

**INFLUENCES OF TEMPERATURE ON THE MORTALITY AND PHYSIOLOGICAL
IMPAIRMENT OF SOCKEYE SALMON AFTER SIMULATED CAPTURE AND
RELEASE**

by

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Abstract

Pacific salmon experience intense fishing pressure as they commence their freshwater spawning migration, frequently encountering commercial net fisheries and recreational hook and line gear. Untold numbers of fish escape by their own volition or are released by fishers at a range of water temperatures, including those above metabolic and physiological optimums. This thesis focuses on the mortality and sublethal consequences of escape or release from fishing gears by migrating adult Pacific salmon, with a specific focus on how temperature mediates those effects.

The role of temperature in the capture and release of fish was investigated in a comprehensive literature review. This revealed that 70% of studies examining mortality or sublethal effects at various temperatures found both to be magnified at warmer temperatures. Collectively, the results suggest that capture-release mortality increases at temperatures within, rather than above, species-specific thermal preferenda. Notably, there were no studies examining temperature effects on capture-release for adult migrating Pacific salmon.

In two experiments, migrating adult sockeye salmon were intercepted during the early part of their freshwater migration held in a laboratory at three temperatures corresponding with the range of temperatures spanning the historic, current and predicted future migration conditions experienced by their run-timing group (13°C, 19°C, 21°C for summer-run fish in 2009, and 13°C, 16°C, 19°C for late-run fish in 2008). Fish were exposed to a simulated capture treatment including three minutes of burst exercise \pm 60 seconds of air exposure. In both experiments, simulated capture treatments resulted in elevations of plasma lactate concentrations, most markedly after air exposure. The highest mortality was seen in the late-run females at 19°C. Late-run fish who died within 24 hours of capture treatment were characterized by higher

hematocrit, plasma lactate and cortisol, and lower glucose, sodium and chloride concentrations than survivors. Air exposure and warm temperatures were associated with longer equilibrium loss and slower ventilation rates post-treatment, which significantly predicted 24-hour survival in late-run fish. Collectively, these results indicate that released or escaped sockeye salmon may be at higher mortality risk when river temperatures are exceedingly high, and that reducing or eliminating air exposure may result in greater survival.

Preface

This research was carried out as a component of a multi-disciplinary research program investigating the effects of climate change on Pacific salmon. I held primary responsibility for research design and experimental protocols, collection and analysis of data, and preparation of manuscripts. I received considerable logistical support from my colleagues and guidance from my supervisors Scott G. Hinch and Steven J. Cooke. Collaborators on individual projects who were instrumental in development, experimentation or manuscript preparation were listed as co-authors on manuscripts submitted for publication. All experimental procedures were conducted with approval from the University of British Columbia Animal Care Committee (#A08-0388) and in accordance with guidelines set forth by the Canadian Committee on Animal Care.

Chapter 2: The role of temperature in the capture and release of fish

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Chapter 1: Introduction

Sockeye salmon (*Oncorhynchus nerka*) are an iconic fish species in British Columbia, with ecological, cultural, and economic significance to the province and its inhabitants. Their complex life history only adds to our fascination. Sockeye salmon eggs are laid in gravelly riverbeds, and newly hatched fry migrate to nearby lakes for their first year of life. As smolts, anadromous sockeye salmon undergo physiological changes that enable them to transition from freshwater to the Pacific Ocean. There they spend the next 2 years feeding, growing, and often becoming prey to larger fish, marine mammals and birds. Those that survive swim thousands of kilometers across the open ocean to the North American west coast, then collectively head south until they reach the mouth of their natal watershed. Sockeye salmon return to the natal streams with remarkable fidelity both in terms of migration timing and spawning location (Dittman and Quinn 1996, Quinn *et al.* 1999). Due to this fidelity to natal spawning streams with very little spatial straying, nearly 100 genetically and geographically distinct sockeye salmon populations (termed “stocks”) have evolved in B.C.’s Fraser River watershed alone (Beacham *et al.* 2004). These sleek, silver salmon have ceased feeding and for the remainder of their lives will rely on endogenous energy reserves accumulated in the ocean while they transition to freshwater, grow their gonads, develop secondary sexual characteristics such as the characteristic dorsal hump, elongated jaws, and brilliant red and green colouring, and perform remarkable feats of aerobic and anaerobic performance to transcend immense hydraulic challenges such as the Hell’s Gate rapids (Hendry and Berg 1999). Some stocks will swim over 1000 kilometers upstream before navigating to their precise place of birth, where they will find a mate, spawn, and die (Burgner 1991). This once in a lifetime event is the only chance sockeye salmon have to pass on their

genes (semelparity), thus conferring zero lifetime fitness to any fish that fails to complete this migration.

The Fraser River is one of the most important salmon-bearing rivers in the world, producing an average of 28 million adult salmon per year and generating hundreds of millions of dollars for B.C.'s economy through commercial and recreational fishing (DFO 2011b). The Fraser River watershed drains 220 000 km², an area approximately the size of the state of California. Global climate change, hydropower development and riparian forest harvest have resulted in the maximum Fraser River water temperature to increase by approximately 2°C in the last 60 years (Patterson *et al.* 2007). Climate models predict this warming trajectory will continue, resulting in an estimated 0.14°C increase in summer temperatures per decade for the next ~90 years (Morrison *et al.* 2002, Ferrari *et al.* 2007). Water temperature has long been considered the “master factor” in the biology of fishes because of its governance over physiological processes (Fry 1947). All fishes have species-specific (indeed sometimes stock-specific) optimal temperatures for growth, feeding, performance, and reproduction. In Pacific salmon, the difference between optimal aerobic temperature and that of complete aerobic collapse may only be 6-7°C (Fry 1947, Lee *et al.* 2003b, Eliason *et al.* 2011). Stock-specific optimal temperatures for aerobic scope in sockeye salmon are ~14.5-17°C (Eliason *et al.* 2011). Since the early 1990's, summer maximum temperatures have exceeded 20°C in many years. This temperature approaches the critical thermal limit for many stocks of sockeye salmon (Farrell *et al.* 2008, Eliason *et al.* 2011). Hodgson and Quinn (2002) suggest that 19°C may be the threshold above which sockeye salmon migration success is limited. High water temperatures have been correlated with high en-route and pre-spawning mortality of Fraser River sockeye salmon (Gilhousen 1990, MacDonald *et al.* 2000, Cooke *et al.* 2004b, Mathes *et al.* 2010).

Commercial, recreational, and First Nations fisheries for sockeye salmon are densely concentrated in the Pacific coastal estuarine and lower Fraser River environments. Migrating sockeye salmon likely experience countless gear encounters as they navigate these densely populated areas, and may escape from nets or hooks by their own volition, or may be released by catch-and-release anglers or as commercial by-catch. Pacific salmon fisheries are managed by Fisheries and Oceans Canada (DFO) and the Pacific Salmon Commission (PSC).

Considerable effort goes into developing predictive models and making in-season adjustments to set catch limits for commercial, First Nations, and recreational fishers, in order to achieve stock-specific escapement targets and thus ensure sustainability of this resource. While many stocks of sockeye salmon co-migrate, they are managed largely in four run-timing aggregates: early Stuart, early summer, summer, and late-run. These run-timing groups experience different river conditions, and stocks have adapted their aerobic capacity to be optimized at the temperatures historically experienced (Farrell *et al.* 2008, Eliason *et al.* 2011). Physiological functioning becomes impaired at temperatures beyond their optimal thermal window.

In recent years there has been increasing research aiming to determine if releasing fish (from a variety of commercial or recreational gears types) is indeed an effective conservation measure. In other words, do released fish survive? There is evidence that severe exercise alone can induce mortality in fish (Wood *et al.* 1983). Fish released as by-catch often experience strenuous exercise coupled with air exposure, net entanglement or hooking injuries, and other physical injuries resulting from handling necessary for their release. Water temperature has been identified as one of the most important factors predicting fish mortality in a catch-and-release context (Bartholomew and Bohnsack 2005, Cooke and Suski 2005, Arlinghaus *et al.* 2007). Sockeye salmon are particularly interesting in this respect since they are a highly sought after species, increasingly subject to catch-and-release fishing, that migrate in summer when

temperatures are at their peak and increasing over time. Additionally, large numbers of late-run sockeye salmon are now migrating several weeks earlier than normal, and thus encountering water several degrees warmer than average (Cooke *et al.* 2004b). Recent policy changes have increased commercial in-river sockeye fisheries, as opposed to ocean/estuarine fisheries where waters are cooler, and recreational sockeye fishing in the Fraser River is dramatically increasing in popularity. In order to effectively manage this resource, managers need an understanding not only of the number of sockeye harvested, but the number of escapees and released fish whose chance of survival may be further reduced by this occurring in warm temperatures.

The over-arching goal of this thesis was to address the paucity of knowledge of how thermal and capture stressors may act in synergy to reduce the fitness of Fraser River sockeye salmon. I endeavored to study the interaction between temperature and acute capture-related stressors, specifically strenuous exercise and air exposure, and how these variables influence mortality and physiological responses of sockeye salmon. My primary objectives were to i) review the existing scientific literature in order to understand how water temperature affects the stress response and survival of captured-and-released fish; ii) to study the responses of adult sockeye salmon exposed to capture-release at various ecologically relevant temperatures; iii) to evaluate predictors of mortality post-capture; and iv) to assess whether stock-specific differences in thermal tolerance confer differences in their responses to combines thermal and capture stressors.

Chapter 2 is a review of the existing literature examining the interaction between capture-release and thermal stressors for all fish species. Therein I assess species studied, research questions addressed, the effects of thermal stress on the mortality and sublethal consequences of various capture techniques, and the context of the experimental temperatures with regard to species

tolerances. As such, this review provides the justification for my experiments (Chapters 3 & 4) and provides a valuable summarization of the current research integrating capture-release and thermal stress in fish.

In Chapter 3, I intercepted adult migrating summer-run sockeye salmon early in their freshwater migration and experimentally challenged fish with strenuous exercise and air exposure in order to simulate capture-and-release stressors that occur when fish are captured in gill, tangle, or seine nets or angled on a hook and line. Injuries that may occur during capture, such as hooking of internal organs or tearing of gill filaments, are often fatal and are not the focus of these studies. Instead, in accordance with methodologies which have been successfully used on other species (Milligan 1996), I simulated capture and release stressors without physical injury, in a laboratory setting where water temperature could be manipulated as part of the experimental design. I analyzed blood chemistry parameters and physiological impairments in order to understand the effects of exhaustive exercise with and without air exposure at a cool (13°C), aerobically optimal (19°C) and critically high (21°C) temperature.

Chapter 4 assesses the survival and physiology on late-run sockeye salmon after the same stressors at corresponding temperatures (13°, 16°, and 19°C). In both experiments (Chapters 3 & 4) I predicted that thermal and capture stressors would be additive, and that lethal and sublethal consequences would be greatest for exercised and air-exposed fish at the warmest temperatures. Logistic regression models were evaluated for predicting 24-hour mortality using plasma metabolites, ions, and hormones. Additionally, two easily quantifiable metrics (ventilation rate post-capture and duration of equilibrium loss) were tested as predictors of mortality.

My concluding chapter (Chapter 5) presents a synthesis of my experimental findings with particular attention to stock-specific differences, and an evaluation of how this thesis contributes

to biological knowledge in general, as well as management implications for Fraser River sockeye salmon fisheries. To my knowledge, the studies described herein are the first to explicitly examine capture-release stressors across an ecologically relevant range of temperatures in any Pacific salmon species.

Chapter 2: The role of temperature in the capture and release of fish¹

2.1 Introduction

Globally, commercial fishers capture and release approximately 7 million tonnes of fish per year (Kelleher 2005), and as many as 19 million tonnes (30 billion fish) per year are estimated to be captured and released from recreational fisheries (Cooke and Cowx 2004). Fish are released because they may have little or no commercial value, they are not of the desired size, legislation prohibits their retention because the species or population is threatened, or in some recreational fisheries release is mandated in order to maintain population characteristics of an unexploited population (Redmond 1986, Ross 1997). Regardless of fishing method or motivation for releasing captured fish, a capture-and-release event commonly consists of multiple separate stressors, including encountering the gear (physical injury), struggling to become free (strenuous exercise), barotrauma (fish caught at depth), human handling (potential further injury, mucous and scale loss, fear response, struggling), and air exposure (oxygen deprivation, collapse of gill structures (Arlinghaus *et al.* 2007)). Sublethal effects of these stressors include altered blood chemistry, behavioural impairments, depressed growth and reproductive rates, and increased vulnerability to disease (Wendelaar Bonga 1997, Barton 2002). Mortality from these stressors has been examined for multiple gear-types and species, and varies from 0-100% of released fish (Alverson *et al.* 1994, Bartholomew and Bohnsack 2005).

While a number of factors can influence post-release mortality, such as species and gear type (Chopin and Arimoto 1995, Bartholomew and Bohnsack 2005), decades of research has

¹ A version of this chapter has been published. Gale, M.K., S.G. Hinch, and M.R Donaldson. 2011. The role of temperature in the capture and release of fish. Fish and Fisheries (Early View). DOI: 10.1111/j.1467-2979.2011.00441.x

revealed that water temperature plays an important but complex role in post-release survival. Indeed, temperature has long been termed the ‘master factor’ in the biology of fishes for its governance over physiological processes (Brett 1971). Being ectotherms, many fish have a relatively narrow range of temperatures in which they are able to thrive, grow, and reproduce (Elliot 1981). When environmental (and thus body) temperatures are elevated above the optima for a particular species, fish may exhibit abnormal behaviour such as bursts of activity, collisions with objects, and rapid ventilation (Elliot 1981), aerobic scope and cardiac function can decline (Farrell 1997, Pörtner 2001), susceptibility to disease generally increases (Ellis 1981), oxygen availability decreases, food conversion efficiency decreases (Kinne 1960, Andrews and Stickney 1972, Wurtsbaugh and Davis 1977), and physiological indices of stress such as plasma cortisol levels are elevated (Wendelaar Bonga 1997, Barton 2002). Physiological homeostasis is disturbed through changes in reaction rates and membrane permeability (Hazel 1984), resulting in increased metabolic demand, decreased blood osmolality and serum electrolytes (Houston and Schrapp 1994, Claireaux and Audet 2000), and decreased probability of survival (Elliot 1981). At temperatures below the thermal optimum, fish have a reduced metabolism and aerobic scope, and thus an impaired ability to catch prey, escape predators, and navigate obstacles. Cold shock (acute decreases in temperature) and very cold temperatures may result in behavioural disturbances such as darting or colliding with objects, loss of dorso-ventral orientation, or coma (reviewed in Donaldson *et al.* 2008b). Theoretically, overcoming a capture stressor may be more difficult for a fish under thermal stress than for one in an optimal thermal environment. Previous reviews have examined fisheries-related capture in relation to physiological stress and survival (e.g. Arlinghaus *et al.* 2007), but the role of water temperature has not been explicitly reviewed in this context.

The focus of this paper was to conduct a quantitative review examining the role of environmental temperature on the survival and physiological condition of ray-finned fishes (class Actinopterygii) in response to capture and release. Our main objectives were to (1) quantitatively summarize and interpret trends across studies with respect to geographic location, year of study, focal species, objectives, duration and methodological approaches, (2) quantify the extent to which elevated water temperatures contribute to mortality from fisheries-related capture and release, (3) determine the role of elevated water temperatures in influencing sublethal parameters, such as physiological stress, and (4) identify thermal ranges in which thermal effects begin to influence mortality, for species where sufficient data enabled such comparisons. Herein, we quantitatively address each of these objectives to summarize existing knowledge and highlight the novel and integrative approaches currently being explored. Further, we discuss challenges faced in the interpretation of existing research to guide management decisions on fisheries regulations and temperature, using salmon fisheries as a key example.

2.2 Methods

2.2.1 Literature search

ISI Web of Knowledge (WK) and Aquatic Sciences and Fisheries Abstracts (ASFA) were used to identify peer-reviewed literature examining the interactions between capture stress and temperature for fishes in the class Actinopterygii. We included papers published from 1965 to December 2009. Keywords were selected using an iterative process, where searches were conducted in both databases and continually revised in order to maximize the number of relevant articles returned. Once the final sets of keywords were established and the database was assembled, we manually removed irrelevant articles by reading abstracts and full articles where

necessary. Articles were excluded if it was not evident from the abstract that the experiment included a capture-type stressor (real or simulated) examined at more than one temperature.

In order to capture as many articles as possible that examined some form of capture stress under more than one temperature, we used combinations of search terms in two separate searches. To qualify for the first search, papers had to include in their title, abstract or keywords (hereafter collectively referred to as keywords) one term from each of four categories: temperature ('temperature', 'thermal', 'climate change', or 'season'), consequences ('mortality,' 'fate,' 'survival,' 'stress,' 'fitness,' 'condition,' 'behaviour,' 'physiology,' or 'injury'), capture ('strenuous exercise,' 'exhaustive exercise,' 'capture and release,' 'catch and release,' 'bycatch,' 'by-catch' 'handling' or 'escape') and taxa ('teleost' or 'fish' or 'Actinopterygii,' WK search only), and must not have any of the exclusion terms ('shellfish,' 'crustacean,' 'invertebrate,' 'mollusc,' 'dolphin,' 'turtle,' 'seabird,' 'bird,' 'shark,' 'whale,' 'shrimp,' 'prawn,' 'nephrop,' or 'lobster'). Similarly, the exclusion terms removed all studies examining species other than ray-finned fishes. The second search required papers to identify in their keywords one of the temperature words identified above, as well as 'hooking mortality,' 'angling mortality,' or 'discard mortality', and to not have any of the exclusion terms listed above. While there is a large body of knowledge studying exercise under different temperatures, we included only those that studied 'strenuous' or 'exhaustive' exercise to represent one of the stressful facets of the capture-release experience (Milligan 1996). All articles resulting from the two searches were put into a database for consideration. Wildcards were used in most search terms (e.g. 'escap*' would capture escapes, escapees, escaped, and escape).

This search process was supplemented by a single-pass reading of papers captured in the database search to find relevant studies cited by other authors. Articles examining only culture-

related stressors such as transport or confinement were removed. This resulted in a total of 83 peer-reviewed articles (Table 2.1). One article in our database involved the collective analysis of data from eight previous studies, two of which were included in this review. We did not exclude this article since the majority of included data was not incorporated elsewhere in this review.

Papers that did not mention temperature in their abstract were eliminated, potentially biasing our results towards papers that found an effect of temperature on the lethal or sublethal effects of capture. Those that found no effect of temperature may have been less likely to report that in an abstract than those that detected an effect. We contend that our approach was justified because temperature is widely considered the master factor in the biology of fishes, and is acknowledged to influence capture-release mortality in the published reviews on this topic (Muoneke and Childress 1994, Chopin and Arimoto 1995, Bartholomew and Bohnsack 2005, Arlinghaus *et al.* 2007). The failure to report the presence or absence of a temperature effect in a capture-release study (if examined) would be a substantial oversight.

2.2.2 Literature review

Articles were queried for publication trends (e.g. continent where research took place, year of publication, journal name), marine or freshwater environment, lab or field experiment (or both), holding method (including free-swimming in the field, fish tanks, temporary holding tanks ashore of study area or on a boat, or large artificial (laboratory) ponds), species, capture method or gear-type used (or imposed stressor such as exercise or air exposure), temperatures used, temperature context for a particular habitat or species, and temperature effects on mortality. In addition, we queried any sublethal indices the authors explicitly chose to examine stress or impairment, including but not limited to physiological metrics such as plasma and muscle metabolites, muscle or tissue constituents such as glycogen, adenosine triphosphate (ATP),

adenosine diphosphate (ADP), and adenosine monophosphate (AMP), ions, and hormones, physical injuries caused by gear or handling, behavioural observations, disease and immune impairment, and vulnerability to predation. We collectively termed these ‘sublethal impairments.’ Within this category, lactate, glucose, cortisol, ATP, ADP, AMP, phosphocreatine (PCr), pyruvate, hematocrit, hemoglobin, glycogen, heart rate, stroke volume, cardiac output, equilibrium loss, ventilation rate, pH, total protein, oxygen consumption, partial pressure of carbon dioxide (PCO_2), and bicarbonate (HCO_3) were classified as measures of stress and exercise physiology. Osmolality, chloride, sodium, and potassium concentrations, and hematocrit were classified as measures of osmoregulation. Any physical trauma or bodily harm was classified as an index of injury. All other sublethal metrics were classified as ‘other.’ It is important to note that if studies evaluated injury as a predictor variable but not as a response variable with respect to both capture stressor and temperature, this was not included in our sublethal impairment category. Variables and classifications used in this review are presented in Table 2.2.

Some variables queried were not always overtly stated in the articles. For example, papers were queried for ‘focal sector,’ which was the target audience or group that results would be applicable to. These included recreational fisheries (sport or leisure fishing), commercial fisheries (fishing for profit), what we termed ‘fisheries science’ (where the fishery method or sector was not explicitly stated in the title or abstract but the study relevance to a particular fishery was discussed in the body of the article) and basic science (fundamental biological questions independent of any fisheries sector). Where unavoidable, subjective decisions were made in order to classify papers. Classes were not mutually exclusive for many of the variables (e.g. some articles examined more than one species, gear type, or physiological metric), and the

result is that percentages of classes within one queried variable do not always sum to one hundred percent.

We queried the papers with regard to several temperature-related questions: what temperatures were studied, were temperatures naturally occurring or manipulated, what was the effect of temperature on stress indices and mortality (e.g. was the effect positive, negative, both or neither), and, what was the biological temperature context of the study? For this last question, we looked for authors to place the temperatures examined into context with regard to the focal species, and classified them as high, within thermal tolerance ('normal'), low, or 'no context given.' All references and summary temperature information are listed by species in Table 2.1. Articles were queried as to whether increasing temperature had a significant effect on mortality or any sublethal indices quantified, and whether this effect was positive (greater survival or lower sublethal impairment parameters), negative, or neutral (no effect).

Thermal preference and/or optimal growth temperature data is available on many species, therefore we attempted to use the existing data in the literature to see if overall patterns in the results presented in this review could illuminate whether final thermal preferendum or optimal temperatures for growth (henceforth "optimal temperatures") corresponded with optimal temperatures for capture and release. Our chain of reasoning for choosing this parameter was as follows: 1) the final thermal preferendum and the optimum temperature for growth closely approximate one another (Jobling 1981, Kellogg and Gift 1983), 2) data on optimal temperatures for growth are available for many species, presumably due to their applications in aquaculture, 3) these parameters may not vary between populations of species that have wide geographical ranges (Beitinger and Fitzpatrick 1979), and 4) using optimal (growth) or preferred temperatures as a context against which to study capture-release mortality is particularly

interesting because within this zone fish are not thermally stressed given the absence of secondary acute stressors (as opposed to critical temperatures, which are lethal in the short- or long-term). This allows us to evaluate whether the optimal thermal window narrows when capture-release stressors are applied.

While it is difficult to compare across studies, since a number of other factors are variable (e.g. air temperature, air exposure, gear types, time in live-wells, water conditioner or aeration, number of monitoring days), we examined the temperature at which mortality began to increase within a given set of circumstances. We examined size classes separately because for many species there are ontogenetic differences in the optimum temperature for growth, with optimal temperatures decreasing with increasing body size (e.g. Björnsson *et al.* 2001, Imsland *et al.* 2005 and references therein). Presented are the optimal temperatures for species that had more than one mortality study included in this review (Table 2.3).

2.3 Results

Klein (1965) was the earliest peer-reviewed study identified in our database. It was published in *The Progressive Fish-Culturist* (became *North American Journal of Aquaculture* in 1999), and studied hooking mortality in rainbow trout (*Oncorhynchus mykiss*, Salmonidae). Eighty-three studies matched our search criteria, with most of these occurring in the last 20 years (Fig. 2.1). Studies occurred predominantly in North America (81%) and Europe (17%; Table 2.2), and 76% were focused on freshwater species (Table 2.2). Studies were published in 18 peer-reviewed journals, with more than half of all studies being from one of the American Fisheries Society publications, which include the *North American Journal of Fisheries Management* (45%), and *Transactions of the American Fisheries Society* (14%; Table 2.2). *Fisheries*

Research and the *Journal of Fish Biology* were also common publication venues (10% and 8%, respectively).

While the target sector was not always obvious or discrete, the majority focused on the recreational sector (64%), followed by the commercial sector (27%; Table 2.2), with considerable overlap. We classified six studies (7%) as ‘fisheries science,’ because while the title and abstract of the paper were not clearly aimed at a particular fisheries sector, the fisheries applications of the research were discussed in the body of the paper. The remaining four studies (5%) addressed fundamental scientific questions and did not express a direct applied research focus. No studies explicitly examined artisanal or Aboriginal fisheries.

Studies examined 21 families of fishes from 9 orders. Perciformes was the most commonly studied order (52%, with 25% of all studies focused on the family Centrarchidae), followed by Salmoniformes (consists of only the family Salmonidae, 28%). Of the 52 species studied, 35 were only examined in one article (Fig. 2.2). Most papers (88%) investigated a single species. Largemouth bass (*Micropterus salmoides*, Centrarchidae) was the most commonly studied species (18% of total), followed by striped bass (*Morone saxitalis*, Moronidae; 11%), rainbow trout (8%) and Atlantic salmon (*Salmo salar*, Salmonidae; 8%; Fig. 2.2).

Most studies focused on real or simulated capture stressors (71 studies, 86%; Table 2.2), which include multiple identifiable stressors such as handling, exercise, confinement, and air exposure. Other studies focused on specific components of the capture-release experience, which authors identified as strenuous exercise (8%), handling (6%), air exposure (4%) and tagging or sampling (4%). Of the 54 studies examining hook and line fishing methods, almost all of these (50 studies, 93%) were focused on the recreational fishing sector. Twelve studies (17% of the 71 capture studies) examined the effects of trawling. Gillnets and purse seines were the capture

method in three studies each (4% of the 71 capture studies). An additional three studies employed manual chasing, including two that used this method to simulate angling (Cooke *et al.* 2003, Suski *et al.* 2006) and a third that discussed their results in a recreational fishing context (Wilkie *et al.* 1997). Other fishing methods examined were traps (two studies), beach seines (one study) and hoop nets (one study). No studies compared electrofishing results at multiple temperatures.

Warmer temperatures resulted in higher mortality in 49 of the 70 (70%) papers that quantified survival after capture (84% of all papers quantified mortality). Only one study found lower mortality in warmer water, and in this case Rutecki and Meyers (1992) speculated that sablefish (*Anoplopoma fimbria*, Anoplopomatidae) mortality was related to disease. Of the 55 studies that were performed in a field setting, most (44 studies, 80% of field studies) used visual assessment to quantify mortality, almost exclusively by utilizing temporary lakeside, streamside, or on-board holding tanks. One exception was Loftus *et al.* (1988), who held lake trout (*Salvelinus namaycush*, Salmonidae) by stringers through the lip and tethered them to a buoy. Telemetry was utilized in six studies (11% of field studies) and mark-recapture was used in two studies (4% of field studies). Mortality occurring within less than 24 hours was examined in 9 studies (13% of 70 mortality studies), and one to two day mortality in 15 studies (21%), whereas 23 studies (33%) quantified mortality greater than two days but less than or equal to one week. Twenty-four studies (34%) examined mortality for longer than one week.

Thirty-seven articles (45% of all 83 studies) measured sublethal impairments, including physiological indices of stress such as elevations of metabolites or stress hormones in the plasma (57% of 37 sublethal studies) or muscle tissues (16%), cardiac parameters (e.g. heart rate, stroke volume, cardiac output, 11%), behavioural impairment (8%), injury (5%), immune

suppression (3%), or vulnerability to predation (3%). Included in these were 23 studies (28% of all studies) that examined both mortality and sublethal indices. Twenty-six of the studies (70% of 37 sublethal studies) demonstrated increasing sublethal impairment with increasing temperature. For studies that presented both survival and sublethal effects, 12 (52% of 23 survival and sublethal studies) showed both increased mortality and a sublethal index of stress or impairment with increasing temperature. Twelve studies compared recovery rates from capture, and warmer temperatures were shown to facilitate or expedite recovery in half of these cases (Dalla Via *et al.* 1989, Kieffer *et al.* 1994, Wilkie *et al.* 1997, Pottinger *et al.* 1999, Galloway and Kieffer 2003, Hyvärinen *et al.* 2004).

Of the 19 studies that included a temperature deemed high for the focal species, all but one (95% of 19 high temperature studies) detected negative effects of increasing temperature on the survival or impairment indices of captured fish. More than half of all studies (58% of 83 studies) did not put their experimental temperatures into any context with regards to species optima; only two of these reported temperatures that were abnormally high for the associated habitat. We found that for 10 of the 15 most studied species in this review (≥ 2 mortality studies), mortality began increasing at temperatures within the optimal growth or preferred temperatures from the literature (Table 2.3).

2.4 Discussion

Most studies were published in the recent decade, likely reflecting the increasing interest in science that links temperature and fisheries management because of the growing awareness and concern of climate change (FAO 2008). Our finding that the majority of studies occurred in freshwater and in North America, and that half focused on recreational fishing, is likely driven by the popularity of recreational catch-and release fishing in that continent, where

management policies mandate or recommend release of captured fish in several jurisdictions (in Canada see the Fishery (General) Regulations – Fisheries Act (1993), or in the United States see the Magnuson-Stevens Fisheries Conservation and Management Act (2006)). In contrast, in recent years some European jurisdictions have banned catch-and-release fishing (described in Arlinghaus *et al.* 2007) on humane or ethical grounds, and these sorts of policy decisions could be limiting the scientific exploration of capture-and-release in those regions. The predominance of scientific studies focused on the Centrarchidae and Salmonidae families (53%), a trend consistent with the general pattern of freshwater recreational fisheries in North America. In the US and Canada, the most common sport fisheries include those for bass (Centrarchidae) and trout (Salmonidae; Fisheries and Oceans DFO 2005, Department of the Interior Fish and Wildlife Service *et al.* 2006).

We found that survival study durations from immediate (Meals and Miranda 1994) to up to two years (Thompson *et al.* 2007) were well represented in the literature. Several authors suggested that physical injury (Plumb *et al.* 1988, Nelson 1998, Cooke and Hogle 2000), physiological mechanisms such as intercellular acidosis (Wood *et al.* 1983, Milligan and Wood 1986, Kieffer *et al.* 1994), or physiological damage caused by air exposure (Ferguson and Tufts 1992, Davis and Olla 2001, Cooke *et al.* 2002) are leading causes of immediate or short-term (hours) mortality. Although it has been shown that long-term mortality and population level effects can be linked with immune suppression and subsequent disease development (Wedemeyer and Wood 1974, Wendelaar Bonga 1997), reduced reproductive success of stressed individuals (Schreck *et al.* 2001, Schreck 2010), disrupted gametogenesis due to reallocation of energy during reproductive maturation (Patterson *et al.* 2004), altered courting or mating behaviour, or interrupted nest-guarding or other parental care activities (Cooke *et al.* 2002), only a few studies in this review examined factors less directly influencing fitness. For example, Lupes *et al.*

(2006) found that sablefish immune function was compromised after the capture stressor (simulated hooking and trawling in laboratory tanks), potentially pre-disposing released fish to disease and delayed mortality, and the response was the same at various water temperatures (up to 16°C). Other innovative and promising new approaches for studying the effects of thermal and capture stressors used indices of reflex impairment (Davis and Ottmar 2006, Davis 2007, 2010) or vulnerability to predation (e.g. Olla and Davis 1989, Mesa *et al.* 2002). Jepsen (2008) found that predation of brown trout (*Salmo trutta*, Salmonidae) by pikeperch (*Sander lucioperca*, Percidae) in laboratory ponds was unaffected by tagging/handling treatments but increased with temperature, however it is unclear whether this was due to decreased predatory avoidance by the trout or increased predatory effort by the pikeperch in warmer water. Regardless, this experiment investigated an important ecological component of the potential effect of capture and thermal stressors acting together. Our results showed that researchers are beginning to study mortality levels and fitness consequences in a broader context, however the ultimate population-level effects of the capture-and release of fish remains unknown for most species.

Many investigators adopted laboratory-based approaches such that temperatures and other stressors could be precisely manipulated (e.g. Barton and Schreck 1987, Kieffer *et al.* 1994). Although many of the ecological complexities of the real world were not incorporated into this type of research, it can be an important starting point for understanding key relationships between thermal and other stressors. Some studies (Cooke *et al.* 2003, Suski *et al.* 2006) utilized manual chasing to exhaustion in laboratory tanks as a means of simulating the ‘playing’ and ‘landing’ components of an angling event under specific thermal conditions, and eliciting a stress response similar to that of angling (Milligan 1996). A limitation of this approach is that in addition to physiological stress and exercise, fish sustain injuries from escaping or being

released from fishing gears (Chopin and Arimoto 1995, Broadhurst *et al.* 1999, Cooke and Hogle 2000, Davis 2002, Bartholomew and Bohnsack 2005, Arlinghaus *et al.* 2007). Therefore, the results of manual chase studies likely represented a best-case scenario for how captured and released fish responded or survived in relation to specific thermal conditions. For example, while Suski *et al.* (2006) observed no mortality in largemouth bass four hours after simulated angling using manual chasing, Meals and Miranda (1994) reported pre-release mortality in multiple largemouth bass angling tournaments at similar temperatures.

Interpreting mortality rates and stress responses in a laboratory setting is difficult because holding wild fish in pens, tanks or cages can be stressful for some fishes (Billard *et al.* 1981, Barton and Iwama 1991, Conte 2004, Roscoe *et al.* 2010), thus captivity could contribute to mortality and indices of stress to an unknown degree that is not related directly to a simulated capture-release event. Most field-based experiments also involved holding fish in tanks, albeit temporarily, to assess survival or stress responses. Only six studies in the current review utilized telemetry to assess survival (Lee and Bergersen 1996, Bettoli and Osborne 1998, Thorstad *et al.* 2003, Bettinger *et al.* 2005, Thompson *et al.* 2007, Thompson *et al.* 2008), which allowed for evaluation of released fish in their natural environment, thus eliminating the effects of captive holding. However, attachment or implantation of transmitters could also contribute to mortality and/or sublethal impairment, and few field studies utilizing telemetry control for tag-effects, since monitoring of non-tagged individuals in the field presents substantial logistic challenges. Ideally, researchers would develop and analyze the procedures best suited to their studies (including quantifying detrimental effects) before collecting data (Bridger and Booth 2003). If methodologies are carefully chosen (e.g. using proven surgical techniques and transmitter specifications for the specific study animals, and choosing study designs with appropriate control and sham treatments, and adequate statistical power; Cooke *et al.* 2011), effects should

be minimal and the benefits in terms of data collected are immense (Bridger and Booth 2003, Cooke *et al.* 2004c, Donaldson *et al.* 2008a). Because telemetry is likely one of the best ways to assess both detailed and long-term effects of capture-release on individual survival, and only a small fraction of all studies have adopted this approach, we thus have only a limited understanding of the full extent of the ecological implications of thermal effects on the capture-release of fish.

The primary objectives of this review were to quantify the extent to which elevated water temperatures contributed to mortality from fisheries-related capture and release, and determine the role of elevated water temperatures in influencing sublethal parameters, such as physiological stress. The majority of studies found that warmer temperatures had a negative effect on fish condition or survival after release. However, less than one-third of the articles we reviewed integrated mortality and some sublethal index of stress or impairment. There are two very good examples of how such an integrated approach, in the lab and field, has helped to elucidate the potential physiological mechanisms responsible for capture-induced mortality. Wilkie *et al.* (1996) examined angling stress by intercepting wild Atlantic salmon in freshwater as they returned to spawn, manually hooking them through the jaw, then playing them to exhaustion. They then sampled fish for blood and white muscle after 0, 2, or 4 hours, or observed them for 12 hours, to investigate the impacts of fishing in warm summer temperatures (22°C) versus those at cool fall temperatures (6°C). They found that summer angling resulted in greater mortality, impaired glycogen resynthesis rates, and slowed white muscle lactate elimination and metabolic proton load correction. Olla *et al.* (1998) simulated trawling in adult sablefish, monitoring mortality in laboratory tanks for 60 days and incorporated some basic measures of stress physiology in plasma after the capture simulation. They estimated that the critical post-capture temperature for sablefish that live at 4-6°C is 12 to 15°C, and discovered

that peak plasma lactate, but not glucose and cortisol, increased with temperature. Plasma lactate or blood pH are both common metrics in capture and release experiments because they are a corollary of intracellular acidosis, which may be the reason that fish sometimes die after strenuous exercise (Wood *et al.* 1983). The slower recovery of pH and greater mortality after angling in warm water observed in Wilkie *et al.* (1996) was consistent with that explanation. While Olla *et al.* (1998) did not speculate as to the mechanism underlying the mortality they observed, the integrative nature of their study was beneficial because it analyzed the effects of ecologically relevant temperatures for sablefish caught in trawls off the northwest coast of the U.S., and suggested that in future studies serum lactate has the potential to be used as a surrogate for mortality. We conclude from the papers we reviewed that the weight of evidence suggests thermal and capture stressors are often additive in nature, such that when experienced together they may be more detrimental to fish than either one experienced alone.

An important, yet surprising finding in this review was the lack of context given for the temperatures used in more than half of the studies included. Considering that each fish species (and sometimes population) has an optimal temperature (see references in Hart 1952, Beitinger and Fitzpatrick 1979, Johnston and Ball 1996, Beitinger *et al.* 2000, Pörtner 2001, 2002, Farrell *et al.* 2008), it is imperative that the reader understands the context of each temperature for the species and life-stage being studied. Indeed, the degree of thermal stress is determined by not only the environmental temperature, but also by the species, their genetics, and their prior thermal experience (i.e. acclimation; Pörtner 2001). It is not clear whether this has occurred because authors have assumed their target audience was thoroughly knowledgeable of their study organism and thus knew the implications of the experimental temperatures, or because they have used the term ‘high’ temperature to suggest that their warmest experimental temperature was not only *relatively* high but also abnormally high for the species or population.

Regardless, this widespread lack of temperature context is problematic as it effectively limits the ability of readers to compare or synthesize results across species and habitats. This lack of clarity could lead to confusion over the ramifications of findings in many of these studies. Moreover, because of the large number of papers that fell into this category, it was difficult for us to accurately and succinctly summarize the overall effects of increasing temperatures on capture and release experiences in an ecologically meaningful way.

Perhaps the most remarkable finding in our literature review was that temperature-mediated capture-release mortality occurred even within temperatures considered to be optimal or preferred for species with sufficient temperature optimum and preference data to warrant comparison (Table 2.3). Capture-release mortality of sablefish, spotted seatrout (*Cynoscion nebulosis*, Sciaenidae), Atlantic cod (*Gadus morhua*, Gadidae), bluegill (*Lepomis macrochirus*, Centrarchidae), smallmouth bass (*Micropterus dolomieu*, Centrarchidae), largemouth bass, striped bass, cutthroat trout (*Oncorhynchus clarkii*, Salmonidae), rainbow trout, paddlefish (*Polyodon spathula*, Polyodontidae), pikeperch, and walleye (*Sander vitreus*, Percidae) began increasing at temperatures within or below their optimal range (see references in Table 2.3). We found the exceptions to this trend were Pacific halibut (*Hippoglossus stenolepis*, Pleuronectidae), Atlantic salmon, and brown trout. Collectively, these results suggest that temperatures even within preferred or optimal ranges may increase mortality to an unacceptable level for many species, representing a potentially unexpected challenge for managing these fisheries. Generally, optimal and preferred temperature experiments are carried out under idealized conditions. Evidence that a secondary stressor such as capture-release narrows or shifts species' optimal temperature ranges suggests that other secondary stressors, such as poor water quality or disease, may similarly constrict or shift the optimal temperature window. Thus,

there is a strong need for researchers to assess the optimal temperature range for a given species under non-idealized conditions.

Fisheries managers may refer to scientific capture-and-release literature if they are considering using closures or restrictions to protect threatened species or stocks by reducing the number of harvested individuals. Our finding of a general trend in warm temperatures exacerbating mortality and sublethal impairments suggests that a better understanding of these processes may aid managers in making decisions on fisheries regulations during times of challenging environmental conditions. Dozens of studies examined in the present review recommended avoiding (catch-and-release) angling or commercial fishing openings (bycatch) when temperatures were relatively high. In some cases authors recommended a specific temperature threshold above which fishing should be avoided or the resulting increased mortality should be accounted for (e.g. 25°C for Puerto Rican largemouth bass, Neal and Lopez-Clayton 2001, 16°C for Hudson River striped bass, Millard *et al.* 2005). Other recommendations from the articles in this review include gear or technique recommendations (Klein 1965, Alós 2009), limiting or eliminating air exposure after capture (Cooke *et al.* 2003), improved sorting techniques (Dunning *et al.* 1989), and minimizing handling times (Meka and McCormick 2005).

Nearly one third (29%) of studies focused on *Oncorhynchus*, *Salmo*, and *Salvelinus* spp., and although climate warming in the next century may have the most serious effects on cool- and cold-water species such as these, assessing impacts of climate change was rarely stated explicitly as a rationale for the research. For Atlantic salmon, there seems to be sufficient information on the effects of temperature upon capture-release stress and mortality (Wilkie *et al.* 1996, Wilkie *et al.* 1997, Anderson *et al.* 1998, Jurvelius *et al.* 2000, Dempson *et al.* 2002, Galloway and Kieffer 2003, Thorstad *et al.* 2003) to aid in the development of specific

guidelines for release of captured fish under different thermal conditions. Of the seven articles we uncovered, five found a significant increase in mortality or some sublethal impairment at the highest temperatures (ranging from 14-24°C). Anderson *et al.* (1998) found that after 72-hours, survival declined from 100% at temperatures less than 16.5°C, to 20% at 20°C. Wilkie *et al.* (1997) found that 30% of fish released after angling perished at 23°C, but none perished following release at temperatures less than 18°C. Post-angling mortality was 40% in Wilkie *et al.* (1996) at 22°C. Dempson *et al.* (2002) detected no statistical differences in survival, however mortality increased from 0% at the coolest temperatures to 12% above 18°C. Two studies found no effects of increasing temperature (Jurvelius *et al.* 2000, Galloway and Kieffer 2003) up to 18°C, although Jurvelius *et al.* (2000) found overall high mortality for (landlocked) Atlantic salmon released from trawls when temperatures were 10-18°C. In summary, temperatures exceeding 20°C were commonly associated with increased mortality of Atlantic salmon released from fisheries capture, and authors often suggested avoiding catch and release above this temperature.

While some important management guidelines have been implemented based on the results of capture-release science, such as recreational Atlantic salmon fisheries closures when temperatures met or exceeded 22°C in Newfoundland rivers (Dempson *et al.* 2001), guidelines in North America (state, provincial, and federal jurisdictions) often fail to provide useful direction to fishers (Pelletier *et al.* 2007). In their recent review of North American guidelines, Pelletier *et al.* (2007) found that only seven of 49 agencies made recommendations about avoiding catch and release fishing in extremely warm water, despite the popularity of angling tournaments in summer months. We reviewed the available online guidelines and discovered that despite the increasing body of knowledge, the proportion of agencies (12 of 61) that warned

that post-release mortality might increase in warm water has remained unchanged. The American National Oceanic and Atmospheric Administration's (NOAA) Code of Angling Ethics makes no mention of warm temperatures (NOAA NOAA 2010). When agency guidelines do suggest avoiding high temperatures, they almost always fail to state temperature thresholds. For example in Canada, Atlantic salmon fishing is governed by the federal government (Fisheries and Oceans Canada), whose 'Angler's Guide' recommends that catch-and-release of Atlantic salmon should cease during 'extreme environmental conditions (low water levels and high water temperatures),' (DFO 2010a). The Atlantic Salmon Federation guide on live-release also recommends avoiding fishing in 'high temperatures,' but also neglects to state how high is too high (Atlantic Salmon Federation 2010). We contend that a specific temperature threshold is imperative to angler compliance, simply because vague recommendations fail to inform anglers, even when they have intentions of using best practices. However, we recognize that such recommendations are challenging given the general paucity of data identified here and our finding that even within species-specific thermal preferenda, capture-release mortality may increase.

Collectively, the studies we reviewed found that temperature stress often contributed significantly to the levels of impairment and mortality of fish released after capture. Very few studies examined the effects of high temperatures that are ecologically meaningful in terms of current peak temperature events in a given habitat or future projections of climate change, as was evident by the lack of supporting context for the experimental temperatures. Our finding that warm temperatures can increase mortality within species-specific optimal temperature ranges demonstrates the importance of evaluating temperature effects in context, in order to improve capture and release research and regulations. Future research should use standardized methodologies to determine how thermal stress interacts with capture stressors. Improved

communication of the ecological context and management implications of research would allow the incorporation of more research findings into the regulatory planning process. Ideally, authors will explicitly compare their results with optimal or preferred temperature ranges for the study species. Because global climate change may result in the capture and release of fish in warming environments, we must attempt to gain greater insight into the synergistic effects of thermal and capture stressors for species that are frequently released from capture. This is especially urgent for species or populations whose numbers are threatened with precipitous declines or extinction. For example, Pacific salmon (anadromous *Oncorhynchus* spp.) are similarly vulnerable to capture-release and warm temperatures as Atlantic salmon, making them excellent candidates for this type of research. To our knowledge, there is a complete lack of peer-reviewed studies combining thermal and capture-release stressors on adult anadromous Pacific salmonids. This paucity exists despite the fact that some populations of Pacific salmon are threatened or endangered and living in environments already affected by climate change (e.g. sockeye (*O. nerka*, Salmonidae) in Washington and British Columbia, and coho (*O. kisutch*, Salmonidae) from California to British Columbia (Brown *et al.* 1994, Gustafson *et al.* 2007)). Further, these species are still highly sought after by fisheries, and climate change projections suggest continuing future warming (Morrison *et al.* 2002, Ferrari *et al.* 2007), making this type of research warranted for these species.

Table 2.1 - All studies included in the current review, listed alphabetically by scientific name of the study species. Symbols indicate studies that included a field component to the research, analysis of mortality, and/or analysis of sublethal impairment metrics are indicated by a symbol in those columns. Temperature range includes the highest and lowest temperatures studied to the nearest °C, (air temperatures in brackets, when measured), but is not suggestive that all temperatures in that range were examined. When no other information is given, means are presented. High temps indicates that authors reported the warmest temperature(s) as high for the species studied. Symbols indicate that warmer temperatures were associated with increased mortality, and/or one or more increased sublethal impairment indices.

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = mortality	Warming = sublethal impairment
Raat <i>et al.</i> (1997)	Effects on growth and survival of retention of rod-caught cyprinids in large keepnets	<i>Abramis brama</i> , <i>Cyprinus carpio</i> , <i>Leuciscus idus</i> , <i>Rutilus rutilus</i> , <i>Scardinius erythrophthalmus</i>		*		12 - 23			
Broadhurst <i>et al.</i> (2009)	Mitigating discard mortality from dusky flathead <i>Platycephalus fuscus</i> gillnets	<i>Acanthopagrus australis</i> , <i>Girella tricuspidata</i> , <i>Platycephalus fuscus</i> , <i>Pseudorhombus arsius</i> , <i>Synaptura nigra</i>	*	*		15 - 18		*	

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = mortality	Warming = ésublethal impairment
Holland-Bartels <i>et al.</i> (1989)	Effects of water temperature on the mortality of field-collected fish marked with fluorescent pigment	<i>Ambloplites rupestris</i> , <i>Lepomis macrochirus</i> , <i>Notropis atherinoides</i> , <i>N. texanus</i> , <i>Perca flavescens</i> , <i>Pomoxis nigromaculatus</i>	*	*		10 - 21		*	
Davis and Parker (2004)	Fish size and exposure to air: potential effects on behavioral impairment and mortality rates in discarded sablefish	<i>Anoplopoma fimbria</i>		*	*	(10 - 18)			
Davis <i>et al.</i> (2001)	Stress induced by hooking, net towing, elevated sea water temperature and air in sablefish: lack of concordance between mortality and physiological measures of stress	<i>Anoplopoma fimbria</i>		*	*	4 - 16		*	*
Lupes <i>et al.</i> (2006)	Capture-related stressors impair immune system function in sablefish	<i>Anoplopoma fimbria</i>			*	10 - 16			
Olla <i>et al.</i> (1998)	Temperature magnified postcapture mortality in adult sablefish after simulated trawling	<i>Anoplopoma fimbria</i>		*	*	4 - 20 (18 - 20)	*	*	*
Rutecki and Meyers (1992)	Mortality of juvenile sablefish captured by hand-jigging and traps	<i>Anoplopoma fimbria</i>	*	*		4 - 9			

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = mortality	Warming = sublethal impairment
Fritz and Johnson (1987)	Survival of freshwater drums released from Lake Erie commercial shore seines	<i>Aplodinotus grunniens</i>	*	*		14 - 20			
Götz <i>et al.</i> (2007)	Comparison of the effects of different linefishing methods on catch composition and capture mortality of South African temperate reef fish	<i>Boobsoidea inornata</i> , <i>Cheimerius nufar</i> , <i>Chrysoblephus cristiceps</i> , <i>C. laticeps</i> , <i>Pachymetopon aeneum</i> , <i>Spondyllosoma emarginatum</i>	*	*		not stated			
Taylor <i>et al.</i> (2001)	Catch-and-release mortality rates of common snook in Florida	<i>Centropomus undecimalis</i>	*	*		22 - 30			
James <i>et al.</i> (2007)	Catch-and-release mortality of spotted seatrout in Texas: effects of tournaments, seasonality, and anatomical hooking location	<i>Cynoscion nebulosus</i>	*	*		16 - 33	*	*	
Murphy <i>et al.</i> (1995)	Mortality of spotted seatrout released from gill-net or hook-and-line gear in Florida	<i>Cynoscion nebulosus</i>	*	*		16 - 31		*	
Alós <i>et al.</i> (2009)	Mortality of <i>Diplodus annularis</i> and <i>Lithognathus mormyrus</i> released by recreational anglers: implications for recreational fisheries management	<i>Diplodus annularis</i> and <i>Lithognathus mormyrus</i>	*	*		14 - 28			

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = émortality	Warming = ésublethal impairment
Storck and Newman (1992)	Contribution of tiger muskellunge to the sport fishery of a small, centrarchid-dominated impoundment	<i>Esox masquinongy</i> <i>x Esox lucius</i>	*	*		22 - 28	*	*	
Milliken <i>et al.</i> (2009)	Survival of discarded sublegal Atlantic cod in the northwest Atlantic demersal longline fishery	<i>Gadus morhua</i>	*	*		<7 - >14	*	*	
Suuronen <i>et al.</i> (2005)	Escape mortality of trawl caught Baltic cod (<i>Gadus morhua</i>) - the effect of water temperature, fish size and codend catch	<i>Gadus morhua</i>	*	*		3 - 19	*	*	
Ross and Hokenson (1997)	Short-term mortality of discarded finfish bycatch in the Gulf of Maine fishery for northern shrimp <i>Pandalus borealis</i>	<i>Glyptocephalus cynoglossus</i> , <i>Hippoglossoides platessoides</i> , <i>Pleuronectes americanus</i> , <i>Pollachius virens</i>	*	*		4 - 18 (6 - 19)	*		
Davis and Olla (2001)	Stress and delayed mortality induced in Pacific halibut by exposure to hooking, net towing, elevated seawater temperature and air: implications for management of bycatch	<i>Hippoglossus stenolepis</i>		*	*	5 - 16	*	*	*
Davis and Schreck (2005)	Responses by Pacific halibut to air exposure: lack of correspondence among plasma constituents and mortality	<i>Hippoglossus stenolepis</i>		*	*	(10 - 16)		*	*

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = émortality	Warming = ésublethal impairment
Gingerich <i>et al.</i> (2007)	Evaluation of the interactive effects of air exposure duration and water temperature on the condition and survival of angled and released fish	<i>Lepomis macrochirus</i>	*	*	*	18 - 27		*	*
Hoxmeier and Wahl (2009)	Factors influencing short-term hooking mortality of bluegills and the implications for restrictive harvest regulations	<i>Lepomis macrochirus</i>	*	*		18 - 35	*		
Muoneke (1992)	Seasonal hooking mortality of bluegills caught on natural baits	<i>Lepomis macrochirus</i>	*	*		17 - 30		*	
Cooke and Hogle (2000)	Effects of retention gear on the injury and short-term mortality of adult smallmouth bass	<i>Micropterus dolomieu</i>	*	*	*	9 - 23		*	*
Schreer <i>et al.</i> (2001)	Cardiac response to variable forced exercise at different temperatures: an angling simulation for smallmouth bass	<i>Micropterus dolomieu</i>			*	12 - 20	*		*
Bennett <i>et al.</i> (1989)	Mortality of tournament-caught largemouth and smallmouth bass in Idaho lakes and reservoirs	<i>Micropterus dolomieu</i> & <i>Micropterus salmoides</i>	*	*		7 - 25		*	
Edwards <i>et al.</i> (2004)	Factors related to mortality of black bass caught during small club tournaments in Connecticut	<i>Micropterus dolomieu</i> & <i>Micropterus salmoides</i>	*	*		12 - 31	*	*	

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = émortality	Warming = ésublethal impairment
Cooke <i>et al.</i> (2004a)	Angling-induced cardiac disturbance of free-swimming largemouth bass (<i>Micropterus salmoides</i>) monitored with heart rate telemetry	<i>Micropterus salmoides</i>	*		*	13 - 25			*
Cooke <i>et al.</i> (2003)	Cardiovascular responses of largemouth bass to exhaustive exercise and brief air exposure over a range of water temperatures	<i>Micropterus salmoides</i>			*	13 - 25			*
Gustaveson <i>et al.</i> (1991)	Physiological responses of largemouth bass to angling stress	<i>Micropterus salmoides</i>	*		*	11 - 30			*
Meals and Miranda (1994)	Size-related mortality of tournament-caught largemouth bass	<i>Micropterus salmoides</i>	*	*		24 - 33		*	
Neal and Lopez-Clayton (2001)	Mortality of largemouth bass during catch-and-release tournaments in a Puerto Rico reservoir	<i>Micropterus salmoides</i>	*	*		23 - 28	*	*	
Plumb <i>et al.</i> (1988)	Survival of caught and released largemouth bass after containment in live wells	<i>Micropterus salmoides</i>		*		10 - 34		*	
Schramm <i>et al.</i> (1985)	Survival of tournament-caught largemouth bass in two Florida lakes	<i>Micropterus salmoides</i>	*	*		12 – 30 (11 - 36)		*	
Schramm <i>et al.</i> (1987)	Evaluation of prerelease, postrelease, and total mortality of largemouth bass caught during tournaments in two Florida lakes	<i>Micropterus salmoides</i>	*	*		17 – 30 (25 - 34)		*	

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = mortality	Warming = sublethal impairment
Suski <i>et al.</i> (2006)	The influence of environmental temperature and oxygen concentration on the recovery of largemouth bass from exercise: implications for live-release angling tournaments	<i>Micropterus salmoides</i>			*	14 - 32	*		*
Thompson <i>et al.</i> (2008)	Physiology, behavior, and survival of angled and air-exposed largemouth bass	<i>Micropterus salmoides</i>	*	*	*	15 - 21			*
Weathers and Newman (1997)	Effects of organizational procedures on mortality of largemouth bass during summer tournaments	<i>Micropterus salmoides</i>	*	*		27 - 33			
Wilde and Pope (2008)	A simple model for predicting survival of angler-caught and released largemouth bass	<i>Micropterus salmoides</i>		*		7 - 27			
Wilde <i>et al.</i> (2002)	Mortality of black bass captured in three fishing tournaments on Lake Amistad, Texas	<i>Micropterus salmoides</i>	*	*		17 - 28		*	
Bettinger <i>et al.</i> (2005)	Hooking mortality and physiological responses of striped bass angled in freshwater and held in live-release tubes	<i>Morone saxatilis</i>	*	*	*	8 - 29	*	*	*
Bettoli and Osborne (1998)	Hooking mortality and behavior of striped bass following catch and release angling	<i>Morone saxatilis</i>	*	*	*	12 - 31 (15 - 31)		*	

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = émortality	Warming = ésublethal impairment
Brick and Cech (2002)	Metabolic responses of juvenile striped bass to exercise and handling stress with various recovery environments	<i>Morone saxatilis</i>		*	*	15 - 25		*	
Dunning <i>et al.</i> (1989)	Reducing mortality of striped bass captured in seines and trawls	<i>Morone saxatilis</i>	*	*		1 - 16		*	
Millard <i>et al.</i> (2005)	Mortality associated with catch-and-release angling of striped bass in the Hudson River	<i>Morone saxatilis</i>	*	*		12 - 18		*	
Nelson (1998)	Catch-and-release mortality of striped bass in the Roanoke River, North Carolina	<i>Morone saxatilis</i>	*	*		16 - 24	*	*	
Thompson <i>et al.</i> (2007)	Seasonal natural and fishing mortality of striped bass in a southeastern reservoir	<i>Morone saxatilis</i>	*	*		not stated		*	
Tomasso <i>et al.</i> (1996)	Physiological responses and mortality of striped bass angled in freshwater	<i>Morone saxatilis</i>		*	*	16 - 32		*	*
Wilde <i>et al.</i> (2000)	Bait and temperature effects on striped bass hooking mortality in freshwater	<i>Morone saxatilis</i>	*	*	*	6 - 31		*	
Hunsaker <i>et al.</i> (1970)	Hooking mortality of Yellowstone cutthroat trout	<i>Oncorhynchus clarkii</i>	*	*		4 - 17		*	
Marnell and Hunsaker (1970)	Hooking mortality of lure-caught cutthroat trout (<i>Salmo clarki</i>) in relation to water temperature, fatigue, and reproductive maturity of released fish	<i>Oncorhynchus clarkii</i>	*	*		3 - 17			

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = émortality	Warming = ésublethal impairment
Strange <i>et al.</i> (1977)	Corticoid stress responses to handling and temperature in salmonids	<i>Oncorhynchus clarkii</i>			*	9 - 23			
Dotson (1982)	Mortalities in trout caused by gear type and angler-induced stress	<i>Oncorhynchus mykiss</i>		*		8 - 16		*	
Kieffer <i>et al.</i> (1994)	Effects of environmental temperature on the metabolic and acid-base responses of rainbow trout to exhaustive exercise	<i>Oncorhynchus mykiss</i>			*	5 - 18			*
Klein (1965)	Mortality of rainbow trout caught on single and treble hooks and released	<i>Oncorhynchus mykiss</i>		*		7 - 14		*	
Meka and McCormick (2005)	Physiological response of wild rainbow trout to angling: impact of angling duration, fish size, body condition, and temperature	<i>Oncorhynchus mykiss</i>	*		*	7 - 17			*
Schisler and Bergersen (1996)	Postrelease hooking mortality of rainbow trout caught on scented artificial baits	<i>Oncorhynchus mykiss</i>	*	*	*	4 - 17		*	*
Simpkins <i>et al.</i> (2004)	Factors affecting swimming performance of fasted rainbow trout with implications of exhaustive exercise on overwinter mortality	<i>Oncorhynchus mykiss</i>		*		4 - 15		*	
Wydoski <i>et al.</i> (1976)	Physiological response to hooking stress in hatchery and wild rainbow trout (<i>Salmo gairdneri</i>)	<i>Oncorhynchus mykiss</i>	*		*	4 - 20			*

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = émortality	Warming = ésublethal impairment
Davis and Olla (2002)	Mortality of lingcod towed in a net as related to fish length, seawater temperature, and air exposure: a laboratory bycatch study	<i>Ophiodon elongatus</i>		*		8 - 20		*	
Bettoli and Scholten (2006)	Bycatch rates and initial mortality of paddlefish in a commercial gillnet fishery	<i>Polyodon spathula</i>	*	*		4 - 29		*	
Dieterman <i>et al.</i> (2000)	Mortality of paddlefish in hoop nets in the lower Missouri River, Missouri	<i>Polyodon spathula</i>	*	*		16 - 25			
Dalla Via <i>et al.</i> (1989)	Temperature-related responses of intermediary metabolism to forced exercise and recovery in juvenile <i>Rutilus rutilus</i> (L.) (Cyprinidae: Teleostei)	<i>Rutilus rutilus</i>			*	4 - 20			*
Pottinger <i>et al.</i> (1999)	Plasma cortisol and 17B-oestradiol levels in roach exposed to acute and chronic stress	<i>Rutilus rutilus</i>			*	5 - 16			*
Anderson <i>et al.</i> (1998)	Remote monitoring of heart rate as a measure of recovery in angled Atlantic salmon, <i>Salmo salar</i> (L.)	<i>Salmo salar</i>		*	*	8 - 20		*	*
Dempson <i>et al.</i> (2002)	Effects of catch and release angling on Atlantic salmon, <i>Salmo salar</i> L., of the Conne River, Newfoundland	<i>Salmo salar</i>	*	*		12 - 25	*	*	

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = émortality	Warming = ésublethal impairment
Galloway and Kieffer (2003)	The effects of an acute temperature change on the metabolic recovery from exhaustive exercise in juvenile Atlantic salmon (<i>Salmo salar</i>)	<i>Salmo salar</i>			*	6 - 18			
Thorstad <i>et al.</i> (2003)	Effects of hook and release on Atlantic salmon in the River Alta, northern Norway	<i>Salmo salar</i>	*	*	*	10 - 14			*
Wilkie <i>et al.</i> (1997)	Influences of temperature upon the postexercise physiology of Atlantic salmon (<i>Salmo salar</i>)	<i>Salmo salar</i>		*	*	12 - 23	*	*	
Wilkie <i>et al.</i> (1996)	Physiology and survival of wild Atlantic salmon following angling in warm summer waters	<i>Salmo salar</i>	*	*	*	6 - 22	*	*	*
Jurvelius <i>et al.</i> (2000)	Mortality of pike-perch (<i>Stizostedion lucioperca</i>), brown trout (<i>Salmo trutta</i>) and landlocked salmon (<i>Salmo salar</i> m. <i>sebago</i>) caught as by-catch in pelagic trawling in a Finnish lake	<i>Salmo salar</i> , <i>Salmo trutta</i> , <i>Sander lucioperca</i>	*	*		10 - 18			
Hyvärinen <i>et al.</i> (2004)	Effects of abrupt cold shock on stress responses and recovery in brown trout exhausted by swimming	<i>Salmo trutta</i>		*	*	0 - 14			
Jepsen <i>et al.</i> (2008)	The level of predation used as an indicator of tagging/handling effects	<i>Salmo trutta</i>		*	*	8 - 14			*
Turunen <i>et al.</i> (1994)	Trawling stress and mortality in undersized (< 40 cm) brown trout (<i>Salmo trutta</i> L.)	<i>Salmo trutta</i>	*	*	*	10 - 20	*		*

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = émortality	Warming = ésublethal impairment
Nuhfer and Alexander (1992)	Hooking mortality of trophy-sized wild brook trout caught on artificial lures	<i>Salvelinus fontinalis</i>	*	*		6 - 18		*	
Lee and Bergersen (1996)	Influence of thermal and oxygen stratification on lake trout hooking mortality	<i>Salvelinus namaycush</i>	*	*		8 - 13	*	*	
Loftus <i>et al.</i> (1988)	An evaluation of lake trout (<i>Salvelinus namaycush</i>) hooking mortality in the Upper Great Lakes	<i>Salvelinus namaycush</i>	*	*		4 - 24			
Hoffman <i>et al.</i> (1996)	Walleye and sauger mortality associated with live-release tournaments on the Lake Winnebago system, Wisconsin	<i>Sander canadensis</i> , <i>Sander vitreus</i>	*	*		24 - 27		*	
Hyvärinen <i>et al.</i> (2008)	Stress and survival of small pike-perch <i>Sander lucioperca</i> (L.) after trawling and chilling	<i>Sander lucioperca</i>	*	*	*	0 - 21		*	*
Reeves and Bruesewitz (2007)	Factors influencing the hooking mortality of walleyes caught by recreational anglers on Mille Lacs, Minnesota	<i>Sander vitreus</i>	*	*		10 - 26		*	
Marçalo <i>et al.</i> (2008)	Sardine early survival, physical condition and stress after introduction to captivity	<i>Sardina pilchardus</i>		*	*	14 - 26	*	*	

Reference	Article Title	Species	Field	Mortality	Sublethal Impairment	Temp range (°C)	High temps	Warming = mortality	Warming = sublethal impairment
Alós (2008)	Influence of anatomical hooking depth, capture depth, and venting on mortality of painted comber (<i>Serranus scriba</i>) released by recreational anglers	<i>Serranus scriba</i>	*	*		16 - 26			
Alós (2009)	Mortality impact of recreational angling techniques and hook types on <i>Trachynotus ovatus</i> (Linnaeus, 1758) following catch-and-release	<i>Trachynotus ovatus</i>	*	*		17 - 25			

Table 2.2 - Summary of variables queried of each study, response classes, and the number of studies that fell into each class. Note that classes are not mutually exclusive, i.e. one article may fall into more than one class per variable. See Methods section for more details on classifications.

Variable	Class	# studies
Journal	North American Journal of Fisheries Management	37
	Transactions of the American Fisheries Society	17
	Journal of Fish Biology	12
	Aquaculture	10
	Fisheries Research	8
	Comparative Biochemistry and Physiology A	4
	Fisheries Management and Ecology	4
	North American Journal of Aquaculture/PFC	3
	Canadian Journal of Fisheries and Aquatic Sciences	2
	Journal of Applied Ichthyology	2
	African Journal of Marine Science	1
	Black Bass: Ecology, Conservation and Management	1
	California Fish and Game	1
	Diseases of Aquatic Organisms	1
	Environmental Biology of Fishes	1
	General and Comparative Endocrinology	1
	Hydrobiologia	1
	ICES Journal of Marine Science	1
	Journal of Evolutionary Biochemistry and Physiology	1
	Journal of Experimental Biology	1
	Journal of Freshwater Ecology	1
	Journal of the World Aquaculture Society	1
	Marine and Freshwater Behavior and Physiology	1
	Physiological Zoology	1
	Physiological and Biochemical Zoology	1
	Texas Journal of Science	1
Order	Perciformes	52
	Salmoniformes	33
	Scorpaeniformes	7
	Cypriniformes	5
	Pleuronectiformes	5
	Gadiformes	4
	Acipenseriformes	3
	Esociformes	3
	Siluriformes	3
	Clupeiformes	2

Variable	Class	# studies
Order cont'd	Gonorynchiformes	1
	Osmeriformes	1
Continent	North America	82
	Europe	27
	Asia	4
	Africa	1
	Australia	1
Environment	Freshwater	84
	Marine	28
	Both	1
	Estuary	2
Experiment	Lab	58
	Field	50
	Both	7
Sector	Recreational	56
	Aquaculture	28
	Commercial	25
	Science	14
Experimental Setup	Holding tanks	57
	Temporary holding tank (lakeside or boat)	42
	Free-swimming - field	16
	Large experimental pond	6
	Black box	3
Stressor	Capture	75
	Handling	19
	Confinement	10
	Transport	8
	Exercise	8
	Tagging / sampling	5
	Air	3
	Disturbance	1
Mortality Assessment	Visual	80
	Mark-recapture	2
	Telemetry	6
	Survival not assessed	29
Physiological Measures	Stress & Exercise physiology	54
	Osmoregulatory physiology	18
	Injury	13
Capture type	Hook / line (includes longline)	55
	None	36
	Trawl	12
	Manual Chase	5

Variable	Class	# studies
Capture type cont'd	Purse seine	4
	Gill net	3
	Dip net	2
	Traps	2
	Beach seine	1
	Electrofishing	1
	Hoop net	1
	Tangle net	0
Species Temperature Context	None	65
	High	22
	Normal	17
	Low	6

Table 2.3 - Comparison of the preferred temperature for growth and/or optimal temperature from the literature with the temperature at which mortality began increasing within a given experiment.

a optimal temperature for growth, b preferred temperature, c optimal temperature for feeding

Species	Optimal / Preferred Temp (°C)	Temp Mortality Increased (°C)	Optimal Temp Reference	Capture / Temp Reference
<i>Anaplopoma fimbria</i> Sablefish	14 - 22 ^a 12 - 15 ^b	14 no temp effect (10 - 18 air) 15 no temp effect (4 - 9)	Sogard and Olla (2001)	Davis <i>et al.</i> (2001) Davis and Parker (2004) Olla <i>et al.</i> (1998) Rutecki and Meyers (1992)
<i>Cynoscion nebulosis</i> Spotted seatrout	28 ^a	27 28	Wohlschlag and Wakeman (1978) Kupschus (2003)	James <i>et al.</i> (2007) Murphy <i>et al.</i> (1995)
<i>Gadus morhua</i> Atlantic cod	7 ^a 13 - 15 ^a 10 - 11 ^a	9 - 14 10	Björnsson <i>et al.</i> (2001) Jobling (1983) Pörtner <i>et al.</i> (2001)	Milliken <i>et al.</i> (2009) Suuronen <i>et al.</i> (2005)
<i>Hippoglossus stenolepus</i> Pacific halibut	10 ^a 3 - 8 ^b	16 16 (air temp)	Björnsson and Tryggvadóttir (1996) Commission (1998)	Davis and Olla (2001) Davis and Schreck (2005)
<i>Lepomis macrochirus</i> Bluegill	27 - 35 ^b	30 27 no temp effect (18 - 35)	Kieffer and Cooke (2009)	Muoneke (1992) Gingerich <i>et al.</i> (2007) Hoxmeier and Wahl (2009)
<i>Micropterus dolomieu</i> Smallmouth bass	30 ^b 28.5 - 32 ^b	21 (one tournament only) 22 20 - 25	Barans and Tubb (1973) Kieffer and Cooke (2009)	Bennett <i>et al.</i> (1989) Cooke and Hogle (2000) Edwards <i>et al.</i> (2004)

Species	Optimal / Preferred Temp (°C)	Temp Mortality Increased (°C)	Optimal Temp Reference	Capture / Temp Reference
<i>Micropterus salmoides</i> Largemouth bass	27 - 30 ^b 29 - 33 ^b	27 23 28 26.5 31 21 <30 no temp effect (15 - 21) no temp effect (27 - 33) 26 no temp effect (7 - 27)	Clugston (1973) Kieffer and Cooke (2009)	Edwards <i>et al.</i> (2004) Bennett <i>et al.</i> (1989) Meals and Miranda (1994) Neal and Lopez-Clayton (2001) Plumb <i>et al.</i> (1988) Schramm <i>et al.</i> (1985) Schramm <i>et al.</i> (1987) Thompson <i>et al.</i> (2008) Weathers and Newman (1997) Wilde <i>et al.</i> (2002) Wilde and Pope (2008)
<i>Morone saxatilis</i> Striped bass	19 - 23 ^b 24 ^a	28 28 25 (in buffered water only) 12 - 16 16 21 27 - 29 26 26	Coutant (1990) Cox and Coutant (1981)	Bettinger <i>et al.</i> (2005) Bettoli and Osborne (1998) Brick and Cech (2002) Dunning <i>et al.</i> (1989) Millard <i>et al.</i> (2005) Nelson (1998) Thompson <i>et al.</i> (2007) Tomasso <i>et al.</i> (1996) Wilde <i>et al.</i> (2000)
<i>Oncorhynchus clarkii</i> Cutthroat trout	13 - 15 ^b	14 - 17 no temp effect (3 - 17)	McMahon <i>et al.</i> (2006)	Hunsaker <i>et al.</i> (1970) Marnell and Hunsaker (1970)
<i>Oncorhynchus mykiss</i> Rainbow trout	14 - 15 ^a 11 ^b 13 - 15 ^b	9 - 11 14 13 15	Barnabé (1994) McCauley <i>et al.</i> (1977) McMahon <i>et al.</i> (2006)	Dotson (1982) Klein (1965) Schisler and Bergersen (1996) Simpkins <i>et al.</i> (2004)

Species	Optimal / Preferred Temp (°C)	Temp Mortality Increased (°C)	Optimal Temp Reference	Capture / Temp Reference
<i>Polyodon spathula</i> Paddlefish	12 - 24 ^b 24 - 29 ^b 7 - 20 ^c	18 no temp effect (16 - 25)	Crance (1987) Paukert and Fisher (2000) Rosen and Hales (1981)	Bettoli and Scholten (2006) Dieterman <i>et al.</i> (2000)
<i>Salmo salar</i> Atlantic salmon	15 ^a 16 ^a 14 ^b	20 14 - 18 no temp effect (10 - 14) 20 23	Barnabé (1994) Elliott and Hurley (1997) Peterson and Metcalfe (1979)	Anderson <i>et al.</i> (1998) Dempson <i>et al.</i> (2002) Thorstad <i>et al.</i> (2003) Wilkie <i>et al.</i> (1996) Wilkie <i>et al.</i> (1997)
<i>Salmo trutta</i> Brown trout	12 - 14 ^a 16 ^b	no temp effect (0 - 14) no temp effect (10 - 20)	Barnabé (1994) Spigarelli <i>et al.</i> (1983)	Hyvärinen <i>et al.</i> (2004) Turunen <i>et al.</i> (1994)
<i>Sander lucioperca</i> Pike-perch	28 - 30 ^{a,b} 12 - 30 ^a	16 no temp effect (10 - 18)	Hokanson (1977) Lehtonen (1996)	Hyvärinen <i>et al.</i> (2008) Jurvelius <i>et al.</i> (2000)
<i>Sander vitreus</i> Walleye	21 - 23 ^b 22 - 28 ^a	25 18	Coutant (1977) Hokanson and Koenst 1986	Hoffman <i>et al.</i> (1996) Reeves and Bruesewitz (2007)

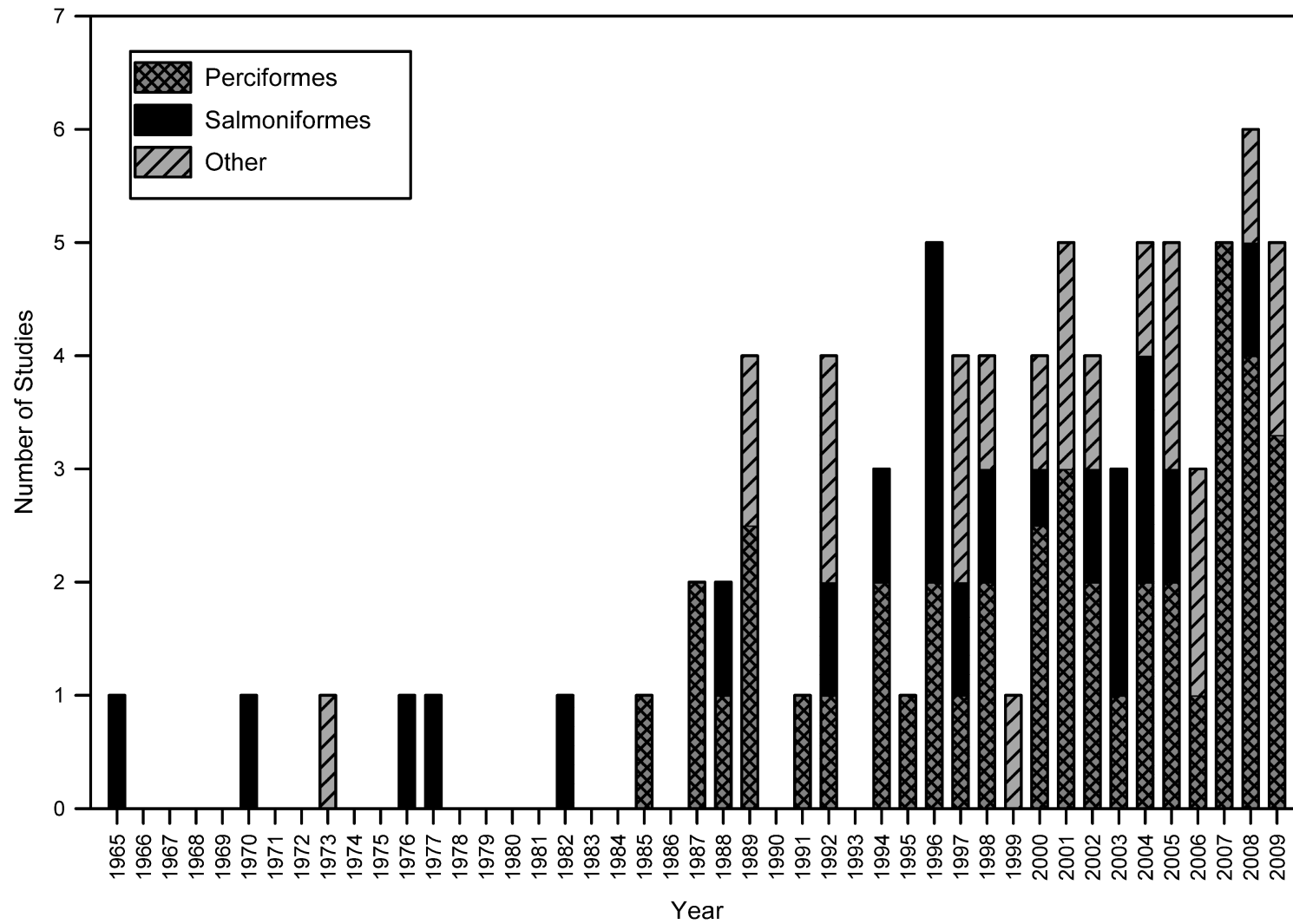


Figure 2.1 - Number of publications by year, with shading indicating taxonomic order.

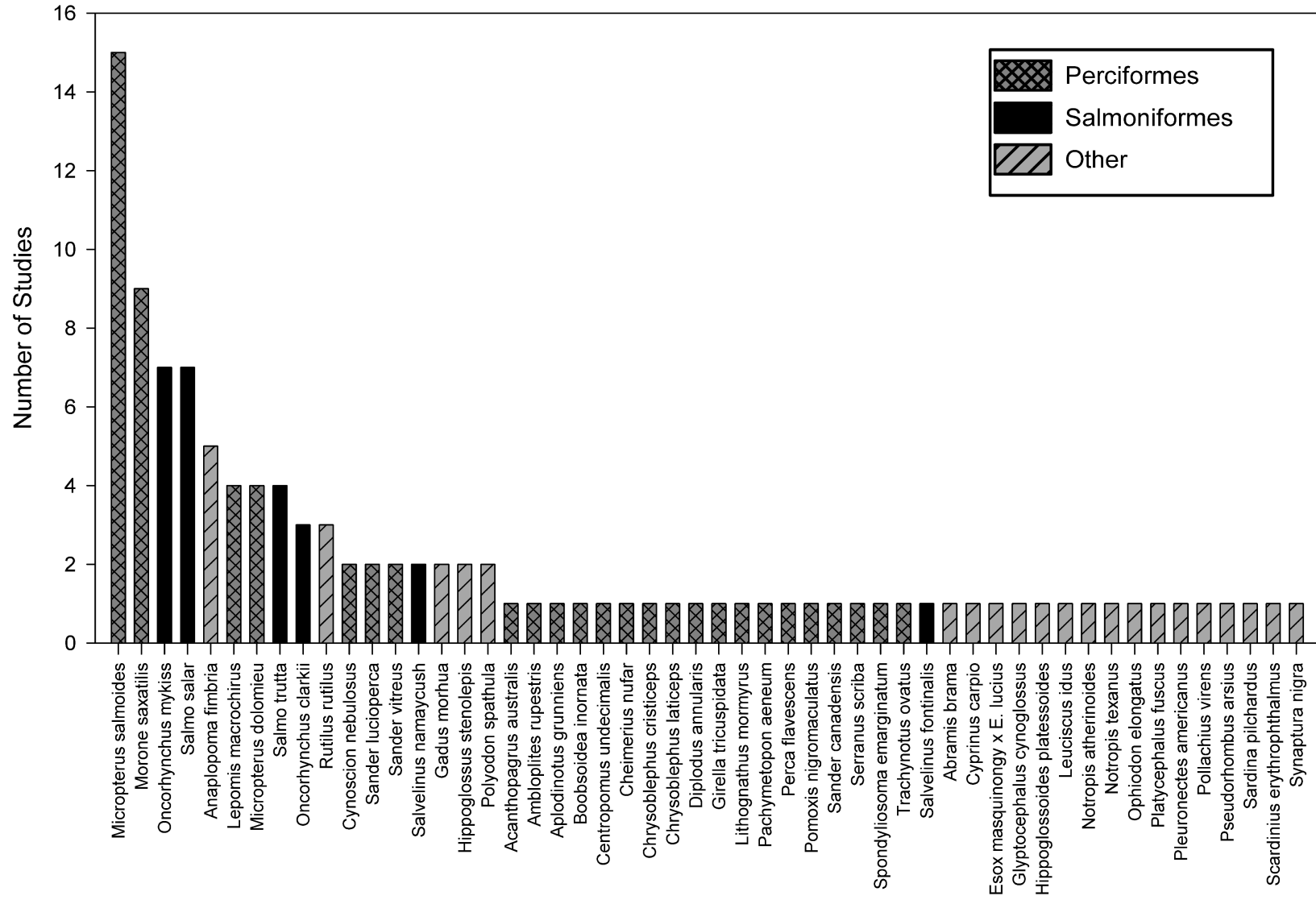


Figure 2.2 - Number of publications by species, with shading indicating taxonomic order.

Chapter 3: Physiological impairment of adult sockeye salmon in fresh water after simulated capture-and-release across a range of temperatures²

3.1 Introduction

Fisheries management agencies frequently impose harvest regulations (e.g., gear selection, bag limits, closed seasons for some species) that require the release of non-target species (i.e., bycatch) in both commercial and recreational fisheries. In the recreational sector, some fish are also released voluntarily due to a conservation ethic among anglers (Arlinghaus et al. 2007). A major assumption involved with capture and release fishing, irrespective of the sector, is that released fish do not have significantly reduced survival or fitness relative to conspecifics that are not exposed to the same stressors (Wydoski et al. 1976, Cooke and Schramm 2007). Although there are a number of inherent differences between commercial and recreational fisheries, fish are exposed to stress and injury in both sectors, with the potential for mortality during the process. Studies have examined the effects of capture and release on immediate, short-term, and delayed mortality of various species and they have found that the survival of released fish can range from zero to almost 100% (Alverson et al. 1994, Muoneke and Childress 1994, Davis 2002, Bartholomew and Bohnsack 2005, Cooke and Suski 2005, Arlinghaus et al. 2007). In these examples, survival was dependent upon species, anatomical hooking location, capture depth, hook, bait, gear types, air exposure, life history stage and/or size, and handling. Mortality arising from capture and release is often not incorporated into management models, which can impede the ability of management agencies to develop sustainable fishing practices (Coggins Jr.

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et al. 2007). In addition, considerable research has examined the specific influence of water temperature on post-release survival of fish (Wilkie *et al.* 1996, Wilkie *et al.* 1997, Davis 2002, Cooke and Suski 2005). Results of this research have been used to develop some general guidelines adopted by management agencies, such as recommending avoiding catch-and-release fishing or reducing air exposure during high temperatures (e.g. DFO 2010a, Atlantic Salmon Federation 2010). However, these guidelines often provide vague or even contradictory advice when it comes to catch-and-release best practices (for example with regard to air exposure and resuscitation; Pelletier *et al.* 2007). It is known that fish have adapted to and depend upon the thermal environment in which they live (Pörtner 2002), and that temperatures exceeding an optimal range can cause impairment of physiological processes and decreased survival (Brett *et al.* 1958, Elliot 1981, Eliason *et al.* 2011). The degree to which the optimal thermal range may narrow when fish experience capture and thermal stress simultaneously remains to be understood.

In British Columbia, sockeye salmon (*Oncorhynchus nerka*) are the most commercially valuable Pacific salmon species (DFO 2011b) and are highly valued by anglers and First Nations (aboriginal) fishers. Owing to an abundant return in 2010, approximately 13 million Fraser River sockeye salmon were caught in commercial seine, troll, and gill-net fisheries (DFO 2011a), and an additional 1.4 million were caught in First Nations gill-net and seine fisheries (DFO 2010b). Both sectors fish primarily where sockeye salmon are approaching, and then transitioning to, fresh water from the Pacific Ocean. The recreational fishery for sockeye salmon in the Fraser River is focused mainly in the lower Fraser River and has grown from being almost non-existent a decade ago (between 1984 and 1990, a total of 370 sockeye were caught by anglers) to a catch of 190 000 (2002), 155 000 (2006) and 300 000 (2010) in dominant cycle years (DFO 2010c). Temporal closures of the sockeye fisheries and catch limits are

implemented to protect threatened stocks and ensure adequate escapement to spawning grounds, forcing the periodic release of captured sockeye salmon. For example, anglers released one third of captured sockeye salmon (100 000 fish) in 2010 in the Fraser River, and on average released 21 000 fish per year in the previous four years (DFO 2010c). There are no direct estimates of how many sockeye salmon escape from different gear types but fail to complete their migration. However, a recent study in Alaska (Baker and Schindler 2009) and a report on Fraser River sockeye salmon (Clarke *et al.* 1994) demonstrate up to 50% of spawning adults had characteristic net mark scars on their bodies. The authors also found that Alaskan sockeye salmon with moderate to severe gillnet injuries were far less likely to successfully enter natal streams than non-injured fish (Baker and Schindler 2009).

A recent review of 83 studies, involving an examination of capture-release and thermal stress (Gale *et al.* 2011a), found that the majority detected deleterious physiological and survival consequences of warm temperatures on released fish. However, more than half failed to put the study temperatures into an ecologically or biologically meaningful context. For most species, there exists little or no data on the consequences of capture and release at ecologically relevant high temperatures. This is true for all Pacific salmon species (*Oncorhynchus* spp.), and perhaps most notably for sockeye salmon, which are well-studied in regards to temperature tolerance (Brett 1971, Cooke *et al.* 2004b, Crossin *et al.* 2008, Farrell *et al.* 2008, Eliason *et al.* 2011) yet there is little known about how temperature affects survival of released sockeye following capture.

Summer water temperatures in the Fraser River have increased by $\sim 2^{\circ}\text{C}$ over the last 60 years (Patterson *et al.* 2007) with 13 of the past 20 years being the warmest on record. Extremely high levels of migration mortality ($> 90\%$ in some populations) have been attributed to high

temperatures in Fraser River sockeye salmon (Cooke *et al.* 2004b, Farrell *et al.* 2008, Martins *et al.* 2011), and are presumed to result from factors including energy exhaustion, collapse of aerobic and cardiac scope, physiological stress, diseases and parasites (Rand and Hinch 1998, Farrell *et al.* 2008, Mathes *et al.* 2010, Eliason *et al.* 2011). Fisheries gear interactions occur as a stressor overlaid on the inherent migration challenges, and consist of burst swimming behaviour in attempt to escape, injury from gear entanglement/hooking, and often air exposure during handling and release. Given that Fraser River sockeye salmon are experiencing temperatures in freshwater that can affect migration survivorship, and that capture and release (or capture and escape) is frequently occurring, there is a pressing need to examine the how temperature and capture-related stressors may interact to influence the survival and physiological responses of fish, particularly Pacific salmon.

The objective of this study was to use sockeye salmon to investigate the interactions between temperature and capture-related stressors and their consequences for post-release blood physiology and survival. To that end, Fraser River sockeye were exposed to three different simulated capture-related stressors - no applied capture stressor, simulated capture, or simulated capture including air exposure - under a range of water temperatures. They were then assessed for the magnitude of physiological impairments using plasma metabolite, ion, and hormone concentrations. Water temperatures reflected a natural range that this run has historically encountered, including temperatures both cooler (13°C) and warmer (19°C) than the window for maximum aerobic scope (Fry 1971, Farrell *et al.* 2008), as well as a high temperature (21°C) that is approaching the critical thermal limit for this group of fish (Farrell *et al.* 2008, Eliason *et al.* 2011). Capture stressors were intended to simulate the flight response and exhaustive exercise, with or without air exposure, that might be experienced by a sockeye salmon caught in a net or on a hook. We hypothesized that the capture stressor coupling exhaustive exercise with

air exposure would cause the highest physiological impairments, and that these effects would be most severe at the highest temperature.

3.2 Methods

3.2.1 Study site and animals

Capture of study animals took place on August 11-12, 2009 in the main-stem of the Fraser River in Chilliwack, British Columbia (Fig. 3.1). Fraser River sockeye salmon are managed as four consecutive “run-timing” groups based on the timing of entry to the Fraser River: early Stuart, early summer, summer-run, and late-run. Adult summer-run sockeye salmon were intercepted soon after they departed the ocean and commenced their freshwater spawning migration towards natal streams. River temperature at this time was measured at approximately $18 \pm 1^\circ\text{C}$. Sockeye salmon were captured using a beach seine deployed from a small boat and pulled close to shore, to allow dip-netting of individual fish into truck-mounted transport tanks. In total, 101 fish were transported approximately 26 kilometers in cool ($\sim 11^\circ\text{C}$) water to the Fisheries and Oceans Canada (DFO) Cultus Lake Salmon Research Laboratory (CLL), where all experiments took place. Dissolved oxygen was monitored continuously throughout transport, and was maintained above 80% by transporting fish in cool water and the diffusion of oxygen from truck-mounted cylinders.

After arrival at the CLL facility, Passive Integrated Transponder (PIT) tags (approximately 8.5 mm x 2 mm size, 134.2 kHz, Biomark Inc., Boise, Idaho) were injected into the coelomic cavity for individual identification and fish were randomly placed into one of nine circular 1400 l aquaria (2 m diameter, maximum 13 fish tank⁻¹, or $\sim 0.028 \text{ kg l}^{-1}$). Aquaria (holding tanks) were supplied with filtered and UV sterilized fresh water ($\sim 40 \text{ l min}^{-1}$; LS-Permabead Filtration System, Integrated Aqua Systems Inc., Escondido, California) from Cultus Lake. All aquaria

were $13^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$ at fish arrival, and were maintained at this temperature for 24 hours to allow fish to recover from the stress of transport. Tank temperatures were monitored carefully in real time (checked at least every 30 minutes during temperature ramp-up periods and every hour between 0700 hrs and 0100 hrs at all other times during the experimental period), and later confirmed using data collected using iButton temperature data loggers (Maxim Integrated Products, Inc., Sunnyvale, California).

3.2.2 Thermal and simulated capture treatments

Summer-run fish can encounter migration temperatures through the lower Fraser River which can range from $< 13^{\circ}\text{C}$ to $> 21^{\circ}\text{C}$ (Patterson *et al.* 2007). We selected temperatures for our experiments that spanned this range. The temperatures of three tanks were maintained at $13 \pm 0.2^{\circ}\text{C}$ while the temperatures of the other six tanks were slowly ($< 1^{\circ}\text{C hr}^{-1}$) ramped up to treatment temperatures of $19 \pm 0.2^{\circ}\text{C}$ (3 tanks) and $21 \pm 0.2^{\circ}\text{C}$ (3 tanks), where they remained until the end of the experiment. Due to logistical constraints, we elected to expose fish to an equal rate of temperature increase at the cost of equal lengths of temperature exposure before capture treatments in order to reduce mortality due to excessively rapid warming. Therefore, after 12 hours (in the case of 21°C treatments) to 24 hours (in the case of 13°C treatments), fish were individually netted into a doughnut shaped aquaria (2 m diameter, 2 fish per tank) at temperatures equal to that of their holding tanks, scanned for PIT tag numbers, and their ventilation rates were counted by observing opercular beats for 30 seconds. Fish were randomly assigned one of three simulated capture treatments: 1) “handling only”, which included handling, transfer, and monitoring in an identical fashion to fish exposed to the other treatments, only the chase, exercise and air exposure protocols were omitted, 2) “capture”, which included three minutes of manual chasing, eliciting a flight response and exhaustive exercise, or 3)

“capture plus air exposure,” which included “capture” immediately followed by one minute air exposure. Fish were stimulated to exercise by four experimenters, who leaned over the perimeter of the tank and touched the tails of the fish or splashed vigorously behind them. Fish were stimulated each time they stopped burst swimming in order to elicit the maximum anaerobic exercise possible using this method, a common approach in studies of fish responses to exercise (Milligan 1996, Kieffer 2000). Air exposure was achieved by rapidly dip netting the individual fish immediately after the three minute exercise had elapsed, and elevating it in the net just above the surface of the water for 60 seconds. Immediately after the assigned treatment, ventilation rates were counted for 30 seconds and observable impairments such as the inability to maintain dorso-ventral equilibrium were recorded for presence/absence and duration. Fish were continuously visually monitored for 25 minutes after the cessation of treatments. Midway through this monitoring period, fish were moved to smaller (100 l, 1 x 0.5 x 0.3 m) individual holding tanks with fresh flowing water until 30 minutes had elapsed fish since were transferred to the initial treatment tanks. For logistic purposes, fish were subjected to treatments in pairs; treatments for a pair of fish occurred in the same tank at the same time, however each fish was netted, moved, handled, exercised, air-exposed, and sampled individually and simultaneously. All procedures and fish care were approved by the Canadian Council on Animal Care (#A08-0388).

3.2.3 Blood sampling, processing and analysis

Thirty minutes after the fish entered the initial treatment tank (onset of stressor), they were moved to a flow-through, foam-lined v-shaped trough, where they were sampled for blood by holding them in a supine position. This sampling time allowed both the detection of elevation of stress indices in the blood, and logistically allowed for the inclusion of 101 individuals over 2

days. The anterior end of their body was kept completely underwater to allow for normal respiratory gas exchange. Three milliliters of blood was collected via caudal venipuncture using a heparinized Vacutainer (Becton, Dickinson and Company - Canada, Mississauga, Ontario), and stored in an ice-slurry until subsequent processing (< 45 mins). This technique took less than one minute to complete, and is a component of a suite of biopsies and sampling techniques used in several past studies involving adult sockeye salmon and have been shown to have negligible effects on fish health and behaviour (Cooke *et al.* 2005).

After blood samples were collected, fish were moved to large (~7000 l, 3 m diameter) circular aquaria supplied with fresh water in the same manner as the smaller aquaria described above. Fish were monitored carefully for morbidity by observing their behaviour and physical condition every 5 minutes for at least 2 hours after blood samples were collected. Thereafter they were observed at least once per hour between 0700 and 0100 hours until the end of the experiment at approximately 72 hours. Fish were judged to be moribund if they exhibited permanent loss of equilibrium or if they became unable to swim, but were still ventilating. Fish that ceased ventilating completely were deemed dead. Moribund and dead fish, as well as fish surviving to the end of the experiment, were removed immediately from the tank by dip net with minimum disruption to the remaining fish, and both moribund fish and those surviving to the end (i.e., 72 hrs post treatment) were euthanized by cerebral concussion. This 72 hr period enabled us to evaluate short-term mortality (frequently regarded as 2 to 3 days post release; Arlinghaus *et al.* 2007), and also provided the opportunity to assess physiological recovery at a standardized time-point. Fish were then immediately sampled for blood in the same manner as the initial sample collection; if more than 10-15 minutes had elapsed since death, fish were not sampled. A small (5 mm) piece of adipose fin tissue was removed to identify individuals to stock (Beacham *et al.* 2004, Beacham *et al.* 2005). For each fish we recorded time of death, sex,

post-orbital-hypural (POH) length, girth (at the fattest point of the fish), somatic fat content (using a handheld microwave fat meter, Distell Fish Fatmeter FM 692, Distell.com Inc., West Lotham, UK; following the protocol and conversion equation described in Crossin and Hinch (2005)), and whole body mass. Morphometric and energetic measures were recorded so that physiological results could not be attributable to differential size or energy status between treatment groups.

3.2.4 Assays

Whole blood was centrifuged at 7 000 g for 6 minutes and plasma was stored at -80°C until further analysis. Plasma was subsequently analyzed for cortisol, testosterone and 17 β -estradiol (Neogen ELISA with Molecular Devices Spectramax 240pc plate reader), lactate, glucose (YSI 2300 Stat Plus analyzer), osmolality (Advanced Instruments 3320 freezing-point osmometer), chloride (Haake Buchler digital chloridometer), sodium, and potassium (Cole-Parmer, model 410 single-channel flame photometer) in the manner described in Farrell *et al.* (2001a).

3.2.5 Statistical analysis

In order to test for an effect of fish sex on physiological responses to treatments, each were analyzed using three-way Analysis of Variance (ANOVA) with interactions to assess the joint effects of sex, capture treatment, and temperature. In cases where sex had no effect we removed it from the analysis and used two-way ANOVA on each variable, and where sex was determined to be a significant effect we separated the genders and used 2-way ANOVA on each separately to determine the effect of capture treatment and temperature. Where statistical differences were detected between capture treatment or temperature groups, Welch's t-tests were performed post-hoc to determine the nature of those differences. Pearson's Chi-square tests were used to detect effects of capture treatment or temperature on the frequency of equilibrium loss after treatment

and mortality prior to the termination of the experiment. Significance levels were set at 0.05. We present the p-values for individual tests and indicate significance using False Detection Rate (Curran-Everett 2000) to correct for multiple comparisons. All tests were performed using R statistical software (R Foundation for Statistical Computing, Vienna, Austria). Data were \log_{10} -transformed if they failed to meet statistical assumptions of normality and equal variance. Prior to other analyses, treatment and temperature groups were checked for differences in size (length, mass) or energy status using two-way ANOVA.

3.3 Results

All 101 sockeye were confirmed to be from the summer run-timing group of stocks, primarily from the Late Stuart/Stellako, Chilko, and Quesnel stocks. There were no morphological or energetic differences between fish in different temperature or capture treatment groups (ANOVA: $p > 0.05$).

3.3.1 Immediate responses to treatment

All fish appeared exhausted before the end of the three-minute exercise component of simulated capture, and were barely responsive to tactile or visual stimuli (no longer bursting away from experimenters hands). Most fish rested on the bottom of the tank or drifted in the current following cessation of treatment, while non-exercised fish generally held position in the current or moved around the tank. Capture treatment had a significant effect on the frequency of equilibrium loss (Pearson's Chi-square: $\chi^2 = 61$, d.f. = 2, $p < 0.0001$), while the effect of temperature was significant only before correction for multiple comparisons (Pearson's Chi-square: $\chi^2 = 6.3$, d.f. = 2, $p = 0.042$). All 23 fish in the 19°C and 21°C air-exposed groups, as compared to five (42%) of the cool-temperature air-exposed fish lost equilibrium after application of the capture-stressor. The duration of equilibrium loss was longer (19 - 98

seconds) for the 19°C and 21°C fish, than for the 13°C fish (5 - 23 seconds; Fig. 3.2). Only two (3%) fish that were not air-exposed demonstrated a loss of equilibrium after treatment (duration of equilibrium loss showed a significant temperature*capture treatment interaction, ANOVA: $F_{4,92} = 21.46$, $p < 0.0001$). Ventilation rates measured before exercise treatments were lower in 13°C fish compared to fish in 19°C or 21°C (ANOVA: $F_{2,92} = 11.6$, $p < 0.0001$), whereas immediately after exercise treatment, ventilation rates were depressed in 21°C air-exposed fish (Fig. 3.2; significant temperature*treatment interaction (ANOVA: $F_{4,92} = 2.9$, $p = 0.027$).

3.3.2 Post-capture samples – 30 minutes post-treatment

Capture treatment had a significant effect on sodium (ANOVA: $F_{2,92} = 19.0$, $p < 0.0001$), potassium (ANOVA: $F_{2,92} = 7.0$, $p = 0.0015$), lactate (ANOVA: $F_{2,92} = 38.5$, $p < 0.0001$), osmolality (ANOVA: $F_{2,91} = 36.3$, $p < 0.0001$; Fig. 3.3), and glucose (females only; ANOVA: $F_{2,44} = 4.2$, $p = 0.022$) measured at 30 minutes (Fig. 3.4). In contrast, temperature treatment did not have a significant effect on any of the plasma parameters at this sampling (ANOVA: $p > 0.2$) with the exception of glucose (females only; ANOVA: $F_{2,44} = 5.3$, $p = 0.0089$). In some cases, capture alone significantly elevated parameters above values for “handling only” fish. Plasma chloride concentrations were higher in captured than in “handling only” fish, however with chloride a significant temperature*treatment interaction (ANOVA: $F_{4,92} = 4.4$, $p = 0.0026$) prevented statistical confirmation of this difference. We detected no effect of capture treatment or temperature on cortisol for either sex (ANOVA: $p > 0.2$).

3.3.3 Terminal samples – 72 hours after treatment

The effects of the capture treatments were no longer evident in any plasma variable at the terminal sampling, 72 hours post-treatment. In contrast, temperature treatment did have a

detectable effect on chloride (ANOVA: $F_{2,89} = 9.2$, $p = 0.00023$), sodium (ANOVA: $F_{2,89} = 7.7$, $p = 0.00084$), lactate (ANOVA: $F_{2,89} = 5.0$, $p = 0.0086$), and osmolality (ANOVA: $F_{2,87} = 4.5$, $p = 0.014$) at terminal sampling (Fig. 3.5). Plasma lactate concentrations had approximately halved for the 13°C and 19°C groups since the first sampling (decreased from $\sim 9 \text{ mmol l}^{-1}$ to $\sim 4 \text{ mmol l}^{-1}$), however lactate for the 21°C fish had not recovered at all ($\sim 12.0 \text{ mmol l}^{-1}$). During terminal sampling, on the last day of the experiment, we began to observe mortality in the 21°C fish and therefore sampled moribund or dead fish between terminal sampling of the survivors. Fourteen female (14%) and six male (6%) fish from the 21°C treatment died before the termination of the experiment (sex not statistically significant, Pearson's Chi-square: $\chi^2 = 2.50$, d.f. = 1, $p = 0.11$; deaths occurred 46 – 76 hours after chase treatments), while no fish from the 13°C or 19°C treatments died during this time. Capture treatment did not have a significant effect on survival (Pearson's Chi-square, 21°C fish only: $\chi^2 = 1.22$, d.f. = 2, $p = 0.54$), however captured fish trended towards higher mortality (45% handling only, 64% captured, and 67% captured and air-exposed fish died).

We evaluated analyses of 72 hour plasma constituents including all 21°C fish, and then repeated the analysis excluding samples taken from moribund or dead fish to account for the fact that these fish were inherently different from the 21°C survivors. Overall, fish that were found dead or moribund had much higher lactate levels ($\sim 16.9 \text{ mmol l}^{-1}$) than 21°C fish that were live-sampled at the end of the experiment (Welch's t-test: $t = 4.77$, $p < 0.0001$), despite the similar time of sampling, although six individuals that died had lactate levels well within the range of the 72 hour samples from 21°C survivors ($\sim 4.9 \text{ mmol l}^{-1}$). When we excluded the 20 moribund or dead fish, there was no significant effect of temperature on terminal lactate levels. All fish were checked for signs of being moribund every 5-10 minutes on the last experimental day

(when mortalities were occurring), therefore we are confident that samples were taken from dead fish were collected only minutes after death. Plasma chloride and sodium concentrations at this sampling were lower for the 21°C and 19°C groups than for the 13°C group, a result that was significant whether or not we excluded mortalities (Welch's t-test: $p \leq 0.011$; and 21°C survivors were not different than 21°C mortalities in terms of plasma sodium, potassium, osmolality, or cortisol after correction for multiple comparisons; Welch's t-test: $p > 0.01$). No other effects of temperature in the plasma were detected at this sample time.

3.4 Discussion

This is the first experiment examining the synergistic effects of ecologically relevant high temperatures and capture stressors on any species of adult river-migrating Pacific salmon. Contrary to our expectations, there was no substantial relationship between direct short-term mortality and capture treatment at any temperature. However, in the only published research quantifying the relative survival of wild migrating sockeye salmon in the Fraser River caught by angling compared to beach seine (at 17 - 19°C, Donaldson *et al.* 2011), lower survival of angled fish became most apparent when evaluated at arrival at sub-natal watersheds (after > 96 hours post-release). Since we observed no mortality of fish held at comparable temperatures for the duration of our study, there remains the possibility that mortality associated with capture treatments would become apparent over a longer time-course. The observed mortality at 21°C was not unexpected, as this temperature is believed to be at or approaching the critical thermal limits for adult sockeye salmon (Eliason *et al.* 2011).

3.4.1 Capture treatment effects

We used manual chasing (e.g. Milligan 1996, Kieffer 2000) to elicit the burst swimming behaviour that is typical of a fish fighting on a hook and line, or struggling to escape from trawl, seine, or gill nets. Three minutes of exhaustive exercise is a capture stressor consistent with angler handling of sockeye salmon during catch and release (Donaldson *et al.* 2011), but it is likely a conservative time estimate in comparison to the experience of sockeye salmon being released from other gear types. Up to one minute of air exposure may occur during release by a commercial or recreational fisher, depending on the difficulty of hook removal or net disentanglement (Donaldson *et al.* 2011). When fish burst swim, they utilize anaerobic respiration fuelled by energy stores found in white muscle tissue, producing lactic acid as a by-product (Wood 1991). The dissociation of a proton results in the production of lactate anions, and a portion of both compounds move from the muscle to the blood. Consequently, elevation of lactate in the blood indicates elevations of these metabolites in the white muscle. We were interested in measuring plasma lactate concentrations after applying simulated capture stressors to assess the relative impacts of our capture treatments. Compared to the handling only treatment (~ 5 mmol l⁻¹; similar to sockeye salmon sampled immediately after beach-seining; Donaldson *et al.* 2011), plasma lactate was doubled in captured fish and tripled in air-exposed fish 30 minutes after treatment. Overall, we detected up to a 13-fold increase in plasma lactate above baseline levels of sockeye being held in the same conditions (~ 1.5 mmol l⁻¹; Jeffries *et al.* 2011), thus it was surprising that we did not see reduced survival of the captured and air-exposed fish. Donaldson *et al.* (2010a) detected equally high lactate levels in hatchery coho salmon (*O. kisutch*) using identical capture simulation procedures at 8°C without significant mortality. These results suggest that Pacific salmon have the ability to recover from substantial (acute) instances of lactic acidosis in fresh water, confirming prior marine work on coho salmon

(Farrell *et al.* 2001b) and in-river work on sockeye salmon (Donaldson *et al.* 2010b). However, Jain and Farrell (2003) found that repeat swim performance was reduced in rainbow trout (*O. mykiss*) with lactate levels above a threshold of $\sim 12 \text{ mmol l}^{-1}$, suggesting that salmonids may be more susceptible to subsequent capture by fisheries or predators if their ability to escape is impaired.

Elevations in cortisol are a characteristic response of fish to stress (Barton 2002). Consequently, cortisol is the principle corticosteroid measured in response to catch and release stressors (Arlinghaus *et al.* 2007). Previous research has shown that female Pacific salmon may demonstrate a greater increase of plasma cortisol than males in response to stress (Donaldson and Fagerlund 1970, McQuillan *et al.* 2003), and cortisol is involved in the regulation of energy metabolism and the hydromineral balance (Barton 2002). Stress hormones trigger mobilization of stored aerobic energy (Gamperl *et al.* 1994, Wendelaar Bonga 1997) resulting in increased glucose levels in the plasma. Therefore, we analyzed the sexes separately when they differed in their response to the treatments. The lack of significant effect of capture stressors on cortisol levels in our study was surprising, however both glucose and cortisol levels did trend higher with the application of capture stressors, and we detected higher plasma glucose in air-exposed compared to “handling only” females. Both cortisol and glucose in the sockeye in our study were high compared to other studies on adult sockeye salmon. Glucose levels from our experimental fish ($4.4 - 22.2 \text{ mmol l}^{-1}$) were double to triple those of bio-sampled migrating sockeye captured by dip-net (Young *et al.* 2006), depending on capture treatment. The rapidity of sampling after capture with a dip-net ensured that glucose levels have not yet had a chance to respond to the stress of capture and handling, and our experimental fish were likely demonstrating elevated glucose and cortisol concentrations in part due to the chronic stress from their days in captivity (Portz *et al.* 2006, Roscoe *et al.* 2011). Sockeye salmon in our experiment

demonstrated a more than 10-fold elevation in cortisol levels above the river-migrating sockeye salmon in Young *et al.* (2006), and an approximately five-fold elevation above quiescent sockeye salmon held in captivity and sampled via catheter in Sandblom *et al.* (2009), presumably in part due to handling and capture stressors.

Exercise and stress can disrupt ionic and osmotic balances within the blood and tissues, by affecting water or ion uptake or elimination mechanisms (Wendelaar Bonga 1997). Plasma sodium and chloride ion levels respond to the accumulation of metabolites in the muscle tissues due to exercise and stress; this osmoregulatory disturbance can cause water to move out of the plasma and into the muscle, increasing plasma ion concentrations (Wood 1991). Consistent with this, captured sockeye salmon in this study had higher plasma concentrations of sodium and chloride ions 30 minutes after treatment than did “handling only” fish. Values from our study were similar to data ranges from other studies on river-migrating sockeye salmon (Young *et al.* 2006, Clark *et al.* 2010, Donaldson *et al.* 2010b) and for capture-simulation treated coho salmon (Donaldson *et al.* 2010a), suggesting that capture treatments had caused some osmoregulatory disturbance, but most fish were still within normal limits for this stage of their life history. Differences in total osmolality were predictable as they are likely driven primarily by differences in the main plasma solutes, lactate, sodium and chloride, among the capture treatment groups. A surprising result of this study was the lower plasma potassium levels in captured fish compared to “handling only” fish, since exercise is known to increase plasma potassium as it is lost from the muscle cells (Thomas *et al.* 1987, Sejersted and Sjøgaard 2000). We can only speculate that the lower levels 30 minutes after exercise are a function of sampling time and the rapid re-uptake of potassium ions from the extracellular space (Nielsen and Lykkeboe 1992). Whereas blood sampling 1-2 hours post-stressor may have yielded different results in the suite of variables measured here, 30 minute post-stressor blood sampling was

chosen in order to capture responses to treatments and to maximize the number of individuals we were able to treat and sample in a short time. Results from an experiment on coho salmon using identical simulated capture protocols yielded the same patterns in blood chemistry when sampled one hour post-stressor (Donaldson *et al.* 2010a).

3.4.2 Temperature effects

Temperature had an observable effect on whole animal physiology both before and immediately after capture treatment, therefore we were surprised at the lack of detectable effect in the plasma constituents measured 30 minutes after simulated capture. We offer two possible explanations:

1) the relatively short exposure to high temperatures prior to capture treatments resulted in minimal disturbance to blood physiology; or 2) while the warmest temperatures were already having physiological consequences, the effects of the different thermal stress levels may have been masked by the more recently imposed simulated capture stressors. It is possible that the effects of capture stressor and temperature on the plasma stress indicators would have been additive had we applied the capture treatment after a longer high temperature exposure (21°C is known to be stressful for sockeye salmon; Brett 1971, Gilhousen 1990, Farrell *et al.* 2008, Keefer *et al.* 2008, Eliason *et al.* 2011, Martins *et al.* 2011). The exposure time to elevated temperatures of 12-24 hours is meaningful, however, as it represents our approximation of fish encountering warm water and concentrated fisheries as they enter and migrate through the lower river.

Warm temperatures had an effect on ventilation rates and the ability of fish to maintain equilibrium immediately after treatment. Compared to fish in 13°C, ventilation rates were 18% higher in 19°C fish and 25% higher in 21°C fish before treatment, likely reflecting an increase in resting metabolism due to warmer body temperature. After exercise, sockeye salmon exhibit

an increased rate of oxygen consumption (termed excess post-exercise oxygen consumption, EPOC) as they re-establish homeostasis (Lee *et al.* 2003a). EPOC has been shown to increase with temperature in juvenile and adult sockeye salmon (Brett 1964, Lee *et al.* 2003a). Oxygen is required to fuel the processes that correct metabolic and ionic biochemical imbalances and restore oxygen and phosphate stores to the tissues (Gaesser and Brooks 1984, Lee *et al.* 2003a). Interestingly, fish that were captured (burst swimming fuelled by anaerobic metabolism) then air-exposed (preventing respiratory gas exchange) in the warmest water demonstrated an 11% decrease in ventilation rate once returned to the water. While we did not quantify ventilatory volume, if we assume that slower ventilation frequency translated to reduced gas exchange and lower oxygen uptake, then fish that presumably had the greatest need to recover oxygen were the least able to do so quickly. This combined with the inability of air-exposed fish in 19°C and 21°C to maintain equilibrium when first returned to the water is evidence that the warm water temperatures were having deleterious physiological effects on the fish at this time. This supports our second explanation that temperature effects were undetectable in the plasma simply because they were masked by the other stressors.

At the end of the experiment fish had been allowed ~72 hours to recover from simulated capture treatments, and at final sampling we detected no legacy effects of those treatments. We elected to terminate the experiment at 72 hours because it allowed us to sample moribund and surviving fish at the same time-point. Also, our previous work on sockeye salmon demonstrated that there were no detectable legacy effects of capture treatment on survival or physiology after approximately 48 hours. In the current experiment, the physiological effects of warm temperatures were evident in the high plasma lactate and depressed chloride and sodium concentrations in the 21°C fish at 72 hours. Being a by-product of glycolysis, plasma lactate is an indicator of anaerobic metabolism, which results when systemic oxygen demand exceeds

supply, such as during burst swimming or high-temperature induced hypoxia (Pörtner 2001). As a group, the 72 hour mean plasma lactate in 21°C fish ($\sim 12 \text{ mmol l}^{-1}$) was similar to those measured after capture treatment, including some fish with concentrations up to 20-fold higher than baseline. Our data comparing surviving fish with mortalities also suggest that lactate levels either elevate drastically immediately before death (Tierney *et al.* 2009, Bradford *et al.* 2010, Hruska *et al.* 2010), and/or that lactate levels this high contributed to mortality. For example, these individuals may have been experiencing oxygen deficiency caused by temperatures beyond critical thermal limits, resulting in passive survival using anaerobic mitochondrial metabolism (Pörtner 2001, 2002). Unfortunately, our design does not permit us to determine whether some mortality may have been attributable to acidosis, but certainly other mechanisms were also important. The lower concentrations of plasma sodium and chloride ions detected in the 19°C and 21°C temperature treatments after 72 hours were still significant when we analyzed only the live-sampled fish. Thus, we are confident that these patterns truly did relate to thermal stress, although potentially indirectly, as it may have been a consequence of impending death (Jeffries *et al.* 2011) or advanced stages of gill and kidney pathogen infection (Bradford *et al.* 2010), both of which may be modulated by warm temperatures. Consistent with these results, chronic stress can be a cause of osmoregulatory dysfunction, which in freshwater would cause a net loss of ions to the environment (Barton and Iwama 1991, Wendelaar Bonga 1997). Studies examining the physiology of sockeye salmon on spawning grounds suggest that metabolite accumulation, elevations of corticosteroids, immunosuppression, and osmo/ionoregulatory dysfunction may all contribute to natural senescence (Morbey *et al.* 2005, Hruska *et al.* 2010).

Through river warming and changes in migration behaviour an increasing proportion of adult Fraser River sockeye salmon are undertaking migrations at temperatures that are well above their optimum and occasionally approaching their critical thermal limits, and hence have

relatively low aerobic and cardiac scope available to migrate (Farrell *et al.* 2008, Eliason *et al.* 2011). Large proportions of the returning runs have perished during migrations as a result of high temperatures (Macdonald *et al.* 2010, Martins *et al.* 2011). Our results confirm that even without physical injury, which is a frequent consequence of gear encounters (Davis 2002), the exhaustive exercise associated with fisheries capture results in substantial physiological stress in sockeye salmon. Air exposure during release results in additional disturbances as was evident from the plasma analyses and the inability of air-exposed fish to maintain equilibrium after release. Even a temporary loss of equilibrium is likely dangerous to fish since it makes them far more vulnerable to repeat fisheries capture, predation, and drifting downstream. Due to the nature of the lower Fraser River fishery, sockeye salmon are very likely to encounter fishing gear (either recreational or commercial) more than once. If release of captured fish is intended as a conservation measure employed by managers, the increased probability of mortality may be a consideration when planning for openings and desired escapement numbers, or when accounting for the impact of non-retention fisheries.

While laboratory experiments such as this one on adult salmon have limitations in their applicability to wild migrants, this study was an important first step to understanding thermal impacts on capture-and-release stressors in sockeye salmon. We must acknowledge the caveats that fish in our study benefitted from the absence of injuries typically incurred when encountering fishing gears, but were artificially challenged with the stress of captivity. However, the findings still have important implications for capture-and-release of river-migrating fish. Sockeye salmon exposed to our simulated capture treatments were characterized by elevated lactate, sodium, and chloride levels and lower potassium levels compared to their “handling only” counterparts, cortisol and glucose concentrations above expected levels for river-migrants, depressed ventilation, and the inability to maintain equilibrium. In order to

survive, released fish will have to cope with ionoregulatory imbalances, oxygen deficits, and altered acid-base status, and clear lactate and other metabolites from the blood and tissues. The elimination of air exposure in sockeye salmon that will be released, particularly in temperatures $\geq 19^{\circ}\text{C}$, will increase the probability of their survival through a reduction in equilibrium loss, as well as reducing the magnitude of physiological impairments. We also suggest that future research should investigate easily observable metrics such as equilibrium loss, ventilation rates, and reflex impairment (Davis and Ottmar 2006, Davis 2010) that could be developed into real-time tools to understand the physiological status of fish as they are being released. Given that temperatures in the Fraser River are expected to continue to warm in future years (Morrison *et al.* 2002, Ferrari *et al.* 2007) and Fraser sockeye salmon have shown declines in productivity over the past 20 years (a federal judicial inquiry is currently examining the potential causes of this decline), field research on survival and fitness consequences on sockeye salmon escaping from fishing gear (e.g. using telemetry to track released fish), particularly on stocks that are less tolerant of high temperatures, is warranted.

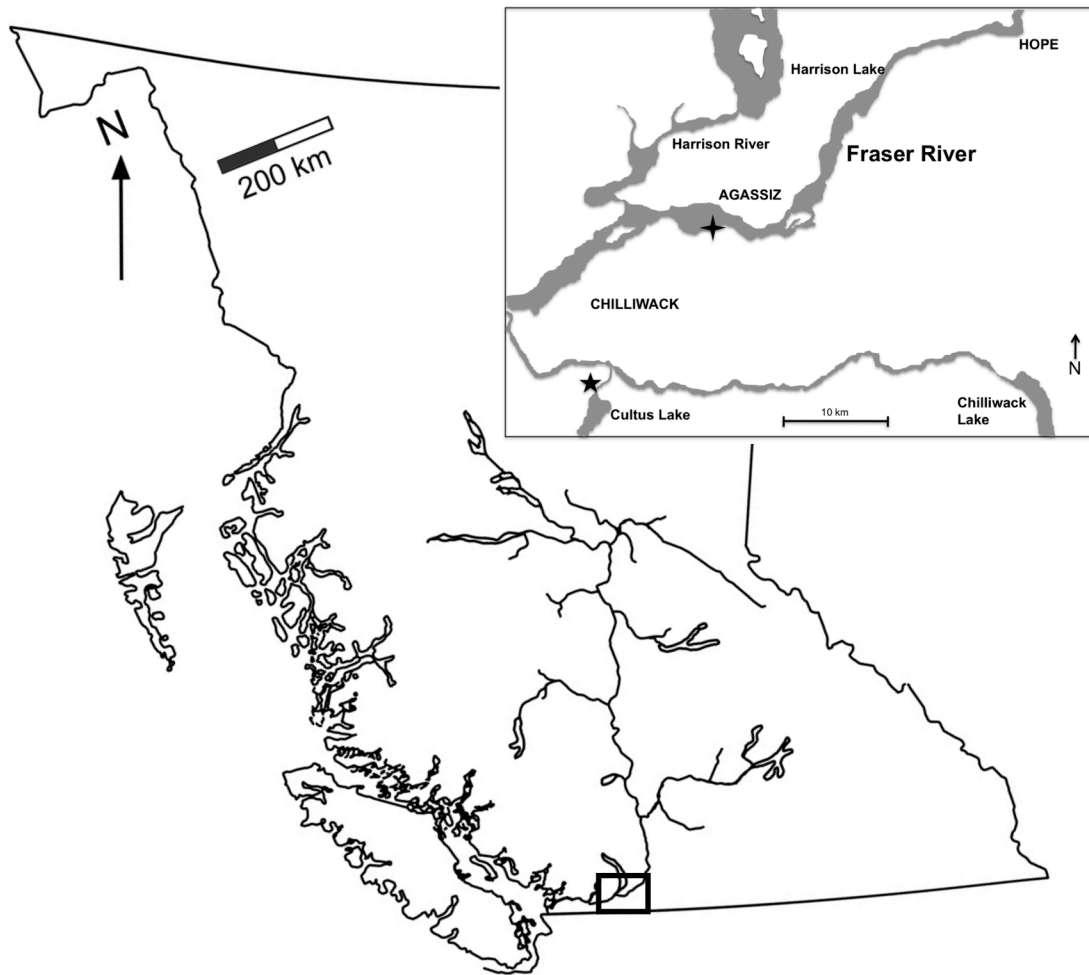


Figure 3.1 - British Columbia and the Fraser River, which drains almost one-third of the province. Inset is the study area, with the cross marking the fish capture site on the Fraser River in Chilliwack, and the star marking the Cultus Lake Salmon Research Laboratory, where experiments took place.

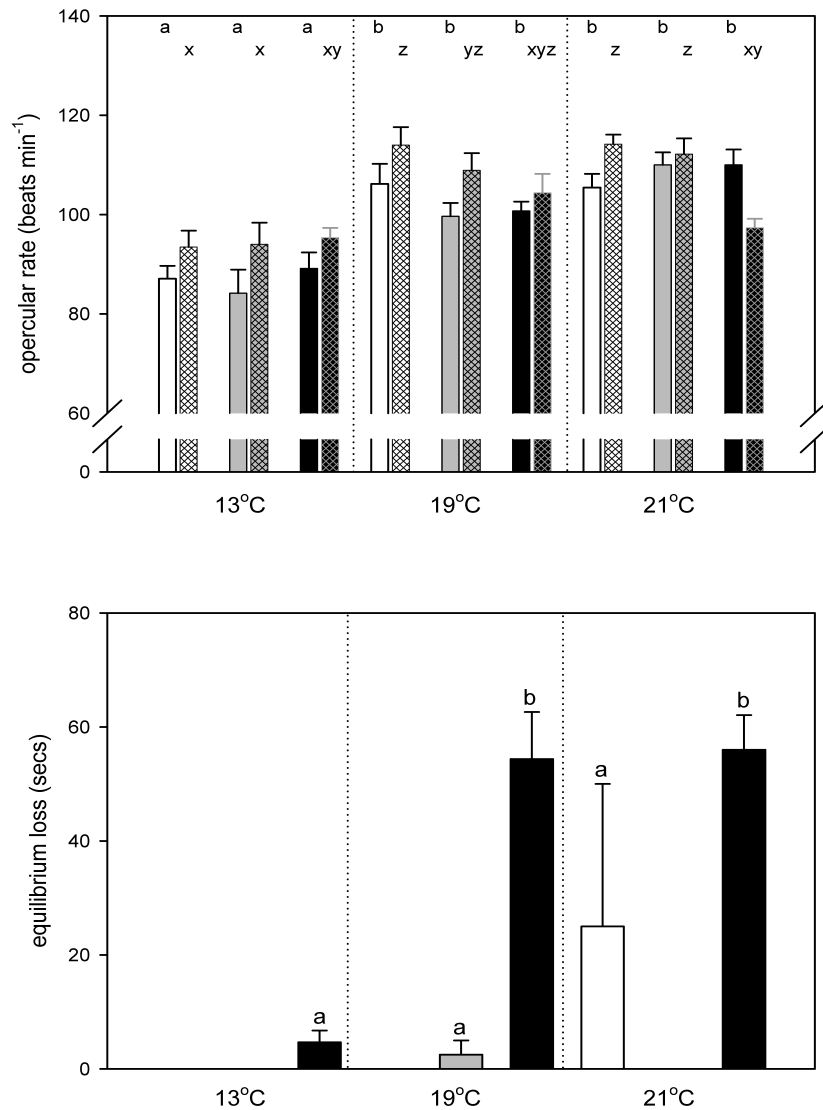


Figure 3.2 - Top - Mean ventilation rate for each capture treatment * temperature group, measured immediately before (no pattern) and after (cross-hatched) capture treatments were applied, with standard error bars. Bar shading indicates capture treatment - handing only (white bars), capture (grey bars), capture + air exposure (black bars). Lower-case letters a,b indicate significant differences between temperatures in ventilation rates pre-treatment (n = 11-12), and lower-case letters x,y,z indicate the significant differences after False Detection Rate correction for multiple comparisons between capture treatment * temperature groups on post-treatment ventilation rates.

Bottom - Mean duration of equilibrium loss immediately after capture treatment, for each capture treatment * temperature group (n = 11-12), with standard error bars. Bar shading indicates capture treatment - handing only (white bars), capture (grey bars), capture + air exposure (black bars). Different lower-case letters represent significant differences after False Detection Rate correction for multiple comparisons. Bars with the small letter (a) are not significantly different from zero.

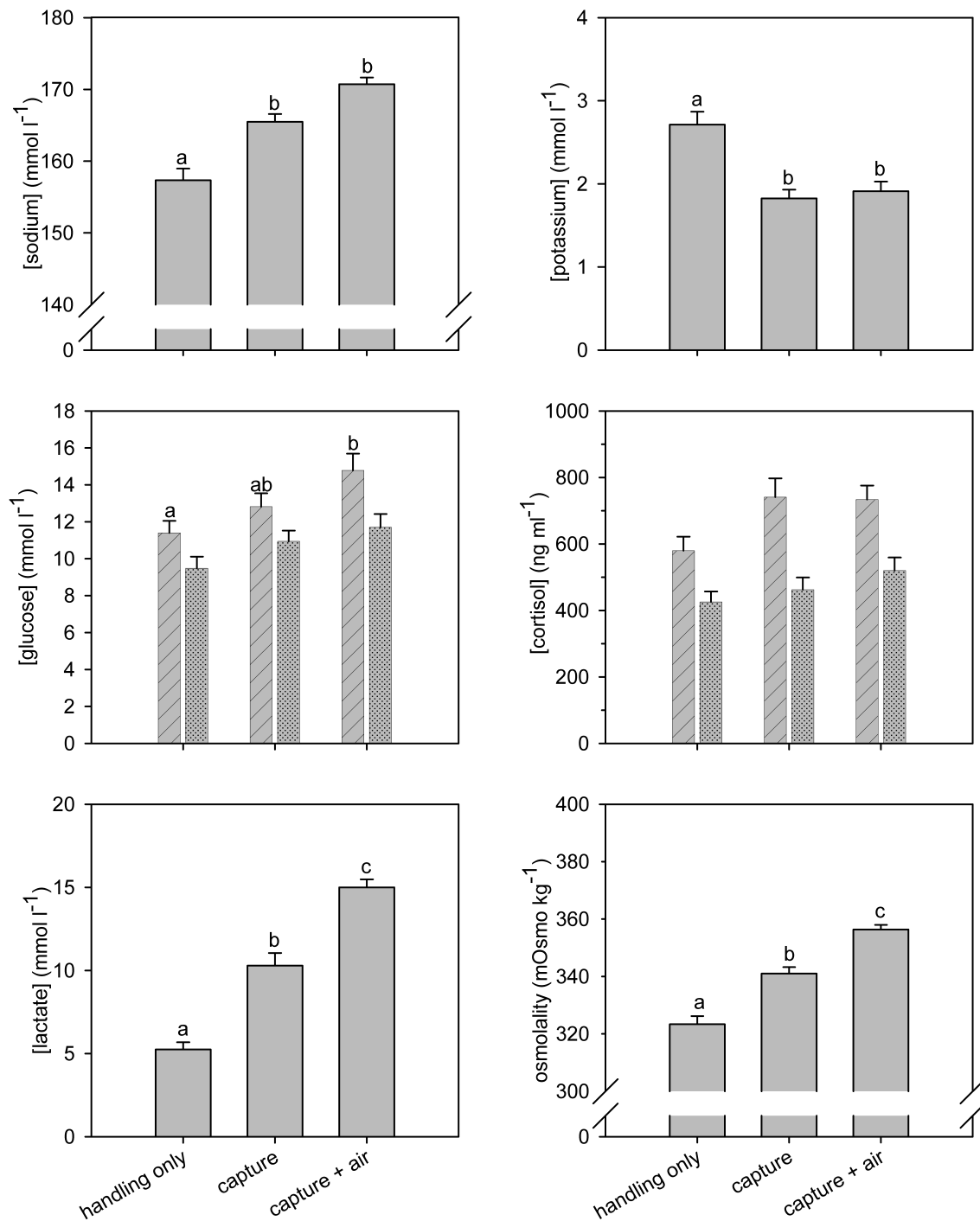


Figure 3.3 - Mean plasma sodium, potassium, glucose, cortisol, and lactate concentrations and osmolality by capture treatment group, collected 30 minutes after capture treatment, with standard error bars ($n = 34 \pm 2$). Where sexes responded differently to capture, bars are patterned (lines indicate females and stipples indicate males, $n = 17 \pm 5$). Different lower-case letters represent significant differences after False Detection Rate correction for multiple comparisons.

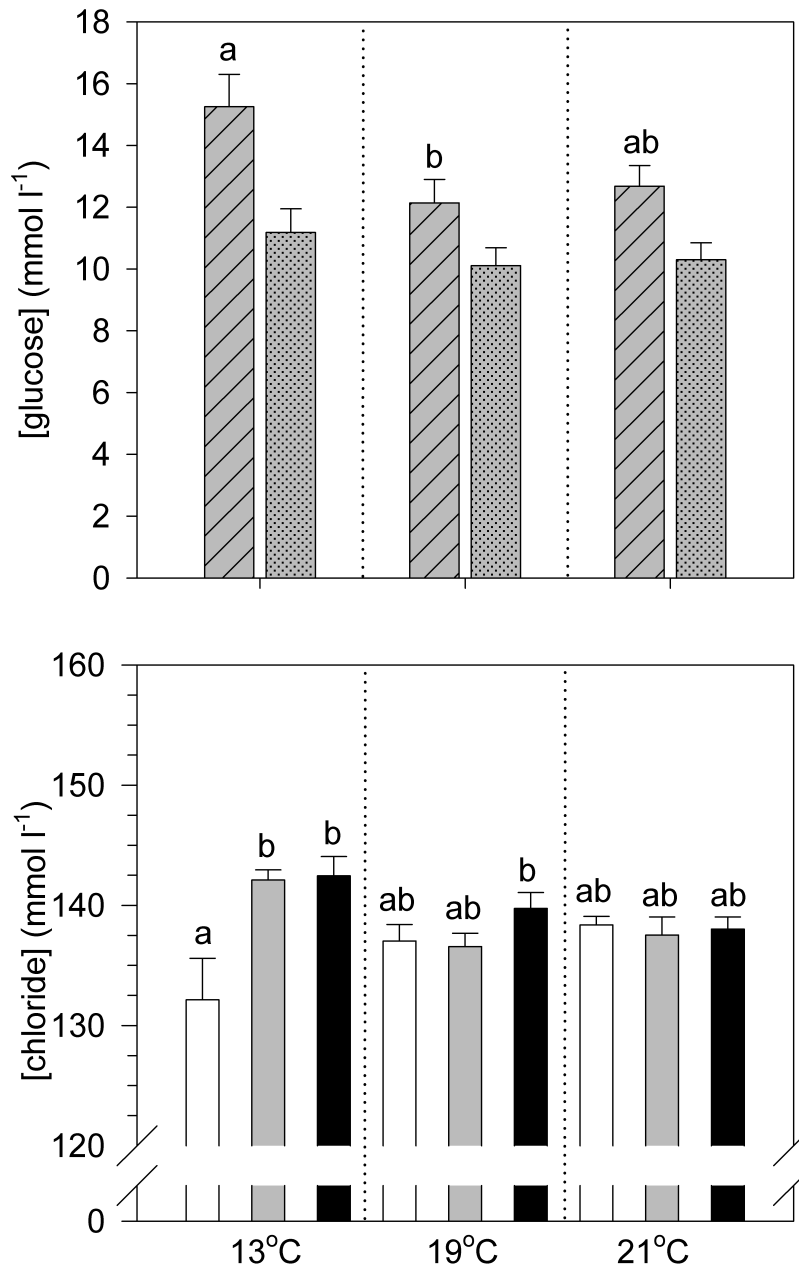


Figure 3.4 - Mean plasma glucose by temperature ($n = 17 \pm 4$) for females (lines) and males (stipples), and plasma chloride by capture * temperature group (sexes pooled, $n = 11-12$), collected 30 minutes after capture treatment, with standard error bars. Bar shading indicates capture treatment - handling only (white bars), capture (grey bars), capture + air exposure (black bars). Different lower-case letters represent significant differences after False Detection Rate correction for multiple comparisons.

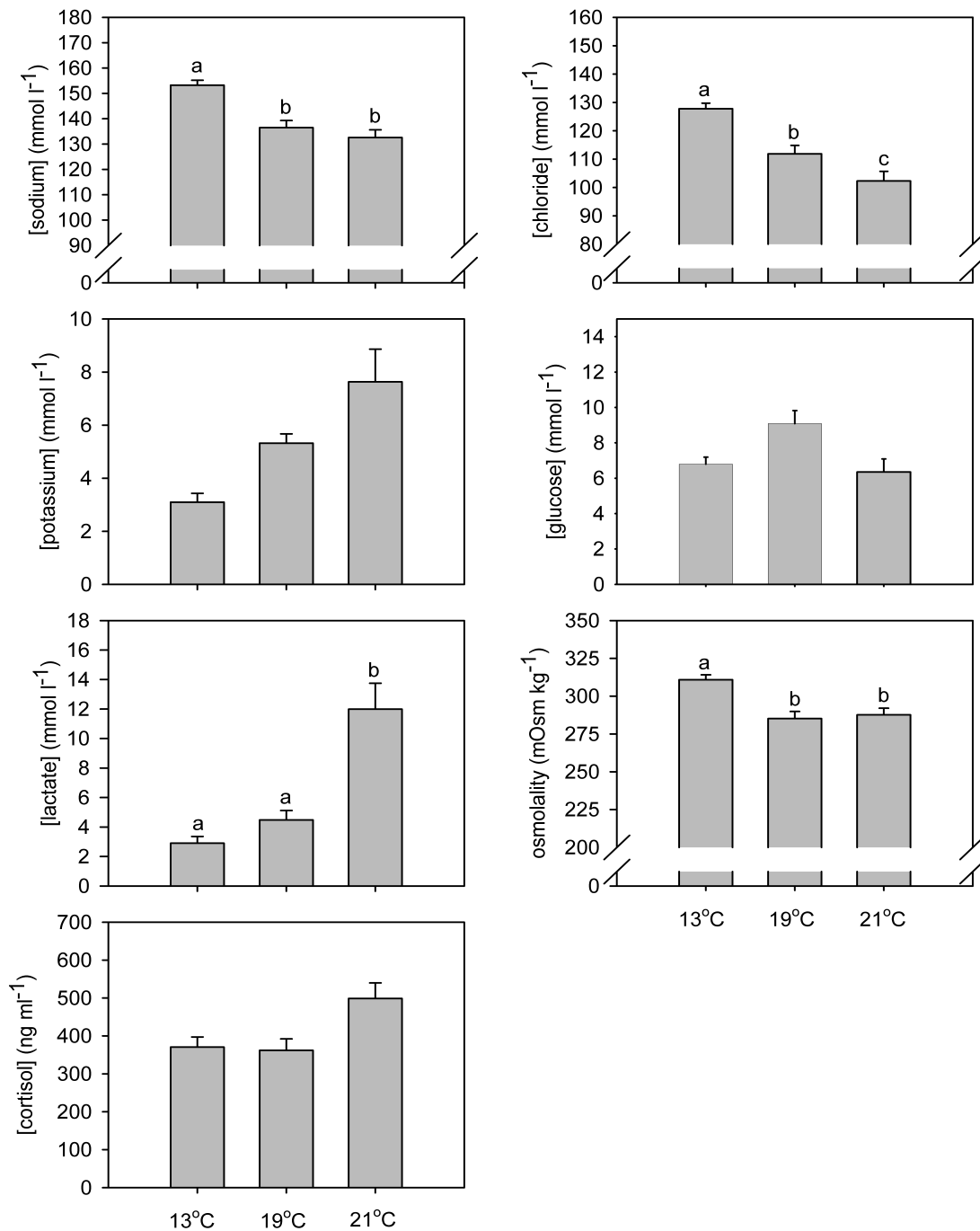


Figure 3.5 - Mean plasma sodium, chloride, potassium, glucose, lactate, osmolality and cortisol by temperature group ($n = 32 \pm 2$), collected 72 hours after capture treatment, with standard error bars. Different lower-case letters represent significant differences after False Detection Rate correction for multiple comparisons.

Chapter 4: Predicting mortality of captured and released sockeye salmon at various temperatures using observational and physiological indices

4.1 Introduction

Capture and release fishing is an important tool used in fisheries worldwide, in an attempt to reduce the impact of fishing on endangered fishes while capitalizing on fishing opportunities for other species. In both commercial and recreational fisheries, non-target species and undersize fish are released with varying levels of care, from negligible to extreme. Some commercial fishers sort their target catch first and “discard” unwanted fishes after most individuals have perished from the stress and air exposure during capture (Alverson *et al.* 1994). However, commercial fishers in Strait of Georgia, for example, use recovery boxes to revive coho salmon (*Oncorhynchus kisutch*) bycatch before release (Farrell *et al.* 2001a). Recreational fishers may employ practices they believe will improve survival of released fish such as gentle handling, keeping the fish in water at all times, and supporting visibly impaired fish until they appear recovered. Even when fish are released carefully, mortality rates reported in catch and release and bycatch studies range from zero to almost 100% (Bartholomew and Bohnsack 2005), and are dependent on species, anatomical hooking location, water temperature, capture depth, hook, bait, or gear types, air exposure, life history stage and/or size, and handling (Muoneke and Childress 1994, Arlinghaus *et al.* 2007). Several excellent reviews exist on the survival and fitness consequences of captured and released fish (Alverson *et al.* 1994, Muoneke and Childress 1994, Davis 2002, Bartholomew and Bohnsack 2005, Suuronen and Food and Agriculture Organization of the United Nations. 2005, Broadhurst *et al.* 2006, Arlinghaus *et al.* 2007), all of which illustrate that water temperature can play a key role in survival after release. A recent review of the capture and release literature specifically examining the effects of

thermal stress during capture, however, found that for most species there is a paucity of knowledge on the effects of ecologically relevant high temperatures on the mortality and impairment of released fish (Chapter 2, Gale *et al.* 2011a). Quantifying the effects of capture and release on fish fitness is challenging, since it involves following individuals after release for the duration of their lifetime in order to compare reproductive success with wild individuals that have not been captured. This type of monitoring can be almost impossible given that fishes are highly vagile, live underwater, utilize external fertilization, produce up to thousands of offspring, and often do not employ parental care. Most often, studies examining the effects on fish released after capture quantify immediate (easy to determine visually), short-term (requires visual or telemetry monitoring for hours to days), or delayed (best studied using telemetry in order to eliminate the confounding effect of long-term holding in captivity) mortality of individuals in order to infer fitness consequences for an entire population.

Some of the challenges of quantifying lifetime fitness effects of capture-and-release can be avoided by studying species which reproduce only once per lifetime (semelparity), and which return from vast marine environments to natal streams to spawn (anadromy), such as Pacific salmon (*Oncorhynchus* spp.). In British Columbia's Fraser River, sockeye salmon (*O. nerka*) are of particular interest in terms of capture and release at high temperatures. Sockeye salmon return to the Fraser River by the millions, and are managed in four run-timing groups based on their date of entry into freshwater: early Stuart, early summer, summer, and late-run. The Fraser River's summer temperatures have increased by $\sim 2^{\circ}\text{C}$ in the past 60 years, and in the last decade sockeye salmon have encountered the highest Fraser River temperatures ever recorded (21.4°C) (Patterson *et al.* 2007). Summer-run stocks migrate during peak high river temperatures, whereas late-run stocks have historically entered the river on the descending limb of the summer thermograph (Burgner 1991, Patterson *et al.* 2007). While all run-timings are experiencing

warmer than historic river temperatures, since the 1990's some late-run sockeye salmon have been inexplicably entering the river up to six weeks earlier than normal, thus encountering temperatures 4-5°C warmer than the historical average for this group (Cooke *et al.* 2004b). This is significant because Fraser River sockeye salmon stocks have adapted their aerobic capacity to be optimized at thermal environments historically experienced (Farrell *et al.* 2008, Eliason *et al.* 2011), and their physiological functioning becomes impaired at temperatures beyond their optimal thermal window. Years of record high temperatures have resulted in catastrophic en-route or in-river mortalities of up to 90% for some late-run stocks (Cooke *et al.* 2004b).

Sockeye salmon are a valuable commercial and recreational resource, and millions are caught each year. For example, in 2010, 13 million Fraser River sockeye salmon were caught by commercial fishers, and 300 000 were caught by anglers (DFO 2010c, 2011a). There are no estimates of how many fish escape from commercial nets, however large proportions of fish are seen on spawning grounds bearing the characteristic scars from their encounters with fishing gears (e.g. gill net wounds, hook wounds). One third of the Fraser River sockeye salmon caught by anglers in 2010 were released, primarily due to mandated closures that prevent anglers from keeping sockeye salmon during much of the season in order to protect threatened stocks. However, we do not yet understand the consequences of capture encounters on released or escaped sockeye salmon, particularly when they are experiencing thermal stress. It is imperative to be able to predict and account for release and escape mortality in order to properly manage this important economic, cultural, and ecological resource. Pre-season and in-season forecasts use complex models already full of uncertainty in order to predict returning run sizes, predominantly to determine how many fish should be available for fisheries while protecting threatened stocks (e.g. Cultus Lake sockeye salmon) and ensuring adequate escapement to the spawning grounds (e.g. Grant *et al.* 2010).

Despite the knowledge that hundreds of thousands of Fraser River sockeye salmon are intentionally released from angling gear, and even more encounter net gears and escape by their own struggle, we currently have no way to account for the number of sockeye salmon that perish after release from gears, nor do we know what impact this stress has on the fitness of surviving fish. Severe exercise is known to cause mortality in fish (Wood *et al.* 1983), and while the precise mechanism for this mortality is not fully understood, it is believed that intracellular metabolic acidosis is a primary cause (Wood *et al.* 1983). Exercise physiology has been well studied in sockeye salmon (e.g. Brett 1967, Brett and Glass 1973, Farrell *et al.* 2003), resulting in an excellent understanding of their primary, secondary, and tertiary stress responses to various exercise protocols. In general, upstream migration of adult sockeye salmon is accomplished by sustained aerobic swimming fuelled by well-perfused red muscle (Webb 1995), with intermittent “burst” swimming fuelled by anaerobic glycolysis in the white muscle to ascend rapids, avoid predators, and escape fishing gears (Wood 1991). Fish may also need to perform anaerobically when swimming at extremely high temperatures, if metabolic demand for oxygen is exceeded by the physiological ability to deliver oxygen to the tissues (Pörtner 2001). The by-product of anaerobic activity is the production of lactate and metabolic protons, which can accumulate in the blood and tissues causing drastic lowering of pH and iono- and osmo-regulatory disturbances (Wood *et al.* 1983, Wood 1991). For these reasons, studies that incorporate physiological measures such as blood plasma constituents and cardiac parameters with survival can help elucidate the mechanisms underlying mortality in released fish.

Our experiment takes the first steps in understanding how thermal and capture-release stressors interact to impact late-run Fraser River sockeye salmon returning to spawn. We simulated various magnitudes of capture stressors, including the exhaustive exercise and air exposure that constitute struggling in fishing gear, in a laboratory setting where temperatures could be

precisely controlled and manipulated. Using temperatures that coincide with those occurring at present during sockeye salmon migrations in the Fraser River, including a cool historic average (13°C), a moderate current average near the optimum for aerobic scope (16°C), and a current high near the critical thermal maximum for aerobic scope (19°C), we employed simulated capture scenarios in order to investigate the following hypotheses: 1) treatments simulating capture and release at various temperatures would result in differential mortality and physiological disturbances, 2) blood plasma ions and metabolites may be used to predict mortality post-release, and 3) easily observable metrics such as ventilation rate and duration of equilibrium loss measured immediately after capture may be useful in predicting mortality. We predicted that mortality and capture stress would be greatest when fish were exercised and air-exposed at the warmest temperature, that the probability of survival could be predicted using plasma lactate, glucose, cortisol, and ion concentrations after capture-and-release, and that because both equilibrium loss and substantially slowed breathing after capture are indicative of physiological impairments, these metrics could be used to predict the probability of individual survival.

4.2 Methods

4.2.1 Study animals and facility

We intercepted adult sockeye salmon in British Columbia's Harrison River, a tributary of the Fraser River located approximately 125 kilometers east of Vancouver (Fig. 4.1). These sockeye salmon were captured by beach seine September 15-18, 2008 while completing their spawning migration, and belonged to the Weaver Creek and Harrison populations. Fish were individually netted from the seine net to truck-mounted tanks and transported (approximately 45 minutes) to the Cultus Lake Salmon Research Laboratory operated by Fisheries and Oceans Canada. Upon

arrival, each sockeye salmon was sampled for adipose fin tissue in order to determine population identification. They were then PIT tagged for individual identification and introduced to a large (20 000 l, 6 meter diameter) artificial holding pond fed continuously with UV sterilized ($\sim 40 \text{ l min}^{-1}$; LS-Permabead Filtration System, Integrated Aqua Systems Inc., Escondido, California) 9°C water drawn from nearby Cultus Lake. On September 22, 2008, after receiving DNA results indicating the stock identity of each fish, 54 Weaver Creek sockeye salmon were moved into nine smaller (1400 l) aquaria (6-7 fish per tank) maintained at 11°C for 24 hours. After this recovery period we began slowly increasing the water temperature ($\text{max } 0.2^{\circ}\text{C hr}^{-1}$) until experimental temperatures were achieved (three tanks each at 13° , 16° and 19°C). Due to logistical constraints, the experimental treatments were applied in two consecutive rounds, with 54 fish in the first round of the experiment, then being removed from the treatment tanks and placed back in the large holding ponds to allow for the experiment to be run on another 52 fish. Rounds were pooled for analyses, unless statistical differences were detected.

4.2.2 Experimental protocol

After all fish had been maintained at their treatment temperatures for a minimum of 12 hours, they were randomly assigned to one of three simulated capture treatments, resulting in a full-factorial design using three levels of temperature and three levels of capture stress. The lowest magnitude stressor involved handling only, in which fish were individually netted from their holding tank to one of the treatment tanks (at the experimental temperature for each fish) and monitored for 30 minutes before being sampled for blood via caudal venipuncture while holding fish supine in a foam-lined trough supplied with flowing water. This treatment was designed as a non-capture control for handling effects other than those employed in the two simulated

capture treatments. Fish were also marked by anchor tag and sampled at this time for a small (<2g) gill sample and 3mm muscle punch for genomics analysis in a separate experiment (Donaldson et al. in prep). These biopsy procedures have been shown to cause minimal stress to adult sockeye salmon in previous experiments by our group and others (e.g. Cooke *et al.* 2005). The capture stressor included stimulating fish to burst swim for three minutes by manual chasing. This technique involved three experimenters standing around the perimeter of the treatment tank, leaning over and splashing vigorously behind the fish or gently touching its tail, and has been used extensively in angling simulation and exercise experiments (Milligan 1996, Cooke *et al.* 2003). The capture plus air exposure stressor we employed was to chase fish as described for three minutes, then gently lift them out of the water using a soft mesh dip-net to air expose them for 60 seconds. Both groups of exercised fish were blood and tissue sampled 30 minutes after the instigation of chasing. Ventilation rates for all fish were counted both immediately after introducing fish to the treatment tank, immediately after capture treatment +/- air exposure, and again before blood and tissue sampling (30 minutes later). Fish were also monitored for the presence or absence of the ability to maintain equilibrium, and the duration of this impairment. Detailed records were kept on swimming and recovery behaviour. After biosampling, fish were returned to their holding tanks. Overall, 47 female and 50 male sockeye salmon completed the experiment. Sockeye salmon that died prior to the simulated capture treatment were excluded from analyses.

Fish were monitored carefully for the duration of the experiment, including checks at least once per one hour from 0700 hrs to 0100 hrs. Dead fish were removed from the tanks, and moribund fish were removed and euthanized by cerebral concussion. All surviving fish were biosampled two days after capture treatments. All fish were biosampled at death or at the termination of the experiment.

4.2.3 Laboratory protocols and assays

Stock identification was determined for all individual fish using DNA analyses (Beacham *et al.* 2004, Beacham *et al.* 2005) and confirmed by analyses of scales. Ninety-seven sockeye salmon were from the late-run Weaver Creek stock. Hematocrit was quantified on whole blood using microcapillary tubes centrifuged at 10 000 g for 2 minutes. The remaining blood was centrifuged at 7 000 g for 6 minutes and plasma was stored at -80°C until further analysis. Plasma was subsequently analyzed for cortisol (Neogen ELISA with Molecular Devices Spectramax 240pc plate reader), lactate, glucose (YSI 2300 Stat Plus analyzer), osmolality (Advanced Instruments 3320 freezing-point osmometer), chloride (Haake Buchler digital chloridometer), sodium, and potassium (Cole-Parmer, model 410 single-channel flame photometer; Farrell *et al.* 2001a).

4.2.4 Statistical analysis

All statistical analyses were performed using the R Statistical Package (R Development Core Team 2008). Three-way ANOVA was used to detect differences in the responses of males and females to temperature and capture treatment. In the absence of a sex effect, two-way ANOVA was used to compare individual plasma indices between capture treatment and temperature groups (including a temperature by capture treatment interaction), using log-transformations to reduce heteroscedacity when necessary. Significance was evaluated at the level of $\alpha = 0.05$, and multiple comparisons were corrected for using the False Detection Rate method (Curran-Everett 2000).

Model selection for survival analysis was performed using the Survival library in R. Survival (in hours) was constrained to be either constant (no effects), or to vary by temperature, simulated capture treatment, sex, and combinations of these (including two-way interactions) as factors in

the model selection process in order to estimate probability of survival over 48 hours post-treatment. The 48 hour time period was chosen for examination based on visualization and preliminary analyses of the survival results; mortality occurring after this period of time strongly appeared to be unrelated to experimental treatments, instead occurring presumably due to the stressors of captivity and natural senescence. Using the Akaike Information Criterion (AIC), we selected the models that best described the survival data. The AIC weight of the models was also computed and can be interpreted as the probability of a given model in the set being the most parsimonious one to describe the data (Burnham and Anderson 2002). To account for model selection uncertainty, model-averaged survival and recovery rate estimates and their associated standard errors were computed using the AIC weight of the models included in a 95% confidence set for the best model (Burnham and Anderson 2002). This resulted in a weighted combination of six models being used to calculate model-averaged survival (Table 4.1).

In order to predict survival using blood plasma metrics, Principal Components Analysis (PCA) was performed in order to reduce whole blood mean cell hemoglobin concentration, plasma cortisol, lactate, glucose, sodium, chloride, potassium, and total osmolality into three principle components (PCs). These PCs were then input to a logistic regression model with survival to 48 hours as the response variable. Total osmolality values for 4 fish were unable to be determined by assay, therefore the values were estimated using a linear regression with the following equation (n=92, R²=0.70, p < 0.0001):

$$\text{osmolality} = (0.8)*([\text{lactate}]+[\text{glucose}]+[\text{sodium}]+[\text{chloride}]+[\text{potassium}]) + 73.1$$

Logistic regression was also employed to create models estimating the probability of mortality using hematocrit, hemoglobin concentration, plasma lactate, glucose, chloride, sodium and

potassium 30 minutes post-treatment, and ventilation rate (opercular beats per minute) and duration of equilibrium loss (in seconds) immediately after release, with survival until 24 hours as the binomial response.

4.3 Results

Ventilation rates measured after fish were transferred to the treatment tank were higher for 16°C and 19°C fish than for 13°C fish (ANOVA: $F_{2,86} = 4.53$, $p = 0.014$). Immediately after simulated capture, temperature effects were no longer evident, however air-exposed fish were ventilating significantly slower than non-air-exposed fish (ANOVA: $F_{2,86} = 4.67$, $p = 0.012$). Air-exposed fish were more likely to lose equilibrium than non-air-exposed fish (Pearson Chi-Square: $X^2 = 74.41$, $p < 0.00001$). For those fish that did lose equilibrium after capture (30 of 31 air-exposed fish, three of 33 capture-only fish and zero of 33 non-captured fish), there was a significant effect of the temperature*treatment interaction on the duration of equilibrium loss (ANOVA: $F_{2,31} = 11.15$, $p = 0.0024$).

4.3.1 30 minutes post-treatment

Water temperature had no effect on any plasma or blood variable we measured at 30 minutes (ANOVA: $p > 0.1$). Simulated capture significantly elevated plasma lactate concentration (Table 4.2, Welch's t : 5.62, $p < 0.0001$), with air exposure exacerbating this elevation (Welch's t : 2.89, $p = 0.0054$). Total osmolality was similarly increased by capture (Welch's t : 2.97, $p = 0.0043$) and air exposure (Welch's t : 2.5, $p = 0.015$). Mean cell hemoglobin concentration (MCHC) was lowered by capture treatment (Table 4.2, Welch's t : 2.7, $p = 0.0088$), however air exposure did not further depress MCHC. Hematocrit trended higher in capture-treated individuals than in controls, while hemoglobin concentration was equal among groups (Table 4.2). Plasma glucose was not affected by capture treatment. Plasma cortisol was higher for females than males,

however capture treatment had no effect on cortisol levels for either sex. Plasma chloride, sodium, and potassium were not different among capture treatment groups. Blood chemistry tests were repeated on surviving fish at 48 hours post-capture, at which time no effect of capture or temperature was detectable after correcting for multiple comparisons.

4.3.2 Survival analysis

The most parsimonious model describing the cumulative mortality data to 48 hours included the effects of temperature and sex (Table 4.1). Similar models with various combinations of capture treatment, temperature and sex (and their interactions) were weakly supported by the data. Model-averaged mortality estimates (and observed mortality) 48 hours after treatment were greater for females than males, and were greater at 19°C than at 13 and 16°C for both sexes (Fig 4.2).

4.3.3 Predicting mortality using physiological indices

Principle components analysis of blood and plasma variables resulted in two significant principle components associated with 48-hour mortality. PC1 (Logistic Regression: $z=2.56$, $p=0.011$) was negatively correlated with total plasma osmolality, plasma sodium, chloride, lactate and glucose concentrations. PC2 (Logistic Regression: $z=4.33$, $p<0.0001$) was positively correlated with plasma cortisol and lactate concentrations, and negatively correlated with mean cell hemoglobin concentration, plasma chloride, sodium, and potassium concentrations. Results of the GLM indicate that for a one unit increase in PC1, the odds of mortality increase by a factor of 1.655, and for a one unit increase in PC2, the odds of mortality increase by a factor of 3.596.

Logistic regression demonstrated that plasma lactate ($z=2.93$, $p=0.0029$), glucose ($z=-2.23$, $p=0.026$), cortisol ($z=2.74$, $p=0.0061$), sodium ($z=-3.14$, $p=0.00017$), chloride ($z=-3.78$, $p=0.00017$), and potassium ($z=-2.02$, $p=0.043$) concentrations, as well as hematocrit ($z=3.76$, $p=0.00017$) and MCHC ($z=-3.96$, $p=0.000074$) predicted survival to 24 hours (Fig 4.3). Logistic regression demonstrated that both slower ventilation rates ($z=-3.40$, $p=0.00067$), and more prolonged equilibrium loss ($z=3.60$, $p=0.00031$), after capture treatment significantly decreased the probability of survival to 24 hours (Fig 4.4).

4.4 Discussion

This study is the first to examine how physiological indices such as blood chemistry, equilibrium loss and ventilation rates may be predictive of mortality after capture and release of sockeye salmon. It is also one of the first, along with Gale *et al.* (2011b) to investigate the synergistic effects of thermal stress and simulated capture on Pacific salmon. We successfully used manual chasing with and without air exposure to elicit a physiological stress response similar to that experienced sockeye salmon migrants encountering fishing gear (Young *et al.* 2006, Donaldson *et al.* 2011), while eliminating the physical injury incurred by these encounters. This has also been shown to be true for other species (discussed in Milligan 1996). The anaerobic exercise stimulated by our capture treatment resulted in 74% higher plasma lactate than in non-captured fish, and air-exposed fish had lactate levels 120% higher than non-captured fish. These results are consistent with other experiments on Pacific salmon using identical capture simulation techniques (Donaldson *et al.* 2010a, Gale *et al.* 2011b). The other significant effect of capture stress was a non-significant elevation in hematocrit (with no associated changes in hemoglobin concentration) that resulted in a significant decrease of MCHC for captured fish. This is likely due to erythrocytic swelling secondary to the adrenaline

response resulting from capture stress (Nikinmaa 1982). Also consistent with our previously published work using simulated capture and release on summer-run sockeye salmon (Gale *et al.* 2011b), we detected no effects of temperature on the blood chemistry parameters measured 30 minutes after capture.

Recent research has shown that sockeye salmon in the Fraser River have adapted to survive and perform optimally at water temperatures coinciding with historic averages for each genetically and geographically distinct population (Farrell *et al.* 2008, Eliason *et al.* 2011). The window of thermal tolerance for sockeye salmon, and indeed most fishes, is relatively narrow. Not only has the Fraser River warmed by approximately 2°C in the past 60 years (Patterson *et al.* 2007), it is expected to continue on this warming trajectory into the future (Ferrari *et al.* 2007, Hague *et al.*). Sockeye salmon are currently experiencing temperatures that sometimes meet or exceed their critical thermal maximum in the Fraser River (Patterson *et al.* 2007, Eliason *et al.* 2011), resulting in substantial mortality (Cooke *et al.* 2004b). Studies on many fish species have shown that capture-release mortality increases at warmer temperatures (Gale *et al.* 2011a), however our group is the first to examine how thermal and capture stress may act in synergy to increase mortality risk to released or escaped sockeye salmon.

Consistent with our prediction, temperatures approaching the critical maximum increased release mortality, however we were surprised to find that sex was a more significant predictor of survival to 48 hours than was capture treatment. While mortality at 24- and 48-hours post-treatment was highest in the 19°C air-exposed group, as predicted, the survival model including temperature and sex was a far more parsimonious fit than any of the models including capture treatment. Our finding that females suffered higher mortality than males was consistent with other studies on sockeye salmon, both wild migrants and captured individuals held in laboratory

conditions (Crossin *et al.* 2008, Cooperman *et al.* 2011, Jeffries *et al.* 2011). These results suggest that adult females experiencing secondary stressors may be at greater risk of failing to complete their migration and successfully spawn, which could have substantial fitness repercussions. The lack of significant treatment effect indicates that capture and release involving a brief strenuous exercise and air exposure may not significantly increase the risk of mortality for sockeye salmon. However, our finding that the physiological impairments resulting from our simulated capture treatments were significantly associated with higher mortality risk suggests that this may not be the whole story. Studies of capture and release on other species have shown that capture stressors and air exposure frequently cause elevations in blood chemistry stress parameters and result in behavioural and other impairments (e.g. Ferguson and Tufts 1992, Davis and Parker 2004, Arlinghaus and Hallermann 2007). In order to more fully understand the mortality of released or escaped sockeye salmon, researchers must incorporate both physiology and telemetry in field studies using a variety of capture methods across a range of river temperatures.

Our finding that statistically significant predictions of survival probability could be made in the lab using individual blood and plasma chemistry indicators is a promising step toward improving our understanding of post-release mortality for sockeye salmon. Elevated plasma lactate, cortisol, sodium, and chloride are consistent with elevated stress, and were associated with higher probability of mortality within the first 24 hours after capture. Lactate anions enter the blood from the muscle tissue after anaerobic exercise and are associated with intracellular acidosis. Extreme intracellular acidosis has been suggested to be causal factors in fish dying after exercise (Wood *et al.* 1983). For this reason episodes of strenuous anaerobic exercise can increase the risk of mortality. Our logistic regression model suggested that sockeye salmon had a >50% probability of mortality within 24 hours when plasma lactate concentrations exceeded

18 mmol L⁻¹. Migrating sockeye salmon caught by tangle net (Donaldson *et al.* 2010b), purse seine (Cooke *et al.* 2008) or beach seine (Clark *et al.* 2010) may reach similarly elevated plasma lactate levels. We detected an association between decreased plasma glucose concentrations and increased mortality risk, which was surprising since glucose levels generally increase with stress. We propose that rather than indicating a less stressed state, the lower glucose concentration could be indicative of reduced stored energy levels or inability to mobilize stored glucose. The trend of higher hematocrit but equal hemoglobin in capture-treated individuals suggests that the depressed MCHC was a result of erythrocytic swelling. On average, plasma chloride and sodium concentration 30 minutes after treatment was similar to conspecifics sampled after river capture (Clark *et al.* 2010) and approximately 15-20% higher compared to quiescent sockeye salmon held in laboratory conditions (Sandblom *et al.* 2009). Our logistic regression models show that fish with relatively low sodium and chloride ion concentrations 30 minutes after treatment had a lower probability of surviving 24 hours. Overall, it appears that fish responded physiologically to our treatment protocols in a similar manner to wild migrants caught in various gears, and that several physiological parameters consistent with a generalized stress response were predictive of mortality. This suggests that the patterns evident in our results may be transferrable to authentic river-capture situations.

The present study found two observable parameters that were predictive of mortality. Other researchers have begun developing novel ways to predict the survival of released fish, perhaps the most promising of which are reflex impairment indices (Davis and Ottmar 2006, Davis 2010). Our work is the first to examine how this type of impairment metric can be used in Pacific salmon in order to predict mortality. Both duration of equilibrium loss and ventilation rate after capture were found to be highly significant mortality predictors. These metrics are easy to observe and quantify by any fisher, and require no specific expertise to evaluate. We

propose that in order for mortality predictions to be practical for fishers, they must involve easily observable metrics with clear thresholds for established unacceptable risk levels. For example, managers could elect to recommend release of fish that had >50% probability of survival but retain any fish that had a lesser probability of survival in order to guide fishers in making decisions that would best maintain a healthy fishing population. We found that fish that were regained equilibrium in <130 seconds, or fish that were ventilating at >60 breaths per minute after release, had a >50% probability of surviving 24 hours after treatment. We were surprised to find that although these impairments were transient for most fish (thirty out of the thirty-two fish that lost dorso-ventral equilibrium after capture appeared recovered within 300 seconds of release, and ventilation rates had returned to pre-capture levels by the next evaluation 30 minutes post-capture), they could still be used to predict 24-hour mortality. Management agencies frequently recommend holding fish until they have recovered orientation and swimming ability, presumably to protect them while they are particularly vulnerable to capture by predators. However if our results are substantiated in the field, that would suggest that even if greatly impaired fish appear recovered before release, they are likely to perish in the following days.

Our results suggest that air exposure increases mortality risk in sockeye salmon by two different mechanisms. Air exposure frequently causes fish to lose equilibrium (e.g. Gingerich *et al.* 2007, Thompson *et al.* 2008), leaving them more vulnerable to predation or secondary capture (e.g. Danylchuk *et al.* 2007). This is a considerable risk in the Fraser River, where commercial, First Nations, and recreational fishers are prolific, and predators including healthy populations of seals, bears and raptors that target returning salmon. Air exposure was also associated with depressed ventilation rates (as in Gale *et al.* 2011b), an effect also seen in largemouth bass (Thompson *et al.* 2008). While we did not quantify ventilatory amplitude, if we assume that

depressed ventilation rates translate to decreased respiratory gas exchange, it appears that oxygen deprivation by air exposure results in an impaired ability to correct oxygen deficits incurred during anaerobic exercise with or without air exposure. Further, our results confirmed the findings of Gale *et al.* (2011b) that elevated temperatures result in greater ventilatory impairment in sockeye salmon, which is particularly troubling considering that excess post-exercise oxygen consumption is greatest for fish in warmer water (Lee *et al.* 2003a). Elevated temperatures also increased the duration of equilibrium loss (also as in Gale *et al.* 2011b). Thus, we have evidence that our initial prediction of increasing mortality with increasing temperature and magnitude of capture stress may have been correct, despite a lack of statistical evidence showing that capture treatment affected 24-hour survival.

In conclusion, the current study demonstrates that while individual sockeye salmon vary in their responses to simulated capture stressors, exhaustive exercise coupled with air exposure at high temperatures can result in a greater mortality risk for released fish than for those not exposed to simulated capture. Fish in our study that died within 24 hours of capture treatment were characterized by higher blood chemistry stress indices (higher hematocrit and plasma lactate and cortisol concentrations; lower hemoglobin, MCHC, and plasma glucose, sodium, chloride, and potassium concentrations), all of which could be used to predict the probability of mortality within 24 hours. Air exposure and warm water temperatures were also associated with prolonged equilibrium loss and depressed ventilation at release, which in turn could also be used to predict the probability of mortality within 24 hours. If our results could be validated in the field, managers would gain a better understanding of the capture-release mortality of sockeye salmon, as well as the ability to predict survival of released individuals.

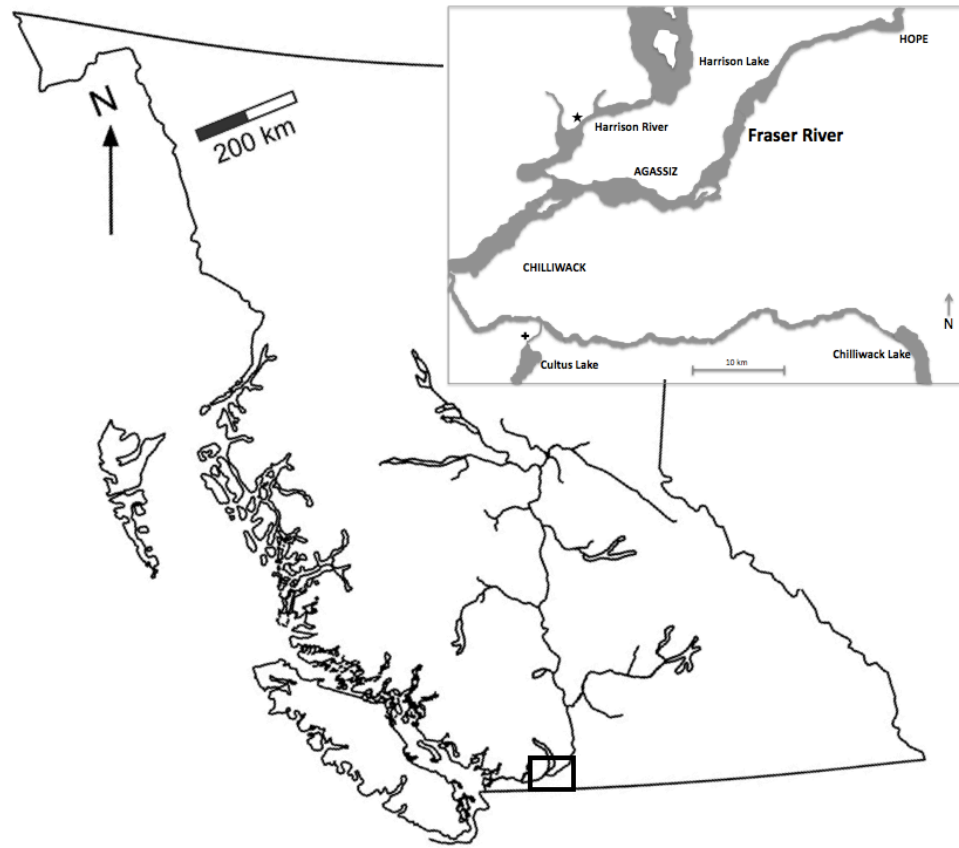


Figure 4.1 - British Columbia and the Fraser River, which drains almost one-third of the province. Inset is the study area, with the cross marking the fish capture site on the Harrison River, and the star marking the Cultus Lake Salmon Research Laboratory, where experiments took place

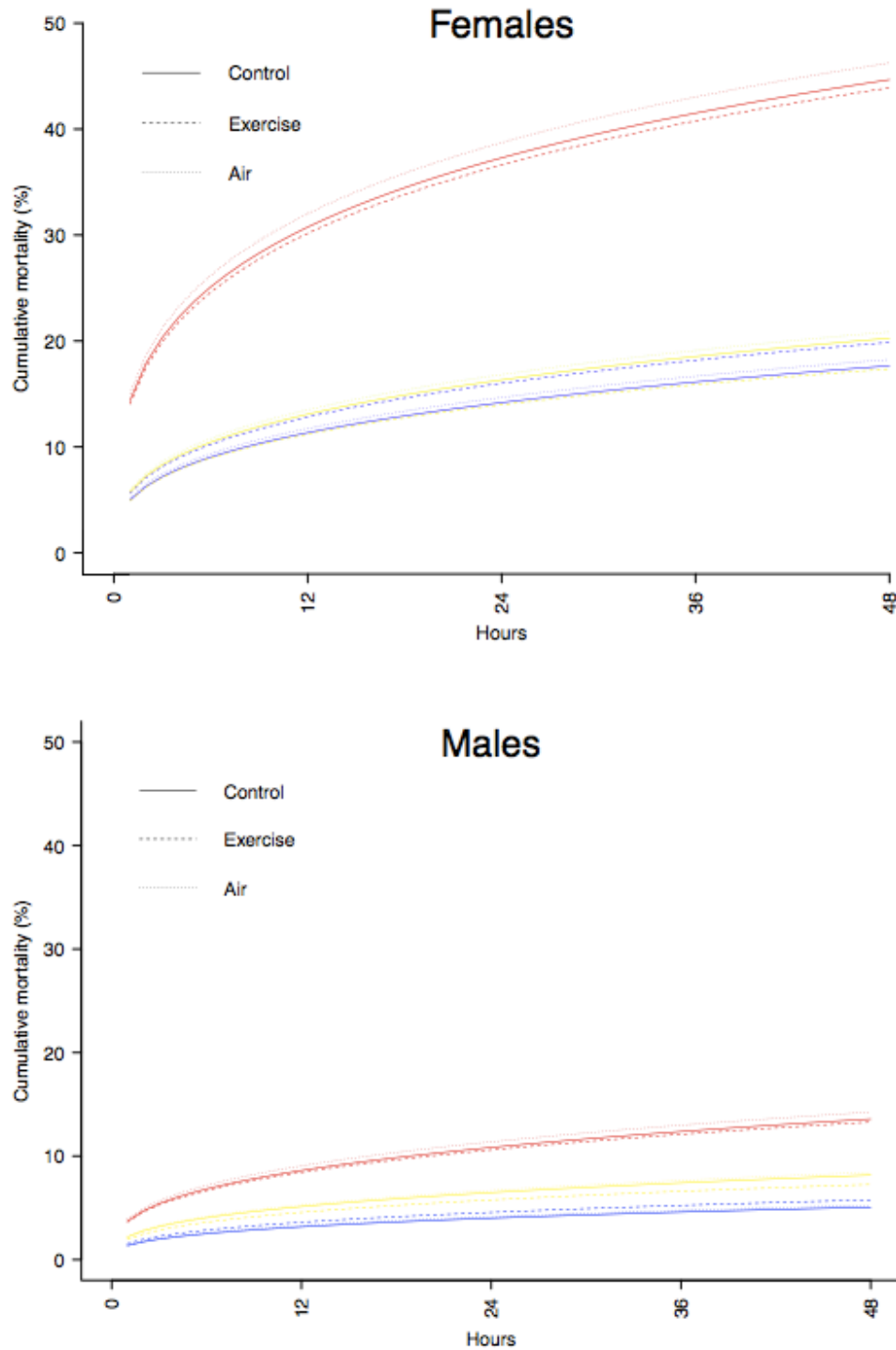


Figure 4.2 - Modeled cumulative mortality of female and male sockeye salmon in hours after simulated capture treatment, with blue lines indicating 13°C, yellow lines indicating 16°C, and red lines indicating 19°C temperature treatments. Line style indicates simulated capture treatment.

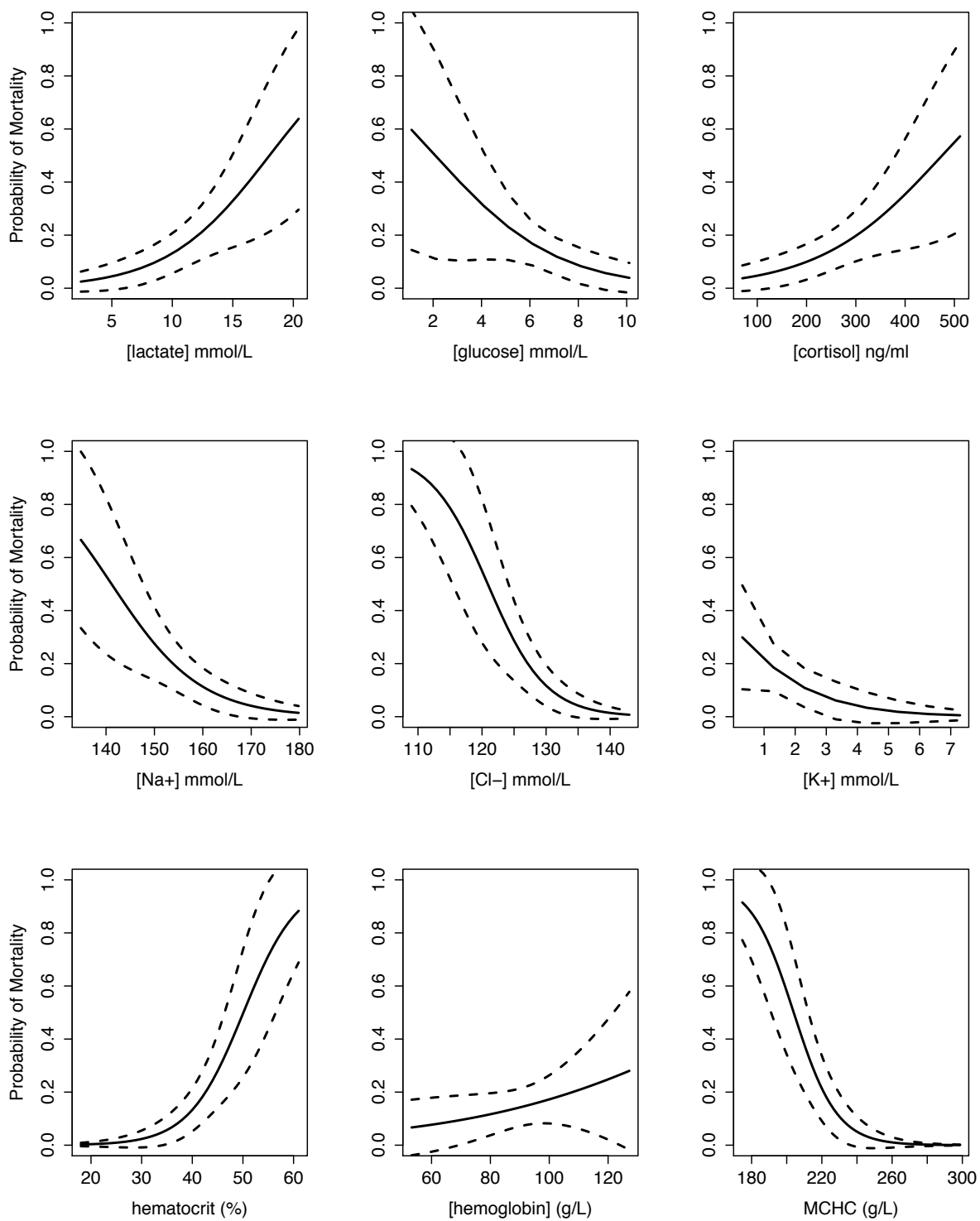


Figure 4.3 – Logistic regression of blood and plasma parameters and mortality within 24-hours of capture treatment, showing probability of mortality (solid lines) and 95% confidence intervals (dashed lines).

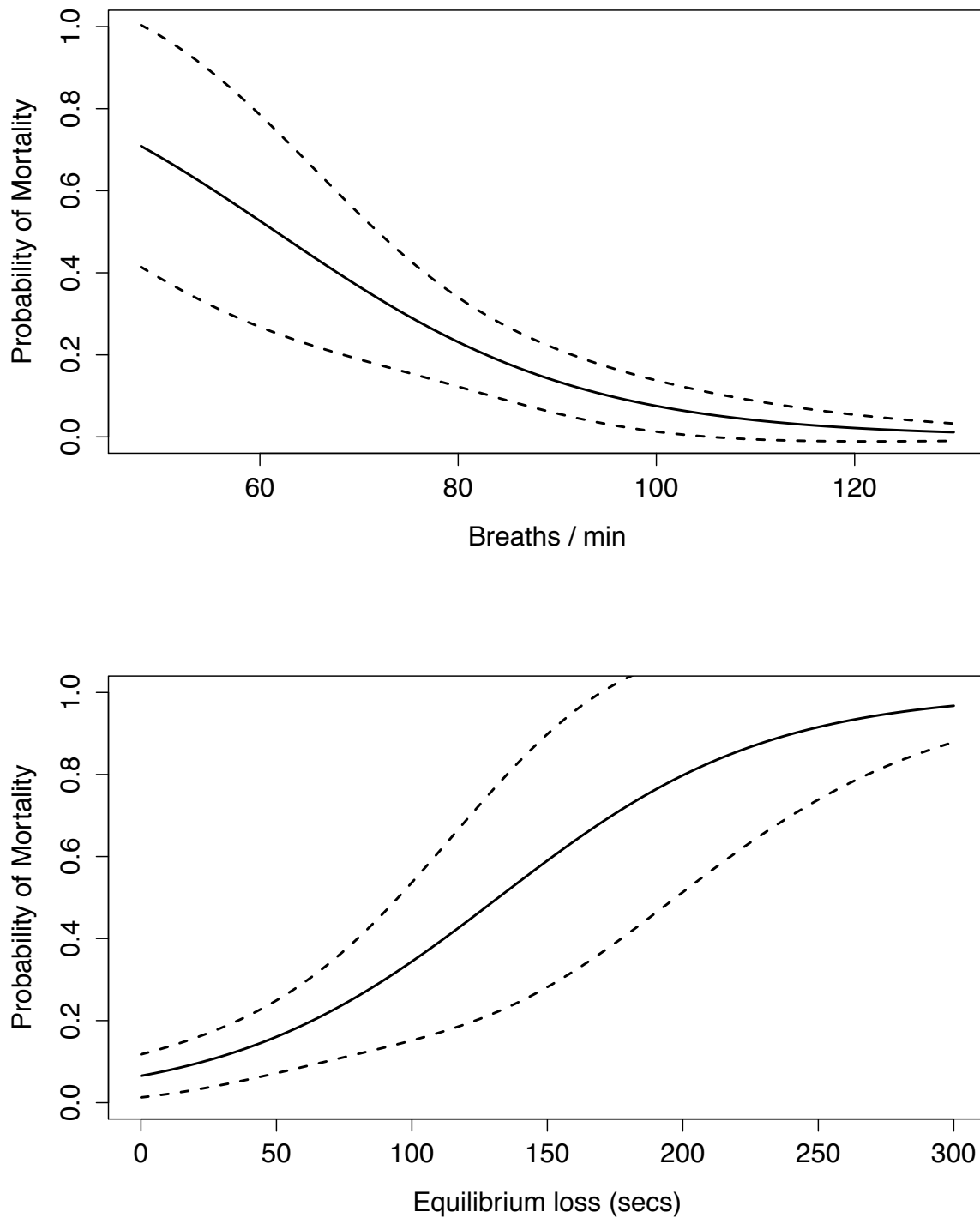


Figure 4.4 - Logistic regression of ventilation rate (top) and duration of equilibrium loss (bottom) immediately post-capture treatment, and mortality within 24-hours of capture treatment, showing probability of mortality (solid lines) and 95% confidence intervals (dashed lines).

Table 4.1 - Experimental factors of the top eight models (95% confidence set) predicting 48-hour mortality of experimental sockeye salmon.

Model	K	AICc	delta.AICc	weight.AICc	Log.likelihood
temp + sex	5.000	397.695	0.000	0.540	-193.518
sex	3.000	400.698	3.003	0.120	-197.220
temp + treat + sex	7.000	400.698	3.004	0.120	-192.720
temp * sex	7.000	401.782	4.087	0.070	-193.262
treat + sex	5.000	403.046	5.352	0.037	-196.193
temp	4.000	404.013	6.318	0.023	-197.789
temp + treat * sex	9.000	404.117	6.422	0.022	-192.024
(no effects)	2.000	404.535	6.841	0.018	-200.204

Table 4.2 - Mean (+/- standard error of mean, SEM) plasma constituent concentrations measured from sockeye salmon at 30 min after the application of a simulated capture stressor at 13, 16, or 19°C. F- and p-values for 2-way ANOVA are presented, (n = 32±1 for treatment groups and n=33±4 for temperature groups), with bold text indicating significance after False Detection Rate correction for multiple comparisons.

Parameter	Capture Treatment	Mean ± SEM	Temp Group (°C)	Mean ± SEM	Capture Treatment		Temperature Treatment	
					F	p	F	p
chloride (mmol/L)	no exercise	130.00 ± 1.00	13	131.52 ± 1.34	2.54	0.084	1.15	0.86
	exercise	131.84 ± 1.48	16	131.61 ± 1.33				
	exercise + air	133.77 ± 1.19	19	132.40 ± 1.03				
cortisol - females (ng/ml)	no exercise	291.58 ± 23.57	13	271.32 ± 18.35	0.0068	0.99	0.29	0.75
	exercise	313.87 ± 25.28	16	291.69 ± 28.65				
	exercise + air	271.40 ± 20.27	19	333.40 ± 21.47				
cortisol - males (ng/ml)	no exercise	162.83 ± 12.68	13	143.16 ± 12.60	0.49	0.61	0.47	0.63
	exercise	165.59 ± 15.15	16	154.12 ± 15.12				
	exercise + air	156.62 ± 12.82	19	188.83 ± 9.33				
glucose (mmol/L)	no exercise	6.22 ± 0.24	13	6.62 ± 0.29	2.55	0.084	0.38	0.69
	exercise	7.17 ± 0.29	16	6.93 ± 0.27				
	exercise + air	7.28 ± 0.30	19	7.15 ± 0.31				
lactate (mmol/L)	no exercise	5.60 ± 0.49	13	8.49 ± 0.69	10.82	<0.00001	0.82	0.44
	exercise	9.75 ± 0.55	16	9.22 ± 0.71				
	exercise + air	12.3 ± 0.69	19	9.82 ± 0.87				
osmolality (mOsm/kg)	no exercise	311.12 ± 2.21	13	320.79 ± 2.86	6.76	0.00187	0.15	0.86
	exercise	321.73 ± 2.80	16	319.52 ± 2.95				
	exercise + air	331.15 ± 2.53	19	323.06 ± 2.88				

Parameter	Capture Treatment	Mean ± SEM	Temp Group (°C)	Mean ± SEM	Capture Treatment		Temperature Treatment	
					F	p	F	p
potassium (mmol/L)	no exercise	2.42 ± 0.19	13	1.74 ± 0.18	1.39	0.25	0.88	0.42
	exercise	2.08 ± 0.27	16	2.14 ± 0.21				
	exercise + air	1.69 ± 0.20	19	2.43 ± 0.29				
sodium (mmol/L)	no exercise	156.70 ± 1.41	13	160.17 ± 1.59	1.33	0.27	0.034	0.97
	exercise	161.49 ± 1.71	16	159.83 ± 1.54				
	exercise + air	163.10 ± 1.60	19	161.16 ± 1.84				
MCHC (g/L)	no exercise	255.23 ± 4.56	13	245.21 ± 4.89	4.87	0.0099	0.74	0.48
	exercise	238.10 ± 4.41	16	244.98 ± 4.86				
	exercise + air	230.82 ± 4.74	19	233.49 ± 4.58				
ventilation (min ⁻¹)	no exercise	104.44 ± 2.21	13	87.39 ± 2.51	4.67	0.012	0.33	0.72
	exercise	96.85 ± 2.86	16	97.19 ± 3.09				
	exercise + air	79.48 ± 2.63	19	98.07 ± 3.71				
hematocrit (%)	no exercise	35.00 ± 1.16	13	36.61 ± 1.16	0.47	0.63	2.02	0.14
	exercise	37.36 ± 1.38	16	36.44 ± 1.51				
	exercise + air	40.23 ± 1.37	19	39.68 ± 1.34				
hemoglobin (g/L)	no exercise	88.42 ± 2.52	13	88.97 ± 2.43	1.51	0.23	0.2	0.82
	exercise	88.14 ± 2.81	16	87.94 ± 3.15				
	exercise + air	91.96 ± 2.77	19	91.73 ± 2.44				

Chapter 5: Conclusion

Exhaustive exercise and air exposure are two primary components of capture-release fisheries, and the resulting physiological disturbances experienced by fish must be overcome if released individuals are to survive. In my review, I found that for many fish species, capture-release events occurring at relatively warm temperatures usually resulted in lower survival and greater physiological disturbances than the same scenarios occurring at a cooler temperature. Mortality and sublethal consequences resulting from capture-release stressors often begin increasing at temperatures within the optimal range (Chapter 2, Gale *et al.* 2011a), although this was not explicitly clear as researchers often failed to put their experimental temperatures into context for the study species.

In my experiments with sockeye salmon (Chapters 3 and 4), blood chemistry confirmed that simulated capture treatments successfully induced anaerobic burst-type exercise, a major component of gear encounters that has been shown by others to result in lactic acid and other metabolites accumulating in tissues (e.g. Wilkie *et al.* 1997, Suski *et al.* 2006). Plasma lactate was significantly elevated in capture-treated fish in both experiments, a result that was magnified in air-exposed fish. Patterns of osmoregulatory disturbance after capture were also evident in both experiments. Sockeye salmon experienced the greatest mortality at temperatures that exceeded stock-specific optima (Eliason *et al.* 2011). I was able to predict the probability of survival of Weaver Creek sockeye salmon after capture-release using a variety of physiological parameters. Collectively, my results suggest that individuals varied in the magnitude of their responses to capture stressors and thus mortality was not associated directly with simulated capture, however fish demonstrating the greatest physiological disturbances post-capture were less likely to survive the following days. The ability to predict mortality using two easily

observable impairment metrics, duration of equilibrium loss and ventilation rate post-capture, is a highly novel finding and has direct management applications (discussed below).

Late-run (Weaver Creek stock) sockeye salmon, particularly females, experienced much higher mortality post-treatment than did summer-run fish that were challenged with a higher temperature. This lends support to previous research that found summer-run sockeye to be more robust at higher temperatures than the other run-timing groups, presumably because they have adapted to run-timing-specific historical river migration conditions (Farrell *et al.* 2008). It also suggests that 21°C may not be the critical thermal maximum for some stocks of summer-run fish given that the late-Stuart / Stellako stock suffered from much higher mortality than did the Chilko stock, despite these stocks being co-migrants and thus having the same migratory thermal experience. Eliason *et al.* (2011) demonstrated that Chilko sockeye salmon have a higher and broader thermal tolerance for aerobic scope compared to other stocks, and Donaldson *et al.* (2010b) saw greater survival of Chilko vs. Adams River sockeye salmon after capture-release and radio tag insertion. Recently, Martins *et al.* (2011) modeled the survival of several hundred telemetry tagged Fraser sockeye from several populations and found that compared with other stocks, survival of Chilko sockeye salmon was not as sensitive to warming temperatures. My research adds to the body of evidence suggesting that stock-specific thermal tolerance exists within (not merely between) run-timing groups, and that these differences are an important consideration in sockeye salmon management and science (Lee *et al.* 2003b, Farrell *et al.* 2008, Eliason *et al.* 2011).

Whereas some captured sockeye salmon died immediately after release in my experiments, most appeared to recover from my simulated capture stressors and swim away in a relatively short time (minutes). However, my results showed that there may be strong latent effects of capture

stress that can result in mortality hours to days after release. Donaldson *et al.* (2011) captured adult Fraser River sockeye by beach seining and angling, then inserted radio transmitters and tracked their fate to spawning grounds using remote telemetry arrays. Both capture approaches involved air exposure and vigorous exercise as in my study. The authors found strong latent effects – one day after release survival, ~ 96% of all tagged fish were alive and migrating, however after 4 days, only ~60-73% of fish were still alive and only 36-52% reached spawning areas. Managers need to consider the scale of such latent mortality, as it is generally not well accounted for when setting escapement targets. The success of capture-release as a conservation measure in any fisheries sector is contingent on high survival rates of released fish. If survival or fitness of released fish is significantly compromised, it may present a major conservation concern when applicable to vulnerable or threatened populations.

My physiological findings in Chapter 4 could aid fishers, particularly anglers, in making decisions about whether captured fish should be released. My results suggest that if fish do not regain upright orientation within 2 minutes of being returned to the water, they should be kept (if permitted), as these fish had a less than 50% probability of survival after 24 hours. An even more rapid test, although perhaps more difficult to perform accurately in the river, is to measure ventilation rate immediately after returning the fish to water. Fish ventilating slower than one breath per second also had less than 50% probability of survival. The findings presented in Chapters 3 and 4 demonstrate that air exposure should always be avoided for sockeye salmon intended for release, in order to maximize survival, decrease stress, and minimize vulnerability to secondary capture by fishers or animal predators. Information regarding latent mortality, rapid survival assessments and the consequences of air exposure could easily be disseminated in annual angler guide pamphlets available online and with fishing licenses, and would provide conservation minded anglers confidence that they are using scientific best practices.

Overall, my results suggest that even relatively brief air-exposure, particularly at warm temperatures, can decrease the probability of survival for released sockeye salmon. Thus, fishers should ensure to minimize air exposure when temperatures are warm and sockeye salmon are to be released. At extremely warm temperatures, sockeye salmon suffer high mortality even without the added stressors of escaping from fishing gear, or being released following capture (Hinch and Martins 2011). In eastern Canada, catch and release angling for Atlantic salmon are closed when river temperatures exceed 18°C in order to facilitate migration survival under difficult conditions (Dempson *et al.* 2002). There are no regulations like this for sockeye salmon in the Fraser River, but my work suggests that thermal criteria need to be incorporated into management decisions about opening and closing river fisheries. Martins *et al.* (2011) clearly showed that for most stocks, when temperatures exceeded 19°C, *en route* mortality became relatively high (>40%) in fish that were handled (e.g. captured, air exposed and tagged) in freshwater. My results support the notion that 19°C is a critical thermal criteria.

My research contributes to the growing body of knowledge demonstrating that sockeye salmon are vulnerable to warming river temperatures, particularly when overlaid by a secondary stressor like fisheries capture. A greater understanding of the stock-specific mortality consequences of capture-release on sockeye salmon will allow managers to improve population-level management. This understanding can be improved through additional laboratory studies involving other stocks of sockeye salmon (not studied in this thesis), as well as the other Pacific salmon species, using ecologically relevant temperature ranges. Findings from laboratory studies will be particularly valuable when incorporated with telemetry research to investigate survival and fitness consequences on wild migrants after fisheries capture and release, with particular attention to the stock-specific role of water temperature. Laboratory and field telemetry studies investigating Pacific salmon capture-release mortality from all fisheries sectors

are currently underway by researchers in our lab and others (Scott Hinch and Steven Cooke, Principal Investigators). Preliminary work evaluating assisted recovery techniques and reflex impairment mortality predictors, such as has been examined in commercially caught coho salmon bycatch (Farrell *et al.* 2001a, Raby *et al.* in press) is also underway (Kendra Robinson, University of British Columbia – personal communication). One telemetry study has shown that sockeye salmon captured and tagged in the marine environment had greater migration success than those tagged in freshwater (Martins *et al.* 2011), thus it would be prudent for future research to evaluate capture-release mortality at various stages of the spawning migration. Sockeye salmon homing from the ocean to natal streams experience numerous concurrent and successive challenges as a backdrop to capture-release stressors, and knowledge of the interaction of these with thermal stressors is in its infancy. Certainly this area of research is of growing importance in the face of threatened fish and fisheries and global climate change.

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