C&R science.

Reliance on a limited set of physiological metrics

The past decade has seen tremendous advances in our ability to characterise stress and deviation from homoeostasis in fishes. Nonetheless, many contemporary studies continue to rely on a small suite of conventional physiological metrics (e.g. plasma chloride, glucose, lactate and cortisol), often without sufficient mechanistic explanation for selecting those particular measures. There is merit in using a variety of conventional metrics, but they are often used without a rational basis or direct links to hypothesis testing. Tools such as microarrays, quantitative PCR, proteomics and other molecular markers have improved understanding of stress across a range of species, in a number of different tissues, for a suite of natural and anthropogenic stressors (dos Anjos *et al.* 2011) and have been advocated for use in studies of fisheries interactions (Renshaw *et al.* 2012). These tools can be broad indices of cellular stress (e.g. heat shock proteins; Heberer *et al.* 2010) or can be specific to certain stressors (i.e. HIF1-α and hypoxia), and often are expressed very quickly after the perception of a stress. Oxidative stress metrics such as those that evaluate oxidative protection [e.g. oxygen radical absorbance capacity (ORAC)] and stress markers [e.g. 8-hydro-2-deoxyguanosine (8-OHdG), protein carbonyls and lipid peroxides] also have potential utility for C&R science (Renshaw *et al.* 2012). To date, despite the power, sensitivity and specificity, these novel molecular and biochemical tools have rarely been applied to studies of C&R. Molecular and biochemical tools could, and likely should, be used in future studies of C&R angling, not only as a way to quantify stressors across tissues of angled fish, but to build knowledge about recovery mechanisms, recovery pathways and to prevent long-term impairment of released fish. Developing links between these variables and population-level processes such as mortality or reproduction or other components of fitness are critical to ensuring their relevance to C&R science and management, and it is only then they will be of relevance. Otherwise, the more sensitive an indicator is, the more impact it will show, but the decisive issue is whether there is a whole-organism effect of the stressor in terms of fitness reduction post-release. Researchers should be encouraged to consider the emerging physiological toolbox in all future C&R studies. Overall, the appropriate tools should be selected *a priori* in response to the question at hand and should be done in a hypothesis testing framework.

What is needed to make physiology more relevant to managers and anglers?

Fisheries managers deal primarily with populations while most C&R studies that involve physiology focus on individuals. Therefore, some managers may have an issue with a purely physiological study because the argument can be made that only a mortality or other more directly fitness-related endpoint is of relevance, often under the further condition that population-level effects are seen in response to total or partial C&R. An alternative perspective is that for maintaining the welfare of an individual fish any avoidable impact is too much (Huntingford *et al.* 2006; Cooke & Sneddon 2007), such that using sensitive physiological metrics may help making C&R fishing less challenging to individual fish. Therefore, some of the issues about the usefulness of physiological tools come back to basic value judgments about what matters in terms of impact, and these judgments are often held implicit. Reconciling how physiological knowledge from individuals can be relevant to management of fish populations remains a critical need for the field (Cooke & O'Connor 2010). Of course, documenting a physiological response does not mean that there are any population-level implications *per se*. Physiological information must always be placed in the context of baseline conditions, performance capacity, thresholds and ability to recover from stressors. It is thus beneficial to establish relationships between physiological metrics and population-level processes not just for C&R, but also more broadly in conservation physiology (Cooke & O'Connor 2010). Indeed, for some stakeholders, establishing a link between physiological reaction to C&R and individual fitness is probably sufficient to induce a management response to avoid the impact on the fish through better handling. The development and validation of macroscopic tools that integrate biological processes (like RAMP) that can easily be used by managers and anglers with negligible economic costs has the potential to empower stakeholders to understand underlying physiological processes better and to use this information to reduce mortality. Because fisheries managers and anglers will be increasingly expected to consider fish welfare as an individual-level concept in their actions (Arlinghaus *et al.* 2007b; EIFAC 2008), physiological tools can provide an objective measure of welfare status and thereby avoid a focus on unmeasurable variables such as pain and suffering (Iwama 2007; Arlinghaus *et al.* 2009b). As all C&R activities induce physiological changes, it remains very important to be careful in the interpretation of physiological data and not to interpret or implicate beyond the scope of the study. The ability to describe and predict the connection between reduced stress and improvements in survival is key for emphasising to anglers the utility and relevance of physiological knowledge, but a focus on fish welfare may equally grow in the future that is not contingent on survival endpoints. In the end, by reducing physiological impact one can assume the fish is released in a better condition, which improves fish welfare without questioning the activity of fishing *per se* (Arlinghaus *et al.* 2009b).

Responsible interpretation and extension of physiological findings

Although physiological tools can play an important role in understanding and mitigating the sublethal consequences of C&R on fishes (Cooke *et al.* 2002; Wikelski & Cooke 2006; Arlinghaus *et al.* 2007a), it is important that the findings of physiological studies be interpreted correctly and used appropriately. It is difficult to translate the physiological results of C&R research into best practices given the limitations listed previously. Where investigators have identified physiological consequences of C&R, findings must therefore be interpreted cautiously with results not extrapolated beyond the boundaries of their study design. For instance, Wedemeyer and Wydoski (2008) examined the physiological response of some economically important salmonids to C&R fishing, and they interpreted many significant trends between angling duration and blood parameters as 'transient' effects, 'generally mild' and of 'little physiological consequence', without fully exploring a broader suite of metrics (e.g. cortisol) shown to be associated with angling stress in other recreational fishes. Moreover, their study was restricted to moderate water temperatures, like many C&R studies (reviewed in Gale *et al.* in press). The results of their study were then noticed by the angling community, which further extrapolated the findings on angling web sites, message boards and blogs, inferring that C&R in general has negligible consequences on trout and without considering how factors not explored in their study such as water temperature could alter the outcome for the fish. Consequently and likely quite unintentionally on the part of researchers, peer-to-peer communication pathways common within the recreational angling community could foster a shift of the social norm about the potential conservation value of C&R. When management implications arising from C&R physiological studies are presented in the peer reviewed literature, authors should thus provide appropriate caveats, context and draw conclusions carefully. Although the interpretation of physiological data can be subjective, it is suggested that such findings always be viewed in the context of the broader stress response and recovery profile for a given species/population (Fig. 1).

Conclusions

Voluntary and mandatory C&R has the potential to be used successfully as a management practice that conserves populations (Arlinghaus *et al.* 2007a; Cooke *et al.* in press), but it is not automatically so (Muoneke & Childress 1994; Coggins *et al.* 2007). From the moment that anglers select a rod and reel combination based on its strength and line limits, to the bait type and hook type they select, to the season when they go fishing, to the water body on which they fish, anglers have already made decisions that can influence the degree of disturbance of a C&R event prior to their first cast. Although there are certainly instances in which we would not expect physiology to be overly informative such as when acute injuries (e.g. owing to deep hooking) lead to severe blood loss and mortality, physiological tools have become common in C&R science and have greatly advanced our understanding of the sublethal effects of C&R angling. A fundamental conservation value of physiological studies on C&R is the ability to inform anglers as to how they can minimise the impacts of the C&R angling event and handling to ensure that recovery of released fish is as rapid as possible (Arlinghaus *et al.* 2007b; Cooke & Sneddon 2007). A variety of success stories based on the use of physiology in C&R research exist including the development of the water weigh-in for bass tournaments (e.g. Suski *et al.* 2004; Tufts & Morlock 2004), identifying thermal thresholds for Atlantic salmon, *Salmo salar* L., fisheries (e.g. Wilkie *et al.* 1996, 1997; Tufts *et al.* 2000) and clarifying air exposure thresholds for a number of fish species (e.g. Cooke *et al.* 2001; Schreer *et al.* 2005; Suski *et al.* 2007b).

Because recreational fisheries is likely to grow in many countries and be a stable activity in others (Arlinghaus & Cooke 2009), C&R in some form or another will continue to be key to sustaining these fisheries for future anglers. In this context, physiology is a tool for understanding mechanisms of C&R impacts. From a management perspective, mortality is the most easily applied endpoint and, if physiological status does not correlate directly with mortality, it is easy to discount the value of physiological metrics in a management context. Nevertheless, the physiological responses to C&R are still important for understanding the relative physiological response of fish under different conditions, regardless of whether or not mortality occurs. Understanding how the responses to C&R differ within (i.e. populations, sex and size) and among species and how angler behaviours, gear types and environmental conditions affect physiological reactions is thus highly relevant to providing robust and tailored management initiatives and results may also inform outreach programmes for anglers. In cases where mortality or other relevant fitness impacts occur in response to C&R, novel measures of physiological disturbance may be used as indicators to determine the mechanisms that may lead to mortality or other fitness impacts (e.g. reduction of reproductive output; Ostrand *et al.* 2004) and, most importantly, to identify opportunities for improving fish welfare. Over the past 20 years there has been a dramatic increase in the use of physiological tools and knowledge in the study of the biological impacts of C&R angling practices on fishes and this trend will surely continue. In this paper, a number of limitations of the use of physiology in current C&R research programmes have been identified, in addition to opportunities for improving future studies. If C&R science is to advance as a subdiscipline and truly inform managers and anglers, there is need for continued innovation and more thought as to how to best conduct physiological C&R studies and how to incorporate biological integrators of suites of interacting physiological processes (e.g. like RAMP). These tools should be of use to managers and anglers to evaluate fish condition in real time to judge the degree of mortality or other impact to be expected after C&R. To facilitate the greater use of physiology-based C&R tools, there remains the need to refine the messaging associated with C&R studies that use physiological tools to ensure that anglers and managers better appreciate and understand how the results are to be interpreted in the context of relevant C&R endpoints such as mortality and in the context of emerging concepts such as to improve fish welfare. In particular, related to the latter concept, physiology (rather than problematic concepts such as pain) offers the most objective approach of all to improve C&R science and management (Arlinghaus *et al.* 2009b).

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