North American Journal of Fisheries Management
© 2021 American Fisheries Society
ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10731

RESEARCH ARTICLE

Temporary Retention in Cold Water Reduces Postrelease Behavioral Impairment in Angled Rainbow Trout

Auston D. Chhor,* Jessica L. Reid, and Peter E. Holder
Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, Ontario K1S 5B6, Canada

Liane B. Nowell
The Kenauk Institute, Kenauk Nature, 1000 Chemin Kenauk, Montebello, Quebec J0V 1L0, Canada

Jacob W. Brownscombe
Fisheries and Oceans Canada, Great Lakes Laboratory for Fisheries and Aquatic Sciences, Burlington, Ontario L7S 1A1, Canada

Andy J. Danylchuk
Department of Environmental Conservation, University of Massachusetts Amherst, Amherst, Massachusetts 01003, USA

Steven J. Cooke
Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, Ontario K1S 5B6, Canada

Abstract

The effectiveness of catch and release as a conservation practice assumes minimal impacts to released fish. In most cases, angling-related stressors can be mitigated via changes to angler behavior that reduce fight duration, handling, and air exposure. In some cases, stressors may significantly impact the ability of fish to engage in normal swimming behavior upon release. In these scenarios, it may be beneficial for anglers to assist recovery or retain fish until they are adequately recovered. We investigated the effectiveness of two assisted-recovery devices at facilitating behavioral recovery in angled Rainbow Trout *Oncorhynchus mykiss*: (1) retention in a flow box, or (2) retention in a water-filled cooler. Additionally, we compared the effects of assisted recovery in surface water (24–27°C) or cool water pumped from the hypolimnion (17–19°C). From July to mid-September 2020, 169 fish were angled from five stocked lakes at Kenauk Nature (Montebello, Quebec). Fish were air exposed for 30 s, for 15 s, or not at all (0 s) and were held in a flow box or a water-filled cooler for 3 min, while fish in a control group were immediately released. Triaxial acceleration and temperature biologgers were temporarily fixed around the trunk of the fish with Velcro to observe postrelease swimming behavior for 10 min. Rainbow Trout that were held in assisted-recovery devices regained equilibrium significantly more quickly than those that were immediately released, and fish that were held in 17–19°C water regained equilibrium the most rapidly. In fish that were air exposed for 30 s, individuals that were held in recovery devices exhibited greater swimming activity compared to those that were immediately released. Our study demonstrates that for Rainbow Trout, assisted-recovery devices can reduce equilibrium impairment, especially when water in the recovery devices is significantly cooler than the relatively warm surface water temperature. Global water temperatures are expected to rise as a result of

---

*Corresponding author: austonchhor1012@gmail.com
Received May 17, 2021; accepted November 16, 2021

anthropogenic climate change, and best practices for angling should be adapted to reflect increased thermal stressors for many game fish species. Ensuring that fish are vigorous upon release is imperative for reducing post-release mortality caused by predation or thermal stress.

Catch-and-release (C&R) angling is a well-established recreational activity for many people around the globe and has been embraced as a conservation tool for the management of a variety of fish species (Arlinghaus et al. 2007). However, the effectiveness of catch and release as a conservation practice is contingent on low mortality in fish that are released and the assumption of minimal sublethal consequences (Wydoski 1977; Cooke and Schramm 2007). In practice, C&R strategies can take the form of regulations or voluntary actions by anglers. Actions that are commonly embraced may involve altering handling practices (i.e., limiting air exposure, limiting contact with dry surfaces, and minimizing fight time) or decreasing angling effort during vulnerable periods (i.e., during spawning, when water temperatures are high; Cooke and Suski 2005; Boyd et al. 2010; Brownscombe et al. 2017a, 2017b) Despite the relative success of some of these measures at reducing mortality (Nelson 1998; Taylor et al. 2001; Bartholomew and Bohnsack 2005), C&R events still trigger a stress response in fish, which can result in a variety of sublethal alterations to physiology (Pankhurst and Dedualj 1994; Gagne et al. 2017) and can impair behavior (Thorstad et al. 2004; Klefoth et al. 2008; Arlinghaus et al. 2009).

Equilibrium loss is one such behavioral impairment that is significantly correlated with physiological stress and has been shown to be a strong predictor of postrelease mortality (Davis 2010). Additionally, fish that are released without equilibrium have limited locomotory function and are therefore more vulnerable to acute predation (Danylchuk et al. 2007b; Holder et al. 2020). In lotic systems, behavioral impairment can also increase displacement of fish downstream (Raby et al. 2012; Gagne et al. 2017), possibly altering migration success or increasing energetic costs. In these scenarios, among others, it can be beneficial for anglers to temporarily retain the fish until they have recovered enough to regain equilibrium and swim away independently. The angling community has supported various interventions that are perceived to help fish recover after capture, although the efficacy of many strategies is unclear (Pelletier et al. 2007). Some interventions require minimal effort (i.e., holding fish upright, positioning the mouth toward the current), while others may be more involved (i.e., live wells, flow boxes, and mesh holding bags); however, there is mixed scientific evidence to support them. For example, Brownscombe et al. (2017a, 2017b) found no evidence to support the efficacy of maneuvering Largemouth Bass *Micropterus salmoides* and Brook Trout *Salvelinus fontinalis* in a figure-eight or back-and-forth pattern in the water for facilitating behavioral recovery. Alternatively, some purpose-built recovery devices, such as flow boxes and mesh recovery bags, have been shown to be somewhat helpful. For instance, Brownscombe et al. (2013) found that Bonefish *Albula vulpes* that were held in flow-through recovery bags exhibited less locomotory impairment and depredation after release, while Farrell et al. (2001) observed a decrease in postrelease mortality of gill-net-caught Coho Salmon *Oncorhynchus kisutch* that were held in a flow box. However, Robinson et al. (2013, 2015) did not observe differences in postrelease survival and migration success of Chinook Salmon *O. tshawytscha* and Sockeye Salmon *O. nerka* that were held in a similar flow box. Although flow boxes force the fish to swim, they also facilitate increased circulation of fresh water over the gills and thus could be beneficial for physiological recovery (Meyer and Cook 1996; Milligan et al. 2000).

The water temperature in which fish are held after capture can play a significant role in their recovery success and postrelease survival. A few promising studies have suggested that holding fish in water that is cooler than the surface water temperatures may decrease recovery times and mortality in angled fish (Gilliland 2000; Loomis et al. 2013; Keretz et al. 2018). Previous studies indicate that the combination of elevated water temperature, air exposure, and exhaustion can have an interactive role in increasing physiological and behavioral distress in angled fish (Cooke and Suski 2005; Brownscombe et al. 2017a). While the popularity of catch and release continues to grow, climate change is expected to increase thermal stressors on fish, especially for coldwater species like salmonids (Eaton and Scheller 1996; Ruiz-Navarro et al. 2016; Chambers et al. 2017). Therefore, identifying strategies that improve the recovery of released fish will be important to sustain healthy recreational fisheries in a warming world.

The Rainbow Trout *O. mykiss* is a temperature-sensitive coldwater species that is native to North America and Asia but has been introduced worldwide (MacCrimmon 1971). As with almost all fish species, Rainbow Trout experience physiological stress in response to exhaustive exercise and air exposure during an angling event, and the stress response is magnified at elevated water temperatures (Wydoski et al. 1976; Meka and McCormick 2005). For Rainbow Trout, a significant portion of C&R science has been conducted in a laboratory setting using simulated C&R techniques, which may not accurately represent the stressors experienced in natural settings. One such laboratory study revealed increased plasma cortisol, blood lactate, and mortality in fish that were exhaustively exercised and air exposed (Ferguson and Tufts 1992). However, the invasive experimental process may have played a role in increasing stress, subsequently leading to artificially increased mortality rates. In contrast, another laboratory study demonstrated a survival rate of over 95% in fish that were subjected to simulated C&R events, which consisted of hooking, chasing, and air exposure (Pope et al. 2007). Another criticism of laboratory studies is that many are conducted in relatively cool water temperatures (~15°C) even though elevated water temperatures are known to play a significant role in capture stress during angling events (Wilde 1998; Wilde et al. 2000; Boyd et al. 2010; Gale et al. 2013; Havn et al. 2015). In the wild, angling of Rainbow Trout has been shown to generate negative effects on reproductive processes, as acute stress associated with capture can decrease the production of gonadal steroids (Pankhurst and Dedualj 1994). Another study conducted on steelhead (anadromous Rainbow Trout) noted that fish caught in warmer water exhibited greater blood lactate concentrations and increased blood acidosis (Twardek et al. 2018). Overall, C&R events can significantly impact the physiology, behavior, and survival of fish that are released; however, the magnitude of such impacts can vary greatly with angling contexts and environmental factors.

The overall goal of our study was to add to the limited research that has tested the techniques and devices for facilitating the recovery of fish that are exhausted from an angling event. Specifically, our first objective was to determine the efficacy of two methods of assisted recovery—a flow box and an uncirculated holding tank—at facilitating recovery from reflex impairment in Rainbow Trout after an angling event. Our experiment used a stocked population of Rainbow Trout in lakes where surface water temperatures exceeded the known lethal limit (>25°C; Hokanson et al. 1977; Matthews and Berg 1997; Bear et al. 2007) and were considerably higher than the optimum temperature for swimming performance and growth in some populations of Rainbow Trout (~15°C; Bear et al. 2007; Yin et al. 2021). As such, we also compared the use of warm (23–27°C) and relatively cool (17–19°C) water in the recovery devices by drawing water either from the surface of the lake or from a depth where waters were cooler. Our second objective was to compare postrelease swimming behavior and temperature usage between recovery treatments by means of externally attached triaxial accelerometer and temperature biologgers. Elevated temperatures can magnify stressors experienced by fish during a C&R event; therefore, we expected the use of cooler (17–19°C) water in assisted-recovery devices to be beneficial for reducing postrelease behavioral impairments in Rainbow Trout.

METHODS

Study site.— This experiment was conducted at Kenauk Nature, a private fish and game reserve in Quebec, Canada. The area contains a variety of small lakes that are stocked with hatchery-grown Rainbow Trout. Angling occurred at five different lakes (Taunton Lake: maximum depth = 12 m, average depth = 6 m, $n = 89$; Mills Lake: maximum depth = 29 m, average depth = 12 m, $n = 59$; Twins Lake: maximum depth = 11 m, average depth = 6 m, $n = 19$; Otter Lake: maximum depth = 15 m, average depth = 7 m, $n = 4$; Pumpkinseed Lake: maximum depth = 8 m, average depth = 6 m, $n = 1$). Almost all angling was conducted on Taunton and Mills lakes due to logistical constraints associated with the nature reserve. Angling was conducted in July and August 2020 between 0900 and 1900 hours. Coolwater treatments were conducted exclusively at Taunton Lake, as water drawn up from 4.6 m on Mills Lake was not cold enough to meet our standardized definition (>5°C difference from surface water temperature).

Capture.— Fish were captured by trolling artificial flies with single barbed hooks on 6-weight fly rods spooled with full sinking line tipped with 2.7- or 3.6-kg fluorocarbon leader. Fight times were measured as the time from initial hookset until the fish was landed with a rubber-mesh net. Fish were dehooked underwater at the side of the boat and immediately transferred to a water-filled trough for measurement of TL (mm). Fish that were hooked in the gills or gullet or that were foul hooked were immediately released and not used for the study.

Recovery methods.— Fish received 1 of 11 treatments, which varied in air exposure, recovery method, and water temperature (Table 1). Fish that were air exposed were

TABLE 1. Summary of the 11 experimental treatments that were conducted on Rainbow Trout. For treatments conducted using “warm” water, the respective recovery device was filled using water from the surface of the lake. For treatments conducted using “cool” water, recovery devices were filled using water pumped from approximately 4.5 m below the surface.

Air exposure duration (s)	Recovery device	Recovery temperature
0	None	N/A
15	None	N/A
15	Flow box	Cool
15	Cooler	Cool
15	Flow box	Warm
15	Cooler	Warm
30	None	N/A
30	Flow box	Cool
30	Cooler	Cool
30	Flow box	Warm
30	Cooler	Warm

held completely out of the water in a rubber net for 30 s, for 15 s, or not at all (0 s) and were transferred to either the flow box or the uncirculated cooler. Air exposure intervals were selected based on preliminary trials that showed significant behavioral impairment or even mortality in fish that were air exposed for 30 s and handled in the trough for a short period (to simulate attachment of the biologger) in water that was 27°C. For treatments that did not include assisted recovery, air exposure was conducted by holding the fish securely with two hands above a water-filled cooler, as attachment of the biologger had to be conducted prior to air exposure. Treatments involving 0 s of air exposure and the use of a recovery method were not included in our study, as immediate release acted as a benchmark against which to measure assisted-recovery treatments.

Our custom-made flow box was wooden and rectangular (77.5 × 14.0 × 17.5 cm; Figure 1). It used a portable bilge pump and 4.6 m of rubber tubing attached to the intake to draw in lake water at one end, and it had a drainage slit at the other end. Incoming water from the pump was diffused by a small showerhead and two panes of screen material, and the box was closed with a hinged lid comprised of a panel of window screen material framed by sealed wood to prevent the fish from escaping. For coolwater treatments, water was drawn from a depth of about 4.6 m, which provided us with temperatures that were consistently between 17°C and 19°C. Water was drawn from the surface for warmwater treatments (24–27°C). Each fish was positioned with its mouth toward the incoming flow to facilitate ventilation. The uncirculated cooler measured 30 × 60 × 30 cm; the cooler was filled with about 23 L of fresh lake water and was closed with a lid for each treatment. Water in the cooler was changed between each treatment, and fish were held in each recovery device for 3 min before being released.

FIGURE 1. Rainbow Trout held in the flow box. Fish were positioned facing the direction of the flow, and the lid was closed during the treatment.

Accelerometer attachment.— To evaluate postrelease swimming activity, we attached biologgers (7.5 g, 12 × 31 × 11 mm; Technosmart Axy-Depth, Rome, Italy; sampling rate: triaxial acceleration = 10 Hz, temperature/depth = 1 Hz; resolution: triaxial acceleration = 8 bit, temperature = 0.1°C, depth = 5 cm, *g* scale = 8) around the trunk of the fish by using custom-made harnesses, which consisted of a length of Velcro tape (length = 20–35 cm, width = 1.5 cm; Scotch Fasteners) threaded through a Plexiglas plate that was epoxied to the logger. With the fish underwater in the cooler or flow box, the length of Velcro tape was wrapped once around the fish anterior to the dorsal fin, positioning the accelerometer on the lateral side above the pectoral fin. We found that this position was the most secure and prevented the harness from slipping off the fish. Although we used harnesses of different lengths to accommodate the variation in girth among individuals, all harnesses were only wrapped once around the fish. The average duration of the attachment process was 22 s and rarely exceeded 60 s. The harness was then connected to a rod spooled with 27-kg braided Spectra line using a snap swivel that clipped through a reinforced hole in the Velcro. All fish were released upside down and immediately assessed for equilibrium status. Equilibrium was defined as the ability of the fish to independently maintain an upright position and engage in forward locomotion. For fish without immediate equilibrium, we recorded the time (s) until the fish righted itself and swam away independently. The fish was then allowed to swim without resistance or on "free-spool" for 10 min before the logger was retrieved by tugging the line, which released the Velcro, allowing us to reel the harness in.

Data processing.— Raw biologger data were processed using techniques derived from Brownscombe et al. (2013) and Lennox et al. (2018). Acceleration data were converted to units of *g* (9.8 m/s) by dividing pitch (*x*-axis), roll (*y*-axis), and yaw (z-axis) by 1.5, the conversion factor for the *g*-scale setting on the tag (8 g). Static acceleration (acceleration from gravity) was calculated by passing a 2-s box smoother over each axis using the rollmean function in the R package zoo (Zeileis and Grothendieck 2005) and was converted to degrees by multiplying values by 180/π. Pitch (*x*-axis) and roll (*y*-axis) were also calculated from these values. Dynamic acceleration (acceleration associated with displacement/locomotion) was calculated by subtracting static acceleration from raw acceleration values for each axis. Overall dynamic body acceleration (ODBA) was calculated as the absolute sum of the dynamic acceleration of each axis. We summarized acceleration data by each second, as the resolution of raw data initially gathered by the tag (10 per second) was too high for realistic estimates of behavior. Data were then trimmed to include only the first 10 min of data collection to remove the period of time during which the accelerometer was retrieved.

Statistical analysis.— Generalized linear models were applied to determine the influence of fight time, time to dehook, biologger attachment time, surface water temperature, and fish TL on the time to regain equilibrium. Backwards model selection resulted in the minimum best fit model of TL, surface temperature, and biologger attachment time as significant predictors. Generalized linear models were also applied with time to regain equilibrium as the response and air exposure, recovery device, or recovery tank as individual predictors. For analysis of ODBA and temperature usage, we used generalized linear models with ODBA or temperature (°C) as the response and air exposure, recovery tank, draw depth, and minutes postrelease as the predictors. One-way ANOVAs were used to elucidate significant differences in each explanatory variable for time to regain equilibrium, ODBA, and temperature usage. We ensured that linear model assumptions were met by analyzing plots of standardized residuals versus theoretical quartiles (*Q*–*Q* plots), residuals versus fitted values, and the square root of standardized residuals versus fitted values (scale–location) and by examining outliers using Cook's distance. Post hoc analyses were conducted using Tukey's range test to interpret pairwise differences between individual factors. For all models, we chose to exclude TL as a predictor because there were no significant differences in TL among treatments (ANOVA: $F = 1.032$, df = 10, $P = 0.419$).

RESULTS

Field Observations

We captured 169 Rainbow Trout between July 13 and September 18, 2020 ($n = 158$ between July 13 and August 28, surface water temperature: 24–27°C; $n = 11$ on September 18, surface water temperature: ~15°C). The number of fish angled was 88 from Taunton Lake, 57 from Mills Lake, 19 from Twins Lake, 4 from Otter Lake, and 1 from Pumpkinseed Lake. Mean TL ± SE of Rainbow Trout in the study was 390.0 ± 4.7 mm, and TL ranged from 320 to 630 mm. Dehooking time ranged between 1 and 60 s, and the mean ± SE was 8.0 ± 0.7 s. Biologger attachment time ranged between 4 and 80 s, with a mean ± SE of 23.0 ± 1.2 s. Mean ± SE fight time was 51 ± 2 s and ranged between 8 and 210 s.

Equilibrium and Postrelease Swimming Activity

Time to regain equilibrium was positively correlated with surface water temperature, TL, and attachment time (ANOVA, temperature: $F = 4.168$, df = 1, $P = 0.042$; TL: $F = 5$, df = 1, $P = 0.04$; attachment time: $F = 5.038$, df = 1, $P = 0.026$). Time to regain equilibrium was also significantly influenced by draw depth (ANOVA: $F = 26.74$, df = 1, $P < 0.01$) and was significantly higher when fish were recovered in warm surface water compared to cool water obtained from 4.6-m depth (Tukey honestly significant difference [HSD] test: $P < 0.01$; Figure 2). Time to regain equilibrium was also influenced by the recovery (or lack thereof) method used (ANOVA: $F = 7.13$, df = 2, $P < 0.01$) and took significantly longer when fish were immediately released compared to fish that were held in the flow box (Tukey HSD: $P < 0.01$) or the cooler (Tukey HSD: $P = 0.030$; Figure 2). Air exposure marginally influenced the time to regain equilibrium, which tended to be longest for fish in the 0-s treatment and shortest in the 15-s treatment (ANOVA: $F = 2.99$, df = 1, $P = 0.053$; Figure 2).

Swimming activity (ODBA) was significantly influenced by minutes after release and the interaction of air exposure and recovery tank (ANOVA, minutes after release: $F = 9.946$, df = 9, $P < 0.01$; air × tank: $F = 6.42$, df = 6, $P < 0.01$). In all fish studied, ODBA was highest in the first minute after release and was significantly higher in the first minute compared to the second minute ($P = 0.05$), third minute ($P = 0.014$), and 4th–10th minutes ($P < 0.01$) after release (Figure 3). The ODBA was also significantly higher in the second minute and the third minute compared to the 4th–10th minutes after release ($P < 0.01$; Figure 3). Overall dynamic body acceleration was higher when fish were immediately released after 0 or 15 s of air exposure compared to fish that were immediately released after 30 s of air exposure (Figure 4). Additionally, ODBA was higher in fish that were held in a recovery tank after 30 s of air exposure than in fish that were immediately released (Figure 4).

By about 1 min after release, fish tended to occupy a water temperature of approximately 15°C, where they stayed for the remainder of the observational period (Figure 5). Temperature usage was significantly influenced by the time (min) after release and its interaction with draw depth (ANOVA, minutes after release: $F = 28.587$, df = 9, $P < 0.01$; minutes after release × draw depth: $F = 2.270$, df = 9, $P = 0.013$; Figure 6). After the fifth minute, fish that were recovered in cool water spent more time in warmer water (~14°C) compared to fish that were recovered in surface water or that were immediately released (~12°C; Figure 6).

DISCUSSION

Even when best practice guidelines for handling are adhered to, fish can still experience significant behavioral impairment after an angling event, especially in unfavorable environmental conditions that increase stress (Cooke and Suski 2005; Arlinghaus et al. 2007). Support for the efficacy of assisted recovery of fish after capture is mixed. Some studies have demonstrated that retention in recovery

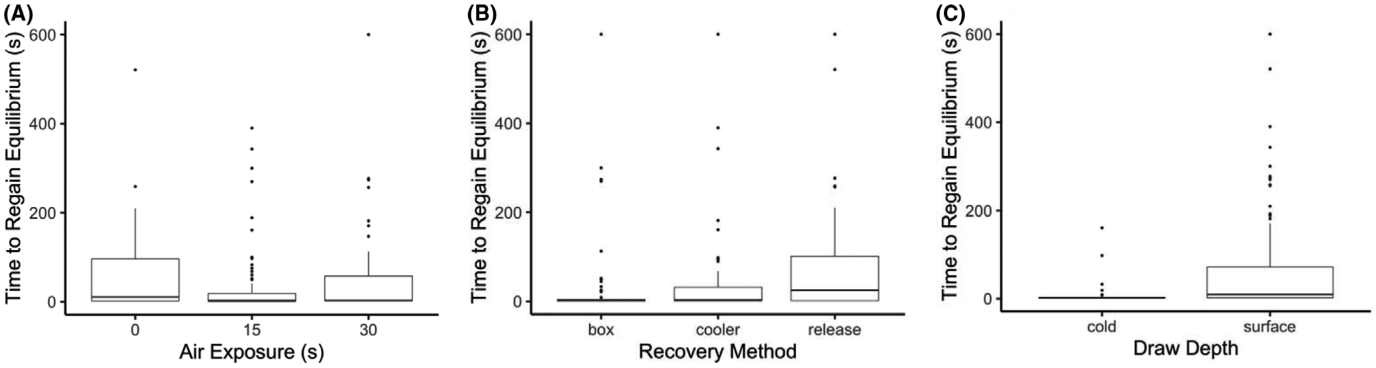

FIGURE 2. Time to regain equilibrium (s) for Rainbow Trout that were subjected to **(A)** air exposure of 0, 15, or 30 s (ANOVA: $F = 2.99$, df = 1, $P = 0.053$); **(B)** recovery in the flow box or cooler or immediate release ($F = 7.13$, df = 2, $P < 0.01$); and **(C)** recovery in cool water or surface water ($F = 26.74$, df = 1, $P < 0.01$). Fish that were immediately released were placed in the surface group.

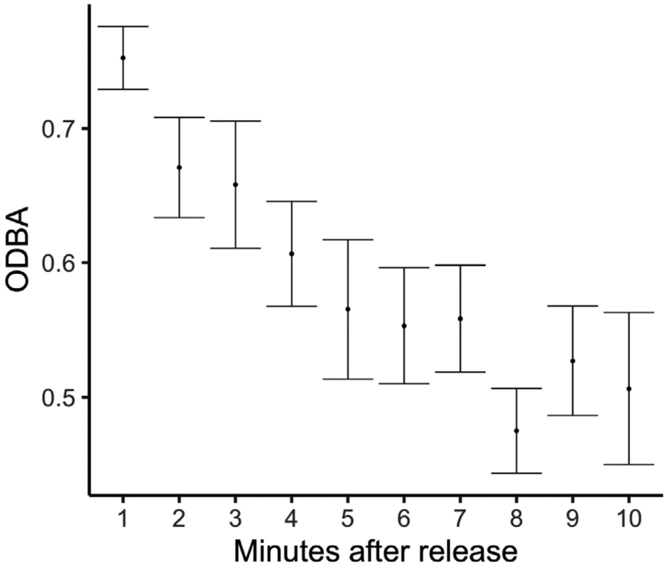

FIGURE 3. Mean (±SE) overall dynamic body acceleration (ODBA) for all Rainbow Trout regardless of treatment for each minute after release.

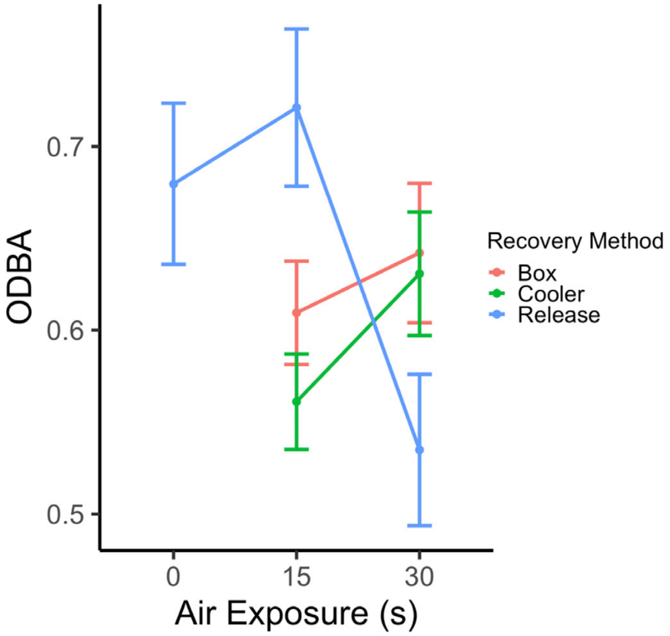

FIGURE 4. Mean (±SE) overall dynamic body acceleration (ODBA) in Rainbow Trout that were subjected to air exposure of 0, 15, or 30 s and that were held in the flow box or cooler or were immediately released.

devices can facilitate physiological recovery in angled fish (Farrell et al. 2001; Brownscombe et al. 2013; Donaldson et al. 2013), whereas others have not found evidence of improved recovery (Robinson et al. 2013, 2015; Brownscombe et al. 2017a, 2017b). These differences could be due to variation in angling contexts, species-specific stress tolerances, and the length of time for which the fish are held in recovery devices (Suski et al. 2007; Nguyen et al. 2014; Raby et al. 2015). Overall, our study determined that holding Rainbow Trout for 3 min in a flow box or water-filled cooler reduced equilibrium impairments, especially when water in the recovery tank was significantly cooler than the surface water temperature. Rainbow Trout also exhibited greater swimming activity when they were held in the flow box or cooler after 30 s of air exposure compared to fish that were immediately released after 30 s of air exposure (Figure 4). Lastly, fish that were recovered in cool water spent more time in a water temperature of about 15°C after release compared to fish that were recovered in surface water or immediately released, which preferred a temperature of approximately 12°C (Figure 6).

Almost all fish that were captured for our study exhibited impaired equilibrium upon landing. In an angling context, loss of equilibrium can be associated with air exposure and handling time (Danylchuk et al. 2007a, 2007b; Pinder et al. 2019), while in our case, measuring TL, attaching the biologger, and transferring the fish

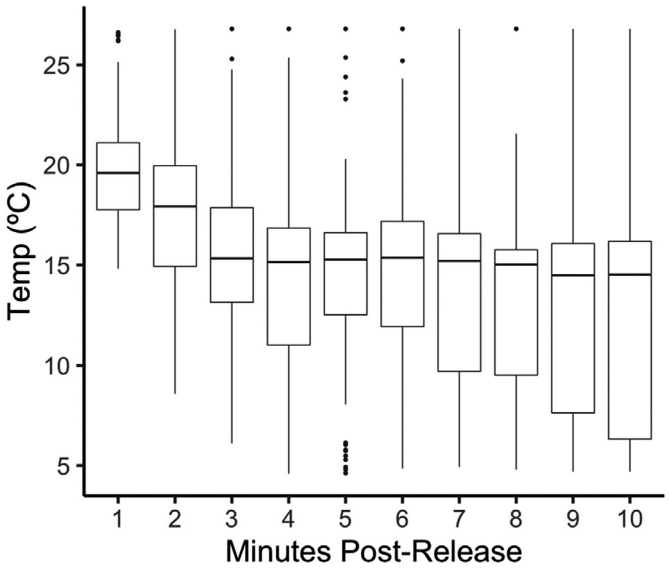

FIGURE 5. Temperature (Temp) usage by all Rainbow Trout regardless of treatment throughout the 10-min observational period. Whiskers indicate min/max values; horizontal lines indicate the lower quartile, median, and upper quartile.

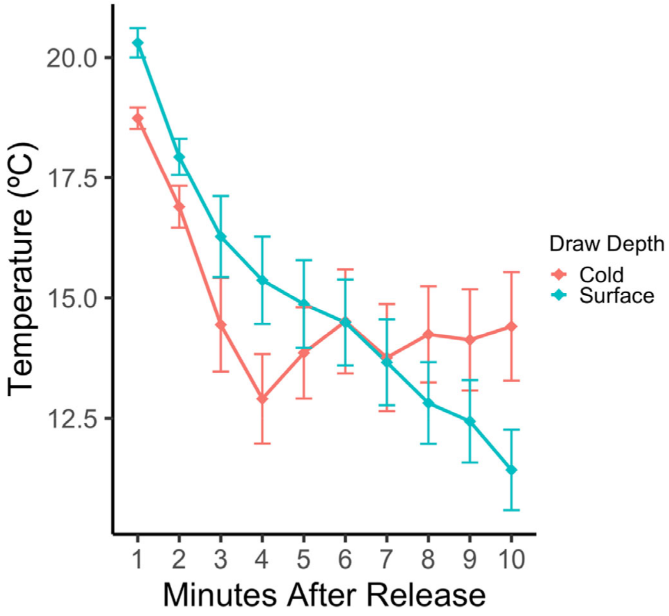

FIGURE 6. Mean (±SE) water temperature usage by Rainbow Trout over a 10-min observational period for fish that were recovered in cool water (17–19°C) or surface water (24–27°C).

between holding tanks may have resulted in increased handling time compared to normal C&R scenarios. Extended fight times, confinement in the flow box or cooler, and elevated surface water temperatures may have also contributed to increased physiological stress. We used a relatively unique angling method of trolling flies on fly rods and sinking line, which involved letting out extremely long lengths of line to ensure that the flies sank to depths of about 4.5 m, at which observed angling success was maximized. This most likely resulted in significantly greater fight times compared to some angling methods for Rainbow Trout but may reflect times associated with the use of light tackle or with novice anglers. We found that fish regained equilibrium most rapidly when held in water that was significantly cooler than the surface water temperature, similar to results obtained by Gilliland (2000), Loomis et al. (2013), and Keretz et al. (2018). However, our results are contrary to those reported by Suski et al. (2006) and Shultz et al. (2011), indicating a threshold temperature for usage of cool water in an assisted-recovery context. The temperature optimum for some Rainbow Trout populations is about 15°C, and the upper incipient lethal temperature is approximately 25°C (Hokanson et al. 1977; Bear et al. 2007; Yin et al. 2021); therefore, it was not surprising that recovery was maximized when fish were held in water temperatures close to optimal. In lotic systems, Rainbow Trout seek coldwater refuge when surface water temperatures are high, in the form of coldwater upwelling areas or cold tributary outflows (Kaya et al. 1977; Ebersole et al. 2001). In lentic systems, coldwater refuge is found at depths below the thermocline. Upon release, fish were observed to immediately descend to seek preferred water temperatures. In our study, equilibrium-impaired fish spent more time in warm surface water and may have continued to be thermally stressed by elevated water temperature. This could have led to a degenerative cascade of events wherein fish required cooler temperatures to regain equilibrium but lacked the ability to descend to those temperatures, compounding the stress that they were seeking to relieve. Retaining fish in cool water before release may reduce equilibrium impairment and can allow fish to quickly descend to cooler water.

Fish that are equilibrium impaired are also more likely to suffer acute predation (Danylchuk et al. 2007b). In our study, attempted predation on equilibrium-impaired fish by ospreys *Pandion haliaetus*, bald eagles *Haliaeetus leucocephalus*, and gulls (Laridae spp.) was observed on multiple occasions. Almost all equilibrium-impaired fish floated at the surface upside down which may have increased their visibility to avian predators, as their light-colored undersides were more visible against the surface of the water (Ross and Hokenson 1997; Fairchild and Howell 2004). In marine environments, fish with impaired equilibrium are at greater risk for predation by other large fish or sharks (Danylchuk et al. 2007b; Holder et al. 2020). In environments with high predator densities, retaining fish until they are able to regain equilibrium quickly could reduce the incidence of postrelease predation (Raby et al. 2014).

We did not find differences in recovery between fish that were held in circulating water and those that were held in static water. Prior research has focused on the use of assisted ventilation methods, which increase the flow of oxygen over the gills (Robinson et al. 2015; Brownscombe et al. 2017); however, our results indicate that water temperature can also influence recovery success in coldwater fish. Retention itself may be beneficial, even if it does not decrease the actual time required to recover. Differences in the time to regain equilibrium between fish that were retained before release and those that were immediately released could be due to the period (3 min) for which fish were held on the boat, which may have allowed the fish to recover before being released into the lake. When predator densities are high, allowing fish to recover in the relative safety of a boat reduces or eliminates the likelihood of postrelease predation if the fish are provided with good water quality.

Swimming activity of Rainbow Trout was greatest in the first minute after release and gradually decreased, reaching an equilibrium at around 5 min postrelease. Most fish spent the entirety of the observational period swimming or alternated between periods of rest and periods of swimming. This was likely due to the habitat structure of the study lakes, as all were deep basins with relatively little cover. Swimming activity was greatest in all fish during the first minute after release, which could be attributed to seeking thermal refugia below the thermocline. Stressors that impact swimming performance immediately after release can have serious implications for short-term survival if fish are unable to reach cooler water. In fish that were immediately released, swimming activity was lowest in fish that were air exposed for 30 s. Across treatments, fish that were air exposed for 30 s displayed lower swimming activity upon release compared to those that were air exposed for 15 or 0 s. Of the two mortalities that were observed in the experiment, both fish were air exposed for 30 s. These individuals did not regain equilibrium and floated at the surface for the entirety of the observational period, presumably dying from physiological stress. Compared to other studies, we selected a relatively short duration of air exposure as our maximum treatment; this was because our early observations determined that air exposure exceeding 30 s significantly increased the probability of mortality. Additionally, Lamansky and Meyer (2016) determined through observations of anglers that the average air exposure time for fly-caught Rainbow Trout was about 30 s. Our results highlight the importance of studying the impacts of angling in the field, as environmental factors can play a significant role in changing the outcome of a C&R event. Overall, fish that were held in a recovery tank after 30 s of air exposure were more active than those that were immediately released. Retention in the flow box may have helped to facilitate ventilation, which has been shown to increase metabolic recovery in other salmonids; however, one study only found benefits after retention for 1–2 h (Farrell et al. 2001). It is unclear why fish retained in the cooler were more active than those immediately released; however, the differences could be attributed to the time course of the physiological response to stress. The biologgers did not start gathering data until the moment of release, so retention in the cooler for 3 min could have allowed for some level of physiological recovery before acceleration data were collected. This could explain the increased swimming activity in retained fish overall, as individuals that were immediately released did not have time to recover before the start of data collection.

In most fish, changes in water temperature influence physiological processes by altering the activity of enzymes. Recovery from physiological stress can therefore be affected by temperature, as the activity of enzymes that facilitate lactate clearance or replenish energy stores in muscle can be altered. Two studies (Galloway and Kieffer 2003; Hyvärinen et al. 2004) have shown that retention in cool water after exercise can delay recovery from physiological stress in Rainbow Trout. However, both studies were conducted with control water temperatures that were relatively cool (~15–18°C), and coolwater recovery treatments were conducted with significantly colder temperatures (~5°C). In our study, Rainbow Trout that were recovered in cool water (~17–19°C) exhibited different temperature preferences compared to those that were immediately released. After recovery in cool water, fish tended to seek water temperatures of about 15°C after 5 min, while fish that were immediately released sought increasingly cooler water over the observational period, with no indication of a preferred temperature by the end of 10 min. These results could indicate that to a certain temperature limit, Rainbow Trout may prefer recovery in water temperatures that are slightly cooler than their typical surroundings.

Ultimately, science supporting the use of assisted-recovery techniques is only effective if anglers are willing to adopt those techniques (Danylchuk et al. 2018). Anglers may be hesitant to adopt practices if they are inconvenient or if they require additional costs. Donaldson et al. (2013) conducted a survey of anglers and found that anglers were generally supportive of the usage of recovery bags, a simple assisted-recovery method, and their support increased if research showed that the method was effective. In our case, recovery in the flow box was considerably more involved compared to recovery in the cooler, but the outcomes for fish that were released did not differ significantly provided that recovery was conducted in cool water. It must be acknowledged that flow boxes are neither commercially available nor simple to construct for those without woodworking knowledge or access to tools. Additionally, flow boxes only serve a single purpose and anglers may be reluctant to bring them during angling trips, especially if there are weight or space constraints. Water-filled containers, such as coolers or live wells, may be more easily adopted as assisted-recovery devices since many anglers already bring them or have them on their boats. Although we used a portable bilge pump to draw cool water to fill the recovery devices, anglers could achieve similar conditions by other methods, such as ice packs. It is important for assisted-recovery methods to be not only effective but also easily implemented and affordable, and the science supporting their benefits should be widely shared.

Conclusions

Our study demonstrated that the assisted recovery of angled Rainbow Trout by means of a flow box or water-filled cooler was successful in reducing postrelease equilibrium impairments and in reducing impacts to postrelease swimming. These benefits were also maximized if water temperatures in the assisted-recovery devices were cooler than the surface water temperature and close to the optimal thermal range of Rainbow Trout (17–19°C). Although it is often noted that increased handling of angled fish increases stressors, there may be certain scenarios (i.e., high-predation environments, elevated water temperatures, and equilibrium-impaired fish) in which the benefits of assisted recovery outweigh the costs of increased handling. As global water temperatures continue to rise, assisted recovery in cool water is a promising strategy for use with angled fish; however, more research is necessary to identify possible benefits for other coldwater species and in lotic ecosystems.

ACKNOWLEDGMENTS

We thank the Kenauk Institute and Kenauk Nature for the use of their facilities and for providing logistical support throughout the project. Daniel Glassman, Jennifer Cooke, and Brittany Leong assisted with data collection. Robert Lennox and Benjamin Hlina provided input on statistical analysis. Scientific collection permits were provided by the Quebec Ministry of Forests, Wildlife, and Parks. There is no conflict of interest declared in this article.

REFERENCES

Arlinghaus, R., S. J. Cooke, A. Schwab, and I. G. Cowx. 2007. Fish welfare: a challenge to the feelings based approach, with implications for recreational fishing. Fish and Fisheries 8:57–71.

Arlinghaus, R., T. Klefoth, S. J. Cooke, A. Gingerich, and C. Suski. 2009. Physiological and behavioral consequences of catch-and-release angling on Northern Pike (*Esox lucius* L.). Fisheries Research 97:223–233.

Bartholomew, A., and J. A. Bohnsack. 2005. A review of catch-and-release angling mortality with implications for no-take reserves. Reviews in Fish Biology and Fisheries 15:129–154.

Bear, E. A., T. E. McMahon, and A. V. Zale. 2007. Comparative thermal requirements of Westslope Cutthroat Trout and Rainbow Trout: implications for species interactions and development of thermal protection standards. Transactions of the American Fisheries Society 136:1113–1121.

Boyd, J. W., C. S. Guy, T. B. Horton, and S. A. Leathe. 2010. Effects of catch-and-release angling on salmonids at elevated water temperatures. North American Journal of Fisheries Management 30:898–907.

Brownscombe, J. W., A. J. Danylchuk, J. M. Chapman, L. F. G. Gutowsky, and S. J. Cooke. 2017a. Best practices for catch-and-release recreational fisheries—angling tools and tactics. Fisheries Research 186:693–705.

Brownscombe, J. W., T. P. Parmar, J. Almeida, E. Giesbrecht, J. Batson, X. Chen, S. Wesch, T. D. Ward, C. M. O'Connor, and S. J. Cooke. 2017b. The efficacy of assisted ventilation techniques for facilitating the recovery of fish that are exhausted from simulated angling stress. Fisheries Research 186:619–624.

Brownscombe, J. W., J. D. Thiem, C. Hatry, F. Cull, C. R. Haak, A. J. Danylchuk, and S. J. Cooke. 2013. Recovery bags reduce post-release impairments in locomotory activity and behavior of Bonefish (*Albula* spp.) following exposure to angling related stress. Journal of Experimental Marine Biology and Ecology 440:207–215.

Chambers, B. M., S. M. Pradhanang, and A. J. Gold. 2017. Simulating climate change induced thermal stress in coldwater fish habitat using SWAT model. Water 9:732.

Cooke, S. J., and H. L. Schramm. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. Fisheries Management and Ecology 14:73–79.

Cooke, S. J., and C. D. Suski. 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? Biodiversity and Conservation 14:1195–1209.

Danylchuk, A. J., S. E. Danylchuk, S. J. Cooke, T. L. Goldberg, J. B. Koppelman, and D. P. Phillipp. 2007a. Post-release mortality of Bonefish, *Albula vulpes*, exposed to different handling practices during catch-and-release angling in Eleuthera, The Bahamas. Fisheries Management and Ecology 14:149–154.

Danylchuk, A. J., S. C. Danylchuk, A. Kosiarski, S. J. Cooke, and B. Huskey. 2018. Keepemwet Fishing—an emerging social brand for disseminating best practices for catch-and-release in recreational fisheries. Fisheries Research 205:52–56.

Danylchuk, S. E., A. J. Danylchuk, S. J. Cooke, T. L. Goldberg, J. Koppelman, and D. P. Phillipp. 2007b. Effects of recreational angling on the post-release behavior and predation of Bonefish (*Albula vulpes*): the role of equilibrium status at the time of release. Journal of Experimental Marine Biology and Ecology 346:127–133.

Davis, M. W. 2010. Fish stress and mortality can be predicted using reflex impairment. Fish and Fisheries 11:1–11.

Donaldson, M. R., G. D. Raby, V. N. Nguyen, S. G. Hinch, D. A. Patterson, A. P. Farrell, M. A. Rudd, L. A. Thompson, C. M. O'Connor, A. H. Colotelo, S. H. McConnachie, K. V. Cook, D. Robichaud, K. K. English, and S. J. Cooke. 2013. Evaluation of a simple technique for recovering fish from capture stress: integrating physiology, biotelemetry, and social science to solve a conservation problem. Canadian Journal of Fisheries and Aquatic Sciences 70:90–100.

Eaton, J. G., and R. M. Scheller. 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnology and Oceanography 41:1109–1115.

Ebersole, J. L., W. J. Liss, and C. A. Frissell. 2001. Relationship between stream temperature, thermal refugia, and Rainbow Trout *Oncorhynchus mykiss* abundance in arid-land streams in the northwestern United States. Ecology of Freshwater Fish 10:1–10.

Fairchild, E. A., and W. H. Howell. 2004. Factors affecting the post-release survival of cultured juvenile *Pseudopleuronectes americanus*. Journal of Fish Biology 65(S1):69–87.

Farrell, A. P., P. E. Gallagher, J. Fraser, D. Pike, P. Bowering, A. K. M. Hadwim, W. Parkhouse, and R. Routledge. 2001. Successful recovery of the physiological status of Coho Salmon on board a commercial gillnet vessel by means of a newly designed revival box. Canadian Journal of Fisheries and Aquatic Sciences 58:1932–1946.

Ferguson, R. A., and B. L. Tufts. 1992. Physiological effects of brief air exposure in exhaustively exercised Rainbow Trout (*Oncorhynchus mykiss*): implications for “catch and release” fisheries. Canadian Journal of Fisheries and Aquatic Sciences 49:1157–1162.

Gagne, T. O., K. L. Ovitz, L. P. Griffin, J. W. Brownscombe, S. J. Cooke, and A. J. Danylchuk. 2017. Evaluating the consequences of catch-and-release recreational angling on Golden Dorado (*Salminus brasiliensis*) in Salta, Argentina. Fisheries Research 186:625–633.

Gale, M. K., S. G. Hinch, and M. R. Donaldson. 2013. The role of temperature in the capture and release of fish. Fish and Fisheries 14:1–33.

Galloway, B. J., and J. D. Kieffer. 2003. The effects of acute temperature change on the metabolic recovery from exhaustive exercise in juvenile Atlantic Salmon. Physiological and Biochemical Zoology 76:652–662.

Gilliland, E. R. 2000. Livewell operating procedures to reduce mortality of black bass during summer tournaments. Pages 477–487 *in* D. P. Philipp and M. S. Ridgeway, editors. Black bass: ecology, conservation, and management. American Fisheries Society, Symposium 31, Bethesda, Maryland.

Havn, T. B., I. Uglem, Ø. Solem, S. J. Cooke, F. G. Whoriskey, and E. B. Thorstad. 2015. The effect of catch-and-release angling at high water temperatures on behavior and survival of Atlantic Salmon *Salmo salar* during spawning migration. Journal of Fish Biology 87:342–359.

Hokanson, K. E. F., C. F. Kleiner, and T. W. Thorslund. 1977. Effects of constant temperatures and diel temperature fluctuations on specific growth and mortality rates and yield of juvenile Rainbow Trout *Salmo gairdneri*. Journal of the Fisheries Research Board of Canada 34:639–648.

Holder, P. E., L. P. Griffin, J. A. Aaron, A. J. Danylchuk, S. J. Cooke, and J. W. Brownscombe. 2020. Stress, predators, and survival: exploring Permit (*Trachinotus falcatus*) catch-and-release fishing mortality in the Florida Keys. Journal of Experimental Marine Biology and Ecology 524:151289.

Hyvärinen, P., S. Heinimaa, and H. Rita. 2004. Effects of abrupt cold shock on stress responses and recovery in Brown Trout exhausted by swimming. Journal of Fish Biology 64:1015–1026.

Kaya, C. M., L. R. Kaeding, and D. E. Burkhalter. 1977. Use of a cold-water refuge by Rainbow and Brown trout in a geothermally heated stream. Progressive Fish-Culturist 39:37–39.

Keretz, K. R., C. P. Dinken, P. J. Allen, M. Colvin, and H. L. Schramm Jr. 2018. The effect of water temperature, angling time, and dissolved oxygen on the survival of Largemouth Bass subjected to simulated angling and tournament handling procedures. North American Journal of Fisheries Management 38:606–622.

Klefoth, T., A. Kobler, and R. Arlinghaus. 2008. The impact of catch-and-release angling on short-term behavior and habitat choice of Northern Pike (*Esox lucius* L.). Hydrobiologia 601:99–110.

Lamansky, J. A. Jr., and K. A. Meyer. 2016. Air exposure time of trout released by anglers during catch and release. North American Journal of Fisheries Management 36:1018–1023.

Lennox, R. J., J. W. Brownscombe, S. J. Cooke, and A. J. Danylchuk. 2018. Post-release behaviour and survival of recreationally-angled Arapaima (*Arapaima* cf. *arapaima*) assessed with accelerometer biologgers. Fisheries Research 207:197–203.

Loomis, J. H., H. L. Schramm Jr., B. Vondracek, P. D. Gerard, and C. J. Chizinski. 2013. Effects of simulated angler capture and live-release tournaments on Walleye survival. Transactions of the American Fisheries Society 142:868–875.

MacCrimmon, H. R. 1971. World distribution of Rainbow Trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 28:663–704.

Matthews, K. R., and N. H. Berg. 1997. Rainbow Trout responses to water temperature and dissolved oxygen stress in two southern California stream pools. Journal of Fish Biology 50:50–67.

Meka, J. M., and S. D. McCormick. 2005. Physiological response of wild Rainbow Trout to angling: impact of angling duration, fish size, body condition, and temperature. Fisheries Research 72:311–322.

Meyer, W. F., and P. A. Cook. 1996. An assessment of the use of low-level aerobic swimming in promoting recovery from handling stress in Rainbow Trout. Aquaculture International 4:169–174.

Milligan, L. C., G. B. Hooke, and C. Johnson. 2000. Sustained swimming at low velocity following a bout of exhaustive exercise enhances metabolic recovery in Rainbow Trout. Journal of Experimental Biology 203:921–926.

Nelson, K. L. 1998. Catch-and-release mortality of Striped Bass in the Roanoke River, North Carolina. North American Journal of Fisheries Management 18:25–30.

Nguyen, V. M., E. G. Martins, D. Robichaud, G. D. Raby, M. R. Donaldson, A. G. Lotto, W. G. Willmore, D. A. Patterson, A. P. Farrell, S. G. Hinch, and S. J. Cooke. 2014. Disentangling the roles of air exposure, gill net injury, and facilitated recovery on the post-capture and release mortality of adult migratory Sockeye Salmon (*Oncorhynchus nerka*) in freshwater. Physiological and Biochemical Zoology 87:125–135.

Pankhurst, N. W., and M. Dedualj. 1994. Effects of capture and recovery on plasma levels of cortisol, lactate, and gonadal steroids in a natural population of Rainbow Trout. Journal of Fish Biology 45:1013–1025.

Pelletier, C., K. C. Hanson, and S. J. Cooke. 2007. Do catch-and-release guidelines from state and provincial fisheries agencies in North America conform to scientifically based best practices? Environmental Management 39:760–773.

Pinder, A. C., A. J. Harrison, and J. R. Britton. 2019. Temperature effects on the physiological status and reflex impairment in European Grayling *Thymallus thymallus* from catch-and-release angling. Fisheries Research 211:169–175.

Pope, K., G. Wilde, and D. Knabe. 2007. Effect of catch-and-release angling on growth and survival of Rainbow Trout, *Oncorhynchus mykiss*. Fisheries Management and Ecology 14:115–121.

Raby, G. D., M. R. Donaldson, S. G. Hinch, T. D. Clark, E. J. Eliason, K. M. Jeffries, K. V. Cook, A. Teffer, A. L. Bass, K. M. Miller, D. A. Patterson, A. P. Farrell, and S. J. Cooke. 2015. Fishing for effective conservation: context and biotic variation are keys to understanding the survival of Pacific salmon after catch-and-release. Integrative and Comparative Biology 55:554–576.

Raby, G. D., M. R. Donaldson, S. G. Hinch, D. A. Patterson, A. G. Lotto, D. Robichaud, K. K. English, W. G. Willmore, A. P. Farrell, M. W. Davis, and S. J. Cooke. 2012. Validation of reflex indicators for measuring vitality and predicting the delayed mortality of wild Coho Salmon bycatch released from fishing gears. Journal of Applied Ecology 49:90–98.

Raby, G. D., J. R. Packer, A. J. Danylchuk, and S. J. Cooke. 2014. The understudied and underappreciated role of predation in the mortality of fish released from fishing gears. Fish and Fisheries 15:489–505.

Robinson, K. A., S. G. Hinch, M. K. Gale, T. D. Clark, S. M. Wilson, M. R. Donaldson, A. P. Farrell, S. J. Cooke, and D. A. Patterson. 2013. Effects of post-capture ventilation assistance and elevated water temperature on Sockeye Salmon in a simulated capture-and-release experiment. Conservation. Physiology 1(1):cot015.

Robinson, K. A., S. G. Hinch, G. D. Raby, M. R. Donaldson, D. Robichaud, D. A. Patterson, and S. J. Cooke. 2015. Influence of post-capture ventilation assistance on migration success of adult Sockeye

Salmon following capture and release. Transactions of the American Fisheries Society 144:693–704.

Ross, M. R., and S. R. Hokenson. 1997. Short-term mortality of discarded finfish bycatch in the Gulf of Maine fishery for northern shrimp *Pandalus borealis*. North American Journal of Fisheries Management 17:902–909.

Ruiz-Navarro, A., P. K. Gillingham, and J. R. Britton. 2016. Predicting shifts in the climate space of freshwater fishes in Great Britain due to climate change. Biological Conservation 203:33–42.

Shultz, A. D., K. J. Murchie, C. Griffith, S. J. Cooke, A. J. Danylchuk, T. L. Goldberg, and C. D. Suski. 2011. Impacts of dissolved oxygen on the behavior and physiology of Bonefish: implications for live-release angling tournaments. Journal of Experimental Marine Biology and Ecology 402:19–26.

Suski, C. D., S. J. Cooke, and B. L. Tufts. 2007. Failure of low-velocity swimming to enhance recovery from exhaustive exercise in Largemouth Bass (*Micropterus salmoides*). Physiological and Biochemical Zoology 80:78–87.

Suski, C. D., S. S. Killen, J. D. Kieffer, and B. L. Tufts. 2006. The influence of environmental temperature and oxygen concentration on the recovery of Largemouth Bass from exercise: implications for live-release angling tournaments. Journal of Fish Biology 68:120–136.

Taylor, R. G., J. A. Whittington, and D. E. Haymans. 2001. Catch-and-release mortality rates of Common Snook in Florida. North American Journal of Fisheries Management 21:70–75.

Thorstad, E. B., C. J. Hay, T. F. Næsje, B. Chanda, and F. Økland. 2004. Effects of catch-and-release angling on large cichlids in the subtropical Zambezi River. Fisheries Research 69:141–144.

Twardek, W. M., T. O. Gagne, L. K. Elmer, S. J. Cooke, M. C. Beere, and A. J. Danylchuk. 2018. Consequences of catch-and-release angling on the physiology, behavior and survival of wild steelhead *Oncorhynchus mykiss* in the Bulkley River, British Columbia. Fisheries Research 206:235–246.

Wilde, G. R. 1998. Tournament-associated mortality in black bass. Fisheries 23(10):12–22.

Wilde, G. R., M. I. Muoneke, P. W. Bettoli, K. L. Nelson, and B. T. Hysmith. 2000. Bait and temperature effects on Striped Bass mortality in freshwater. North American Journal of Fisheries Management 20:810–815.

Wydoski, R. S. 1977. Relation of hooking mortality and sublethal hooking stress to quality fishery management. Pages 43–87 *in* R. A. Barnhardt and T. D. Roelofs, editors. Catch-and-release fishing as a management tool: a national sport fishing symposium. Humboldt State University, Arcata, California.

Wydoski, R. S., G. A. Wedemeyer, and N. C. Nelson. 1976. Physiological response to hooking stress in hatchery and wild Rainbow Trout (*Salmo gairdneri*). Transactions of the American Fisheries Society 105:601–606.

Yin, L., L. Chen, M. Wang, H. Li, and X. Yu. 2021. An acute increase in water temperature can decrease the swimming performance and energy utilization efficiency in Rainbow Trout (*Oncorhynchus mykiss*). Fish Physiology and Biochemistry 47:109–120.

Zeileis, A., and G. Grothendieck. 2005. zoo: S3 infrastructure for regular and irregular time series. Journal of Statistical Software 14: 1–27.