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At the intersection of fisheries and climate change: Emergent challenges for Pacific
salmon management in a warming world

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Abstract

At the intersection of fisheries and climate change: Emergent challenges for Pacific salmon management in a warming world

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A changing environment is not a new challenge for Pacific salmon (*Oncorhynchus* spp.). This group of fishes has proven resilient, persisting over millions of years while surviving massive changes in climate and physical habitats. There is therefore reason to believe that salmon will be able to adapt to the changes anticipated in association with global climate change. Indeed, the level of warming predicted for the coming century seems a surmountable challenge for salmon at the genus level. However, climate change is impacting and will continue to impact individual populations, driving marked changes in their ecology, abundance and life-histories. The distinction between species and population is important because the majority of ecological, cultural and economic values provided by salmon are manifest at local or regional scales and tied to specific populations, species and life-history types. Furthermore, it is typically at these scales that fisheries and fish habitats are managed. Although the influence of past climate variability on the productivity of salmon populations demonstrates sensitivity of these species to environmental change, unanticipated and unintuitive outcomes are possible given the complexity and diversity of the species and their life-histories. Understanding past variability and predicting future

trajectories of salmon populations therefore requires an in-depth understanding of the mechanisms that link environmental change to population productivity. This information can help to ensure that fisheries management serves to increase resilience of salmon populations and avoids actions that amplify potential negative consequences of climate change.

This dissertation seeks to contribute to the informed management of Pacific salmon in a warming world through development of theory and in-depth exploration of cases where salmon populations have responded to changing environments. Chapter 1 considers the underappreciated phenomenon of temporal selection in fisheries and its implications for climate adaptation by salmon and other fishes. Chapter 2 tests a series of hypotheses that link observed warming in Lake Iliamna, Alaska to changes in sockeye salmon life-history and productivity. Chapter 3 describes a novel pattern of adult mortality in spawning sockeye salmon and demonstrates that low streamflow can create habitat conditions under which density-dependent spawning failure may occur. Chapter 4 describes changes in reproductive timing of Cedar River, Washington sockeye salmon and examines the relative influence of natural and artificial selection on phenological change and climate change resilience. Collectively, this research demonstrates some of the diverse responses that can be expected in salmon populations responding to climate change, emphasizes the importance of life-history and phenological diversity as adaptive pathways for populations impacted by climate change, and argues for management that maximizes these forms of diversity.

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DEDICATION

I dedicate this work to my family, who have inspired and encouraged me to pursue my passion since I first looked toward the water in wonder.

Without their support I would not have had the means – financially, emotionally, intellectually or otherwise – or motivation to see this through.

My grandparents, Robin and Don, Helen and Lee.

My parents, Doug and Jan

My sister, Nicole

My wife, Kara and our very soon to be named baby

GENERAL INTRODUCTION

Identifying and predicting climate impacts on population productivity is vital for natural resource management and the conservation of rare or threatened species. Observed warming in recent decades has provided opportunity for empirical, *in situ* research on the biological impacts of climate change across a broad geographic and taxonomical range (Parmesan and Yohe 2003; Parmesan 2006). Biological responses to these physical changes have been diverse and have been documented in a wide variety of species including mammals, birds, fish, amphibians, plants and invertebrates (Walther et al. 2002). Species and population-level climate change impacts including alterations in spatial distribution, the timing of key life history events, demographics, growth and survival have all been observed in multiple cases (Schmitz et al. 2003; Parmesan 2006; Burrows et al. 2011; Doney et al. 2012).

A changing environment is not a new challenge for Pacific salmon (*Oncorhynchus* spp.). Indeed, despite (or perhaps because of) a complex life-cycle that typically requires distant migrations through diverse habitats, salmon have proven extremely successful at adapting to environmental change on timescales ranging from minutes to eons (Waples et al. 2008). Of course, the pathways to adaptation vary depending on the timescale over which change is experienced. At one end of the spectrum, actions such as behavioral thermoregulation allow salmon to optimize their experienced environment in heterogeneous and dynamic habitats such as dendritic river systems (Newell and Quinn 2005; Keefer et al. 2009). At the other end, evolutionary processes including local adaptation and – at the extreme – speciation have enabled the genus *Oncorhynchus* to persist despite massive changes to physical habitats and global climate (Waples et al. 2008; Hendry 2010). In between, life-history plasticity and variability including partial migration and alternative reproductive tactics have buffered against year-to-year

variability in environmental conditions by spreading risk across time and space (Quinn 2005). These adaptive processes are also intertwined as behavior and life-history commonly have a genetic basis and can evolve in response to selection (Dunlop et al. 2007).

Pacific salmon have persisted over millions of years and survived massive changes in climate (Waples et al. 2008). As such, the level of warming predicted for the coming century seems a surmountable challenge for *Oncorhynchus*. Nevertheless, although the genus is unlikely to vanish in the near term because of climate change, individual populations will experience marked changes in their ecology, abundance and life-histories; with local extirpations and new colonization likely (Crozier et al. 2008). The majority of ecological, cultural and economic value provided by salmon are manifest at local or regional scales and tied to specific populations, species and life-history types. Furthermore, it is typically at these scales that fisheries and fish habitats are managed (Schindler et al. 2008). Thus, although it is important to consider Pacific salmon climate adaptation and resilience at boarder spatial scales, it is at the local scale which the mechanisms of change must be understood and managed. And although the influence of past climate variability on the productivity of salmon populations demonstrates sensitivity of these species to environmental change (Hare et al. 1999; Beamish et al. 1999; Irvine and Fukuwaka 2011), unanticipated and unintuitive outcomes are possible given the complex life histories of the species. Understanding past variability and predicting future trajectories of salmon populations therefore requires a more in-depth understanding of the mechanisms that link environmental change to population productivity. Such an understanding seems possible only by investigating change at finer spatial and taxonomic scales.

Moving from the species level to the stock or population level changes the type of impacts likely result from warming waters. At the species level, it is possible to envision the

response to climate change as a movement through space. In simplistic terms, it is expected that species track shifting temperature windows poleward as their optimal thermal habitat moves towards higher latitudes. Such shifts have indeed been documented, particularly in marine environments where physical barriers to movement are scarce (Pinsky et al. 2013). However, this coarse scale of observation obscures the diverse processes that may be occurring at the local level. In species such as salmon with high levels of local adaptation and relatively limited connectivity between populations, it seems unlikely that movement through space is commonly occurring in response to a warming (Lin et al. 2008; Piou and Prévost 2013). Rather, local changes in abundance, life-history, habitat capacity, phenology and demographics are likely to be the more widespread and visible consequences of climate change (Crozier et al. 2008). Interestingly, when observed collectively across populations these local processes may mimic a spatial shift if southern populations living near physiologically limiting conditions are extirpated, or if northern populations take advantage of improved growth conditions and increase in abundance.

Biological responses to climate change will in turn have important implications for fisheries management. In the face of changing ecosystems and altered the distributions of fishes modern management regimes will need to be adaptable, and consider the ways in which future conditions may reduce the efficacy of regulations based on historical conditions (Melnychuk et al. 2014). Maintaining diversity across multiple scales, will also be necessary. Recent research highlights the importance of life-history diversity as a buffer against a variable and uncertain environment (Hilborn et al. 2003; Schindler et al. 2010). Mounting evidence also suggests that genetic diversity is important for productivity. This type of diversity may be negatively impacted by human activities, including fishing which can exert selective pressures on populations, driving

evolutionary responses that impact productivity (Kuparinen and Hutchings 2012). Climate change and fishing are likely to interact in shaping responses of salmon populations, as both can alter the relative fitness of different life-history pathways with consequences for productivity and population dynamics. Such changes may also serve as forces of natural or artificial selection with long-term evolutionary consequences (Quinn et al. 2002). Benchmarks for biological success in salmon management will thus need to evolve in light of the challenges posed by climate change and unintended consequences of fisheries and management induced selection.

In a warming world Pacific salmon face an uncertain future. Although the long-term consequences of climate change may be impossible to avoid, in the near-term fisheries management can serve to either exacerbate or ameliorate these impacts. An improved understanding the mechanisms by which salmon respond to environmental change can ensure that management actions do not reduce the adaptive capacity of populations. This dissertation contributes to such an understanding by examining the intersection of climate change and salmon management. Chapter 1 considers the underappreciated phenomenon of temporal selection in fisheries and its implications for climate adaptation. Through literature review, simple mathematical and graphical illustrations, I demonstrate the diverse management actions and fishermen's behaviors that cause mortality rates to vary through time and impose selection on phenological traits. I then reviewed the likely biological impacts of such selection for populations and stock complexes before considering the ways in which temporal selection may reduce adaptive capacity or drive maladaptation to climate change. Chapter 2 tests a series of hypotheses that link observed warming in Lake Iliamna, Alaska to changes in sockeye salmon (*O. nerka*) life-history and productivity. I found that although warming waters have contributed to dramatic changes in life-history patterns in the lake's sockeye populations there has been no

observable impact on fisheries productivity at the basin scale, suggesting that current management targets remain effective despite observable impacts of climate change. In Chapter 3 I describe a novel pattern of adult mortality in sockeye salmon spawning in Hansen Creek, Alaska. I demonstrated that low streamflow can create habitat conditions under which density dependent spawning failure may occur. Finally, in Chapter 4 I use a series of statistical and mathematical models to describe changes in reproductive timing of Cedar River, Washington sockeye salmon and examine the relative influence of natural and artificial selection on phenological change. I find that trends in spawning timing are best explained by a combination of hydrologic change and artificial selection imposed by hatchery supplementation. In particular, since the mid-1990s hatchery selection has contributed to an advance in median spawning date of over three weeks. I argue that this artificial selection may be driving maladaptation to climate change as earlier spawning individuals appear to experience lower fitness than their later spawning counterparts. Collectively, this research demonstrates some of the diverse responses that can be expected in salmon populations responding to climate change, emphasizes the importance of life-history and phenological diversity as adaptive pathways for populations impacted by climate change, and argues for management that maximizes these forms of diversity.

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CHAPTER 1 Selection on the timing of migration and breeding: A neglected aspect of fishing-induced evolution and trait change

ABSTRACT

Fishing can drive changes in important phenotypic traits through plastic and evolutionary pathways. Size-selective harvest is a primary driver of such trait change, has received much attention in the literature, and is now commonly considered in fisheries management. The potential for selection on behavioral traits has received less study, but mounting evidence suggests that aggression, foraging behavior, and linked traits can also be affected by fishing. An important phenomenon that has received much less attention is selection on reproductive phenology (i.e. the timing of breeding). The potential for this type of “temporal selection” is widespread because there is often substantial variability in reproductive phenology within fish populations, and fisheries management strategies or fishermen’s behaviors can cause fishing effort to vary greatly over time. For example, seasonal closures may expose only early or late breeding individuals to harvest as observed in a range of marine and freshwater fisheries. Such selection may induce evolutionary responses in phenological traits, but can also have demographic impacts such as shortened breeding seasons and reduced phenotypic diversity. These changes can in turn influence productivity, reduce the efficacy of management, exacerbate ongoing climate-driven changes in phenology and reduce resilience to environmental change. In this essay we describe how fisheries management can cause temporal variability in harvest, and describe the types of selection on temporal traits that can result. We then summarize the likely biological consequences of temporally-selective fishing on populations and population complexes, and conclude by identifying areas for future research.

INTRODUCTION

The management and conservation of animal populations has traditionally focused on abundance and demographics as indicators of sustainability (Ricker 1946; Hilborn 1985a). More recently, the effects of human activities including harvest and habitat alteration on phenotypic traits have become broadly recognized (Hendry et al. 2008; Allendorf and Hard 2009; Darimont et al. 2009). Through phenotypic plasticity and microevolution, traits such as growth rate, behavior, morphology, and age at maturity have responded to anthropogenic influence in various taxa (Palkovacs et al. 2012). Notable examples of human-induced trait change include reduced age and size at maturity in many commercial fish stocks (Sharpe and Hendry 2009), altered travel patterns in migratory birds resulting from habitat alteration (Berthold et al. 1992), declines in body weight and horn size in wild sheep (*Ovis canadensis*; *Ovis dalli stonei*, Bovidae) subjected to trophy hunting (Coltman et al. 2003; Douhard et al. 2016), and changes in feeding and reproductive behavior of recreationally harvested largemouth bass populations (*Micropterus salmoides*, Centrarchidae) (Cooke et al. 2007). Such changes can profoundly affect the ecology, productivity and viability of animal populations (Palkovacs et al. 2012), and understanding the drivers of trait change is therefore critical to the sustainability of affected species (Stockwell et al. 2003).

A range of human activities may drive rapid trait change in wild populations such as habitat alteration (Berthold et al. 1992; Franssen 2011), modification of thermal regimes (Bradshaw and Holzapfel 2006), pollution (Mooney and Cleland 2001) and harvest (Hendry et al. 2008; Palkovacs et al. 2012). Exploited populations are especially susceptible to human-induced trait change – both plastic and genetic – because hunting and fishing methods are commonly selective with regard to size and behavior, and because reduced densities often

increase growth rates via compensatory density dependence (Allendorf and Hard 2009; Sharpe and Hendry 2009; Kuparinen and Festa-Bianchet 2017). Furthermore, artificial selection from harvest is often strong relative to forces of natural selection, and so rapid phenotypic change is possible (Edeline et al. 2007; Allendorf and Hard 2009). Because harvest can impose particularly strong selection (Edeline et al. 2007), and because fishes and aquatic invertebrates make up the majority of harvested wild taxa, fisheries-induced trait change is particularly widespread and well-documented (Fenberg and Roy 2008; Palkovacs et al. 2012). Indeed, it has long been recognized that fishing can be selective with regard to morphological and life-history characteristics (Miller 1957; Hamley 1975; Handford et al. 1977). Large fish are often preferentially harvested through some combination of regulations on fish size or gear, or from harvester preference, exerting selection on phenotypic traits including size, growth rate, and age at maturity (Birkeland and Dayton 2005; Edeline et al. 2007). Interest in the consequences of size-selective harvest on fisheries ecology and sustainability has grown rapidly in recent decades (Policansky 1993; Fenberg and Roy 2008). By 2008, size-selective harvest had been documented for over 120 species of fish and marine invertebrates (Fenberg and Roy 2008) and many papers warned of the dangers of fisheries-induced evolution for fisheries sustainability (Law 2000; Conover and Munch 2002; Kuparinen and Merilä 2007; Fenberg and Roy 2008; Kuparinen and Hutchings 2012). However, selective fishing is not limited to size-related traits. Recent research has documented selection on various behavioral traits (Heino and Godo 2002) including removal of aggressive individuals by angling (Cooke et al. 2007) and individuals with bold foraging behavior by gillnets (Biro and Post 2008).

While the impact of size-selective fisheries have been widely examined, the potential for reproductive phenology to be altered through anthropogenic selection as been largely ignored,

despite the fact that variation in the timing of breeding and associated physiological and behavioral changes plays a critical role in the productivity of fish populations. Constraints on fishing effort imposed by management, behavior of fishermen, or environmental conditions can cause fishing intensity to vary over time, and fisheries mortality can therefore be selective with regard to important temporal traits such as spawning or migration date (Quinn et al. 2007; Loher 2011; Peer and Miller 2014). In this essay we call attention to the phenomenon of temporally-selective fishing and review relevant literature from related areas of research. We argue that it is likely to be very common, can reduce the diversity, productivity, and sustainability of fish populations and stock-complexes, and therefore merits further research. We first describe how management and harvester behavior can cause temporal variability in mortality rates within exploited populations, and use a hypothetical population to illustrate the types of selection on temporal traits that can result. We then summarize the likely biological consequences of temporally-selective fishing on single populations and population complexes composed of multiple stocks with unique timing traits, and conclude by suggesting important avenues for future research.

THE PREVALENCE OF TEMPORAL SELECTION IN FISHERIES

In most fishes and macroinvertebrates, breeding and migration occur predictably in association with seasonal, semilunar or other environmental cycles (Ims 1990; Yamahira 2004; Asch 2015). The typical timing of these events is thought to reflect evolutionary optima given the selective pressures on adults and offspring, and reproductive phenology therefore plays a central role in the biology of many species (Lowerre-Barbieri et al. 2011; Quinn et al. 2016). A series of interrelated behavioral and physiological processes commonly precede reproduction in

fishes, including gametogenesis, migration, altered feeding behavior, aggregation, and courtship (Figure 1.1). Variation in any of these traits can influence susceptibility to fishing within or between populations, and fisheries can therefore selectively remove fish based on various aspects of their reproductive phenology. Furthermore, fishing practices and regulation are commonly centered around these events, either to exploit or protect the migrants or breeders (van Overzee and Rijnsdorp 2014; Sadovy de Mitcheson 2016). As a result, there is significant potential for fishing to interact with biologically important phenological traits (Hard et al. 2008) which may result in what we hereafter refer to as temporal selection.

Temporal selection occurs when a) individuals within a population vary in the timing of migration, spawning, or other important life history events and b) vulnerability to capture in a fishery depends on the timing of those same events. Temporally-selective fishing is therefore any pattern of harvest that results in variable mortality rates across individuals as a result of their reproductive phenology. Figure 1.2 illustrates how several common forms of selection may act on a phenological trait. For example, directional temporal selection can occur when either early or late migrating or spawning individuals are more susceptible to harvest than other parts of the population (Figure 1.2a,c), resulting in a directional change of the mean phenotype. When both early and late migrants are harvested at high rates, the resulting stabilizing selection can reduce variability in timing (Figure 2b). Lastly, disruptive selection results when early and late individuals are harvested at lower rates than the central portion of the population. This can increase variability in timing, though it may also result in fewer individuals spawning at the optimum time (Figure 1.2d).

Direct temporal management

Many fishes undertake spawning migrations or form large groups during reproduction (Harden Jones 1981; Neuenfeldt et al. 2013; van Overzee and Rijnsdorp 2014; Sadovy de Mitcheson 2016), aggregating a fisheries resource in time and space. Indeed, the majority of global fisheries catch is comprised of species that display seasonal movement patterns (Harden Jones 1981). Fishermen have long exploited these movements and aggregations, and management measures such as spatial and seasonal closures – restricting fishing in certain areas, during certain times of the year or a combination of the two – are common for protecting fish during these vulnerable periods (Loher 2011; Erisman et al. 2012; Sadovy de Mitcheson 2016). Because they are explicitly temporal in nature, typically consistent across multiple years and commonly have some basis in the reproductive biology of the targeted species, seasonal closures are a likely cause of temporal selection in fisheries; almost inevitably some fish migrating or breeding outside the closed period are vulnerable to harvest. When migratory or reproductive behavior is distributed across several weeks or months it is often technically or politically difficult to enforce a seasonal closure that protects all breeders equally. This is the case in many river fisheries for Pacific salmon (*Oncorhynchus* spp., Salmonidae), where efforts to balance the conservation of depleted stocks with full exploitation of more abundant stocks has produced a complex system of seasonal closures that can lead to differential exploitation between early and late migrating fish (Larson and Ward 1955; Washington Department of Fish and Wildlife 2016). A similar type of selection occurs in the Canadian Pacific halibut (*Hippoglossus stenolepis*, Pleuronectidae) fishery which utilizes a winter closure (typically mid-November through mid-March) to protect fish during their offshore migration and spawning. However, telemetry studies have revealed that the traditional closure does not completely protect migrants in either the

spring or fall, and the fishery can therefore exert either directional or stabilizing selection (Loher and Seitz 2008).

Non-migratory species can also be subjected to temporal selection because spawning date often varies by weeks or months within populations (Martell et al. 2000). For example, lingcod (*Ophiodon elongatus*, Hexagrammidae) typically spawn between January and April, and fisheries in Washington, British Columbia and Alaska all observe seasonal closures intended to protect nest-guarding males. Guarding males are sedentary, aggressive, and highly susceptible to both hook and line and spearfishing mortality (Martell et al. 2000; Withler et al. 2004; Stahl et al. 2014). However, in each of these regions at least some males have been observed guarding after the spring opening dates (Smith et al. 1990). Nest-guarding species in freshwater including important recreational species such as largemouth bass could also be susceptible to similar temporal selection (Gwinn and Allen 2010). This type of incomplete spawning closure selects strongly against late reproduction because such guardian males would be vulnerable, and their death also exposes the clutch to egg predators (Withler et al. 2004).

Indirect temporal management

In addition to the fixed-date seasonal closures described above, flexible closures also occur (Melnychuk et al. 2014). In such cases fishery openings vary from year to year, depending on in-season monitoring of abundance, environmental conditions, physiological state (e.g. proportion ripe, spawned or molted) or presence of non-target species. For example, in some Pacific herring (*Clupea pallasii*, Clupeinae) fisheries, harvest is delayed until the majority of females have fully developed (and therefore marketable) roe (Thynes et al. 2016). This effectively reduces the harvest rate on early spawning fish and may impose directional selection

on spawning date (Ware and Tanasichuk 1989). Fisheries that target anadromous species often are managed to allow a fixed number of individuals – “the escapement” – to pass upstream for spawning (Walters 1981). Even when managers endeavor to distribute the escapement evenly throughout a salmon run, several temporally-selective mortality patterns can result from limited harvest capacity or management uncertainty (Sethi et al. 2005). If the capacity of a fishing fleet is limited, then a “predator swamping” effect may occur during the period of peak abundance. This results in stabilizing selection by lowering harvest rates during the middle of the migration relative to the beginning and end (Figure 1.2b; Ims 1990). Alternatively, precautionary management can limit fishing during the early portion of the migration because of uncertainty in overall abundance, shifting to higher exploitation rates once the management targets have been met (i.e., directional selection as in Figure 1.2c). Quinn et al. (Quinn et al. 2007) demonstrated both patterns of selective mortality in the Egegik fishing district of the Bristol Bay sockeye salmon (*Oncorhynchus nerka*, Salmonidae) fishery. During the early 1970s harvest rates were lower during peak abundance, (as in the generalized example in Figure 1.2b), but in recent decades the managers have been reluctant to allow fishing early in the season, resulting in strongly directional selection on migration date (as in Figure 1.2c with data shown in Figure 1.3).

The case of Bristol Bay sockeye salmon demonstrates that even when management is “conservation minded” and not explicitly temporal in nature, selective harvest may nevertheless occur. Efforts to control overfishing have led to the introduction of strict harvest quotas in many fisheries, and in some cases there is a “race for fish” as fishermen strive to fulfill these quotas over very short time periods (Chu 2009). Annual quotas that lead to early closure of fisheries result in the same temporal pattern of fisheries mortality as seasonal closures (Fig 2a.), whereas daily quotas or trip limits impose stabilizing selection by reducing harvest rates during periods of

peak abundance (Figure 1.2b.). While comprehensive statistics on the prevalence of fisheries management strategies are not available, fixed or variable temporal closures are very common management practices (Melnychuk et al. 2013). The increasing focus on preventing overfishing around the world is likely to bring more fisheries under seasonal or quota management systems capable of producing temporally-selective fishing mortality (Anderson et al. 2012).

Fishermen's behavior

In addition to management actions, the behavior of fishermen is likely to result in temporally-selective fishing effort because people tend to fish when it is most economical, safe, or productive. In many areas of the world seasonally bad weather or other environmental conditions (e.g. ice, high river flows, etc.) limit fishing at certain times of the year (Smith and Wilen 2005). Because migration and breeding commonly coincide with seasonal changes in environmental conditions (ice, storms, high river flows, etc.), selection can occur if part of the population has already reproduced or migrated by the time fishing becomes safe or practical (Figure 1.2a). Fishermen are also sensitive to economic forces, and fishing effort commonly changes throughout the year in response to seasonal variability in the absolute or relative profitability of targeting different species or stocks (Katsukawa and Matsuda 2003). Fishing that targets periods of abundance (such as spawning aggregations or migrations) can increase profitability, but might also impose disruptive selection if less abundant early and late migrants or breeders experience lower fishing mortality (Figure 1.2d). Thus, various forms of temporal selection can result from intentional management actions, or as unintended consequences of management and the behavior of fishermen. Furthermore, the phenomenon is likely widespread

in both commercial and recreational fisheries, freshwater and marine environments, and across a range of taxa.

BIOLOGICAL CONSEQUENCES OF TEMPORAL SELECTION

Although little research has directly focused on the issue of temporal selection, and indeed relatively few empirical estimates of fishing selection on any trait exist (Quinn et al. 2007; Kendall and Quinn 2011, 2012), a sizeable body of literature suggests that adverse effects are probable in populations with artificially altered phenology. While biological responses will no doubt be species, fishery and context-specific, three main categories of impacts are likely to result from temporal selection. First, evolutionary responses within populations are possible if the phenological traits experiencing selection are heritable. Second, temporal selection can drive plastic and demographic trait change by altering the spawning period or by selective removal of individuals with other traits that covary with phenology (Wright and Trippel 2009). For example, early breeders often differ in size or age from later breeders (Horrall, 1981; Hutchings & Myers, 1994; Quinn et al., 2016). Finally, when fisheries target stock-complexes, temporal selection can lead to overexploitation of stocks with specific timing patterns, altering the overall timing of the complex and reducing intraspecific variability (Collie et al. 1990). Regardless of the pathway, the biological impacts of temporally-selective fishing are likely to interact with ongoing changes in reproductive phenology driven by climate change (Parmesan 2006), and this interaction may dampen or enhance the effect of temporal selection on fisheries productivity and sustainability.

Evolutionary impacts

Following evolutionary theory, spawning should be timed to maximize reproductive success by optimizing the balance between survival of parents and their progeny; reproductive phenology should reflect the prevailing environmental and ecological conditions experienced throughout the period of maturation, spawning and hatching (Cushing 1969; Sinclair and Tremblay 1984; Wright and Trippel 2009). In some cases reproductive phenology can be very plastic, responding to environmental changes such as water temperature (e.g., American shad, (*Alosa sapidissima*, Clupeinae) Leggett and Whitney 1972; striped bass (*Morone saxatilis*, Moronidae) Peer and Miller 2014). However, in other cases, especially in salmonids, the genetic control over timing of upstream migration and reproduction is much stronger, as inferred from 1) population-specific differences in timing (Webb and McLay 1996; Hodgson and Quinn 2002), 2) selective breeding experiments (Siitonen and Gall 1989; Neira et al. 2006), 3) evolution of timing in hatchery populations (Quinn et al. 2002; Hard 2004; Tipping and Busack 2004) 4) estimates of heritability in wild populations (Dickerson et al. 2005; Lin et al. 2016) 5) changes in response to fishery selection (Quinn et al. 2007), and 6) the rapid evolution of timing outside the native range of the species (Quinn et al. 2000). Indeed, there is often substantial variation in reproductive phenology – both migration and spawning timing – among and within salmon populations (Quinn et al. 2016), and heritability in these traits appears quite high (Dickerson et al. 2005; Carlson and Seamons 2008; Lin et al. 2016). In some populations more than half the variability of spawning timing in progeny can be predicted by spawning timing in adults (Quinn et al. 2000; Thériault et al. 2007). Thus, at least in salmonids the key ingredients for adaptive evolution of reproductive phenology are both present; variability on which selection can act and heritability of timing traits.

Quinn and Adams (Quinn and Adams 1996) hypothesized that because the environments experienced by anadromous salmon during migration and spawning are temporally distant from the conditions experienced by their progeny, the optimal strategy is to track long term mean conditions rather than short term variation. In contrast, for other anadromous fish such as American shad and striped bass that have shorter incubation periods, environmental conditions at the time of migration or spawning better predict conditions at hatching, thus favoring plasticity in spawning date (Peer and Miller 2014). The strength and rate of evolutionary responses to temporal selection is therefore expected to vary between taxa and salmonids may represent a somewhat extreme case. Nevertheless, even in species with more plastic reproductive phenology, evolution of timing traits is possible because trait variability commonly reflects an underlying, genetically controlled norm of reaction to external cues (Crozier and Hutchings 2014). Reaction norms such as size at maturity evolve in response to size-selective fishing (Kendall et al. 2014), and similar responses in both the mean and variability of timing traits seem probable responses to temporal selection. Fisheries-induced evolution of timing traits could have significant and long-lasting impacts on fisheries sustainability by disrupting the relationship between phenology and the ecological conditions that optimize reproductive success (Sinclair and Tremblay 1984; Cushing 1990; Beaugrand et al. 2003). However, even in the absence of a genetic response, temporal selection can drive trait changes that influence the productivity of populations and stock complexes (Wright and Trippel 2009; Lowerre-Barbieri et al. 2011).

Ecological and demographic impacts

Although reproduction follows predictable cycles in most fishes, there is often significant variation in timing between individuals from the same population (Scott et al. 2006). This

variation can buffer the population against an uncertain environment by ensuring that at least some offspring are likely to encounter favorable conditions. This variation in larval survival, commonly known as the match-mismatch hypothesis, is foundational in fisheries oceanography (Cushing 1990) and has often been demonstrated in marine systems where fishes rely on secondary productivity of zooplankton and other small pelagic prey (Sinclair and Tremblay 1984; Cushing 1990; Mertz and Myers 1994; Beaugrand et al. 2003). These fundamental principles apply to freshwater systems as well, so alteration of the normal phenology is likely to affect recruitment in lakes (e.g. Ludsin et al. 2014). Consistent with the match-mismatch hypothesis, empirical (Mertz and Myers 1994) and simulation (James et al. 2003) studies have found that longer spawning seasons increase a population's productivity and reduce recruitment variability in uncertain environments.

Because mortality from fishing reduces the probability of fish growing old and large, exploited populations – even in the absence of any size or temporal selectivity – can nevertheless experience reductions in the duration and shifts in the peak of spawning activity as a result of altered demographics (Hixon et al. 2014). Size and reproductive timing are commonly correlated; early migrating and spawning salmonids are commonly (though not universally) larger or older than those later in the run (Anderson and Beer 2009; Doctor and Quinn 2009; Bracis and Anderson 2013; Quinn et al. 2016). Indeed, this pattern occurs in many fishes, though in some cases the reverse pattern is seen (Horrall 1981). For example, in Atlantic cod the larger and older individuals tend to spawn later and over a longer period compared to younger ones (Hutchings and Myers 1994). Thus, the loss of large, old individuals in heavily exploited populations is likely to reduce overall reproductive output, but also shorten the spawning season, potentially reducing the likelihood of a 'match' of juveniles with abundant prey (Cushing 1990;

Mertz and Myers 1994). Indeed, Wright and Trippel (2009) reviewed the potential impact of demographic-driven changes in spawning timing and duration on reproductive success in fishes and argued that this is likely a major component of reduced productivity in age-truncated populations. In similar fashion to this process of demography-driven contraction of spawning seasons in exploited populations, directional and stabilizing temporal selection both serve to reduce the number individuals spawning at the extremes of the temporal distribution. As such, temporal selection may result in the same negative outcomes for impacted populations including increased variability and reduced productivity.

Size selectivity, especially the common pattern of increased exploitation of large individuals, only serves to exacerbate the issue of spawning season contraction as it further reduces the abundance of large individuals with particularly early or late spawning timing (Hixon et al. 2014). Additionally, because timing often co-varies with size and age, there is the potential for complex interactions between multiple forms of selection and demographic impacts of fishing (Anderson et al. 2008; Wright and Trippel 2009); just as size-selective fishing may influence timing, temporally-selective fishing may in turn influence size. Depending on the temporal pattern of fisheries mortality, the direction of size selectivity and the relationship between size and timing, various outcomes seem plausible in the case of dual selectivity including counteracting and reinforcing effects on correlated traits. To further complicate matters, size and phenology may also be associated with other behavioral traits such as boldness or aggression (McPhee and Quinn 1998; Biro and Post 2008). These interactions highlight the fact that both the process of, and biological responses to, all forms of fisheries selection do not happen in a vacuum and trait changes in exploited fish populations may result from selection on ostensibly unrelated traits.

Impacts on stock complexes

Advances in population genetics have revealed that many commercially exploited fish populations once thought to be relatively homogeneous have complex stock structure (Stephenson 1999; Waples and Naish 2009). Sub-populations with unique morphology, phenology, population dynamics, and ecological interactions commonly comingle despite reproductive isolation, and can therefore be harvested by a single fishery (Hilborn 1985b). When populations vary in their productivity or are differentially vulnerable to harvest, management as a single stock can lead to population-specific depletion or extirpation (Hilborn 1976). Populations exploiting even subtly different ecological niches commonly vary in productivity, thus applying a single harvest rate to a stock complex will often deplete the less productive populations (Ricker 1958; Hilborn 1985b). In salmon, differences in migratory timing between populations returning to the same river system have been exploited by managers through temporal closures to protect the weaker stocks while harvesting the more abundant (Collie et al. 1990). However, in cases where populations overlap significantly in migration timing, or timing differences are not appreciated, temporally-selective fishing can shift the overall run-timing by altering the relative abundances of the sub-stocks (Figure 1.4). For example, the sockeye salmon run to Bear Lake, Alaska is characteristically bimodal, with distinct early and late peaks, and management was based on the idea that there were distinct early and late populations. However, Boatright et al. (Boatright et al. 2004) revealed a series of populations with a continuum of migration timing. The higher exploitation rate in the middle of the season had created the appearance of bimodality by suppressing the populations migrating at that time.

Long-term monitoring of stock-complexes with fine-scale population structure has demonstrated that the relative productivity of individual stocks fluctuates significantly over time, and increased diversity therefore stabilizes overall variability in abundance; a phenomenon now commonly referred to in ecology as the portfolio effect (Schindler et al. 2010). Thus, reduced genetic and phenotypic diversity resulting from overexploitation of individual stocks serves to erode the portfolio effect and can therefore increase overall variability (Hilborn et al. 2003) and reduce the long-term resilience of stock complexes to environmental change (Moore et al. 2010). The importance of maintaining population structure and intra-specific diversity has been appreciated for decades in Pacific salmon management (Thompson 1959) but has been less widely known in marine fishes until more recently (Stephenson 1999). Reproductive timing in Pacific herring varies significantly between populations spawning in discrete locations (Haegele and Schweigert 1985; Hay 1985). However, many populations come together in the winter and during pre-spawn staging periods in coastal areas where they are fished (Ware and Tanasichuk 1989). Variability between populations in spawning date or the duration of staging are likely to influence susceptibility to fisheries, and population-specific overexploitation might occur. Such losses of genetic and phenotypic diversity may also impede the recovery of depleted stocks. For example, Ames (2004) reported that prior to intensive fishing, the Atlantic cod stock-complex in the Gulf of Maine was composed of many smaller sub-populations with unique spatial and temporal migration patterns. Many of these sub-populations were extirpated during decades of intensive harvest and even after years of drastically reduced fishing the historic diversity in migratory routes and spawning areas has not recovered (Ames and Lichter 2013).

IMPLICATIONS OF TEMPORAL SELECTION FOR FISHERIES SUSTAINABILITY

Here we have called attention to the prevalence of temporal selection in fisheries and briefly considered its causes and potential consequences. Many common fisheries management strategies and fishermen's behaviors can result in mortality that is selective with regard to reproductive phenology, and various evolutionary and plastic changes in temporal traits can result from such selection. Although the potential consequences of temporal selection have received little attention from researchers and managers, the phenomenon nevertheless has the potential to impact exploited fish populations, particularly in combination with rapid changes in phenology resulting from global climate change (Parmesan 2006). In order to clarify the risks to fisheries sustainability resulting from temporally-selective fishing we encourage further research on several key topics.

First, a prerequisite for understanding the potential impacts of temporal – or indeed any type – of fisheries selection is determining the stock structure of the exploited population or stock-complex (Stephenson 1999). Within- and between-population variability in phenology may indicate genotypic variability on which temporal selection can act, but may also reflect plastic responses to a variable environment. As noted previously, such intraspecific variability in traits can also arise from either differences between individuals or differences between populations that co-occur in time and space and may therefore be captured in the same fishery. As such, the interpretation and consequences of an observed trait change depend fundamentally on these two facets of variability. Both within- and between-population variability can produce a stabilizing portfolio effect (Schindler et al. 2010), and fisheries that erode diversity in traits including reproductive phenology are likely to have negative consequences for population productivity and resilience (Smith et al. 1991; Ames 2004; Carlson and Satterthwaite 2011). Diversity in

phenology may be particularly important as temporal traits appear to be the most likely path for adaptive evolution in response to climate change (Bradshaw and Holzapfel 2006, 2008). Thus, an improved understanding of stock structure will be critical for identifying and interpreting phenological change in response to fisheries selection and to crafting appropriate management responses.

Second, there is limited understanding of the impacts of fisheries selectivity in general (Kuparinen and Hutchings 2012) and selection on reproductive phenology in particular will have on fish population dynamics and productivity. Although theory predicts that human-driven shifts in reproductive timing could cause a larger portion of a population to spawn during less favorable periods, the consequences of such changes are difficult to observe in the real world and may be confounded by environmental modulation of reproductive phenology (Wright and Trippel 2009). As such, it is difficult to predict how different species or populations will respond to temporal selection. Simulation and experimental studies are needed to explore the consequences of human-induced changes in phenological traits and to differentiate plastic and genetic components of trait change. Individual based models have been used to explore the relative importance of genetic, plastic and demographic factors in other instances of fisheries-induced trait change, (e.g. Dunlop et al. 2007; Kuparinen and Hutchings 2012), and the demographic impacts of fisheries-induced evolution (Kuparinen and Hutchings 2012), and should also be valuable for studying changes in reproductive phenology. Such studies will help to identify the circumstances under which temporally-selective fishing reduces productivity and will also be useful for guiding conservation and management efforts by identifying species and life-history strategies that are particularly susceptible to temporal selection.

Third, the impacts of fisheries-induced changes in reproductive timing are likely to interact with ongoing change in environmental drivers of phenology such as temperature (Crozier and Hutchings 2014; Asch 2015). Depending on the form and direction of selection, these independent forces may reinforce or dampen phenological change. For example, in a case where both environmental and selective fishing impose reinforcing directional selection on spawning date, reproductive timing could change rapidly. In contrast, if environmental change and selective fishing oppose each other, it is possible that timing would remain the same but temporal selection would nevertheless be driving maladaptation to climate change and could drastically reduce productivity. This type of counteracting selection was observed in a hatchery population where unintentional artificial selection drove a rapid advance in spawning timing in Chinook salmon, despite a warming environment that favored later spawning (Quinn et al. 2002), ultimately requiring refrigeration to avoid mortality of embryos from high water temperatures in the hatchery. In light of the complex and potentially cryptic outcomes of simultaneous artificial and natural selection, we encourage researchers and managers observing phenological change in exploited populations to consider the role of temporally-selective fishing in addition to climate change.

Finally, the effectiveness of temporal fisheries managements such as seasonal closures will be impacted by changes in phenological traits, whether induced by selective fishing or climate change (Melnychuk et al. 2014). For example, as the reproductive phenology shifts away from historical conditions a closed season may become more or less protective of spawners (e.g. Peer and Miller 2014), or a closure that once protected all spawners may become temporally selective if management fails to respond to altered phenology. In response to these challenges we encourage thoughtful examination of temporal fisheries management strategies and their

potential interaction with timing traits. In particular, the biological basis of management measures that target or protect reproductive periods should be critically evaluated, and their effectiveness in light of environmental change should be considered.

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FIGURES

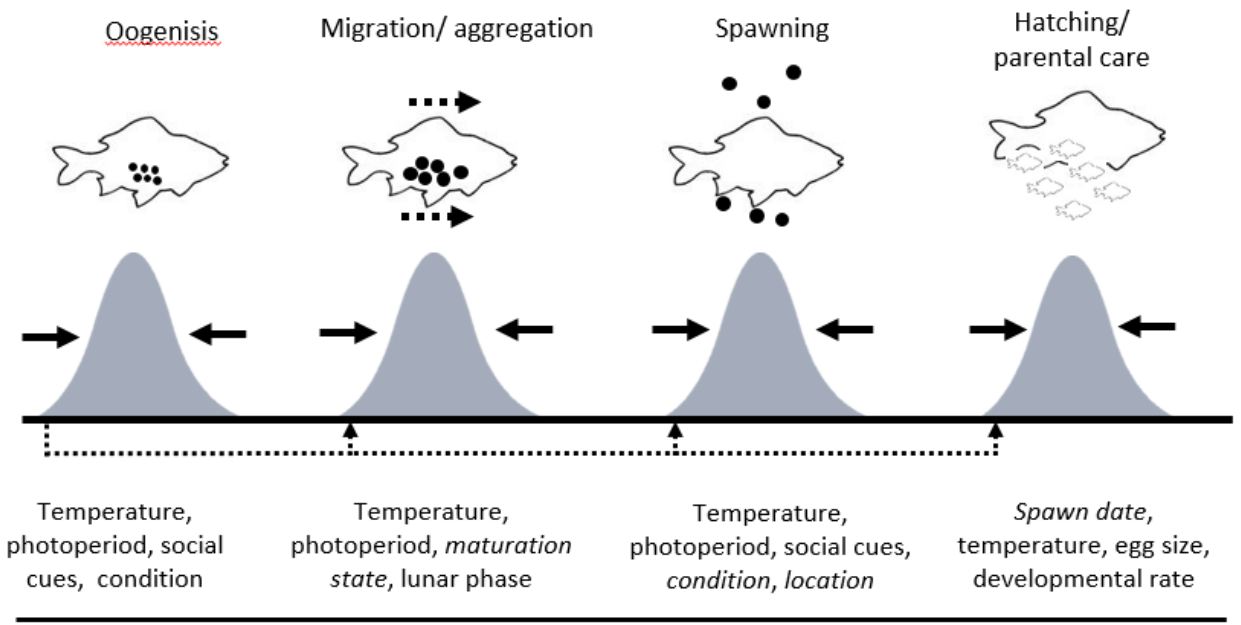


Figure 1.1. Generalized fish reproductive phenology showing variability in the timing of important life history events that can influence susceptibility to fishing. Dashed lines and italics indicate that the timing of later events may be influenced by earlier events. Bold arrows represent processes of natural selection that can shape the timing of various reproductive events.

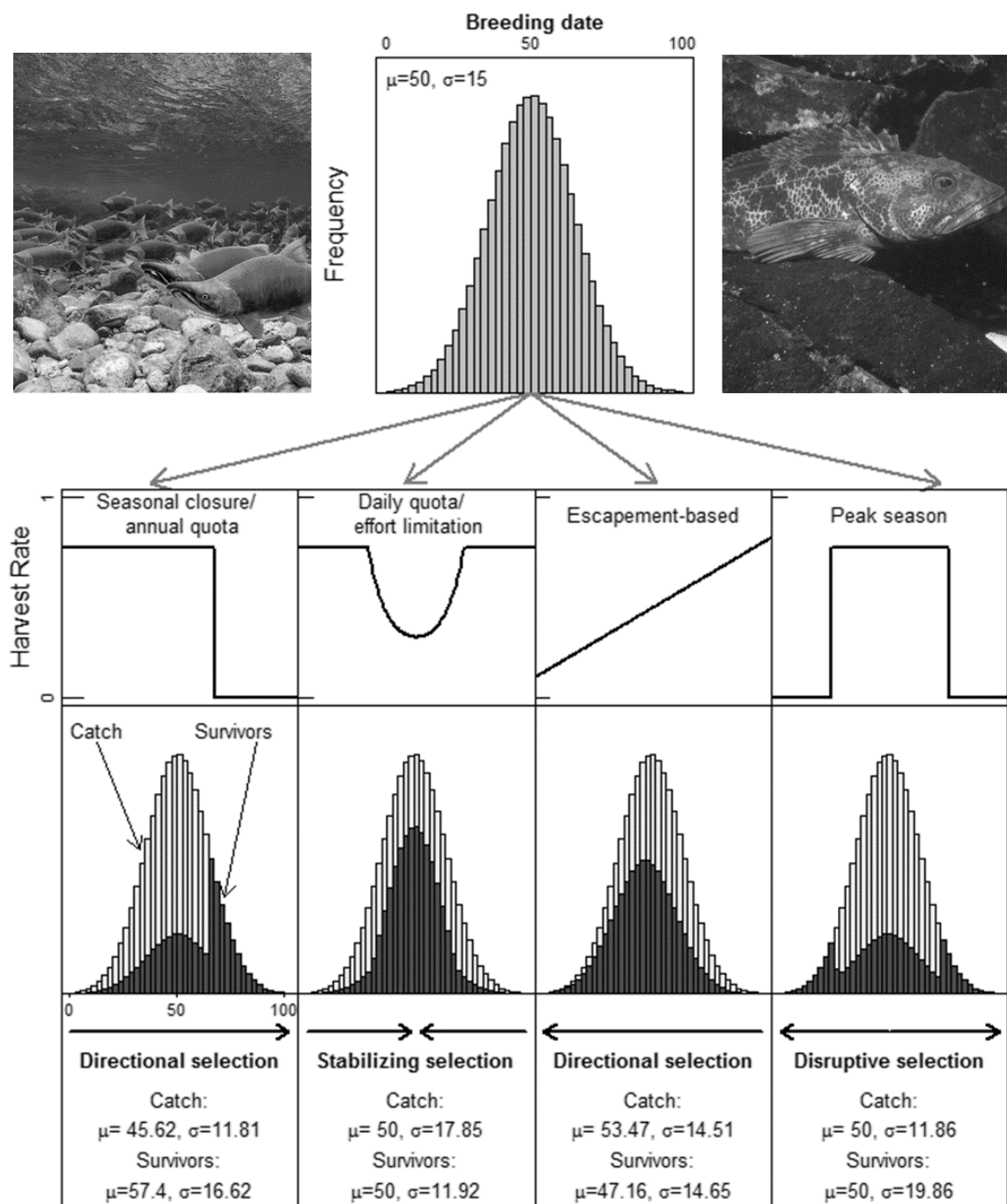


Figure 1.2. Selective pressure on a normally distributed quantitative timing trait in response to several common harvest regimes. Top row shows unfished frequency distribution of breeding date including distribution parameters. Second row shows typical temporal patterns in harvest rate for different fishing regimes. The third row shows the resulting frequency distributions for catch and survivors. The bottom row indicates the type of resulting selection and the parameters for the temporal distribution of survivors; μ = mean, σ = standard deviation. Left image: sockeye salmon during their spawning migration (photo by Morgan Bond). Right image: Male lingcod guarding a nest (photo by Tom Quinn).

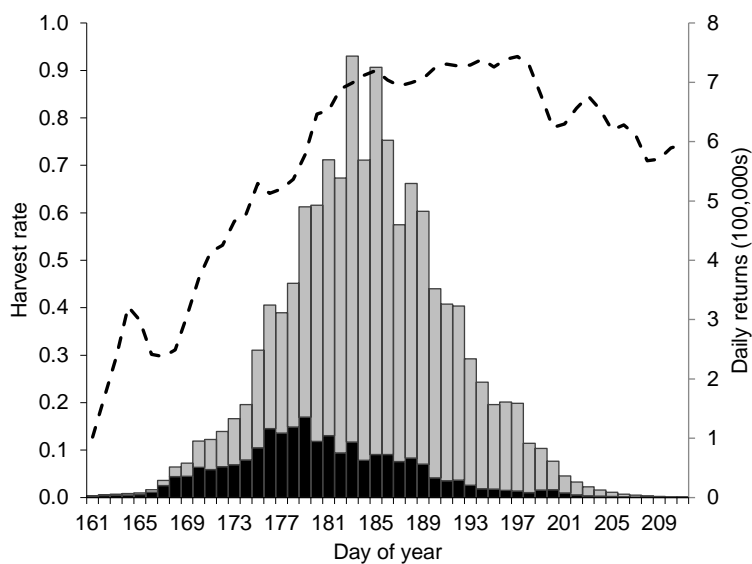


Figure 1.3. Average daily catch, escapement and harvest rate in the Egegik commercial fishing district 1990-2003. Bars show the number of salmon arriving each day in the fishing district (on the right y-axis); daily escapement is in black and catch is grey. Dashed line shows daily harvest rate (left y-axis). Day 1 of the year is 1 January.

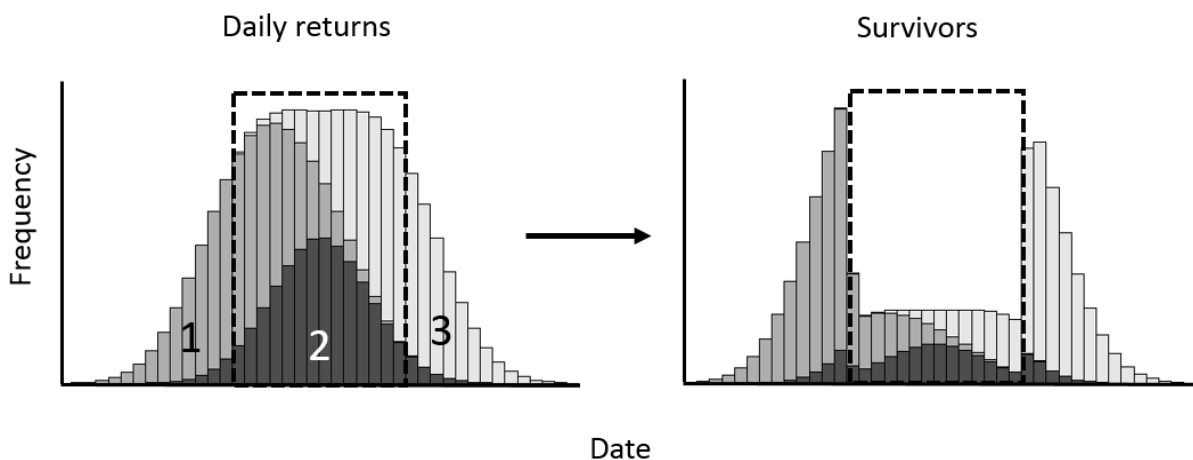


Figure 1.4. An example of stock-specific depletion in a mixed stock fishery altering temporal patterns of migration. Three populations of equal size, differing only in mean migration date are subjected to an 80% harvest rate during the middle third of the overall migration (dashed line). Populations 1 and 3 experience and ~48% harvest rate while population 2 is harvested at ~80% resulting in strongly bimodal migration timing in the surviving fish.

CHAPTER 2 **Life history plasticity mediates climatic influence on sockeye salmon (*Oncorhynchus nerka*) productivity**

ABSTRACT

Detecting the biological impacts of climate change is a current focus of ecological research and has important applications in conservation and resource management. Owing to a lack of suitable control systems, measuring correlations between time series of biological attributes and hypothesized environmental covariates is a common method for detecting such impacts. These correlative approaches are particularly common in studies of exploited fish species because rich biological time-series data are often available. However, the utility of species-environment relationships for identifying or predicting biological responses to climate change has been questioned because strong correlations often deteriorate as new data are collected. Specifically stating and critically evaluating the mechanistic relationship(s) linking an environmental driver to a biological response may help to address this problem. Using nearly 60 years of data on sockeye salmon from the Kvichak River, Alaska we tested a mechanistic hypothesis linking water temperatures experienced during freshwater rearing to population productivity by modeling a series of intermediate, deterministic relationships and evaluating temporal trends in biological and environmental time-series. We found that warming waters during freshwater rearing have profoundly altered patterns of growth and life history in this population complex yet there has been no significant correlation between water temperature and metrics of productivity commonly used in fisheries management. These findings demonstrate that pairing correlative approaches with careful consideration of the mechanistic links between populations and their environments can help to both avoid spurious correlations and identify

biologically important, but not statistically significant relationships, ultimately producing more robust conclusions about the biological impacts of climate change.

INTRODUCTION

The response of animal populations, biological communities, and entire ecosystems to global climate change has become a dominant theme in the field of ecology (Parmesan et al. 2013). Observed warming in recent decades has provided opportunities for empirical, *in situ* research on the biological impacts of climate change across a broad geographic and taxonomical range (Parmesan and Yohe 2003; Parmesan 2006). Biological responses to these physical changes have been diverse, documented in a wide variety of species including mammals, birds, fishes, amphibians, plants, involving altered spatial distribution, timing of key life history events, demographics, growth and survival (Schmitz et al. 2003; Parmesan 2006; Burrows et al. 2011; Doney et al. 2012). Despite abundant evidence that climate change affects species' distribution, growth and phenology, the implications of these effects for population productivity and persistence are less clear. Even in the absence of a clearly specified mechanism, correlations between environmental variables and population productivity are frequently reported, and may serve as the basis for predicting future abundances (Myers 1998). However, a variety of intrinsic ecological processes may mask or confound such relationships (Foley 2010; Hoffmann and Sgrò 2011). Population level responses including phenotypic and demographic plasticity, evolution, and altered behavior may affect observed species-environment relationships (Parmesan 2006; Rogers and Schindler 2011). In populations subject to significant density dependence, compensatory growth or survival may moderate or exacerbate the impacts of environmental change (Reed et al. 2013, 2014). Furthermore, environmental change is often spatially or

temporally heterogeneous and therefore a negative impact at one life-history stage may prove beneficial in later stages (e.g. Dybala et al. 2013). It is therefore not surprising that environment-productivity correlations frequently break down when confronted with new data (Myers 1998).

Understanding the ongoing and future impacts of climate change is especially pressing for commercially important fish species because environmentally driven changes in productivity can have severe economic, social and cultural consequences (Sumaila et al. 2011). For example, Pacific salmon (*Oncorhynchus* spp.) populations have fluctuated in response to large-scale climate variability in recent decades with impacts on fishermen felt around the Pacific Rim (Hare et al. 1999; Beamish et al. 1999; Irvine and Fukuwaka 2011). Across the North Pacific salmon populations tend to display prolonged periods of high and low productivity, often correlated with climate indices (Mantua et al. 1997; Ruggerone et al. 2010). However, the mechanisms by which large scale climate forcing influences salmon populations are not well understood, and individual populations often diverge significantly from the average pattern (Rogers and Schindler 2011). In part this among-population variability can be explained by strong population-specific density dependence and differences in freshwater habitats. Additionally, life history variability may result in diverse responses to common environmental conditions (Hutchings 2011). In these fishes the timing of key ontogenetic shifts including seaward migration (smolting) and homeward migration (maturation) depends on size and growth rate (Quinn 2005). As a result, even salmon from the same population and cohort may be subject to disparate environmental conditions and schedules of mortality. For example, individuals spawned in the same year but migrating to sea after one or two years of freshwater residence will enter the ocean in different years, and thus experience different environmental conditions at sea. They will also differ in size during the stressful ocean entry phase, and may spend different lengths of time at sea prior to

maturation and return (Quinn et al. 2009). Climate, life history and productivity are therefore interdependent, and accounting for these relationships is necessary to interpret past variability and predict future responses to environmental change in species such as salmon that display complex life histories (Ruggerone et al. 2013).

The life history patterns of Pacific salmon exemplify the complex links between climate and population productivity, and the rich data collected on the commercially valuable species allow us to test critical hypotheses regarding these links. In this study we examine over five decades of data on the largest complex of sockeye salmon populations in the world, produced in the Kvichak River basin in Bristol Bay, Alaska. Beginning in the late 1990s sockeye salmon from the Kvichak River system experienced a decrease in productivity at the same time that many other parts of the Bristol Bay population complex increased (Figure 2.1) (Schindler et al. 2010). Although asynchronous changes in productivity among the major rivers is characteristic of the Bristol Bay stock-complex (Hilborn et al. 2003), the decline was nonetheless alarming. With significant warming observed in the region during the past two decades (Chapin III et al. 2014) there has been much speculation about what role climate change could be playing in this apparent decline, and what characteristics of the Kvichak River population might make it particularly vulnerable to warming (Ruggerone and Link 2006; Rogers and Schindler 2011).

Lew (2003) proposed a mechanistic hypothesis for climate induced productivity declines in the Kvichak River system; increased juvenile growth opportunity associated with climate warming has resulted in a shift from predominantly age-2 to age-1 seaward migrants. In turn, average marine survival has declined because these younger migrants are smaller than they would have been had they remained in the lake for an additional year, and marine survival in salmon is generally size-dependent. Juvenile growth in the system is also density dependent

(Rich Jr. et al. 2009) so a positive feedback occurs with even faster growth of juveniles as abundance declines, enhancing their tendency to leave the lake young, hence small. The Kvichak River could be particularly susceptible to this change because – more than other Bristol Bay rivers – large returns have historically been dominated by age-2 smolts (Ruggerone and Link 2006). Overall, this hypothesis predicts a negative correlation between temperature experienced during freshwater rearing and population productivity; an environment-productivity relationship that can be easily evaluated using a typical correlative approach.

Alternatively, several nested hypotheses can be tested to shed light on the mechanisms relating climate change and productivity. These intermediate hypotheses include: 1) a positive relationship between fry growth and growing season temperature, 2) a negative relationship between fry growth and average age at seaward migration, 3) a positive relationship between marine survival and smolt age, and 4) marine survival accounts for an appreciable proportion of variation in total lifetime survival. In this study we utilized a multi-step approach to test the hypothesis that warming waters and the earlier age at juvenile migration are indeed resulting in reduced productivity of Kvichak River sockeye. First, we described temporal trends in a suite of environmental variables and population attributes to evaluate their general consistency our hypotheses and to identify potentially confounding factors. We next modeled the hypothesized intermediate, deterministic relationships to test the strength of the mechanistic link between climate and productivity. Finally, in order to allow for comparison between the correlative and mechanistic approaches we evaluated the influence of climate change on sockeye salmon productivity by incorporating growing season temperature as an environmental covariate in a stock- recruit model.

METHODS

Study Site and Population Characteristics

The river systems that drain to Bristol Bay in southwest Alaska comprise the world's largest sockeye salmon producing region (Figure 2.2.). Intensive commercial fishing with gillnets has occurred for over 100 years in five districts located near river mouths within the bay (Quinn et al. 2009). Each river drains one or more large lakes where sockeye salmon generally rear for one or two years before migrating to the Bering Sea and Gulf of Alaska (Blair et al. 1993). Iliamna Lake is the largest in the watershed (and in Alaska) with a surface area of approximately 2622 km². The Kvichak River drains from Iliamna Lake approximately 30 km to Kvichak Bay and the Naknek-Kvichak fishing district where most of the population's fishery mortality occurs (Rich Jr. et al. 2009).

Sockeye salmon return to the Kvichak River during June and July and spawn on the beaches of Iliamna Lake or in its many tributaries throughout the summer and early autumn. Fry emerge the following spring and enter the lake where they feed – almost always for one or two years – before migrating to sea (Rich Jr. 2006). Ocean residence typically lasts two or three years, though a small fraction of the males returns after only one year. Thus, the majority of Kvichak River sockeye mature at ages designated 1.2 (i.e. one year of freshwater rearing and two years at sea), 1.3, 2.2 and 2.3 (note that the winter of incubation is not accounted for in these age distinctions so a fish returning at age 1.2 is 4 calendar years old; see Figure 2.3). The age composition of the Kvichak River population has varied through time (Fair 2003). Both seaward and homeward migration are at least somewhat dependent on growth, and patterns in age composition are therefore thought to reflect both external (i.e. environmental) and internal (i.e. density dependent) processes (Quinn 2005; Quinn et al. 2009; Rich Jr. et al. 2009).

Data collection and processing

For salmon populations, productivity is generally measured in terms of returns per spawner (R/S); the number of salmon surviving natural mortality and returning to spawn or be caught as adults that was produced by the parental generation in a given previous year (i.e. brood year). Because age at maturity varies sockeye salmon of the same cohort will return to spawn over several years. To accurately measure productivity it is thus necessary to know both the abundance and age of returning fish. Sampling of catch and escapement has been conducted in Bristol Bay since the mid-1950s and is reported annually by the Alaska Department of Fish and Game (ADF&G) in regional management reports (e.g. Westing et al. 2006; Jones et al. 2012). Catch is enumerated daily by dividing the total weight of landings by average fish weight for each district. Fish that survive through the fishing district are termed ‘escapement’ and are enumerated by counting towers located on the major rivers in Bristol Bay (Minard and Meacham 1987). Age can be determined from scales that are collected from sample of the catch at processing facilities and from the salmon that escaped the fisheries using beach seines near the counting towers. Age composition samples are expanded based on total catch and escapement to estimate the total number of returning fish of each age (Jones et al. 2012). Catch data as reported by ADF&G did not always account for potential interceptions of Kvichak River fish in non-terminal fisheries including the South Alaska Peninsula, on the high seas, and other Bristol Bay districts. Run reconstructions using retrospective genetic studies have made it possible to correct bias in productivity estimates that can be introduced by these interceptions. We therefore use an updated version of the corrected catch and escapement data set described in Cunningham et al. (2012) to calculate returns by age class.

Brood tables were constructed by assigning returns to the year in which they were spawned. Abundance and age composition of catch and escapement have been estimated using consistent methods since 1956 and validated data were available through the 2014 return. The large majority of fish (>99%) return by age six and we were therefore able to construct brood tables and estimate productivity for brood years 1956-2009. Brood tables were used to calculate several population attributes. First, total R/S was calculated for each brood year. Next, to account for potential declines in productivity at high spawner abundances (i.e. density dependence) a density-independent index of productivity was developed. We fitted a Ricker (Ricker 1954) model to brood table data using a linear regression of the natural logarithm of R/S on spawner abundance. We then extracted the model residuals as an index of density-independent productivity (R/S index; Peterman *et al.*, 1998). In order to examine freshwater and marine productivity independently, in years where data on seaward migrating juveniles were available (see below) total smolts per spawner (S/S) and smolt-to-adult survival (SAS) were also calculated.

In addition to metrics of abundance and productivity we also sought to describe age composition which may be sensitive to environmental variability and could therefore be influenced by climate change. Because on average four age classes – 1.2, 1.3, 2.2 and 2.3 – make up over 99% of the return (minimum of 97.8% in our time-series) both freshwater and marine age can be considered as a binary responses, and thus each is described by a single proportion. For each brood year freshwater age composition of fish surviving to maturity is as the total return of freshwater age-1 individuals divided by the total return while marine age composition is described by the proportion of ocean age-2 fish in the return.

Efforts to annually monitor the juvenile life-history phase of Kvichak River sockeye began in 1956. Initially, smolts (seaward migrating juveniles) were sampled throughout the spring migration season at a location just downstream of Iliamna Lake on the Kvichak River. Over the history of the sampling program consistent methods have been used to estimate the age composition, mean age and mean weight of the migrating smolts on a daily basis; daily values are then aggregated in to seasonal averages. We calculated smolt condition factor as the residuals of a linear regression of the natural logarithms of weight and length across all smolt years with available data (Pope and Kruse 2007). Daily relative abundance is used to characterize migration timing and can be used to estimate benchmarks including median migration date. Additionally, smolt abundance has been estimated in most years. In total, age-specific smolt abundance estimates are available for 1956-2001 and 2008-2014 (Ruggerone and Link 2006; Nemeth et al. 2014). While age and size sampling methods have remained consistent the smolt enumeration methodology has varied over time and included standardized fyke net sampling, hydroacoustics, and modeling. Several efforts have been made to correct for the changes in sampling methods (Rogers and Poe 1984; Ruggerone and Link 2006). We use the estimates given by Ruggerone and Link (2006) and update them with data from recent annual reports (e.g. Nemeth et al. 2014). After accounting for the two or three year lag between brood year and migration year we estimated the total smolt production and juvenile age composition for 53 brood years: 1956-1998 and 2006-2012.

In addition to smolt sampling, the length and weight of sockeye salmon fry at the end of their first growing season in Iliamna Lake have been estimated annually since 1962. Fry are sampled using a standardized tow-netting procedure at two index areas in the eastern end of the lake (Pedro Bay and Knutson Bay; see Rich et al. 2009 for complete methodology). Spawning

occurs primarily in this region of the lake and juveniles tend to migrate westward as they become older (Rich Jr. 2006). As a result the vast majority of individuals sampled were age-0; those spawned the previous autumn. Average fish lengths were weighted by the surface area of the sampling areas (a constant among years) and adjusted to a common date of 1 September using observed growth rates to account for variation in the precise sampling date among years (Rich Jr. 2006). The time series for fry length, after accounting for a one year lag between spawning and capture covers brood years 1961-2014, except for 1997 when sampling did not occur, for 52 years in total.

Although we are primarily interested in the influence of spring water temperature on population productivity, we recognized that environmental changes influencing other portions of the sockeye salmon life-history may also influence the population. To evaluate consistency in the magnitude and direction of environmental changes, we examined trends in a broad range of environmental variables that potentially influence Kvichak River sockeye salmon throughout their life-cycle. Water temperature mediates many important processes including growth, survival and phenology in salmon. Water temperatures collected at the outlet of Iliamna Lake during smolt sampling operation were obtained from ADF&G and generally span June 1 – 15. Direct measurements of water temperature were not available for other seasons, but air temperature has been a useful proxy for water temperature (Rich Jr. et al. 2009). Long-term records of daily air temperature from the Iliamna Airport are available spanning the complete biological time series (National Oceanic and Atmospheric Administration 2014a). To identify potential heterogeneity in rates of change between seasons we considered monthly mean temperatures independently. During several years Iliamna Airport did not report temperature data but data were available from the weather station at Intricate Bay, on the southern shore of

Iliamna Lake. Temperatures at the two sites were highly correlated ($\rho > 0.95$) and combined to complete the time series from 1955-2014. In lakes with seasonal ice coverage the spring thaw effectively initiates the phytoplankton growing season; as such ice out date is an important determinant of growth at higher trophic levels (Hodgkins et al. 2002). For Iliamna Lake dates of ice out based on observations from local pilots and other residents are available for most years from 1955-2014. Missing values comprised $< 5\%$ of all years and were estimated using linear regression with winter mean low temperature and spring mean high temperature as predictors.

During the marine portion of their life history Bristol Bay sockeye salmon are distributed widely in in the Gulf of Alaska and North Pacific Ocean as they grow to maturity (Pyper et al. 2001). To account for possible environmental influences on the ocean life history phase we considered indices of large scale climate patterns thought to influence the Bering Sea and North Pacific ecosystems. Following Litzow *et al.* (2014) we considered a suite of basin scale indices – notably the Pacific Decadal Oscillation (PDO; Mantua et al. 1997) and El Nino Southern Oscillation (ENSO) – and regional conditions including sea surface temperature (SST) and surface low pressure (Ruggerone et al. 2010). We also included in our trend analysis two regional time series of SST recorded at the Pribilof Islands and at NOAA mooring TsfcM2 over the eastern Bering Sea shelf (National Oceanic and Atmospheric Administration 2014b). Complete source information for all marine environmental variables is provided in Table 2.1.

Statistical analyses

Ordinary least squares (OLS) regression with year as the independent variable was used to test for directional trends in biological and environmental time-series. Data represented as proportions were first square root arcsin transformed to approximate normality. To account for

the influence of possible autocorrelation, ρ – the degree of autoregressive first order autocorrelation – was calculated and all relationships were subsequently modeled using a generalized least squares (GLS) regression with a biologically plausible first order autoregressive error structure. The quality of the two models was compared using a likelihood ratio test and coefficients and standard errors from the preferred model were considered more reliable.

Generalized linear and additive models were used to evaluate the strength of these intermediate relationships hypothesized to link growing season temperature and sockeye productivity. For marine survival, a mixed modeling approach was used to account for high interannual variability. In order to minimize the possibility of identifying spurious correlations we restricted our candidate models based on preexisting hypotheses. For each modeled relationship the quality of candidate models was compared using Akaike's Information Criterion (AIC). Models were further compared by calculating AIC weights which represent the conditional probability of a model relative to all candidate models.

The first intermediate relationship links temperature and density to juvenile growth during lake rearing. Rich and colleagues (2009) identified the average mean Iliamna air temperature during March through June as the strongest environmental predictor of fry growth in Iliamna Lake. We utilized OLS regression to evaluate the predictive power of alternative environmental covariates but failed to identify any stronger relationships. No direct estimates of juvenile abundance prior to smolt migration are available. Fry density was therefore indexed as the natural logarithm of the spawning escapement that produced the cohort (e.g. $\ln(1990$ spawners) for 1991 fry) to account for the assumed density dependent reduction in fry production by large escapements. Yearlings – juveniles spawned in the previous year that delay migration until age two – may also compete for food with fry and therefore influence growth. Yearling

density was indexed as the natural logarithm of age-2 smolts migrating in the following spring (Rich Jr. 2006). Because no direct measurements of growth are available, we used average fry length on 1 September as an index of growth in a given year. In order to allow for potential nonlinearity in the relationship between temperature and fry growth we considered generalized additive model (GAM) forms of each linear model in which the coefficient for spring temperature was replaced by an optimal smoothing function fit using penalized regression splines and selected via generalized cross validation (Wood 2006). In total we considered ten candidate models (Table 2.2.)

The next intermediate relationship links fry growth to age at seaward migration. Because the vast majority of individuals go to sea after either one or two years, migration was considered a binary response variable and therefore required a generalized modelling approach. The data were overdispersed under a binomial model, and we therefore used the more flexible beta distribution – which allows for an independent estimate of variance – with a logit link to model the proportion of smolts migrating after one year. . The smolt transformation that precedes seaward migration is complex and includes physiological, morphological and behavioral changes that develop over a period of months (Björnsson et al. 2011). As such, an individual fry must commit to these changes well before the period in spring during which seaward migration occurs or else delay and remain in the lake for another year. This ‘decision’ is apparently based on an evaluation of physiological condition and depends on size, with larger individuals tending to migrate while smaller individuals delay (Mahnken et al. 1982). Because there is little opportunity for additional growth after August in Iliamna Lake, length on 1 September was used as the primary explanatory variable. Initial models showed strong autocorrelation of residuals, indicating that for a given fry length the probability of migrating at age-1 has increased over time

and suggesting omission of an important explanatory variable. To achieve independence of residuals we considered several potential explanations for this trend including condition factor (weight at a given length), environmental conditions during the spring of migration, and a linear temporal trend that may capture other unobserved changes. In total we considered six candidate models (Table 2.2.)

We next modeled marine survival as a function of smolt size and age to test the hypothesis that age-2 smolts are more likely to survive and return to breed. As a response variable we used freshwater age-specific marine survival by year of seaward migration (i.e. freshwater age-1 smolts/ freshwater age-1 returns produced by those smolts). Marine survival in sockeye salmon is generally size dependent (Henderson and Cass 1991; Koenings et al. 1993) and in the Kvichak River population age-2 smolts are on average 23% longer and 80% heavier than age-1 smolts (Ruggerone et al. 2013). However, slower growing individuals are more likely to be age-2 smolts, and age may therefore influence survival independent of length. Additionally, survival in salmon is highly stochastic (Henderson and Cass 1991) and as such we anticipated a strong year effect in addition to any size effect. To account for this interannual variability in survival we also considered each model with and without year as a random effect by allowing a unique intercept for each migration year. In total we compared six candidate models (Table 2.2).

It is in theory possible that variation in total productivity is dominated by fluctuations in survival during the freshwater life history phase and that marine survival is much less variable. To exclude this possibility we modeled the logarithm of recruits per spawner in response to smolt-to-adult survival (S/S) and smolts per spawner SAS. By definition these predictor variables explain 100% of the variation in productivity. However, by standardizing both predictors to zero mean and unit variance the coefficients of the model can be directly compared

to evaluate the relative contribution of freshwater and marine factors to total productivity. We also conducted deviance partitioning by dropping either smolts per spawner or SAS from the model and comparing the explained deviance of each. Finally, we evaluated the direct environment-productivity correlation by including spring temperature as a covariate in a linear form of the Ricker stock-recruit model (Ricker 1954), and – to be consistent with the intermediate hypotheses – allowing for a non-linear relationship between temperature and productivity with a smoothing function. All analyses were conducted in R 3.1.3 (R Development Core Team 2015) using packages ‘mgcv’ (Wood 2006, 2011), ‘nlme’ (Pinheiro et al. 2015), ‘betareg’ (Cribari-Neto and Zeileis 2009), ‘glmmML’ (Broström 2013) and ‘lme4’ (Bates et al. 2014).

RESULTS

Trend analysis

Significant directional trends were identified in many environmental and biological time series. However, in general even statistically significant trends explained little of the total variation in the time series (maximum $R^2 = 0.26$). For freshwater environmental variables all slopes were consistent with a general warming trend. Nine of twelve trends in monthly mean temperatures were significant at $\alpha = 0.1$. June Kvichak River water temperature and Iliamna Lake ice breakup date showed significant positive and negative trends respectively, neither with significant autocorrelation. Complete results for trend analysis of freshwater environmental variables are provided in Table 2.3 and selected trends are shown in Figures 3.4a-b. For the marine environmental variables both the direction and magnitude of temporal trends varied. Three of ten variables displayed directional trends at a significance level of $\alpha = 0.1$ and eight of

ten time series were significantly autocorrelated. Both the annual and winter PDO indices displayed marginally significant positive trends ($p = 0.068$ and 0.032 respectively). Of the three time series of regional SST only one – southeastern Bering Sea spring temperature (May SST) – showed a directional trend; in this case cooling ($p = 0.004$). Complete results for trend analysis of marine environmental variables are provided in Table 2.4 and trend for May SST is shown in Figure 2.4c.

In total eight of 25 biological variables trended significantly over the period of observation at a significance level of $\alpha = 0.1$. Changes were not uniformly distributed across variable categories. Of 14 abundance and productivity variables only one – age 1.3 abundance – changed over time with a significant positive trend ($p = 0.048$). On the other hand, all three age composition variables displayed directional trends with proportions of freshwater age-1 increasing and marine age-2 decreasing. Three of six freshwater growth indices indicated directional change with negative trends in length for both age-1 and age-2 and increasing condition factor for age-1 smolts. Finally, the only phenological variable – median smolt migration date – showed a declining trend (i.e., earlier migration: $p = 0.007$). Growth variables were generally autocorrelated at a one year lag with ρ values between 0.12 and 0.36, whereas abundance variables were not. However, of all biological variables the R/S index displayed the strongest autocorrelation with a ρ of 0.50. Complete results for trend analysis of biological variables are provided in Table 2.5 and selected trends are shown in Figures 3.5a-d.

Intermediate relationship models

For the relationship between environmental conditions and fry growth the AIC selection process favored a model which included a positive and slightly nonlinear effect of March-June

average air temperature (i.e., bigger fish with warmer conditions: estimated $DF = 4.012$) and a negative, linear effect of fry density (FL-3gam). Several other models in which these two predictors were also included received smaller, but non-zero AIC weights. The selected model received a weight of 0.52. Although a model in which yearling density was added as a predictor (FL-1gam) explained slightly more of the total deviance, it also had a marginally higher AIC and received a weight of only 0.33. The highest ranked model explained over 62% of total deviance (Figure 2.6a.). Across all candidate models spring temperature was a highly significant predictor ($p < 0.001$). When included, fry density was always highly significant ($p < 0.003$) whereas yearling density was never significant ($p > 0.208$). For the preferred model the effect of temperature was essentially flat below 1.5°C , and nearly linear above with fry length increasing ~ 4.5 mm per $^{\circ}\text{C}$ (Figure 2.6b.). The effect of density was negative with fry length decreasing ~ 2.6 mm per order of magnitude of adults in the parental generation (Figure 2.6c.).

The AIC-preferred smolt age composition model linking freshwater growth and age at seaward migration included fry length on 1 September (Figure 2.7a.), March-June average temperature in year of migration (Figure 2.7b.) and a linear temporal trend (Figure 2.7c.) as predictor variables. The preferred model (AC-1) had the lowest AIC score and received a 0.55 AIC weight. Most of the remaining AIC weight went to models which were nested within the selected model and dropped either the temperature or temporal predictor. The highest ranked model explained over 72% of total deviance (Figure 2.7d.). Fry length was included in all models and was always a highly significant predictor of smolt age ($p < 0.001$). Age-1 smolt condition factor was not included in the selected model and was not significant in any candidate model ($p > 0.228$). Where included, both year and spring temperature were always significant ($p < 0.023$ and $p < 0.045$ respectively). For AC-1 the effects of fry length and spring temperature on the

probability of migrating at age-1 were both positive; the odds of migration increased at ~12% per mm and ~14% per °C, respectively. After accounting for the effects of these other predictors an increasing temporal trend of ~2% per year in the odds of age-1 migration remained significant.

For the smolt survival models the AIC selection process strongly favored SAS-1R which included smolt length and age as fixed effects and migration year as a random effect. No other model received any AIC weight and the selected model explained over 86% of total deviance. However, the large majority of deviance explained is attributable to the random intercepts of migration year; model SAS-1 had the same fixed effects, but no random effects and explained only 9.4% of total deviance. The fixed effects of age and length were highly significant ($p < 0.001$) in all cases where included in a candidate model. In SAS-1R – the highest ranked model – the odds of survival increase ~6% per mm of smolt length. For a given length the effect of age is negative with the odds of survival for age-2 smolts 30% lower than age-1. The effect of the random intercept by year was very large with expected probability of survival for a smolt of average length ranging from 0.006 to 0.518 for age-1 smolt and 0.014 to 0.70 for age-2 smolt (Figure 2.8.). Full results of the model comparisons are provided in Table 2.6.

For the remaining two hypothesized relationships we modeled productivity in terms of recruits per spawner, first evaluating the relative influence of freshwater and marine life-history phases, and then directly evaluating the effect of temperature during freshwater rearing. Because both predictors were standardized prior to analysis, the coefficients for SAS and smolts per spawner in model RS-1 represent the change in R/S in response to a one standard deviation increase in the predictor. Not surprisingly, both predictors were highly significant ($p < 0.001$), but direct comparison of the coefficients revealed a ~16% larger response in productivity to SAS than S/S. Deviance partitioning of the model further supported this result as SAS individually

explained 46.3% of total deviance while S/S explained only 32.6%. Finally, incorporation of spring temperature as a covariate in the linear Ricker model revealed a slightly convex, but non-significant environmental effect (Figure 2.9.). Thus, no direct correlation between temperature during freshwater rearing and overall population productivity was apparent.

DISCUSSION

Identifying and accurately attributing biological responses to climate change is, and will continue to be, vital for conservation and management of animal populations in a warming world. This field of research will inform important policy decisions and as such, requires a particularly thoughtful and deliberate approach. Because of the challenges of conducting large-scale ecological experiments, correlative approaches will be required. Here we utilized a multi-step approach with a series of intermediate mechanistic hypotheses to address the shortcomings of a purely correlative approach between climate and productivity. We also contextualized the productivity-environment relationship by examining trends in potentially confounding environmental and biological variables. Taken together, these analyses allow for robust conclusions regarding the importance of freshwater climate in determining Kvichak sockeye productivity; by extension, they also provide lessons for climate effects on other species with complex life histories and migratory cycles.

Considering first the intermediate, deterministic relationships that link temperature during freshwater rearing to population productivity, there appears to be strong support for a link between freshwater climate and productivity. As predicted, freshwater growth as measured by fry size on 1 September was positively related to average March-June air temperature and negatively related to density; these two variables explained over 60% of deviance in fry growth.

This finding is consistent with other studies of sockeye salmon growth though the relative importance of temperature and density vary among systems (Edmundson and Mazumder 2001; Schindler et al. 2005). Also as predicted, and consistent with previous research on Kvichak River sockeye (Blair et al. 1993; Rich Jr. et al. 2009), the probability of seaward migration at age-1 was positively correlated with fry size, which alone explained over 50% of the deviance in migration probability. We also identified an unexpected increasing propensity over time for age-1 migration that was independent of size. Spring temperature in the year of migration may partially explain this phenomenon, but a linear temporal trend capturing other, unknown processes was also significant. Possible explanations for this phenomenon include evolution and shifting stock composition of the Kvichak sockeye run (Hilborn et al. 2003). It is possible that this trend indicates evolution of the reaction norm between size and probability of age-1 seaward migration (Dieckmann and Heino 2007). Maturation reaction norms respond to selection in fishes, and a shift in the relative lifetime survival of the two smolt ages could provide the selection necessary in this case (Olsen et al. 2004). Alternatively, this trend may be explained by a change in the relative contribution of different populations within the Kvichak basin to system's total productivity. Although abundance data are available only at the basin level, many distinct populations make up the total Kvichak run and population-specific propensities for freshwater age have been documented (Blair et al. 1993).

Marine survival was positively and significantly related to smolt size; the larger age-2 smolts experienced on average 95% higher survival than age-1 smolts at their respective median lengths. This magnitude of size selective smolt mortality is consistent with patterns observed in sockeye salmon throughout their range (Koenings et al. 1993) as well as with previous studies in the Kvichak River system (Ruggerone and Link 2006; Ruggerone et al. 2013). Finally, marine

survival accounted for the majority of variation in population productivity. However, although all the intermediate deterministic relationships were statistically significant with reasonably strong explanatory power, the predicted negative correlation between growing season temperature and overall productivity was not. Indeed, based on the correlative approach spring temperature appears to have had little or no influence on population productivity of Kvichak River sockeye salmon.

The trend analyses can provide some insight into this disconnect between the significant deterministic intermediate relationships and lack of an overall influence of spring temperature on productivity. In the freshwater environments there is strong evidence of a long-term warming trend and environmental indices previously linked to juvenile sockeye salmon growth and phenology including spring air temperature, ice out date and water temperature during smolt migration each display directional change over the period of record (Martins et al. 2012; Kovach et al. 2013, 2014). Despite this, freshwater growth has not displayed the increasing trend that might be expected under warming conditions. Mean fry length on 1 September has remained stable over the past five decades despite inter-annual variation > 25 mm. Meanwhile – and somewhat counterintuitively – mean length of both age-1 and age-2 smolts has declined. This has likely resulted from a combination of factors. First, timing of smolt migration has advanced by over a week since 1955, and earlier migrating fish forego some growth opportunity in the lake. Second, this trend could result from shifting smolt age composition. Individual fry near the margin of migrating at age-1 and age-2 will fall near the low end of the age-1 length distribution, but at the high end of the age-2 growth distribution. Thus, if more of these individuals migrate at age-1 there are more relatively small age-1 smolts and fewer faster growing, larger age-2 smolts. The trend analysis indicates a significant shift toward lower smolt age which is therefore

consistent with the observed patterns in mean smolt length. Indeed, age composition showed the most significant changes over time of all biological variables. Kvichak sockeye are on average migrating to sea at a younger age and spending longer at sea as indicated by increasing proportions of freshwater age-1 (rather than 2) and marine age-3 (rather than 2) individuals. Despite these shifts and the observed ~95% marine survival advantage of age-2 smolts overall smolt-to-adult survival has not declined. This apparent paradox is key to understanding the disagreement between the mechanistic and correlative approaches

Mixed effects modeling of smolt-to-adult survival allows for examination of the relative importance of the fixed effects of smolt size and age, and random interannual variation in marine survival. Consistent with the meta-analysis of sockeye marine survival conducted by Koenings and colleagues (1993), our analysis revealed that although both age and length were significant predictors of marine survival, they together explained little of the total variability. Similarly, Henderson and Cass (1991) found that in Chilko Lake sockeye marine SAS was positively correlated with length within a cohort, but length was not a significant predictor of survival over a 34 year time series. As such, although the intermediate hypotheses demonstrate a mechanism by which declining smolt age should reduce average marine survival, exogenous factors dominate the signal of variability in marine survival and effectively break the chain of relationships that link spring temperatures during freshwater growth to population productivity. Additionally, our analysis necessarily ignored differential freshwater survival of the two smolt ages because freshwater survival and the proportion of a brood year migrating at age-1 are confounded. Our estimates of differential SAS therefore represent an upper bound on the lifetime survival advantage of age-2 smolts. In reality, some portion of this advantage is offset by the risk of mortality associated with a second year of lake residence; though this risk is thought to be low

relative to the marine environment (Quinn et al. 2009). Therefore, contrary to our prediction, any potential negative influence of increased freshwater growth on population productivity is either compensated for by reduced freshwater mortality in age-1 smolts or unobservable in our time-series as a result of the stochastic nature of marine survival. Despite this, the results of testing the intermediate hypotheses clearly show that changes in temperature during freshwater rearing have profound consequences for growth, life history and demographics in Kvichak River sockeye. Observed warming over the past six decades has shifted the dominant life-history strategy towards earlier seaward migration which in turn has altered the average length of marine residence. Together, these changes impact generation time, size at maturity and the relative importance of the marine and freshwater environments in determining lifetime survival. Thus, relying solely on correlation with productivity for identifying the influences of climate change on Kvichak River sockeye would have overlooked important changes with implications for the biology and management of the stock.

In addition to demonstrating the shortcomings of a purely correlative approach to studying climate change impacts on productivity, our analyses also highlight heterogeneity in patterns of environmental change. While in the freshwater environment there has been a clear warming trend, the rate of change differed among seasons, with spring and summer temperatures increasing most markedly. Associated with rising spring air temperatures, the typical date of ice out has advanced by nearly two weeks, resulting in a longer ice free growing season in Iliamna Lake. In addition to controlling growth opportunity through primary production, ice out also largely determines when water temperatures begin to increase in spring. Both ice out date and water temperature modulate the seasonal timing of smolt migration (Burgner 1962; Quinn et al. 2009), and as such warming is likely responsible for the observed trends in smolt size and

median migration date discussed previously. In other salmon populations, early marine survival may depend on the degree of synchrony between ocean entry date and favorable environmental conditions (Scheuerell et al. 2009). Smolts can only respond to freshwater environmental cues to initiate migration (Stewart et al. 2006), and matching migration timing with the period of optimal survival is therefore mediated by the long term relationship between freshwater and marine environments. Thus, our observation of declining spring SST in the Eastern Bering Sea is particularly interesting because it indicates that optimal marine conditions may be occurring later while freshwater environmental cues are initiating migration earlier. Further research in this area may help to explain some of the large year effect identified by our model of marine survival.

Taken together, our results describe a salmon population complex that has experienced directional environmental change that is both spatially and temporally heterogeneous and displayed multiple, simultaneous biological responses. This type of complexity is likely to be the rule rather than the exception for animal populations faced with environmental change. Because of this complexity, even when robust, deterministic relationships link environmental conditions to survival climate change impacts on productivity may remain difficult to detect using strictly correlative approaches. Previous studies have highlighted the issue of false positives in the search for environmental drivers of biological change (Myers 1998; Rogers and Schindler 2011); our results demonstrate the reciprocal issue of false negatives. If, instead of working from an *a priori* hypothesis we explored correlations between Kvichak River sockeye salmon productivity and a broad range of environmental covariates, spring temperature during freshwater rearing would have been dropped as non-significant. By instead considering the explicit mechanisms by which environmental drivers elicit biological responses, we revealed that although a direct

correlation with productivity is not apparent, climate warming has precipitated other important biological changes in the world's largest sockeye salmon stock complex.

Although our analyses were facilitated by an unusually rich data set with large sample sizes at multiple life history stages over many decades, the implications of our results are broadly applicable to the study of biological responses to climate change. Identifying and predicting climate impacts on population productivity is vital for natural resource management and the conservation of rare or threatened species. While testing for significance of environment-productivity relationships is a fast and relatively low cost way of detecting potential climate change impacts, type 1 and type 2 errors are both major concerns. Stating and testing the mechanisms that link environment and species can improve the method by helping to simultaneously identify significant, but spurious and biologically important, but non-significant correlations. Even in the absence of extensive data on life-history, phenology or physiology, logical consideration of the mechanisms that link environmental and biological change is possible. Moving beyond correlation can inform more robust conclusions from existing data and help ensure that future research is targeted toward the most relevant questions as climate change continues to impact populations and ecosystems.

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TABLES

Table 2.1. Summary of marine environmental variables and sources

Variable name:	Description:	Data Source:
NPI	North Pacific Index	beringclimate.noaa.gov
AO	Arctic Oscillation	beringclimate.noaa.gov
NPGO	North Pacific Gyre Oscillation	www.o3d.org/npgo
PNA	Pacific North American Pattern	beringclimate.noaa.gov
PDOa/w	Pacific Decadal Oscillation; winter and annual means	www.jisao.washington.edu
PISST	Pribilof Islands surface temperature	beringclimate.noaa.gov
ENSO	El Nino Southern Oscillation	beringclimate.noaa.gov
SSTM2	Sea surface temperature at mooring TsfcM2	beringclimate.noaa.gov

Table 2.2. Candidate models for intermediate, deterministic relationships

Response:	ID:	Predictors:	Distribution:
Fry length	FL-1	$\alpha + \beta_1 * \text{spring temperature} + \beta_2 * \text{fry} + \beta_3 * \text{yearlings} + \varepsilon_t$	Normal
	FL-1gam	$\alpha + f(\text{spring temperature}) + \beta_1 * \text{fry} + \beta_2 * \text{yearlings} + \varepsilon_t$	
	FL-2	$\alpha + \beta_1 * \text{spring temperature} + \beta_2 * (\text{fry} + \text{yearlings}) + \varepsilon_t$	
	FL-2gam	$\alpha + f(\text{spring temperature}) + \beta_1 * (\text{fry} + \text{yearlings}) + \varepsilon_t$	
	FL-3	$\alpha + \beta_1 * \text{spring temperature} + \beta_2 * \text{fry} + \varepsilon_t$	
	FL-3gam	$\alpha + f(\text{spring temperature}) + \beta_1 * \text{fry} + \varepsilon_t$	
	FL-4	$\alpha + \beta_1 * \text{spring temperature} + \beta_2 * \text{yearlings} + \varepsilon_t$	
	FL-4gam	$\alpha + f(\text{spring temperature}) + \beta_1 * \text{yearlings}$	
	FL-5	$\alpha + \beta_1 * \text{spring temperature} + \varepsilon_t$	
	FL-5gam	$\alpha + f(\text{spring temperature}) + \varepsilon_t$	
logit (age-1)	AC-1	$\alpha + \beta_1 * \text{fry length} + \beta_2 * \text{spring temp.} + \beta_3 * \text{year}$	Beta
	AC-2	$\alpha + \beta_1 * \text{fry length} + \beta_2 * \text{condition} + \beta_3 * \text{year}$	
	AC-3	$\alpha + \beta_1 * \text{fry length} + \beta_2 * \text{year}$	
	AC-4	$\alpha + \beta_1 * \text{fry length} + \beta_2 * \text{spring temperature}$	
	AC-5	$\alpha + \beta_1 * \text{fry length} + \beta_2 \text{ condition factor}$	
	AC-6	$\alpha + \beta_1 * \text{fry length}$	
logit (SAS)	SAS-1	$\alpha + \beta_1 * \text{age} + \beta_2 * \text{length}$	Binomial
	SAS-1R	$\alpha + a_i + \beta_1 * \text{age} + \beta_2 * \text{length}$	
	SAS-2	$\alpha + \beta_1 * \text{age}$	
	SAS-2R	$\alpha + a_i + \beta_1 * \text{age}$	
	SAS-3	$\alpha + \beta_1 * \text{length}$	
	SAS-3R	$\alpha + a_i + \beta_1 * \text{length}$	
log(R/S)	RS-1	$\alpha + \beta_1 * \text{SAS} + \beta_2 * \text{Smolt / Spawner} + \varepsilon_t$	Log-normal
	RS-2	$\alpha + \beta_1 * \text{SAS} + \varepsilon_t$	
	RS-3	$\alpha + \beta_1 * \text{Smolt / Spawner} + \varepsilon_t$	
log(R/S)	DC-1	$\alpha + \beta_1 * \text{escapement} + \beta_2 * \text{spring temp.} + \varepsilon_t$	Log-normal

Model ID key: FL = fry length model, AC = age composition model, SAS = marine survival model, RS = freshwater/ marine survival variance partitioning model, DC = direct temperature-productivity correlation model, gam = generalized additive model, R = includes random

Table 2.3. Summary of trend analysis results for freshwater environmental variables

	slope	R ²	p-value	AR (1) slope	ρ	LRT p-value
Iliamna Airport air temperatures (°C):						
January mean	0.006 (-0.009,0.021)	0.01	0.438	0.006 (-0.012,0.024)	0.15	0.14
February mean	0.016 (0.001,0.03)	0.08	0.033	0.016 (0.001,0.031)	0.05	0.538
March mean	0.007 (-0.008,0.022)	0.01	0.379	0.007 (-0.011,0.024)	0.12	0.231
April mean	0.021 (0.007,0.035)	0.13	0.004	0.022 (0.004,0.04)	0.20	0.062
May mean	0.026 (0.013,0.039)	0.21	< 0.001	0.027 (0.01,0.045)	0.23	0.035
June mean	0.024 (0.01,0.038)	0.17	0.001	0.024 (0.007,0.042)	0.20	0.061
July mean	0.022 (0.008,0.036)	0.14	0.003	0.022 (0.005,0.04)	0.20	0.065
August mean	0.020 (0.006,0.034)	0.12	0.007	0.020 (0.004,0.037)	0.15	0.147
September mean	0.013 (-0.002,0.028)	0.05	0.079	0.013 (0.001,0.025)	0.20	0.201
October mean	0.015 (0.001,0.03)	0.07	0.039	0.015 (0.004,0.027)	0.21	0.155
November mean	0.003 (-0.012,0.018)	0.00	0.67	0.003 (-0.012,0.018)	0.03	0.962
December mean	0.019 (0.004,0.033)	0.10	0.012	0.018 (0.005,0.032)	0.07	0.776
Spring (Mar.- Jun.) mean	0.020 (0.006,0.034)	0.12	0.006	0.021 (0.001,0.041)	0.32	0.005
Autumn (Sep. - Nov.) mean	0.008 (-0.007,0.023)	0.02	0.307	0.008 (-0.007,0.023)	0.01	0.852
Spawning season mean high	0.010 (-0.005,0.025)	0.03	0.174	0.012 (-0.011,0.035)	0.39	0.001
Growing season degree days	0.030 (0.017,0.042)	0.26	< 0.001	0.032 (0.011,0.053)	0.41	< 0.001
Winter mean low	0.019 (0.005,0.033)	0.11	0.01	0.021 (0.002,0.04)	0.25	0.022
H ₂ O temp. at smolt migration	0.014 (0,0.029)	0.06	0.056	0.014 (-0.002,0.031)	0.10	0.302
Ice breakup (Day of Year)	-0.022 (-0.036,-0.008)	0.14	0.003	-0.022 (-0.038,- 0.005)	0.14	0.178

OLS = Ordinary least squares models. GLS = Generalized Least Squares models with first order autocorrelation. LRT = Likelihood ratio test between OLS and GLS models. Bold indicates significance at $\alpha = 0.10$, boxes indicate preferred model based on likelihood ratio test.

Table 2.4. Summary of trend analysis results for marine environmental variables

	slope	R2	p-value	AR (1) slope	ρ	LRT p-value
PDOa	0.013 (-0.001,0.026)	0.05	0.0681	0.012 (-0.015,0.038)	0.56	<0.001
NPI	-0.008 (-0.022,0.005)	0.02	0.2282	-0.008 (-0.023,0.006)	0.02	0.6648
PDOw	0.015 (0.001,0.028)	0.07	0.0321	0.015 (-0.003,0.032)	0.23	0.0342
ENSO	0.007 (-0.007,0.021)	0.02	0.2910	0.008 (-0.013,0.028)	0.35	0.0016
AO	0.01 (-0.003,0.024)	0.04	0.1331	0.01 (-0.007,0.027)	0.18	0.0958
NPGO	0.015 (0.001,0.028)	0.07	0.0332	0.016 (-0.011,0.044)	0.59	<0.001
PNA	0.008 (-0.006,0.022)	0.02	0.2630	0.008 (-0.005,0.02)	-0.11	0.5278
MaySST	-0.024 (-0.036,-0.011)	0.19	0.0004	-0.022 (-0.044,0)	0.45	<0.001
STM2	-0.009 (-0.023,0.005)	0.03	0.2130	-0.009 (-0.027,0.009)	0.25	0.0236
PISST	0.009 (-0.005,0.023)	0.03	0.1925	0.009 (-0.01,0.029)	0.29	0.0081

OLS = Ordinary least squares models. GLS = Generalized Least Squares models with first order autocorrelation. LRT = Likelihood ratio test. Bold indicates significance at $\alpha = 0.10$, boxes indicate preferred model based on likelihood ratio test.

Table 2.5. Summary of trend analysis results biological variables

Variable	Slope (95% C.I.)	R ²	p-value	Slope (95% C.I.)	ρ	LRT p-value
Abundance:						
Run Size	-0.131 (-0.302,0.041)	0.04	0.133	-0.132 (-0.329,0.065)	0.12	0.239
Escapement	-0.057 (-0.132,0.019)	0.04	0.137	-0.057 (-0.133,0.02)	0.01	0.758
Age 1.2	-0.013 (-0.083,0.058)	0.00	0.725	-0.013 (-0.079,0.054)	-0.07	0.777
Age 2.2	-0.103 (-0.259,0.053)	0.03	0.192	-0.102 (-0.261,0.058)	0.01	0.756
Age 1.3	0.019 (0,0.037)	0.07	0.048	0.019 (-0.001,0.038)	0.05	0.542
Age 2.3	-0.002 (-0.02,0.017)	0.00	0.850	-0.002 (-0.021,0.018)	0.04	0.573
Total return	-0.112 (-0.329,0.106)	0.02	0.309	-0.111 (-0.327,0.104)	-0.02	0.928
Smolt abundance	-1.141 (-3.18,0.898)	0.03	0.266	-1.141 (-3.135,0.853)	-0.03	0.986
Age-1 smolt abund.	-0.128 (-1.041,0.785)	0.00	0.779	-0.122 (-1.183,0.938)	0.15	0.189
Age-2 smolt abund.	-1.095 (-2.473,0.283)	0.05	0.117	-1.093 (-2.466,0.281)	-0.01	0.874
Productivity:						
R/S	0.000 (-0.034,0.033)	0.00	0.992	-0.003 (-0.055,0.048)	0.39	0.001
R/S Index	0.004 (-0.011,0.019)	0.01	0.604	0.002 (-0.025,0.028)	0.50	<0.001
Smolt/ spawner	-0.150 (-0.394,0.095)	0.03	0.224	-0.158 (-0.436,0.121)	0.13	0.253
SAS	0.001 (-0.001,0.002)	0.02	0.350	0.001 (-0.001,0.003)	0.10	0.206
Age Composition:						
% FW age-2 (return)	0.006 (0.003,0.009)	0.22	<0.001	0.006 (0.003,0.01)	0.10	0.309
% Ocean age-2 (return)	-0.003 (-0.005,-0.001)	0.16	0.002	-0.003 (-0.005,-0.001)	-0.15	0.385
% Age-1 smolts (brood)	0.003 (0,0.006)	0.07	0.064	0.003 (0,0.006)	0.01	0.696
Freshwater Growth:						
Age-1 smolt length	-0.088 (-0.15,-0.027)	0.13	0.006	-0.086 (-0.169,-0.003)	0.26	0.019
Age-2 smolt length	-0.098 (-0.196,0)	0.07	0.049	-0.098 (-0.231,0.036)	0.24	0.023
Age-1 smolt weight	-0.011 (-0.026,0.004)	0.04	0.144	-0.010 (-0.03,0.01)	0.27	0.013
Age-2 smolt weight	-0.025 (-0.056,0.006)	0.05	0.110	-0.024 (-0.072,0.023)	0.29	0.002
Age-1 condition factor	0.002 (0.001,0.003)	0.18	0.001	0.002 (0,0.003)	0.35	0.0028
Age-2 condition factor	0.000 (-0.001,0.001)	0.00	0.720	0.00 (-0.001,0.002)	0.36	0.002
Fry length	0.023 (-0.09,0.135)	0.00	0.687	0.033 (-0.107,0.172)	0.12	0.101
Phenology:						
50% smolt migration	-0.140 (-0.24,-0.04)	0.14	0.007	-0.139 (-0.241,-0.037)	0.02	0.764

OLS = Ordinary least squares models. GLS = Generalized Least Squares models with first order autocorrelation. LRT = Likelihood ratio test. Bold indicates significance at $\alpha = 0.10$; boxes indicate preferred model based on likelihood ratio test.

Table 2.6. Summary of intermediate relationship model results

ID	Coefficients (p-values)			AIC	AIC weight	% Dev. Explained	
	Spring temp.	Fry	Yearlings				
<u>FL-1</u>	2.01 (<0.001)	-2.27 (0.002)	-0.05 (0.328)	267.3	0.03	53.6	
FL-1gam	NA (<0.001)	-2.52 (<0.001)	-0.05 (0.452)	262.8	0.33	63.1	
FL-2	1.88 (<0.001)	-1.10 (0.006)		269.6	0.01	49.0	
FL-2gam	NA (<0.001)	-1.15 (0.003)		267.0	0.04	57.2	
FL-3	2.08 (<0.001)	-2.36 (0.002)	--	266.3	0.06	52.5	
<u>FL-3gam</u>	<u>NA (<0.001)</u>	<u>-2.61 (<0.001)</u>	--	<u>261.9</u>	<u>0.52</u>	<u>62.3</u>	
FL-4	2.38 (<0.001)	--	-0.68 (0.208)	276.0	0.00	41.1	
FL-4gam	NA (<0.001)	--	-0.69 (0.452)	274.3	0.00	49.7	
FL-5	2.02 (<0.001)	--	--	275.7	0.00	38.8	
FL-5gam	NA (<0.001)	--	--	274.3	0.00	47.7	
	Fry length	Spring temp.	Cond. Factor	Year			
<u>AC-1</u>	<u>0.106 (<0.001)</u>	<u>0.146 (0.045)</u>	--	<u>0.021 (0.023)</u>	<u>-24.2</u>	<u>0.55</u>	<u>72.1</u>
AC-2	0.119 (<0.001)	--	0.109 (0.961)	0.026 (<0.001)	-20.2	0.07	67.0
AC-3	0.100 (<0.001)	--	--	0.026 (<0.001)	-22.2	0.20	66.9
AC-4	0.119 (<0.001)	0.187 (0.011)	--	--	-21.5	0.14	68.7
AC-5	0.114 (<0.001)	--	2.55 (0.228)	--	-16.2	0.01	61.5
AC-6	0.116 (<0.001)	--	--	--	-16.8	0.01	59.1
	Length	Age	Year (var.)				
SAS-1	-0.018 (<0.001)	0.775 (<0.001)	--		$2.9 \cdot 10^8$	0.00	9.4
<u>SAS-1R</u>	<u>0.060 (<0.001)</u>	<u>-0.402 (<0.001)</u>	<u>1.023</u>		<u>$4.4 \cdot 10^7$</u>	<u>1.00</u>	<u>86.6</u>
SAS-2	--	0.503 (<0.001)	--		$3.0 \cdot 10^8$	0.00	8.6
SAS-2R	--	0.745 (<0.001)	0.931		$4.8 \cdot 10^7$	0.00	85.3
SAS-3	0.02 (<0.001)	--	--		$3.2 \cdot 10^8$	0.00	4.4
SAS-3R	0.040 (<0.001)	--	0.977		$4.5 \cdot 10^7$	0.00	86.4
	SAS	Smolt/Spawner					
RS-1	0.702 (<0.001)	0.609 (<0.001)			NA	NA	100
RS-2	0.569 (<0.001)	--			NA	NA	46.3
RS-3	--	0.464 (<0.001)			NA	NA	32.6
	Escapement	Spring temp.					
DC-1	-0.011 (0.621)	NA (0.533)			NA	NA	4.12

Best fit model values are underlined. Model ID key: FL = fry length model, AC = age composition model, SAS = marine survival model, RS = freshwater/ marine survival variance partitioning model, DC = direct temperature-productivity correlation model, gam = generalized additive model, R = includes random effects (i.e. mixed model).

FIGURES

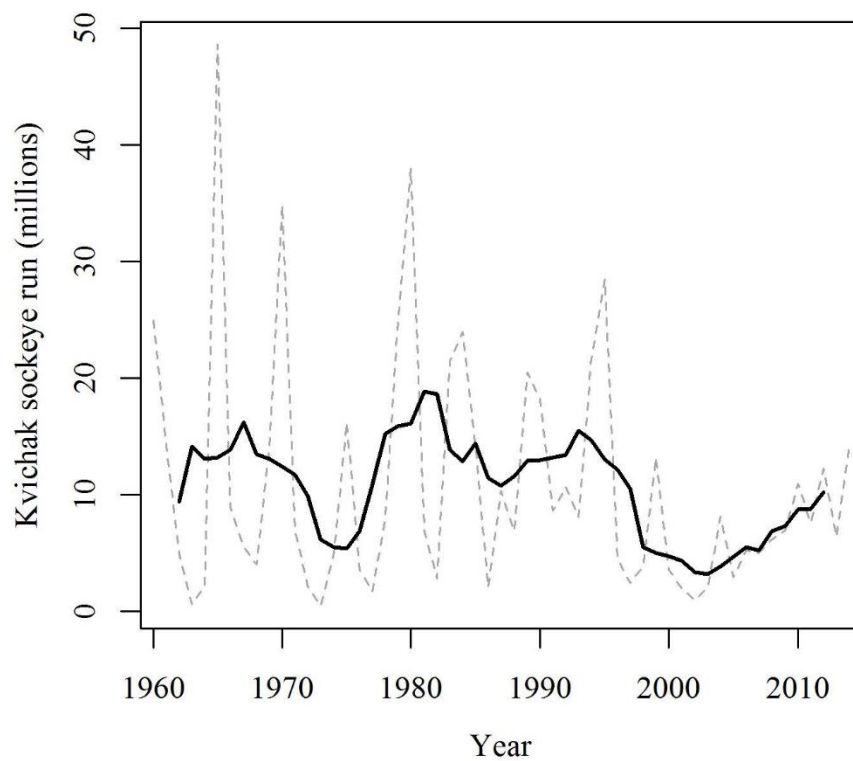


Figure 2.1. Kvichak River annual sockeye run size and 5-year moving average, 1960-2014.

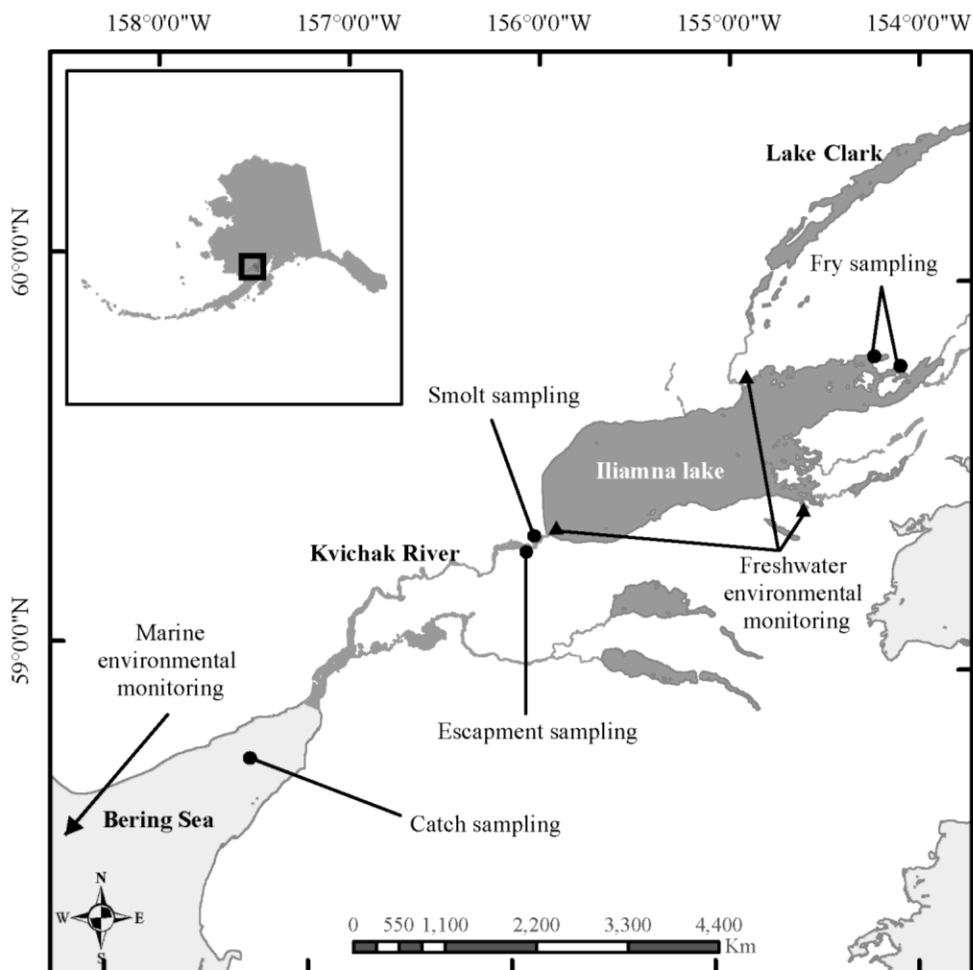


Figure 2.2. Kvichak River drainage, Alaska showing biological and environmental data collection sites. Spatial data retrieved from the USGS National Hydrography Dataset (nhd.usgs.gov).

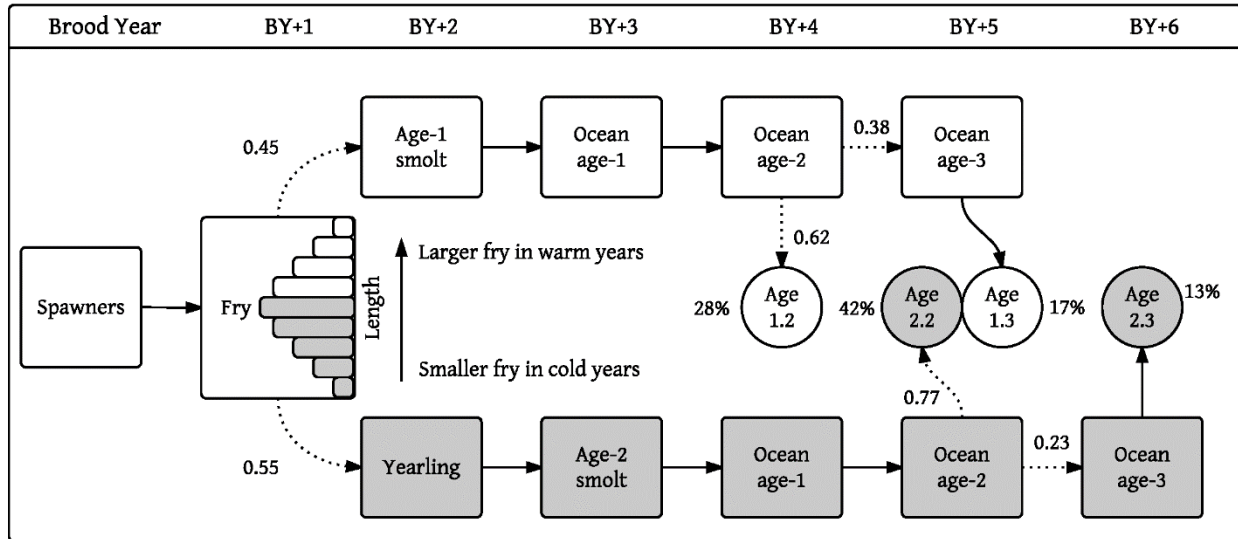


Figure 2.3. Kvichak sockeye salmon life-history and main life-history pathways. Percentages give long-term average age composition. Dotted lines indicate variable life history pathways and are labeled with the long-term average proportions of individuals following each pathway. Fry length frequency histogram shows relationship between freshwater growth and smolt age.

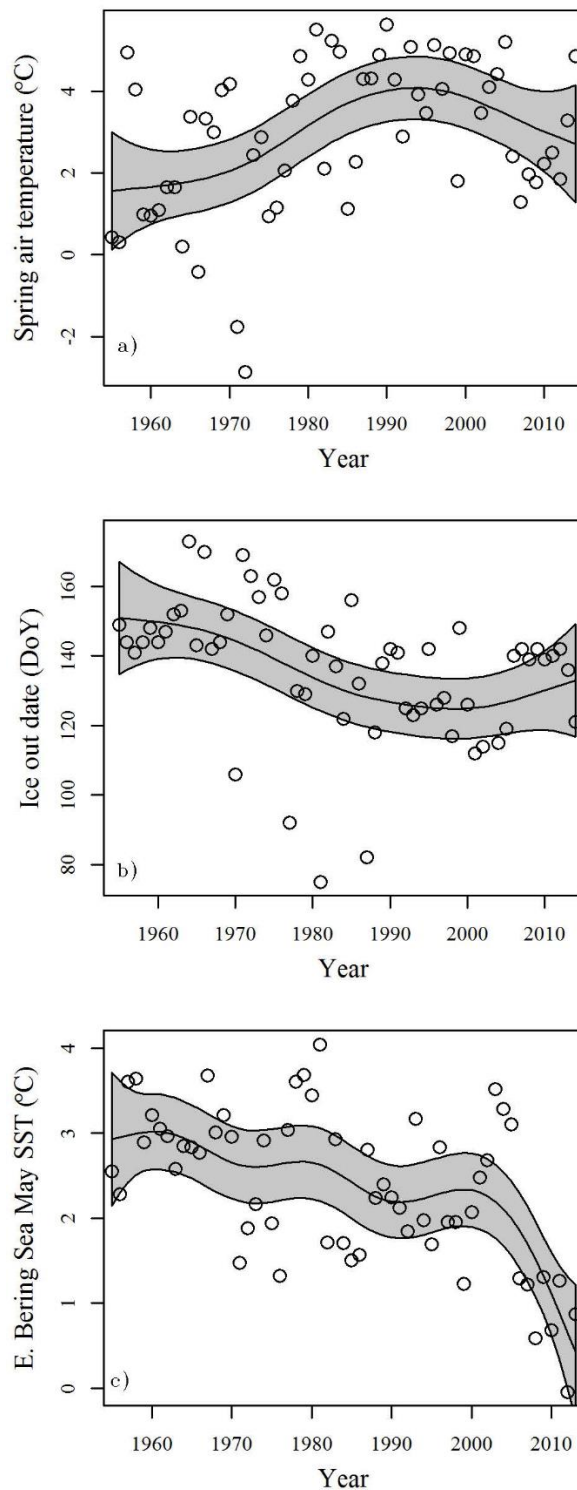


Figure 2.4. Temporal trends in environmental variables. a) March-June spring air temperature at Iliamna Airport, b) day of year on which ice breakup on Iliamna Lake is complete, c) mean May sea surface temperature in the eastern Bering Sea. Lines indicate GCV-selected best fit penalized regression spline; shaded areas show 95% confidence intervals and are included to highlight general trends.

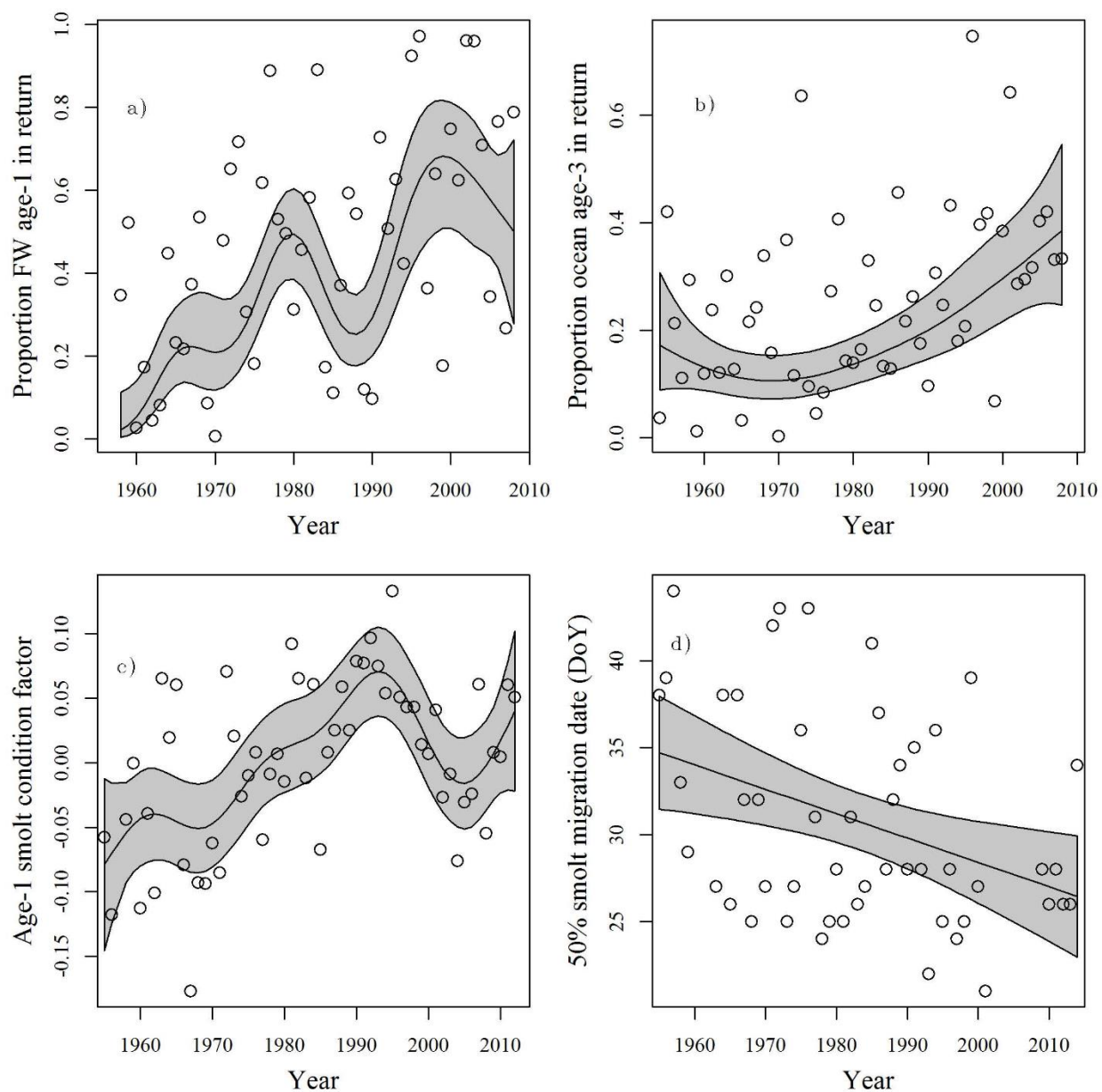


Figure 2.5. Temporal trends sockeye salmon biological variables. a) Proportion of brood year returning as freshwater age-1, b) proportion of brood year returning as ocean age-3, c) condition factor of age-1 sockeye smolts, d) date on which 50% of total smolt migration is reached. Lines indicate GCV-selected best fit penalized regression spline; shaded areas show 95% confidence intervals and are included to highlight general trends.

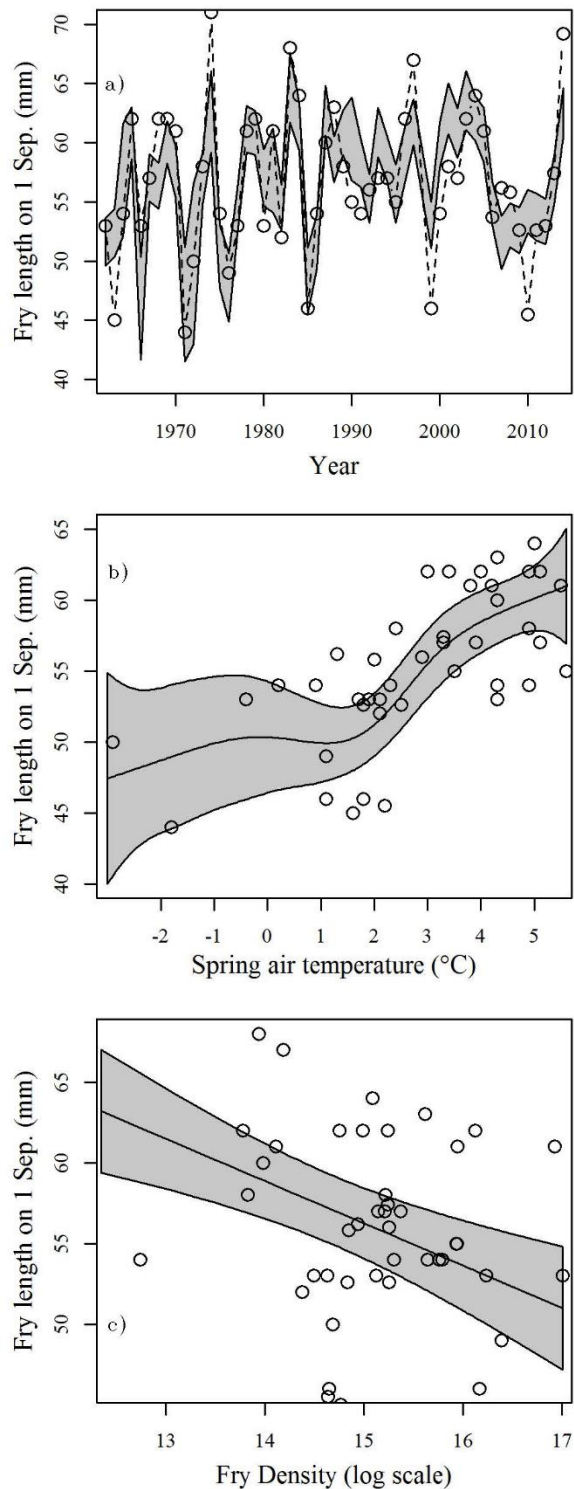


Figure 2.6. Results from AIC selected fry length model. a) Observed (points and dashed lines) and predicted (shaded area: 95% confidence interval) fry length. Partial plots showing effects of b) March-June mean air temperature and, c) sockeye fry density on growth during freshwater rearing.

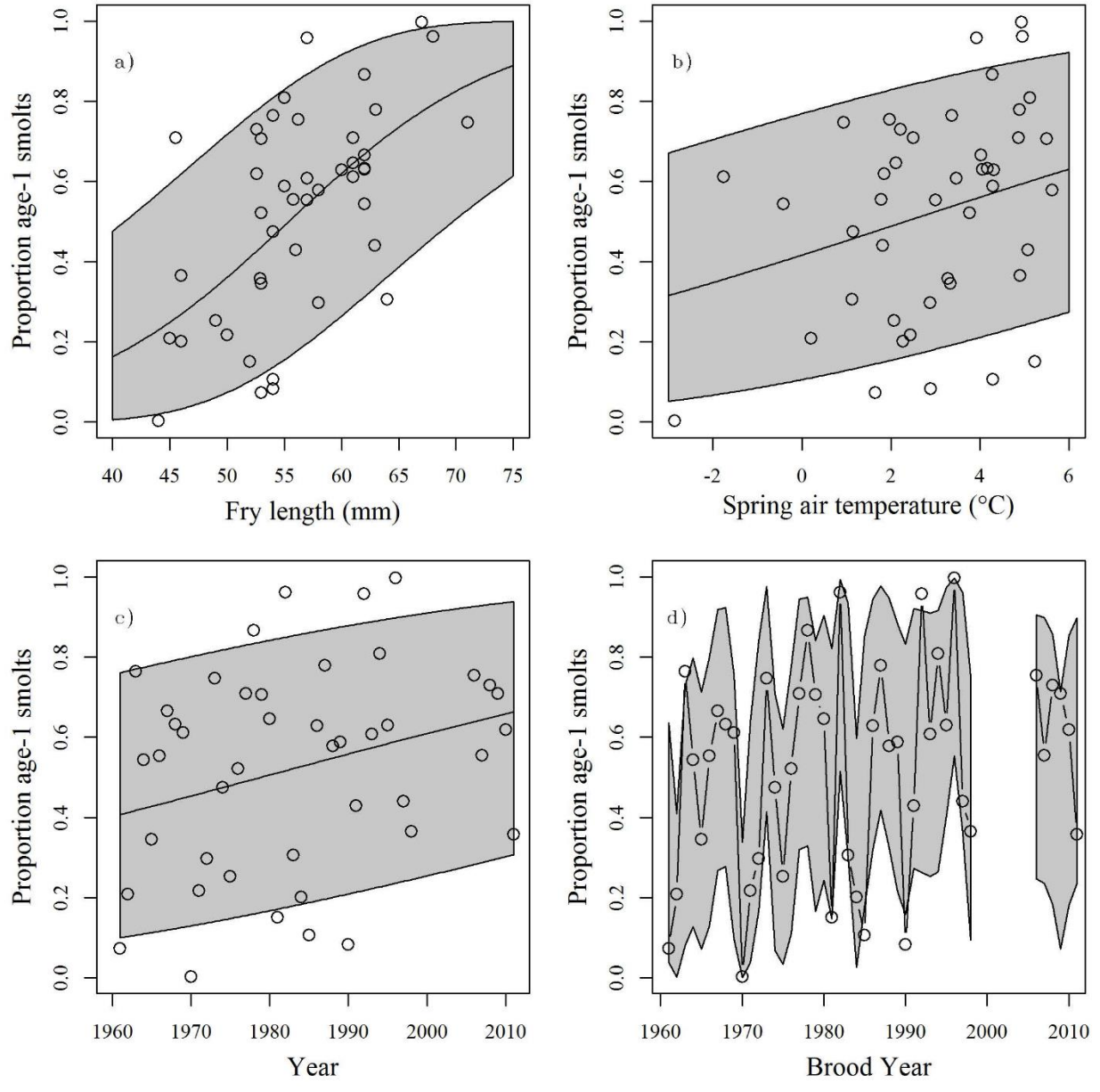


Figure 2.7. Results from AIC selected smolt age composition model. Partial plots showing the effects of a) fry length, b) spring air temperature in year of migration and c) year of migration on proportion of a brood year migrating at age-1. d) Observed (points and lines) and predicted (shaded area: 95% confidence interval) proportions.

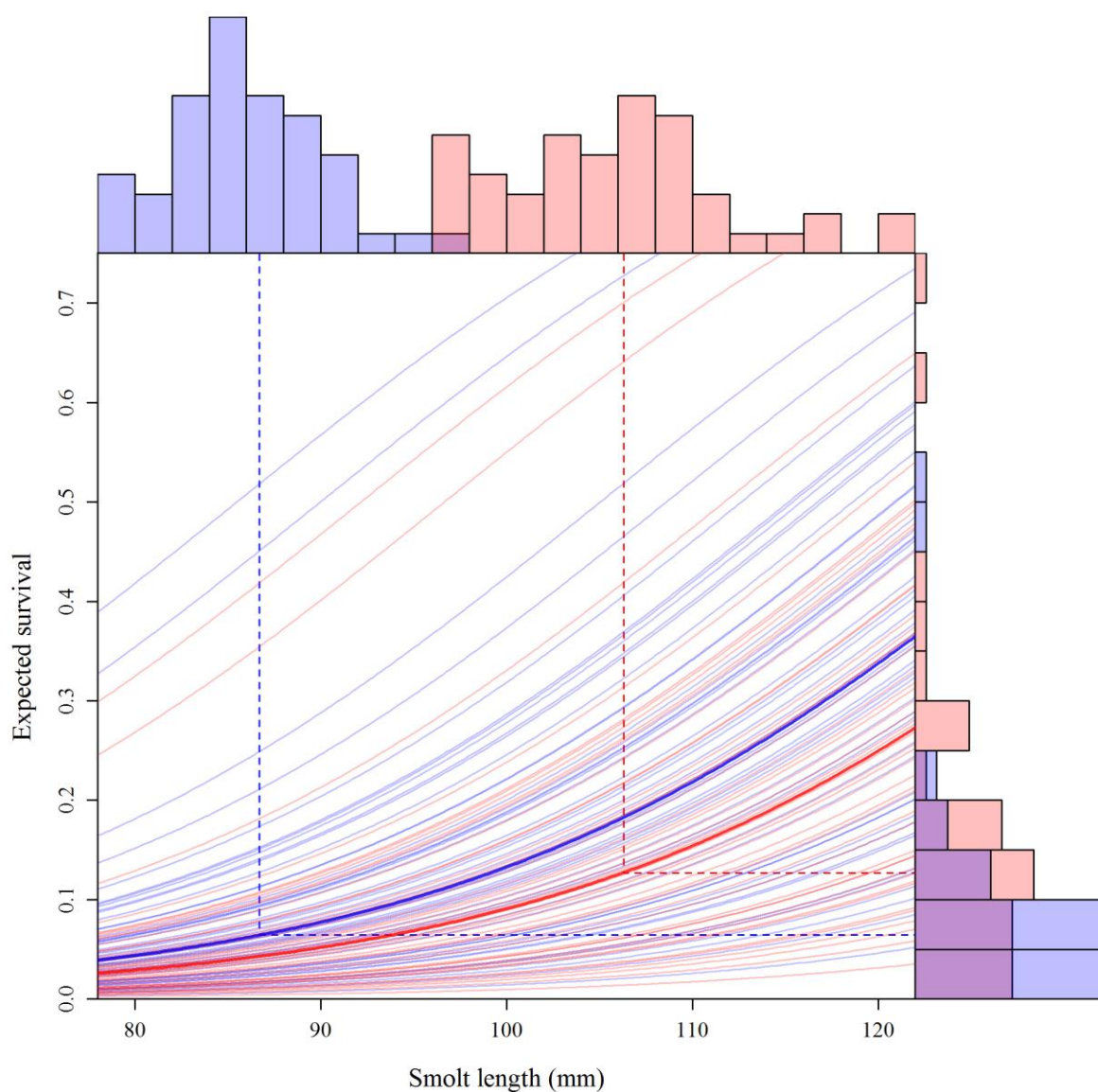


Figure 2.8. Results from AIC selected smolt survival model. Expected marine survival is shown in relation to length for age-1 (blue) and age-2 (red) smolts. Light colored lines show predicted survival as a function of length for each age in each year (random intercepts from model SAS-1R). Bold lines indicate mean values across all years. Histograms show frequency distributions of smolt length (x-axis) and expected survival at mean length (y-axis) for age-1 and age-2 smolts; dashed lines indicate medians of each frequency distribution, for each smolt age.

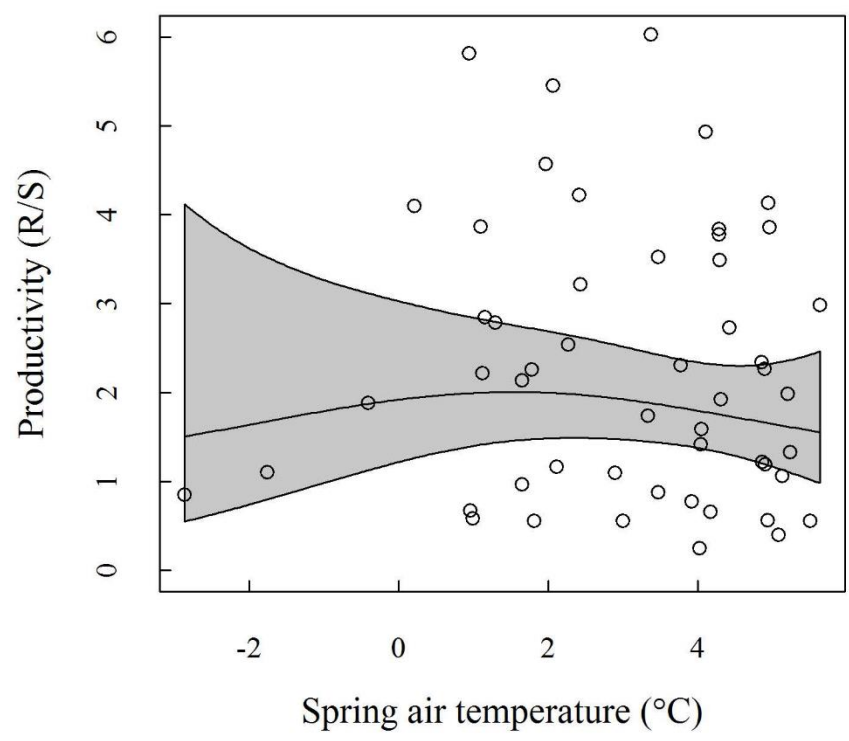


Figure 2.9. Non-significant relationship between Iliamna Lake temperature and sockeye salmon productivity. Partial plot of the influence of spring air temperature during freshwater rearing on productivity (R/S). Points show observed data, lines indicates GCV-selected best fit penalized regression spline; shaded area show 95% confidence interval.

CHAPTER 3 Climate and conspecific density trigger pre-spawning mortality in sockeye salmon (*Oncorhynchus nerka*)

ABSTRACT

Pre-spawning mortality (PSM) has been occasionally observed in association with high densities of adult Pacific salmon (*Oncorhynchus* spp.), but because large escapements are rare, the phenomenon remains poorly understood. A large spawning escapement (~12 times the 54 year median, and 3X the previous maximum) to a small stream in Alaska provided a unique opportunity to explore the factors that contribute to density-driven spawning ground mortality. After comparing patterns of mortality in 2014 with over 20 years of prior abundance and environmental data, we identified low dissolved oxygen (DO) as likely contributing to PSM. We then utilized a fish habitat-DO model to explore the roles of density-dependent and -independent factors in reducing DO. Stream flow and spawning density were identified as primary drivers of oxygen availability. Despite suboptimal oxygen levels the salmon did not die abruptly. Rather, on average they lived as long as in previous years (mean = 9.99 d), but many (55%) failed to complete spawning prior to death. Our results suggest that this mortality was ultimately a density-dependent process, exacerbated by low-flow conditions. Given projected effects of climate change on river flows and temperatures, similar events may occur more frequently in parts of the range of salmon where abundances remain high.

INTRODUCTION

The regulation of populations through density-dependent processes is one of the most salient themes in ecological research and provides the theoretical basis for classic methods of natural resource management (Turchin 1995). Indeed, maximum sustainable yield – a pervasive

target in fisheries management – fundamentally depends on compensatory processes of density-dependent population dynamics (Punt and Smith 2001). Although debate over the relative importance of abundance and environmental factors in determining fisheries recruitment remains unresolved (Myers 2001; Rose et al. 2001; Vert-Pre et al. 2013), density dependent reproductive success has long been observed in Pacific salmon (*Oncorhynchus* spp.) (Ricker 1954, 1962). Notwithstanding this empirical relationship between high densities of breeding adults and reduced per capita production of offspring (Quinn 2005), carrying capacity is difficult to measure and varies through time in response to environmental change or ecological factors (Kaeriyama et al. 2009; Irvine and Fukuwaka 2011; Rogers et al. 2013; Tillotson and Quinn 2016). Furthermore, fisheries management operates to largely preclude the very high densities that would be needed to fully observe compensatory processes in populations (Walters et al. 2004). Consequently, the true capacities of freshwater habitats to produce salmon are rarely tested, the processes that regulate populations at very high densities are seldom observed, and changes in carrying capacity may go unnoticed. Observations of high-density spawning can provide valuable insight into the processes that limit reproductive output in salmon populations and help to identify habitat or climate variables likely to affect the carrying capacity of spawning grounds (Battin et al. 2007).

Although density-dependent reductions in growth and survival have been documented throughout the salmonid life-cycle, competition for limited freshwater habitat is thought to be a critical determinant of abundance (Bradford 1995; Sharma and Hilborn 2001). The primary periods of freshwater density dependence vary predictably between species (Quinn 2005). Stream-rearing species such as coho salmon (*O. kisutch*) and steelhead trout (*O. mykiss*) are generally limited by freshwater rearing habitat as juveniles compete for food and territory (Quinn

2005). The most abundant species of Pacific salmon – sockeye (*O. nerka*), pink (*O. gorbuscha*) and chum (*O. keta*) – often spawn at much higher densities than those stream-rearing species because they make little if any use of riverine habitat for feeding as juveniles. Consequently, the primary density-dependent process regulating population growth is often competition for breeding habitat where females deposit fertilized eggs in gravel nests and guard them from disturbance by other females (McNeil 1964; Fukushima et al. 1998). Thus, for the salmon species that are most abundant, freshwater carrying capacity is commonly controlled by the quantity and quality of suitable spawning habitat (Quinn 2005).

Mortality rates of adult salmon in freshwater prior to spawning are normally very low, but can be elevated by anthropogenic impacts such as chemical contaminants (Scholz et al. 2011) and sub-lethal injury after escape from gillnets (Baker and Schindler 2009). Mortality along the freshwater migration corridor (“*en route mortality*”) can be caused by exposure to pathogens (Bradford et al. 2010) or environmental factors including high temperatures, and high flows that slow migration (Gilhousen 1990; Martins et al. 2012). Predators can be a significant source of mortality in small streams (Quinn et al. 2016), but otherwise most female salmon successfully spawn the great majority of their eggs if they reach the spawning grounds (Manzer and Miki 1986). Although it is relatively uncommon, unexplained premature mortality on the spawning grounds has long been observed (Gilhousen 1990). Williams et al. (1977) reported high rates of spawning ground mortality (5-62% of females) over several years in Horsefly River sockeye salmon – one of the larger populations returning to the Fraser River, Canada, and associated the losses with difficult migration conditions as well as an unknown bacterial infection. This “pre-spawning mortality” (PSM) is typically observed when female carcasses are recovered

containing a substantial proportion of their available eggs. Despite the long history of study, in many cases the underlying causes of PSM are unclear (Hinch and Martins 2011).

Because maturing Pacific salmon cease feeding upon freshwater entry, migration, maturation and reproduction must all be accomplished with a fixed energy budget prior to inevitable senescence (Crossin et al. 2009). Any conditions that delay migration or increase its energetic costs may therefore reduce in-stream lifespan. In many cases PSM may therefore be an extension of *en route* mortality (Hruska et al. 2010) and share the same underlying causes including disease, or exposure to stressful environmental conditions that increase energy expenditure (Williams et al. 1977; Hinch and Martins 2011). Delayed effects of migratory challenges may be the ultimate cause of PSM, but even sub-lethal migratory stress could reduce the duration of spawning ground occupation by increasing the rate of senescence or delaying arrival (Gilhousen 1990). Consistent with this process, Hruska et al. (2011) found that females that lived longer or established redds earlier after arrival on the spawning grounds retained fewer eggs, suggesting that reproductive lifespan can influence spawning success. However, PSM is not always associated with energy limitation (Hinch and Martins 2011). Pathogens affecting the gills and kidneys have also caused PSM in some Fraser River sockeye salmon populations (Bradford et al. 2010). Disease, poor environmental conditions and other sources of physiological stress may also impair the complex maturation processes that precede spawning (Barton and Iwama 1991; Jeffries et al. 2012). Because the causes of PSM are varied, there is also variability in how the term is defined. For the purposes of this study we use PSM to mean any fish that died prior to spawning all or most of its eggs, and the rate of PSM as the proportion of total spawners dying prematurely (see 2.1.2 for details on mode of death classification).

Density has not typically been implicated as a driver of PSM (Gilhousen 1990), but some mortality has been reported under high densities in adverse conditions such as the loss of 300 pink salmon or about 1% of a run during neap tides and low stream flows (Murphy 1985). In this case the PSM was apparently related to a combination of high temperature and low dissolved oxygen (DO) from crowding. Quinn et al. (2007) documented high levels of PSM and egg retention (i.e., incomplete spawning) in atypically large escapements of Alaskan sockeye salmon. They hypothesized that the mortality was driven by the joint influence of density and warm, dry environmental conditions, but could not identify an ultimate cause of mortality or evaluate the relative influence of each factor. Nevertheless, these findings suggest that PSM may be a density dependent process which could have been a common source of mortality prior to reductions in spawning density from fisheries. Here we explore the relative influence of density and environmental factors on spawning success during an anomalously large escapement of sockeye salmon to Hansen Creek, a small southwest Alaska stream in which PSM had not been previously observed in over two decades of intensive study. We first identify potential causative factors by comparing environmental conditions and run characteristics in 2014 with several decades of historical data. We then examine spatial and temporal patterns of mortality and environmental variation within Hansen Creek to test the hypothesis that reduced oxygen availability was a proximate cause of PSM. Finally, we model DO concentration in relation to habitat characteristics and salmon abundance to evaluate the relative contribution of density-dependent and –independent factors in producing sub-optimal oxygen conditions.

METHODS

Site and species characteristics

Hansen Creek meanders from a beaver pond ~2 km to Lake Aleknagik in the Wood River watershed of southwestern Alaska, with only one small tributary entering from a spring-fed pond (hereafter “side pond”) ~0.5 km below the beaver dam (Quinn and Buck 2001). The stream is narrow (average 4 m), shallow (average 10 cm) and during the sockeye salmon spawning season (mid-July to mid-August) flows clear with little fluctuation in discharge, even following rain events (Marriott 1964). The stream contains ~7,800 m² of accessible habitat during the spawning season and the side pond and beaver pond provide an additional ~800 m² and 4,000 m² respectively. The side pond has an average depth of 18 cm and the beaver pond areas used for spawning are almost all < 25 cm deep. The physical characteristics of Hansen Creek make it highly amenable to visual surveys of spawning salmon (Quinn et al. 2014). During these surveys, no other Pacific salmon species have been recorded and sampling of small fishes revealed only very low densities of juvenile Arctic char, *Salvelinus alpinus*, Dolly Varden, *S. malma*, and sculpins, *Cottus* spp. Consequently, adult sockeye salmon completely dominate the fish biomass in the stream, simplifying many ecological studies.

Stream surveys

From 1962-1990 annual surveys were conducted to estimate the number of sockeye salmon returning to Hansen Creek by walking the entire stream during or near the first week of August (typically the traditional peak of the run) and counting all live and dead salmon. Since 1990 the stream has been surveyed daily from mid-July through mid-August, which allows for more precise enumeration of total escapement than the peak count methodology. Pre-1991

escapement estimates were therefore expanded using the methods described by Quinn et al. (2014) to allow for comparison across all years. During the more recent period the stream has been surveyed in six sections: the mouth, lower, middle and upper portions of the main channel, and the two ponds (Figure 3.1.). To avoid double counting, dead fish are removed from the stream and tossed at least 3 meters beyond the bank. Starting in 1992, in addition to counting live and dead fish daily, survey teams also recorded the sex and cause of death for each fish, and measured body length from the mid-eye to hypural plate (ME-H) of a subsample of the dead.

Spawning salmon in Hansen Creek may die from several causes. Many fish become stranded while crossing the delta at the mouth of the stream when the lake level is low, and some strand in other shallow reaches but the main causes death are predation by brown bears (*Ursus arctos*) and glaucous-winged gulls (*Larus glaucescens*) (Quinn and Buck 2001). Those fish not killed or stranded typically spawn and die of senescence in within a few weeks of stream entry. Each mode of death is characterized by specific carcass attributes (described previously in: Carlson et al. 2007; Cunningham et al. 2013) that allow for reliable classification. Prior to 2014 PSM had not been regularly observed or recorded in Hansen Creek; fish were characterized as PSM if they had intact fins, lacked rough skin patches typical of senescent fish, were not obviously stranded in shallow water and showed no wounds indicating predation. These criteria likely resulted in conservative estimate of PSM rates because many fish are scavenged by gulls and bears after death (Quinn and Buck 2000), and therefore were not classified as PSM. For the analyses reported here we group all fish into three categories: those that were killed by predators or stranded (“killed”), those that spawned successfully (“senescent”) and those that died prematurely without any obvious cause (PSM). Field classification for cause of death is more reliable in females than males. Females spawn their eggs with a few days and so the pre-

spawning and post-spawning fish are distinguishable whereas males breed throughout their lives in the stream; as a result gonads are depleted more gradually and physical appearance is less indicative of spawning status in males (Carlson et al. 2009). Although all carcasses were classified based on mode of death, because we could not confirm the accuracy of our classification for males, analyses involving this variable are restricted to females.

Although time constraints precluded body cavity examination of all individuals, to test our ability to visually identify PSM we estimated the proportion of total eggs spawned for a subset of females classified as either PSM or senescent. During the 2006-2010 spawning seasons a total of 124 completely unspawned females found stranded at the mouth of Hansen Creek were measured for length and gonad volume. Using these measurements we established the relationship between body length and egg volume (egg number and average egg mass) for Hansen Creek female sockeye using linear regression ($r^2 = 0.53$). With this relationship and the lengths of the 2014 subsample we calculated an expected gonad volume for 49 females blindly classified as senescent and 67 classified as PSM. The body cavities of these fish were then examined and the volume of any retained eggs measured. Retained eggs were separated from any body cavity fluid in a colander and then placed in a graduated cylinder with 100 ml of stream water to remove air pockets trapped between eggs. Dividing observed egg volume by expected gonad volume therefore estimates the proportion of total eggs spawned. Robust visual identification methods would be indicated by a high average proportion in senescent individuals and low proportion in PSM individuals.

Tagging

In addition to the spawner surveys, a portion of the sockeye salmon run to Hansen Creek has been captured and tagged in Lake Aleknagik near the mouth of the stream since 1999 to measure reproductive lifespan and observe the spawning behavior and movements of individuals. Fish staging at the creek mouth were captured using a beach seine, anesthetized, and fitted with a pair of individually coded, brightly colored disk tags. Previous research suggests that the tagging procedure does not noticeably affect spawning behavior or lifespan (Carlson et al. 2007). Tagged fish were observed and recorded during daily surveys. Stream entry date was recorded as the first day a tagged fish was observed in the creek, though in practice the fish might have arrived the previous day, after that survey had been completed. Date of death was assumed to be the day after the last live observation. In-stream lifespan was calculated as the difference between date of death and date of entry, so a fish first seen in the stream dead would have an instream life of 1 d, meaning that it died within its first day in the stream. Any tagged females recovered that showed no visible signs of predation or scavenging were inspected for retained eggs and if present, measured for volume as described above.

Environmental monitoring

Unfavorable environmental conditions have been implicated in prior studies of PSM (Quinn et al. 2007). High water temperatures are of particular concern for sockeye salmon (Eliason et al. 2013), but given the high densities of fish observed in Hansen Creek in 2014 oxygen limitation was also a concern. Water temperatures were monitored throughout the spawning season with DS1921 iButton® temperature loggers (Maxim Integrated, San Jose, CA, USA) deployed at five locations throughout the stream. Temperature loggers were situated to

capture the range of thermal regimes present in Hansen Creek, recording data at 2 h intervals from 21 July 2014 through 12 August 2014. A complete profile of stream temperature and DO was collected on 30 July 2014 at ~100 m intervals from Lake Aleknagik to the two primary springs that feed Hansen Creek. At each sampling location coordinates were recorded using a handheld GPS and water temperature, oxygen saturation (%) and DO concentration ($\text{mg}\cdot\text{L}^{-1}$) were measured using a YSI model 85 multimeter (YSI incorporated, Yellow Springs, OH, USA). In total 31 stations were sampled in the main stem of the stream (M1-M31 from downstream to upstream) and six were sampled in the side pond and its channels (S1-S6). A subset of locations was also sampled on 31 July and 4 August 2014.

To provide context for weather conditions in 2014, historical climate data from the King Salmon airport were retrieved from the NOAA National Centers for Environmental Information (www.ncdc.noaa.gov). Although located 130 km from Hansen Creek, King Salmon is the closest weather station with sufficient coverage of both historical and recent time periods and should capture synoptic trends in Bristol Bay weather that affect the Lake Aleknagik region. In total 73 years of climate data (1942-2015) were available. High and low temperatures and precipitation observed at King Salmon were averaged over the typical Hansen Creek peak spawning season (15 July – 15 August). Stream flow is an important environmental variable for which no suitable historic record was available. Discharge of Hansen Creek has been measured opportunistically throughout the spawning season since 2008, and qualitatively suggest that in 2014 flows were lower than average, though this stream has perennially low discharge. However, because these data were not systematically collected and cover only a short time period they are unsuitable for quantitative analysis. Snowmelt is important for maintaining summertime flows in southwest Alaska streams, either as direct runoff or indirectly through the recharge of alluvial aquifers (Lisi

et al. 2015). Snowpack and the timing of spring melt therefore have a strong influence flows in Hansen Creek during the spawning season (Barnett et al. 2005). Cumulative snowfall for April through June was therefore used as a simple metric that integrates spring precipitation and temperature and should provide a coarse estimate of summer base flow conditions.

Historical comparisons

Climate and run characteristics in 2014 were compared with previous years to identify anomalous conditions that might have contributed to high rates of PSM. Histograms, ordered bar plots and box plots provided qualitative comparisons of 2014 observations with historical records of environmental conditions and run characteristics. Run characteristics evaluated included the number of salmon that returned (escapement) to Hansen Creek, total return to Hansen Creek (i.e., escapement plus estimated number caught in fisheries that would have returned to Hansen Creek), probability of successful spawning, spawning density, natural in-stream lifespan, and realized in-stream lifespan (see definitions below). Environmental conditions included mean, mean high, and mean low air temperatures for 15-July through 15-August, cumulative precipitation during that same period, and spring (April-June) snowfall. Spawning escapement was calculated as the sum of all dead and the final live count within a year. Total return was calculated as the sum of escapement plus the catch, estimated based on age and sex specific harvest rates reported by the Alaska Department of Fish and Game for the Nushagak commercial fishing district and the age composition in Hansen Creek that year (Quinn et al. 2014). Probability of successful spawning was calculated as the proportion of total escapement recorded as senescent in a given year. Natural in-stream lifespan – the number of days a senescent fish had been alive in Hansen Creek – was estimated from tagging records. Realized in-stream lifespan –

the average number of days alive in Hansen Creek for all fish regardless of ultimate cause of mortality – was estimated using an inverse area-under-the-curve (AUC) method by dividing the integral of the live-count curve by total escapement (Bue et al. 1998). Spawning density was calculated the sum of the total dead and live counts on a given date divided by the wetted area of the stream or survey reach.

Patterns of mortality

Differences in the frequency of PSM between stream reaches or through time can provide information on the factors that contributed to early mortality. For example, high rates of PSM or a more rapid increase in cumulative deaths relative to other portions of the stream could indicate unfavorable conditions in a survey reach. Cumulative deaths observed in each survey reach were plotted by mode of death (senescence, PSM, killed) to compare the temporal and spatial distribution of the different causes of mortality. Multinomial logistic regression was utilized to evaluate the statistical significance of apparent differences in the causes and timing of death between stream reaches. The conditional probabilities of dying by each of the three modes of death were modeled as a function of stream reach, a factor; and day-of-year, a continuous variable. Because no spawning occurs in the delta area, all fish recovered at the mouth of the creek were classified as ‘killed’ and we therefore excluded this survey reach from spatial comparisons. Analysis was completed using the ‘nnet’ package in R version 3.2.5. Variation in the overall timing of mortality between reaches was further compared with a pairwise Wilcoxon signed rank test using the `pairwise.wilcox.test` function in the ‘stats’ package. This method was utilized to test for significant horizontal shifts in the empirical cumulative distributions of total

dead between stream reaches. The Bonferroni correction was applied to resulting p-values to account for the influence of multiple tests.

Dissolved oxygen supply and demand

Suboptimal dissolved oxygen conditions were observed throughout Hansen Creek during the 2014 spawning season, but the primary cause of oxygen drawdown was uncertain. To evaluate the relative influence of several factors on DO concentrations in Hansen Creek we modeled and conducted sensitivity analyses on oxygen supply and demand, generally following the methods of Willis *et al.* (2015). In particular, we were interested in the influence of respiration by spawning salmon on DO concentration within a survey reach which can be described as

$$DO_r = (DO_i - DO_c)/(A \cdot D)$$

where DO_i is the available DO (mg) within the entire survey reach, DO_r is the remaining DO (mg/L) at the lower extent of the reach, DO_c is the net oxygen consumption (mg) within the reach. The denominator in the equation gives reach volume and includes the reach area, A (m²) and average depth D (m). DO_c is comprised of several components including respiration by salmon, other respiration (e.g. decay), physical reaeration and photosynthesis. Initial examination of the DO profiles indicated that oxygen drawdown was occurring in the pond reaches of Hansen Creek. We constrained our analysis to the beaver pond because the side pond contributes so little to the stream's total discharge. Given the large negative oxygen flux and relatively brief water residence times observed in the ponds we assumed that the reoxygenating processes of photosynthesis and physical aeration were negligible in these areas. The influence of respiration sources other should be relatively minor given that Hansen Creek is cool and clear, and that

salmon carcasses were removed from the stream each day (Jankowski et al. 2014). In any case, if any of these unobserved variables contributed significantly to net oxygen consumption it should be indicated by poor model performance (i.e. consistently large differences in predicted and observed DO_r).

The initial DO available within the survey reach is calculated as

$$DO_i = DO \cdot Q \cdot \theta$$

where DO is the concentration (mg/L) at the upstream extent of the survey reach, Q is the discharge (m^3/s) and θ is the residence time of water in the reach (min). The total net oxygen flux (assumed to approximate oxygen consumed by spawning salmon) is given by

$$DO_c = R \cdot m \cdot \theta \cdot N$$

where R is the rate of oxygen consumption (respiration) by spawning sockeye salmon ($mg \cdot min^{-1} \cdot kg^{-1}$), m is the average mass of an individual fish and N is the number of fish present within the reach. θ is equivalent to residence time of water in the reach and represents the length of time that DO is available for salmon respiration. The rate of oxygen consumption – an approximation of metabolic rate – has been extensively studied in salmonids and has typically been modeled as a function of mass, water temperature, swimming speed, and salinity. We utilize the model of Ware (1978) which Trudel *et al.* (2004) found to more accurately predict sockeye salmon oxygen consumption than other common models. Total metabolic rate (R ; mg/h) is calculated as the sum of standard metabolic rate (R_s ; mg/h) and swimming cost (R_a ; mg/h). We ignore the cost of digestion because spawning sockeye salmon cease feeding well before arriving on the spawning grounds. Standard metabolic rate is calculated as

$$R_s = \alpha_1 \cdot m^\beta \cdot e^{\phi \cdot T}$$

where α_1 , β , and φ are constants derived empirically from experiments and T is temperature ($^{\circ}\text{C}$). Swimming cost is calculated as

$$R_a = \alpha_0 \cdot m^{\delta} \cdot U^{\lambda}$$

where α_0 is the swimming cost at zero velocity, U is swimming speed (cm/s) and δ and λ are empirically derived constants. Updated values for all constants from Ware (1978) were taken from Trudel *et al.* (2004) and are as follows: $\alpha_1 = 0.0799$, $\beta = 0.80$, $\varphi = 0.069$, $\delta = 0.44$, $\lambda = 2.42$. For a given temperature and salinity α_0 was estimated using equation 5 from Trudel *et al.* (2004). Plausible values for U were taken from Brett (1965), who estimated swimming speeds at varying activity levels (e.g. $\frac{1}{4}$ active, full active) in sockeye salmon.

The model was first run with best estimates of all variable model parameters based on field observations from 30 July, 2014, the date of the most comprehensive environmental monitoring. To address uncertainty in model parameters and explore the relative impact of parameters on the model output (DO_r) we conducted a sensitivity analysis using Monte Carlo simulation. Random draws from continuous probability distributions were taken for reach depth (D), water temperature (T), discharge (Q), average fish mass (w), oxygen concentration at top of reach (DO), swimming speed (U) and number of fish within the reach (N); ranges for each distribution are given in Table 3.1. Distributions and parameters were chosen based on available observations and informed by literature values where necessary. The ranges are intended to capture all plausible values for the beaver pond on 30 July 2014. For each set of randomly selected parameters DO_r was calculated. Results from 1,000,000 runs were summarized by calculating – for a given range of each parameter – the probability of DO_r falling below 3 mg/L, a level below which acute mortality is observed (Bjornn and Reiser 1991). For simplicity we did not model a feedback between DO concentration and fish density, and as a result negative DO

remaining values are possible. For the purposes our analyses negative DO values were replaced with 0 mg/L which indicates that all available oxygen would be consumed given the selected parameter values.

RESULTS

Season Overview

Hansen Creek was surveyed 27 days during the 2014 spawning season. Sockeye salmon were aggregated off the mouth of the creek by 15 July and were entering the creek by 18 July when the first complete survey was conducted: 2,779 live fish and 1,042 dead – mostly stranded or killed by bears and gulls in the delta area. Surveys were conducted daily from 21 July through 11 August and then every 2-3 days through 20 August. In total 59,692 dead salmon were counted and 1,017 fish remained alive in the stream at the end of the survey season for a spawning escapement of 60,709 (59.5% females). Both the live count and spawner density (live + dead) peaked on 5 August at 27,195 and 32,415 respectively. Most fish did not successfully spawn. Of the 33,378 females that entered the creek, 35% fully spawned (senescent), 9% were killed, and 55% died prematurely or retained the majority of their eggs (PSM). Analysis of expected vs. observed gonad volume confirmed that field classification procedures were sufficient for identifying PSM. Forty-nine females classified as senescent spawned $91 \pm 0.5\%$ (mean \pm s.e.) of their predicted eggs whereas 67 females classified as PSM spawned only $25 \pm 0.5\%$ of their eggs. Applying these rates across all females suggests that in total ~44% of available eggs were lost to PSM and incomplete spawning.

Across all monitoring stations, water temperatures ranged from 2.9 to 17.4 °C during the spawning season. Temperatures at all stations followed a similar temporal pattern that was

dominated by diel variation. Aside from the uppermost station located immediately downstream of the headwater spring, all water temperatures generally tracked the ambient air temperature with the warmest period extending from 25-30 July. Despite daily and seasonal variation, water temperatures rarely exceeded 15° C, the upper threshold for preferred sockeye spawning temperature (Bjornn and Reiser 1991). Water temperature generally increased from upstream to downstream as cold water from springs gradually equilibrated with air temperatures. In total, 71 mm of rain fell at Aleknagik during the spawning season with the large majority (65 mm) falling after 5 August. On 30 July, the date of the most comprehensive dissolved oxygen monitoring, 35 stations were sampled and DO ranged from 2.1 – 11.9 mg/L and 18.4 – 90.4% saturation (Figure 3.2). Recommended DO levels for migrating and spawning salmonids are at least 80% saturation and not even temporarily below 5 mg/L (Bjornn and Reiser 1991). Only four sampling stations met the saturation criterion, the two uppermost and two lowermost. Nearly half of the stations were below the 5 mg/L threshold and several areas within the beaver pond and side pond were below 3 mg/L, a level at which acute responses are expected (Davis 1975). Stations resampled on 31 July (9 stations) and 4 August (6 stations) had varied little from 30 July concentrations (\pm 0-2 mg/L), and overall the shape of the DO profile remained consistent. There were high DO concentrations and saturation levels near the side pond and beaver pond springs, a rapid drawdown in the ponds, and gradual increase approaching saturation near the mouth (Figure 3.2).

Historical comparisons

Environmental conditions during the 2014 Hansen Creek sockeye spawning season were warmer and drier than average, though not record setting. Average air temperatures during the traditional spawning season were in the top 10% of the 73 year record. Cumulative precipitation

at King Salmon was close to average, though fell almost exclusively toward the latter half of the run, and spring snowfall was well below average (Table 3.2) which collectively support the qualitative observation of lower than average flows during the spawning season. The number of sockeye salmon returning to Hansen Creek was exceptionally large relative to historical records. The observed escapement was three times the previous maximum and the estimated total run (i.e., including the estimated number of salmon taken in the fishery) almost doubled the standing record. Natural stream life and the overall probability of spawning success were average, but realized stream life was higher than average, an apparent result of the atypically low rates of bear predation and stranding. The combined effect of a large escapement and low predation rate was record high densities of salmon in the stream day after day (Table 3.2; Figure 3.3).

Patterns of mortality

Mortalities were clustered in the beaver pond, upper, and middle reaches which contained 74% of the observed dead. On a per-area basis, 10.2 dead/m² were counted in the upper reach and 5.7 dead/m² in the middle reach. The beaver pond and side pond each had 3.8 dead/m² while in the lower reach only 1.5 dead/m² were recovered. The mouth is a dynamic environment for which effective wetted area cannot be easily determined because it depends on lake level, but ~9% of total dead were recovered in this reach. Proportionally, PSM was most prevalent in the side pond where 90% of females died without fully spawning, compared to 46% in the beaver pond, 78% in the upper, 54% in the middle, and 13% in the lower reaches. The spatial differences in PSM rates were significantly and inversely related to average DO concentration (adjusted R²=0.90, p=0.009; Figure 3.4).

Multinomial logistic regression confirmed the significance of these differences and also indicated changes in mode-of-death through time; all coefficients were highly significant ($p < 0.0001$). For the response variable (mode-of-death) senescence was used as the reference category. The relative risk of being killed vs. dying of senescence decreased over the course of the spawning season while the relative risk of PSM increased (Figure 3.3). For the categorical predictor variable (survey reach) the lower reach was used as the reference category. The lowest proportion of salmon died of PSM in the lower reach; the proportion ranged from 6.8 to 77.8 times greater than the lower reach in the other reaches (Table 3.3). There were also significant differences between survey reaches in the cumulative distributions of deaths: earliest in the side pond, followed by the upper reach, with mortality occurring later in the remaining three reaches (paired Wilcoxon signed rank test; Table 3.4; Figure 3.5).

Dissolved oxygen supply and demand

Model and sensitivity analysis results indicated that observed sockeye salmon densities would be sufficient to cause significant oxygen drawdown in the Hansen Creek ponds given environmental conditions on 30 July 2014. Using the best estimate point values, the model predicted a DO concentration of 2.94 mg/L at the beaver pond outlet, similar to the observed value of 3.25 mg/L. Across all Monte Carlo model runs the median final DO concentration was 2.78 mg/L and the overall probability of DO staying above 3 mg/L was only 40%. The sensitivity analysis further indicated that remaining DO was most sensitive to stream discharge and fish swimming speed (i.e., activity) and least sensitive to temperature and depth (Figure 3.6).

DISCUSSION

The patterns of mortality observed in Hansen Creek during the 2014 sockeye salmon spawning season likely resulted from the combination of an unusually large number of spawning salmon and warm, low-flow conditions, producing sub-optimal DO levels. Several lines of evidence implicate density-driven oxygen depletion as a proximate cause of PSM. DO monitoring conducted during the peak of the run found conditions consistently below levels recommended for spawning and migrating salmon throughout the large majority of the stream (Figure 3.2). In many portions of the stream oxygen concentrations were even lower, frequently at levels that cause avoidance reactions (< 5 mg/L) and at some sites acutely harmful (< 3 mg/L; Bjornn and Reiser 1991). Modeling of oxygen availability in response to density, activity, habitat and environmental conditions indicated that even using a conservative estimate of activity level, the observed number of fish in 2014 would be sufficient produce dangerously low oxygen conditions. Meanwhile, water temperatures remained largely within the optimal range for adult sockeye migration and spawning and temperature is therefore unlikely to have caused PSM as has been observed elsewhere (e.g. Martins et al. 2012). Spatial and temporal patterns of mortality were consistent with the hypothesis that oxygen depletion contributed to PSM. The rates of PSM varied significantly between survey reaches and showed a strong negative correlation with mean DO (Figure 3.3). Furthermore, in the reaches with the lowest mean DO (upper and side pond) cumulative mortality increased more rapidly than the other reaches indicating reduced duration of survival in these areas.

However, despite suboptimal oxygen conditions throughout much of Hansen Creek in 2014, PSM does not appear to have resulted from rapid suffocation. Comparison of natural and realized stream life with historical records revealed that on average fish actually lived as long, or

longer after stream entry compared to other years when salmon densities were ca. 10% of the 2014 densities (Table 3.3). Moreover, tagging data showed no significant difference in stream life-span between females that spawned successfully in 2014 and those that died prematurely. High density apparently contributed to a low *per capita* risk of bear predation, which typically limits in-stream survival time because bears tend to kill newly arrived salmon (Gende et al. 2004). As a result, fish survived in-stream for longer than average with a mean realized in-stream lifespan of over 7 days, which far exceeds the 23-year median of 4.18 d (Table 3.2). The widespread failure to spawn is therefore paradoxical because under typical conditions female sockeye enter Hansen Creek and deposit all their eggs within 3-5 days (McPhee and Quinn 1998) so stream life of 7 days should be more than enough time to complete spawning. Observations of the carcasses indicated that the PSM females did not have the scars and frayed tails typical of females that have been fighting to obtain nesting sites, digging nests, and fighting to defend the completed nest. Indeed, their outward appearance belied how long they had been in the stream; they resembled newly arrived salmon which suggests that many fish died without even attempting to spawn despite an abundance of potential mates and high quality breeding habitat that characterizes Hansen Creek. Fish may have instead been holding in areas with relatively benign environmental conditions – large aggregations of fish were commonly observed near springs and other sources of oxygenated water – or unable to initiate spawning due to space limitation or physiological stress. Thus, reduced oxygen availability cannot alone account for the prevalence of PSM in 2014; atypical in-stream behavior appears to have also played an important role.

There are a number of potential explanations for this abnormal delay in reproductive activity. Social factors associated with the extreme crowding may have inhibited the formation of

redds and completion of spawning. Alternatively, oxygen limitation may have had physiological impacts that disrupted spawning. Recent investigations of cardiorespiratory physiology in Pacific salmon suggest that energy intensive activities such as upstream migration can be limited by aerobic scope, especially when temperatures exceed optimum levels (Eliason et al. 2013). Though not previously investigated, reductions in DO would be expected to similarly reduce aerobic scope. Such a reduction in scope could potentially curtail the energy intensive activity of nest construction or lead to cardiac collapse if exertion continued in sub-optimal oxygen conditions (Eliason and Farrell 2016). A final possibility is that physiological responses to external stressors could have delayed maturation (Barton and Iwama 1991). Under experimental conditions, female sockeye salmon exposed to stressful thermal conditions (19° C) experienced delayed maturation and increased mortality relative to fish held at 13° C (Jeffries et al. 2012). Although temperatures in Hansen Creek remained largely within acceptable levels for sockeye salmon, a similar physiological stress response could result from persistent sub-optimal oxygen conditions. Regardless of the particular mechanism the delay in spawning appears to be density-related; either directly through space limitation and social factors, or indirectly through oxygen limitation.

Despite no visual indication of infection, the possibility cannot be ruled out that a virus, parasite or other pathogen contributed to the observed mortality in Hansen Creek as has been reported in other cases of PSM (Gilhousen 1990; Guillen 2003; Bradford et al. 2010). On the other hand, an infection as the sole cause of mortality seems unlikely given the distinct spatial patterns of mortality in Hansen Creek; in particular the low incidence of PSM in the lower reach where densities were lowest and DO concentrations highest. Furthermore, significant PSM was not observed in sockeye populations from nearby creeks that share migration and staging areas

with Hansen Creek fish. Nevertheless, environmental stress during upstream migration can increase the virulence of many pathogens that commonly afflict Pacific salmon (Gilhousen 1990; Jeffries et al. 2012), so infection may have been the ultimate cause of mortality in this case. However, because the stressful conditions (low DO) resulted in part from high fish densities, even if infection was the ultimate cause of death, the PSM observed in Hansen Creek remains a fundamentally density-dependent process.

The ultimate impact of the 2014 mortality event on the population's productivity is uncertain because no data were available on the number of fry emerging from Hansen Creek. Low per capita predation partially offset the effect of egg retention and PSM on overall spawning success (Table 3.2) and despite the levels of PSM – completely unprecedented in the period of record – the total number of successful spawners was above average. However, given the extremely high densities it is possible that many of these eggs were lost to superimposition. In any case, it seems likely that the *per capita* fitness of 2014 spawners was artificially inflated by our sampling scheme. Daily removal of the dead from the stream was necessary to avoid double counting, but if they had been left undisturbed the decaying carcasses would have further reduced oxygen levels, potentially suffocating eggs as well as adults. Furthermore, given how shallow (~10 cm) and narrow (~4 m) Hansen Creek is and the sheer number of dying salmon, the carcasses would probably have created a physical barrier to upstream migration. Thus, conclusions cannot be drawn regarding the effect of density-driven spawning ground mortality on the productivity of the population, though the return of the 2014 run's progeny – primarily in 2018 – will provide some insight in to this issue.

Despite these limitations, our findings shed light on an underappreciated source of density-dependent mortality in anadromous fishes. While historical accounts of “walking across

the backs of fish” may be exaggerated, there is little doubt that prior to habitat alteration and industrial fishing many species returned in remarkable densities to rivers throughout the northern hemisphere (Schindler et al. 2006; Limburg and Waldman 2009). Here we show that these densities can still occur. Indeed, in the absence of fishing in 2014 Hansen Creek would have had about 160,000 rather than the 60,709 that we observed (assuming the 63% harvest rate reported for the Wood River in 2014). Such densities are not common but neither are they unprecedented, as a number of cases of exceptionally high densities of Pacific salmon have been reported (e.g., pink salmon: Heard 1978; Murphy 1985). Our findings suggest that under projected regional climate change this currently uncommon cause of density-dependent mortality may become more prevalent.

Given the generally poor state of anadromous fish populations (Honea et al. 2009; Limburg and Waldman 2009) and possibility of further declines resulting from climate change (Jonsson and Jonsson 2009; Healey and Bradford 2011), density-dependent mortality in spawning adults may not seem to be the most pressing concern for fisheries managers. However, despite severe depletions of individual stocks, overall salmon abundance in the North Pacific is near historic highs as a result of favorable environmental conditions and industrial-scale hatchery production (Irvine and Fukuwaka 2011). In particular, the abundance of pink salmon – already the most numerous species – has increased sharply since the 1970s (Heard and Wertheimer 2012), even in the Puget Sound region where other salmon species are listed as threatened or endangered (Ruggerone and Goetz 2004; Dorner et al. 2008). The co-occurrence of stocks with divergent productivity creates complex management challenges which can result in restricted fishing to protect one population and thus large escapements of more productive populations that migrate together and so cannot be selectively caught (Collie et al. 1990; Quinn et al. 2007).

Additionally, straying salmon from large hatcheries can greatly increase densities in small streams nearby (Brenner et al. 2012). Therefore, although spawning densities such as those observed in Hansen Creek in 2014 are uncommon, they are certainly possible and could occur more often in the future if recent trends in salmon hatchery production and ocean conditions persist.

Meanwhile, climate change will likely reduce oxygen availability in many salmon streams as a result of higher water temperatures and lower discharge during periods of peak salmon migration and spawning. Under projected warming trends, rivers in the western United States, Canada and Alaska are generally expected to experience more extreme summer low flows and higher water temperatures (Stewart et al. 2004; Hinzman et al. 2005; Mantua et al. 2010). In this context, oxygen limitation can be seen as an additional stressor for species already facing increasingly difficult conditions during migration and spawning. Thus, it appears possible that – at least in the near-term – increasing numbers of adult salmon could return to freshwater habitats with decreasing carrying capacity. The influence of spawning density on rates of PSM therefore remains an important area of study with direct relevance to salmon management in a warming world. More broadly, our observation of unprecedented premature mortality in an intensively studied population serves as a reminder that biological responses to climate change may not be incremental. Rather, complex interactions between climate, habitat and density-dependence can produce novel dynamics in animal populations faced with a changing environment.

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TABLES

Table 3.1. Dissolved oxygen consumption model parameters.

Variable	Distribution	Point estimate
Temperature (°C)	$N(5.45, 1.45)$	5.45 ^a
Depth (m)	$U(0.25, 1.00)$	0.60 ^b
Area (m ²)	N/A	4,220 ^a
Discharge (m ³ /s)	$\ln N(-3.03, 0.40)$	0.0479 ^a
$\alpha_0, \alpha_1, \beta, \phi, \delta, \lambda$	N/A	See text
# sockeye	$N(6,678, 1,000)$	6,678 ^a
Sockeye mass (g)	$N(2,300, 150)$	2,300 ^c
Swimming speed (m/s)	$U(30, 107)$	71.5 ^d
Initial DO conc. (mg/L)	$N(11.84, 1.5)$	11.84 ^a

^a Direct field measurement; distribution allowing for significant observation error.

^b No depth measurements were taken from the beaver pond, range is based on best estimate of researchers.

^c Meehan et al. (2005)

^d Range captures 1/4 - 3/4 active swimming speeds from Brett (1965); point estimate is 1/2 active.

Table 3.2. Summary of 2014 Hansen Creek environmental conditions and sockeye salmon run characteristics in relation to historical records

Variable	N	Median	Interquartile Range	2014 value	2014 percentile
Mean high air temperature (°C) ^a	73	17.35	16.78 - 18.15	19.5	93.15
Mean air temperature (°C) ^a	73	12.97	12.23 - 13.77	14.67	94.52
Mean low air temperature (°C) ^a	73	8.70	8.13 - 9.18	9.84	89.04
Cumulative precipitation (mm) ^a	73	70.4	49.6 - 89.6	66.0	45.21
Cum. Spring snowfall (Apr-Jun, mm)	68	109.22	34.29 - 212.09	12.7	7
Total Return	54	10,230	5,846 - 22,370	164,994	100
Escapement	54	5,171	2,373 - 9,606	60,709	100
Natural stream life (days)	17	9.99	8.65 - 11.61	8.78	35.29
Realized stream life (days)	23	4.18	2.79 - 6.00	7.07	86.96
Daily spawning density (fish/ m ²)	23	0.14	0.07- 0.33	2.14	100
Probability of spawning success	23	0.34	0.16 - 0.45	0.34	56.52
Proportion killed	23	0.66	0.48 - 0.84	0.19	8.7

^a All climate data are from King Salmon airport weather station (www.ncdc.noaa.gov) and except where noted are summarized for 15 July – 15 Aug, the traditional spawning season in Hansen Creek.

Table 3.3. Relative risk ratios (exponentiated coefficients of multinomial logistic regression) and p-values (subscript) for causes of death as a function of stream reach and day of year

	Beaver Pond	Middle	Side Pond	Upper	Day of Year
Killed	4.37 _{<0.001}	0.26 _{<0.001}	2.06 _{<0.001}	0.46 _{<0.001}	0.93 _{<0.001}
PSM	8.14 _{<0.001}	6.81 _{<0.001}	77.84 _{<0.001}	21.62 _{<0.001}	1.02 _{<0.001}

All risk ratios are compared to a base case of senescence in the lower stream reach.

Table 3.4. Pairwise comparisons of cumulative deaths between stream reaches using a Wilcoxon signed rank test.

	Beaver Pond	Lower	Middle	Side Pond
Lower	1.000	-	-	-
Middle	1.000	1.000	-	-
Side Pond	0.002	0.007	0.002	-
Upper	0.002	0.034	0.004	0.021

Bonferroni corrected p-values given. Bold indicates significant differences in the timing of mortality between the column and row stream reaches.

FIGURES

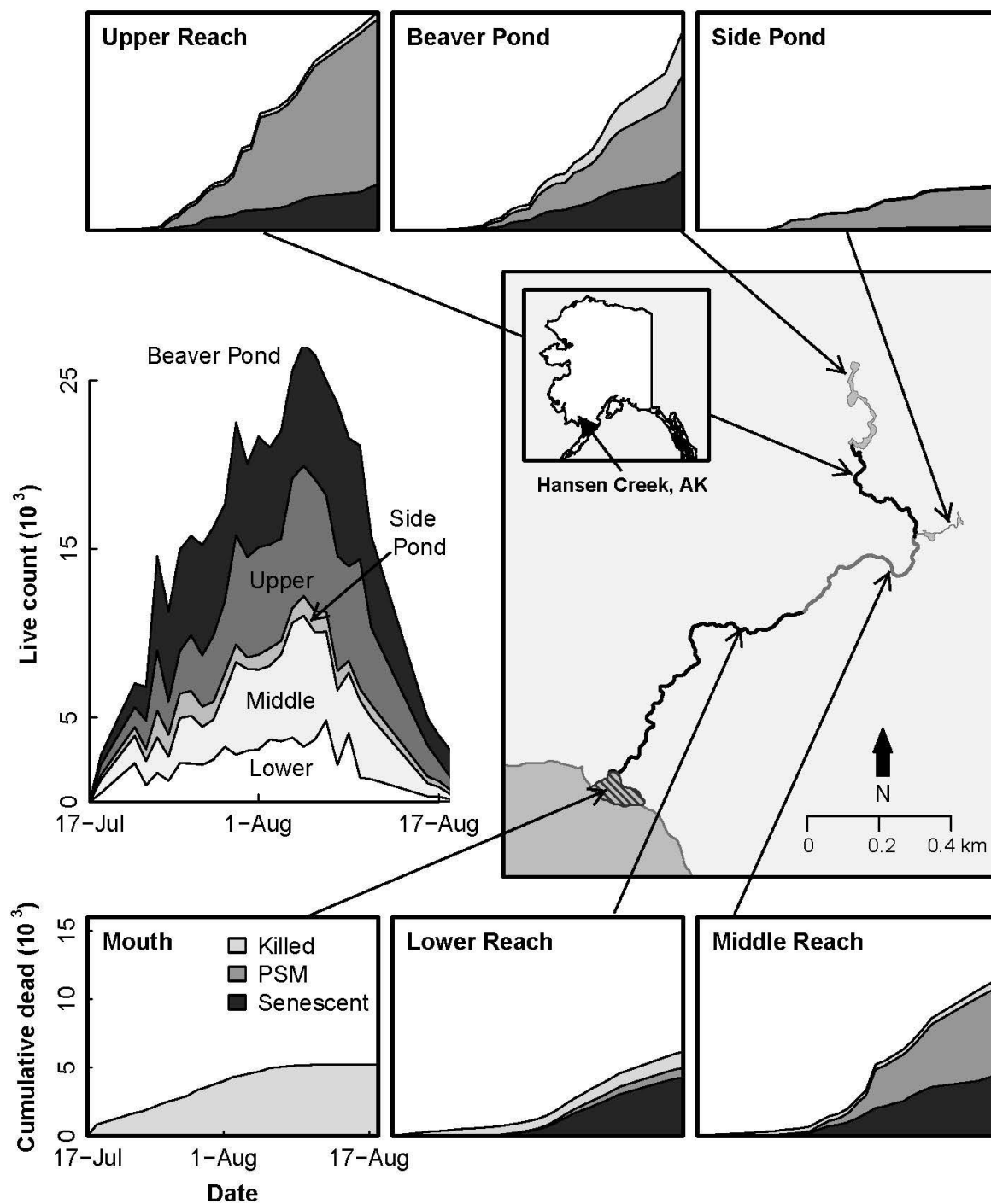


Figure 3.1. Map of Hansen Creek, located in the Wood River watershed in Alaska's Bristol Bay region with live and cumulative dead for the 2014 sockeye salmon spawning season.

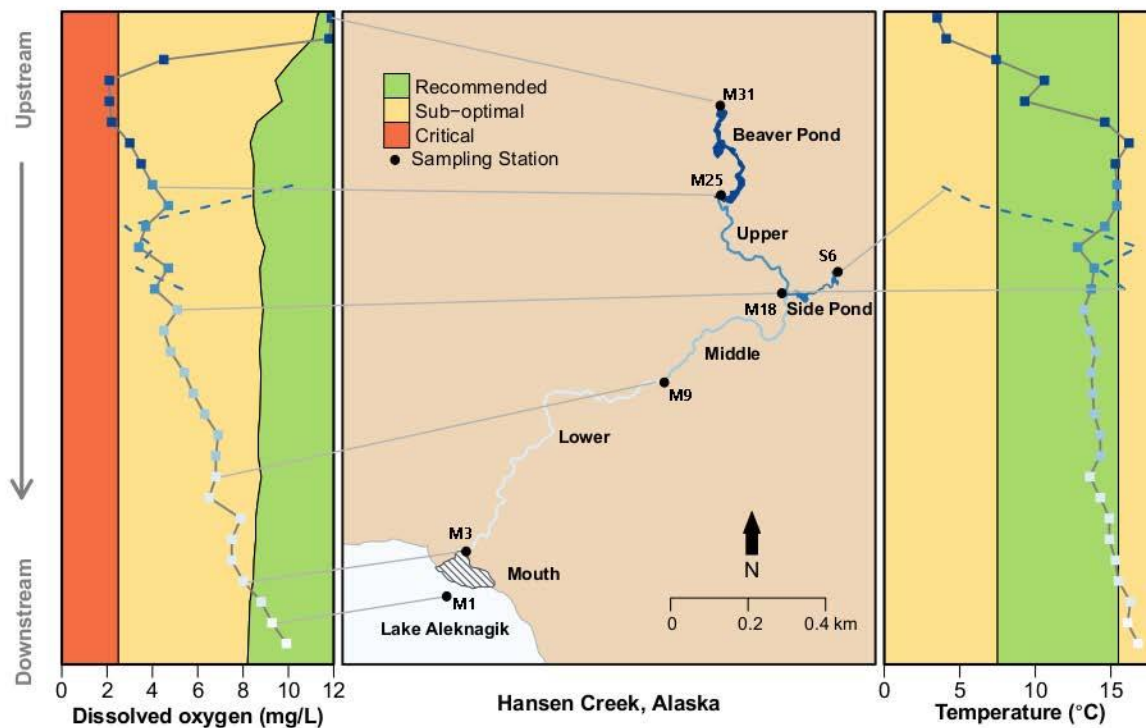


Figure 3.2. Environmental profiles of Hansen Creek on 30-July 2014. Center panel shows the stream divided in to six survey reaches. The left panel shows a profile of dissolved oxygen and the right panel a profile of water temperature. Colored points show main stem profiles while dashed line shows the side pond tributary. Grey lines locate select survey stations and point colors in profiles correspond to survey reaches in map. For DO the recommended range for sockeye salmon spawning and migration is $> 85\%$ saturation; for temperature the optimal range is $7.2 - 15.6$ °C. Exposure to critical DO levels (< 2.5 mg/L) can cause acute mortality.

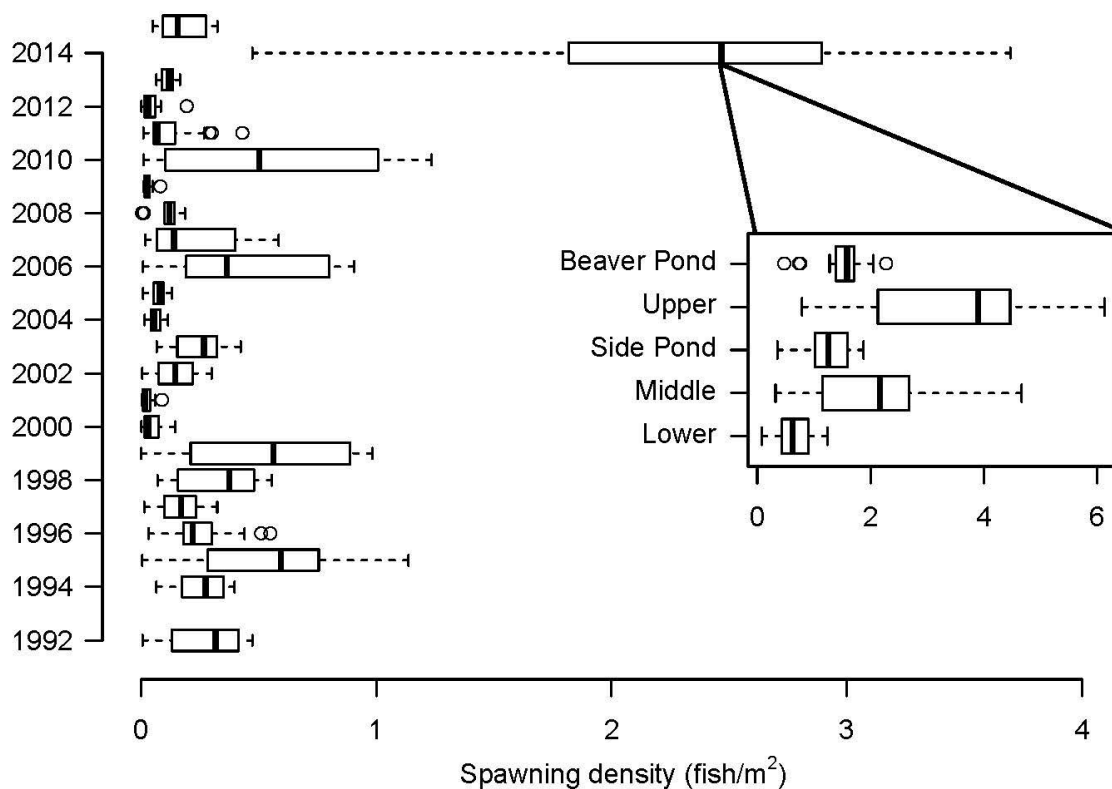


Figure 3.3. Daily spawning density in Hansen Creek 1992-2015. Bold lines indicate median daily spawning density for each year or – within 2014 – survey reach. Boxes indicate the interquartile range and dashed lines indicate maximum and minimum values absent of outliers (greater than 3*IQR from the median) which are shown as open circles.

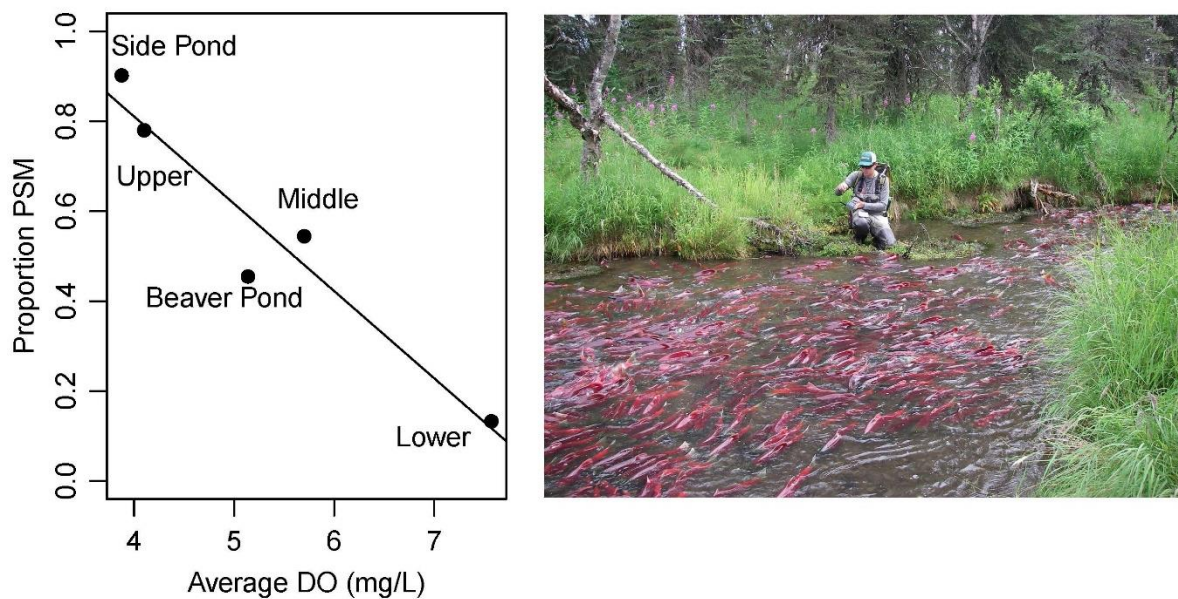


Figure 3.4. Relationship between average dissolved oxygen and PSM prevalence by stream reach. Scatterplot shows that proportion of salmon dying prematurely is negatively related to average DO concentration within the survey reach (adjusted $R^2=0.90$, $p=0.009$). Image shows high sockeye densities in the upper survey reach of Hansen Creek on 30 July, 2014.

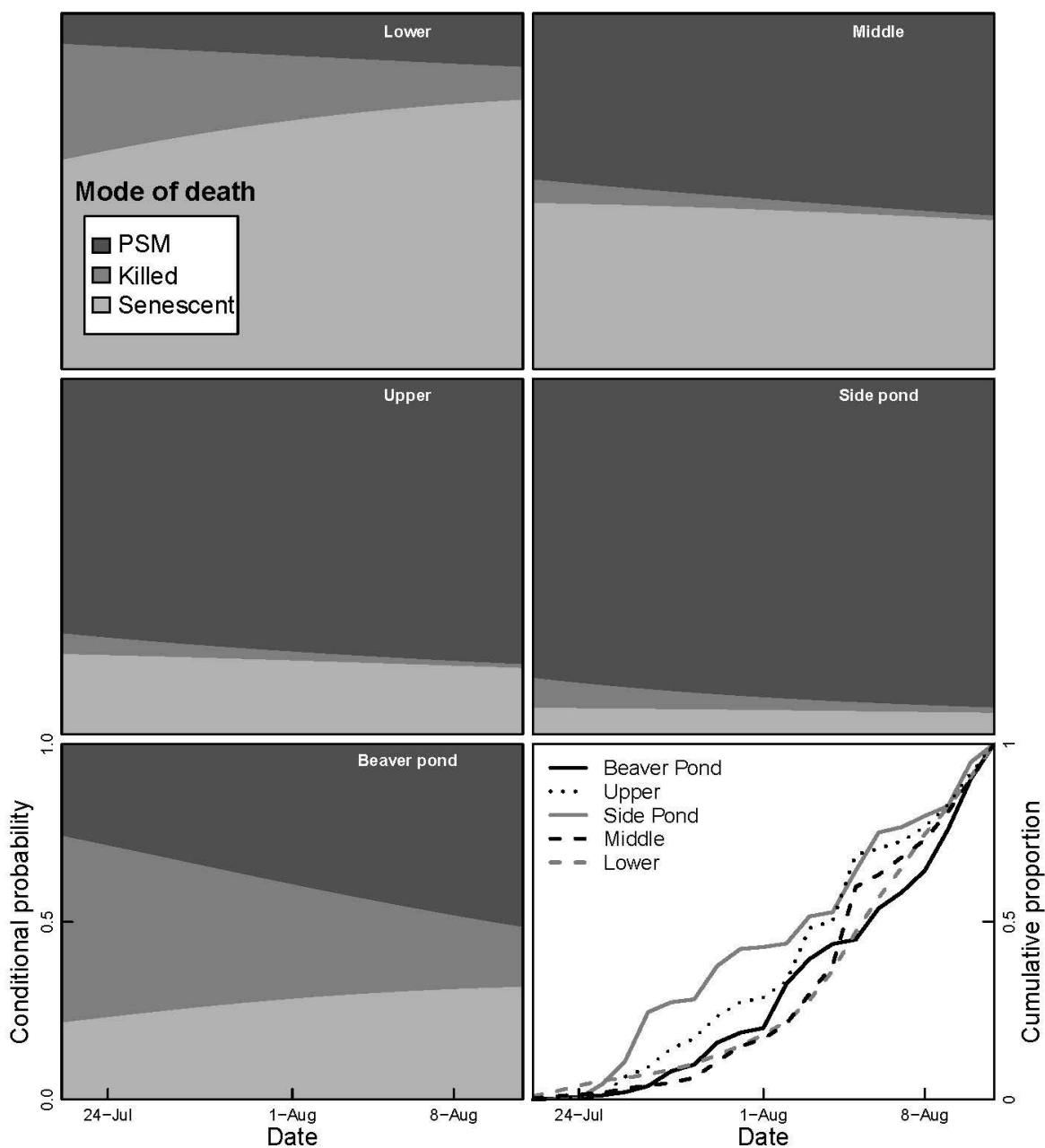


Figure 3.5. Conditional probabilities for each mode of death predicted by multinomial logistic regression, by stream reach and date. Area plots show predicted probabilities of each mode of death for a given stream reach and date and indicate i) significant differences in PSM risk between survey reaches and ii) increasing risk of PSM over the spawning season. Bottom right panel shows the empirical cumulative density curves of total deaths for each stream reach and indicates earlier mortality in the side pond and upper survey reaches.

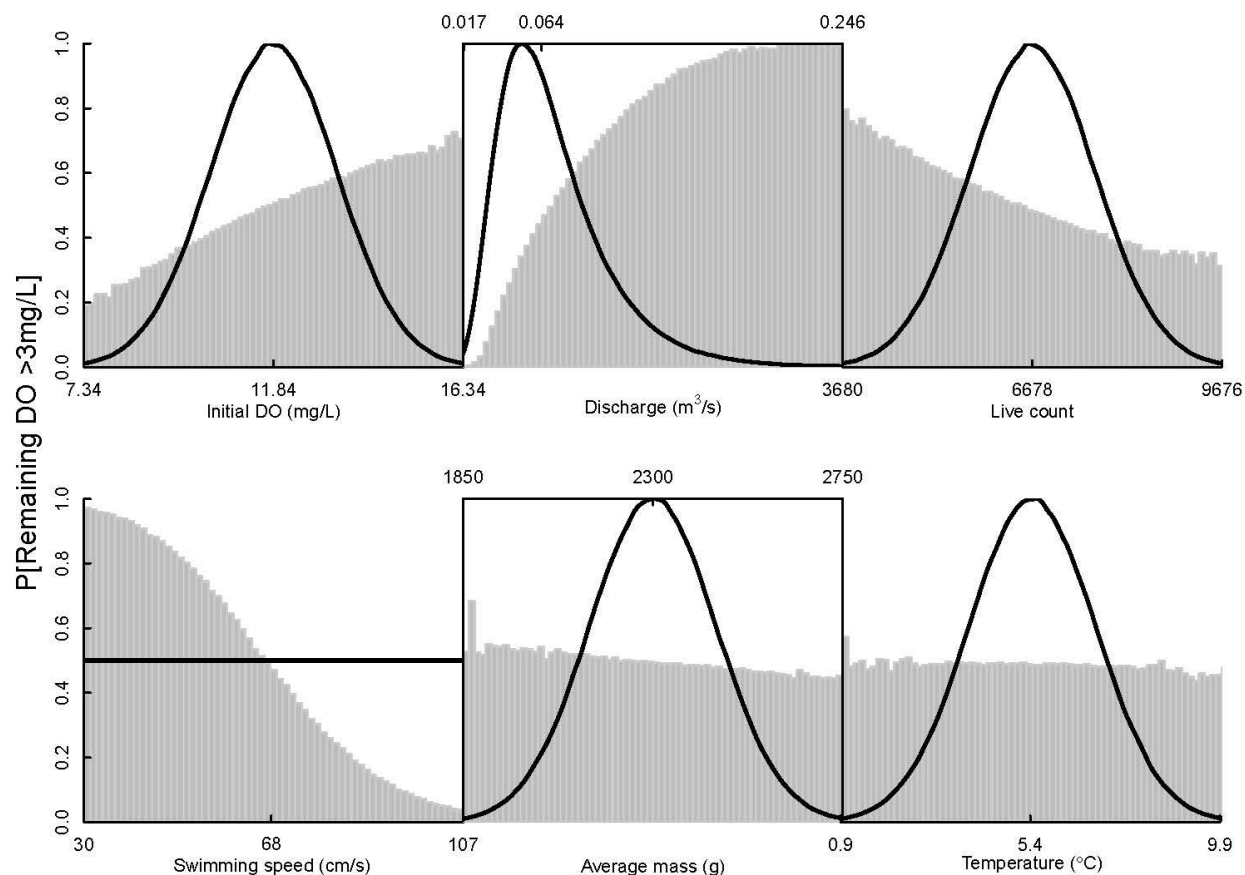


Figure 3.6. Sensitivity of remaining dissolved oxygen to DO-habitat model parameters. Bars show change in probability of modeled DO remaining above 3mg/L from mean-3 to mean +3 standard deviations for each variable except swimming speed for which the full uniform distribution range is shown. The model output is insensitive to depth and as such a depth plot is not shown. Black lines show density curves for parameter values used in the Monte Carlo simulation and for visualization purposes are scaled arbitrarily along the y-axis relative to their peak value.

CHAPTER 4 Artificial selection on reproductive timing in hatchery salmon drives potential maladaptation to warming waters

ABSTRACT

Reproductive phenology – the timing of spawning and associated events such as migration – is an important trait that links generations and substantially influences individual fitness. In salmonids, phenological events including return to freshwater and spawning occur during predictable periods within a given population suggesting local adaptation of these traits to prevailing environmental conditions. Changing reproductive phenology has been observed in many populations of Atlantic and Pacific salmon, potentially reflecting an adaptive response to climate change, but the mechanisms by which change occurs are seldom well understood. The sockeye salmon spawning in the Cedar River near Seattle, Washington have displayed dramatic changes in spawning timing over the past 50 years, trending generally later through the early 1990s, and then, approximately concurrent with the initiation of an integrated hatchery program, changing course and again becoming earlier. During the more recent period, and in spite of substantial hatchery production, the abundance of Cedar River sockeye has declined markedly. In this study we explored the question of whether artificial selection in the hatchery has resulted in maladaptation to ongoing environmental changes in the Lake Washington basin including warming waters and lower late-summer flow. We found that prior to the mid-1990s median spawning date in Cedar River sockeye was primarily influenced by Cedar River flow and Lake Washington temperature, but in the most recent 20 years these relationships have deteriorated. Since its initiation in 1991 the hatchery has on average imposed directional selection for earlier spawning, and, depending on trait heritability, would be expected to have advanced spawning by 1-3 weeks over this period. We estimated heritability of spawning date to be high ($h^2 \sim 0.8$), and

so the upper end of this range is not improbable. Recent observations of increased prespawning mortality in early spawners and relatively lower survival of early emerging juveniles, suggest that artificial and natural selection are acting in opposite directions. Because both of the apparent fitness costs of early spawning are expected to be exacerbated by future warming, we conclude that artificially altered phenology is a likely contributor to reduced productivity of Cedar River sockeye salmon, and may limit the capacity of the population to adapt to climate change.

INTRODUCTION

The ability of animal populations to respond to and ultimately persist in the face of myriad human-induced environmental changes is a key concern for scientists, natural resource managers, and the individuals and communities that rely on fish and wildlife for their livelihoods (Dolan and Walker 2006; Badjeck et al. 2010). In the face of rapid and often unpredictable environmental change, maintaining or increasing resilience – the capacity of individuals, populations and ecosystems to adapt to and persist in the face of such change – is now a commonly stated goal of resource management and conservation (Gunderson 1999; Walker et al. 2004; Allen et al. 2011; Quinlan et al. 2016). The general pathways for adaptation include phenotypic plasticity (i.e. behavioral, morphological and physiological changes at the individual level), range shifts and evolution (Parmesan and Yohe 2003; Bernhardt and Leslie 2013). However, because of uncertainty regarding environmental changes and resulting biological responses, the specific traits, populations or species most likely to persist under future conditions are seldom known (Webster et al. 2017). As such, management strategies that seek to maximize resilience often focus on genetic, phenotypic and species diversity, and the connectivity of populations and habitats. Indeed, benefits of maintaining diversity at multiple scales are widely

recognized (Schindler et al. 2015) and include increased abundance and reduced variability (Hilborn et al. 2003; Schindler et al. 2010). On the other hand, a range of human activities including certain management and conservation strategies may unintentionally erode the diversity on which resilience relies (Carlson and Satterthwaite 2011; Webster et al. 2017).

Although difficult to identify definitively, evidence of human-induced evolution has been observed in a wide range of taxa (e.g. fishes (Heino et al. 2015), mammals (Douhard et al. 2016)), in response to diverse anthropogenic influences (e.g. harvest (Allendorf and Hard 2009), climate change (Bradshaw and Holzapfel 2006), pollution (Medina et al. 2007)) and across many different traits (e.g. growth rate (Conover and Munch 2002), age at maturity (Olsen et al. 2004), aggression (Sutter et al. 2012), phenology (Quinn et al. 2007)). It is clear that human activities – harvesting in particular (Hendry et al. 2008) – can impose strong directional selection resulting in dramatic changes in phenotypic traits with consequences for population dynamics and ecological interactions (Darimont et al. 2009; Palkovacs et al. 2012). While human-induced trait changes can be detrimental alone, they may also interact with climate change, causing amplified negative ecological outcomes, though there has been little research in this area. The issue could be particularly acute for phenological change because timing (e.g., of reproduction) has high adaptive potential in response to climate change (Bradshaw and Holzapfel 2008), but can also be influenced by selective harvest (Quinn et al. 2007; Wright and Trippel 2009; Loher 2011; Tillotson and Quinn 2018). For example, directional or stabilizing selection on reproductive timing by fisheries may reduce genetic variability (and therefore adaptive capacity) or in the most extreme case drive maladaptation to climate change if selection from fishing and climate change act in opposite directions.

Artificial propagation of species in captivity is an increasingly common tool for conservation in the face of habitat degradation and environmental change. Divergence in traits between wild populations and portions of those same populations subject to artificial propagation is a common side effect of this conservation approach (Frankham 2008). If propagated individuals are later integrated with wild breeders, these trait changes may be manifest in the broader population, and if the trait changes reduce fitness in the wild, then conservation efforts may actually undermine the population's productivity or persistence (Baskett and Waples 2013). The approach is particularly common in anadromous fishes where propagation methods are well established and freshwater (i.e. spawning) habitat degradation often limits populations while the marine (i.e. growth) environment remains relatively intact (Lorenzen 2005). Indeed, billions of juvenile salmonids are released from fish hatcheries around the globe each year (Ruggerone et al. 2010) in order to increase harvest opportunities in some cases, and to supplement depleted wild populations in others (Naish et al. 2007). Artificially propagated salmon commonly experience reduced fitness in the event that they stray from the hatchery and spawn in the wild (Brenner et al. 2012; Westley et al. 2013), in some cases as a result genetic and phenotypic differences arising from domesticating selection in the hatchery environment (Grant 2011; Lorenzen et al. 2012).

The specific trait differences that impact fitness are not always clear, but may include growth rate, predator avoidance and disease resistance among others (Araki et al. 2007, 2008). One common change in hatchery salmon populations is altered reproductive timing; a trait which is highly heritable in salmonids (Quinn et al. 2002; Tipping and Busack 2004; McLean et al. 2005). In some hatchery salmon populations, reproductive timing has been intentionally selected upon to create temporal separation between hatchery and wild runs or to enhance the efficiency

of the hatchery operations (Crawford 1979). In other cases, risk aversion on the part of hatchery managers (e.g. tendency to spawn early arriving fish because of uncertainty in how many fish will eventually return) or practical challenges to obtaining later migrating fish (e.g. high stream flows) have caused unintended advances in spawning timing (Quinn et al. 2002). In either case, such selection may reduce fitness because earlier adult migration can expose fall spawning adults to higher summer water temperatures (Quinn and Adams 1996) and earlier spawning can greatly advance hatching and emergence in juveniles, potentially leading to a mismatch with environmental conditions or prey resources (Quinn et al. 2000).

Given the prevalence of salmon hatcheries, their potential influence on migratory and reproductive timing and the fact that such phenological traits are likely to be vital for adaptation to climate change, an interaction between these two selective forces seems probable. In this study we examine a potential case of such counteracting selection in a population of sockeye salmon (*Oncorhynchus nerka*) that has undergone marked change in reproductive timing over the past four decades, and has been supplemented with hatchery propagated fish since the early 1990s (Figure 4.1). Between the early 1970s and early 1990s reproduction by sockeye salmon in the Cedar River, Washington (Figure 4.2) appeared to be shifting later in the year; a pattern consistent with local environmental change during this period (i.e. increasing water temperatures and decreasing late-summer flow). In the mid-1990s – approximately coincident with the initiation of a hatchery supplementation program – this pattern reversed and spawning is now occurring earlier in the year. Despite an absence of targeted harvest since 2006 and hatchery supplementation, the population has declined in abundance in recent years as well. Because the hatchery program is integrated (i.e. naturally spawned and hatchery fish interbreed freely) there is concern among managers that unintended selection in the hatchery may have contributed to the

recent trends in reproductive timing and abundance. Here we investigate the patterns and causes of changing run timing in Cedar River sockeye, with particular focus on the strength and direction of artificial selection during hatchery propagation. We then compare the influence of artificial selection to observed changes in run timing, and conclude by considering the potential fitness consequences of artificially altered reproductive phenology.

METHODS

Study system

Lake Washington, WA, USA is a large, urban lake located near Seattle, WA. It is a natural lake, but has been substantially altered over the past century by human development. Today, the primary input is the Cedar River, which enters from the south and contributes over 50% of the annual inflow (Arhonditsis et al. 2004); the lake drains to the marine waters of Puget Sound through the Lake Washington Ship Canal. Prior to the construction of the ship canal and the Hiram M. Chittenden locks (commonly, and hereafter called Ballard locks), and diversion of the lower river reaches in the early 20th century, the Cedar River did not flow into Lake Washington; rather, the lake drained through the now dry Black River (Edmondson 1991). Because sockeye salmon typically require lakes for juvenile rearing, it is generally thought that the Cedar River had few if any sockeye salmon prior to hydrological modifications of the Lake Washington system (Darwin 1917). Lake Washington sockeye are therefore thought to be primarily descendants of fish from Baker Lake, Washington, a tributary to the Skagit River located ~120 km north of the Cedar River that were stocked in the Cedar River and other tributaries between 1934 and 1944 (Ames 2006; Spies et al. 2007). Although sockeye spawning also occurs on Lake Washington beaches and in other tributaries, the Cedar River has produced

on average more than 85% of total returns since counting efforts began in the 1960s. Since 1991 a portion (2-61%; mean 14%) of returning Cedar River sockeye have been captured for spawning in a hatchery and their offspring released back in to the river as fry to complete the rest of their lives naturally. Both hatchery and naturally spawned fish typically spend one year rearing in the lake and two or three years at sea, and thus achieve a total age of four or five years before returning to complete their life cycle.

Environmental data

Water flow data for the Cedar River were obtained from USGS gaging stations located at river kilometer (rkm) 2.6 near Renton, WA and rkm 32.8 below the Landsburg diversion dam; daily average discharge was available for all study years. Water temperature data for Lake Union, Lake Washington and the ship canal were obtained from the King County (<https://green2.kingcounty.gov/lake-buoy/>) and the University of Washington (Edmondson 1994). Temperatures were typically recorded monthly or every other week, in which case observations were averaged by month. Monthly temperature data are available for the ship canal nearly continuously since 1975 and range from the surface to 5 meters, while in Lake Washington observations begin in 1965 and range from the surface to 60 m. Daily surface water temperatures recorded at a marine site along the migration route into Puget Sound (Race Rocks, British Columbia) were obtained from racerocks.com and are available for all study years. A summary of data sources including location, temporal resolution, and years available is shown in Figure 4.2.

We then summarized flow and temperature data in to potential covariates of timing based on prior observations of their influence on sockeye salmon run timing in general (Hodgson and

Quinn 2002) or the Cedar River in particular (Ames 2006). For Lake Washington water temperatures, we calculated seasonal means (spring: Mar-May, summer: Jun-Aug, autumn: Sep-Nov) and annual maxima. For marine water temperatures (i.e. Race Rocks) we calculated monthly mean temperatures during the typical period of sockeye migration, May – July. For Cedar River flows we calculated mean discharge during peak spawning (1 – Sep through 30 – Nov), number/ duration of early spawning season high flow events (number of days between 1 Aug and 30 Sep that discharge exceeded the long-term 75th percentile) and cumulative discharge increase during September (sum of all positive day-to-day differences in flow).

Salmon timing data

Sockeye salmon returning to Lake Washington enter fresh water at the Ballard Locks which separate the Lake Washington Ship Canal from the marine waters of Puget Sound. Since 1972 state and tribal fisheries personnel have conducted daily counts sockeye passing through the locks and/or the fish ladder during an index (12 June – 31 July) period that captures on average >95% of the run. Expansion factors are used to account for proportions of the run that occur at night or during uncounted locking cycles (Ames 2006). Although imperfect, these daily visual counts were very similar to estimates from hydroacoustic methods, and are considered unbiased with regards to the hypotheses addressed herein (Thorne 1979).

Surveys of live adult salmon in the Cedar River have been conducted by Washington Department of Fish and Wildlife (WDFW) or other agencies using standardized methods since 1969 (Ames 2006). An index reach extending from rkm 6.8 upstream to the Landsburg diversion dam (rkm 34.3) has been surveyed since 1969. Occasional surveys of the lower section of the river (below rkm 6.8) documented few fish and little spawning activity prior to 1987, but use of

this reach by sockeye salmon has increased dramatically in recent decades (Timm and Wissmar 2014). Thus, since 1987 survey counts have been reported for all available habitat (rkm. 0.0 – 34.3) in addition to the traditional index reach. The inclusion of the lower reaches in more recent years is not expected to bias our analysis because a) few fish were present in this reach prior to the late-1980s and b) fish spawning in the lower river tend to arrive later, which should lead to a delay in observable run timing; the opposite of the recent trend. In order to summarize run timing, survey counts were converted to estimated daily counts through linear interpolation (Barnett et al. 2013). Interpolated daily counts of sockeye salmon for 1969-2012 were obtained from prior reports on Cedar River sockeye run timing (Cascade Environmental Services Inc. 1995, Barnett et al. 2013) and updated through 2015 with field data from WDFW. As in previous reports, the years 1970, 1973, 1974, 1975 and 1990 were excluded from run timing analysis because too few surveys were conducted to be reliable (Barnett et al. 2013).

Although river occupancy estimates derived from survey counts allow for interannual comparison of run timing, they do not allow for evaluation of selection on migration and spawning timing within a year, because individual fish may be observed multiple times throughout the spawning season. We therefore used a simple accounting model based on interpolated daily in-river abundance and estimated in-stream lifespan to calculate the number of fish dying each day. Then, deaths were added to the change in live fish between days to give the number of new fish in the river. Mathematically,

$$deaths_t = arrivals_{t-stream.life}$$

and

$$arrivals_t = live_t - live_{t-1} + dead_t$$

Because of observation error (i.e., error estimating live fish from stream surveys) and process error (i.e. variability in true stream-life), the model can produce negative estimates of

arrivals which result in oscillations as the estimates are used in the calculation of future deaths. To accurately calculate descriptive statistics for the distribution of arrivals we stabilized such oscillations by fitting a cumulative normal distribution to the cumulative distribution of modeled arrivals using ordinary least squares. This process produced good visual fits and the fitted distributions were used for further analysis of arrival timing. The temporal distribution of spawning in the river was then estimated by offsetting arrival timing by the average number of days that fish are in the river before completing spawning. Cedar River sockeye mature while holding in Lake Washington for several months prior to river entry (Newell and Quinn 2005, Newell et al. 2007) and then typically initiate spawning relatively quickly after arriving in the Cedar River. Tagging studies in both the river and hatchery suggest this delay is slightly more than one week on average (Ames 2006; WDFW, unpublished data).

Baker Lake sockeye, the ancestral population of introduced Lake Washington sockeye, are trapped approximately 88 river km upstream from marine waters and are counted and transported daily above two hydroelectric dams. Similar to the Lake Washington populations, Baker Lake sockeye arrive in the lake primarily during June and July, but do not spawn until September-December. Daily counts of transported sockeye were obtained from the WDFW and the Skagit River System Cooperative for the years 1965-2016. Prior to 1992 Baker Lake sockeye were severely depleted and terminal harvest was negligible and so the counts at the collection facility represented essentially the entire run. The population expanded in recent years and was exposed to some fishing, so for the period from 1992-2016 daily counts were corrected for commercial and sport catches in terminal areas (i.e. Skagit Bay and the Skagit River). For this period daily catches were assigned trap arrival dates by adding a harvest-location dependent travel time to landing date; travel times were based on tagging studies and are assumed to remain

constant between years (Personal communication. Peter Kairas, Skagit River Cooperative, September 29, 2016). No attempt was made to correct for any harvest of Lake Washington or Baker Lake sockeye salmon in distant fisheries; interception by coastal fisheries for Fraser River sockeye salmon is minimal because the Puget Sound runs are earlier than those returning to the Fraser River (Starr and Hilborn 1988).

Hatchery operations data

Comparisons between reproductive timing of hatchery-spawned and naturally-spawning fish were used to evaluate the presence and strength of artificial selection on timing by hatchery practices. In the hatchery all females were checked regularly (i.e., every few days) and those with eggs free from the connective tissue were euthanized and the eggs removed. At this stage they would be expected to spawn in the river, and so the dates of spawning were used as an approximation of the timing of natural spawning. Daily counts of eggs taken were obtained from WDFW for all years of hatchery operation (1991-2015). All hatchery fish are exposed to controlled thermal shifts during embryonic development such that their otoliths have a permanent set of marks that can be examined in adult salmon after death. These marks not only indicated that the fish was produced in the hatchery but in many years there were also specific marks applied to fish based on the timing in the fall when their parents were spawned (early, middle, or late in the season). For fish returning between 2005 and 2012 a sample of otoliths was collected during each hatchery spawning event, and for these years we were able to compare the timing of spawning in the parental and offspring generations.

Run timing trend analysis

We calculated median run timing for daily fish passage counts at Baker Lake and the Ballard Locks, interpolated daily counts for the Cedar River, and egg take dates (i.e., spawning of females) in the Cedar River hatchery by calculating daily cumulative counts, dividing these by the annual total at each site, and taking the first date with greater than 50% run completion as the median. We then employed an information theoretic model selection approach to evaluate the shape, magnitude and influence of environmental covariates on trends in median run timing for Lake Washington entry (i.e. passage of the Ballard Locks), occupancy of the Cedar River, and Baker River entry.

Because migration and reproductive timing in salmonids have ostensibly evolved to maximize fitness given prevailing environmental conditions, long-term change in such conditions may also explain contemporary evolution or plastic changes in these traits (Quinn and Adams 1996; Crozier et al. 2011). Water temperature and stream flow influence reproductive phenology in many salmonid species, including sockeye salmon throughout their geographic range (Hodgson et al. 2006). Changes in temperature and flow regimes have also been implicated in altered migration timing of other sockeye salmon populations (Major and Mighell 1967; Crozier et al. 2011). Trends in timing that are not explained by environmental change may indicate that some other process is responsible. To partition these sources of variability in phenology sixteen candidate models were fit to time-series of median run timing for the Cedar River, Baker River and Ballard Locks using the `glm()` function in the ‘stats’ package in R.

Models included combinations of stationary or linearly changing mean migration dates with one or two potential environmental covariates. For each site, the two included environmental covariates were the two most highly correlated with timing. Each model was also

tested for a break point; optimal breaks were identified by sequentially fitting the models using all possible years or combination of years. The break point(s) returning the lowest AIC was then used for model comparison. For each site, model performance was compared using Akaike's Information Criterion (AIC) which balances model fit (likelihood) with model complexity (number of parameters). The model with the lowest AIC was considered the most parsimonious, and the relative support for candidate models was evaluated by comparing AIC between models, and the relative likelihood of each model was compared by calculating AIC weights (i.e. $\exp(-0.5 (AIC_{\text{best}} - AIC_i))$).

In addition to this examination of trends in median run dates, we also calculated 10%, 25%, 75% and 90% run dates to qualitatively explore changes run duration, and to make comparisons between sites. Correlations between run timing reference points at different locations or different populations may indicate a shared underlying driver of timing (e.g., marine conditions for arrival timing of Baker River and Lake Washington populations). Conversely, a lack of a relationship may indicate that timing is more strongly influenced by population-specific factors or local environmental signals. Pearson correlation coefficients were calculated between pairs of run timing reference points in order identify the strength and direction of any relationships.

Heritability of spawning timing in Cedar River sockeye

Between 2005 and 2015, all returning hatchery adults had received otolith markings as juveniles which indicated the period when their parents were spawned (i.e. early, middle, or late). During hatchery spawning, otoliths were collected from a consistent proportion of these adults; allowing for determination of age and parental spawning period. For each timing group,

in each year we calculated mean dates of spawning for the parental generation weighted by the number of released juveniles spawned on each date. For the offspring generation, we used the hatchery otolith sample data to calculate mean date of spawning. Finally, depending on age at return we matched the means from each offspring timing group back to its parental generation. Because fish returning at age-4 tend to spawn later than age-5 fish we analyzed these ages separately. We standardized both generations to zero mean and unit variance, and performed a linear regression of offspring mean timing against parental timing for each age-at-return. The slope coefficients of these regressions can be interpreted as the realized heritability in spawning timing (Hard et al. 1993).

Artificial selection on spawning timing

In order to estimate the direction and strength of artificial selection on spawning timing imposed by hatchery operations we developed a simple evolutionary model based on the breeder's equation, which has been previously utilized in studies of changing salmon run timing (Quinn et al. 2000; Crozier et al. 2011; Abadía-Cardoso et al. 2013). The equation is commonly written as:

$$\Delta Z = h^2 S$$

Where Z is the population mean for a trait of interest and the change in Z over one generation equals the product of the heritability of the trait, h^2 , and a selection differential on that trait, S . Linear selection differentials measure the difference in trait means between the original population and the selected population, typically the portion of the population surviving to reproduce. In the case of hatchery selection in an integrated population, this raw selection differential overstates the strength of selection because fish not spawned in the hatchery can

nevertheless produce offspring. Egg-to-fry survival is substantially higher in the hatchery setting than in the wild and S can therefore be weighted by this fitness advantage to estimate the effective strength of any selection imposed by the hatchery. For each year of hatchery operation, a raw linear selection differential was calculated as the difference in mean spawning date between fish spawned in the hatchery and the total population (calculated as the mean of hatchery timing and natural timing weighted by the proportion of the return spawned in each setting). The proportional survival advantage of selection for hatchery spawning was then calculated as $((\text{hatchery survival} - \text{natural survival}) / \text{hatchery survival})$. Survival in the hatchery was estimated from the total number of eggs spawned (mean fecundity, determined empirically for this population, times number of females spawned) minus the number of dead embryos removed during standard culling procedures. The survival of embryos in the river was estimated from the total number of eggs potentially spawned (mean fecundity and number of females) and the number of fry migrating from the river into Lake Washington in annual operations based on regular trapping throughout the spawning season (Hovel 2015). Final selection differentials were then the product of the raw differentials and this survival advantage. Expected change in spawning timing (ΔZ) in the next generation was determined by the breeder's equation. Uncertainty exists in model parameters including stream-life, the time between river entry and spawning, the hatchery survival advantage and the heritability of timing traits. A Monte Carlo sensitivity analysis was therefore conducted to explore the impact of parameter uncertainty on the direction and strength of trait change resulting from hatchery selection.

For all parameters, the Monte Carlo procedure took 10,000 random draws from a broad uniform distribution intended to encompass all plausible values. While area under the curve (AUC) escapement estimation for the Cedar River uses a fixed 15 day stream-life estimate based

on tagging (Ames 2006), studies from many other salmon streams, and anecdotal observations in the Cedar River suggest that early arriving salmon live longer than those arriving later (Ames 2006; Perrin & Irvine, 1990). There is also some evidence that average Cedar River stream-life may be declining in response to spatial shifts in spawning activity, or increased rates of pre-spawning mortality (Ames 2006). The sensitivity analysis therefore explored the impact of average stream-life as well as the influence of declining stream-life within (i.e. early arrivals live longer than late arrivals) and between (i.e. stream-life is declining over time) years. The Monte Carlo procedure was conducted three times, with high, moderate and low levels of spawning timing heritability (h^2). Table 4.1 shows the range of values used in the sensitivity analysis and the point estimates considered to be best estimates for each model parameter.

RESULTS

Run timing trend analysis

Temporal trends in run timing varied markedly between sites, with the most parsimonious models varying between the Ballard Locks, Cedar River and Baker River. In general, the timing of sockeye salmon arrival at the Ballard Locks and Baker River changed minimally between ~1970 and 2016 (Figures 4.3d,e). For each of these time-series, the selection procedure did not identify a single, strongly favored model. Rather, nearly every model had a >1% support, and at least three had a >10% probability of being the best model (Table 4.3). There was reasonable support for an influence of nearshore marine conditions on Ballard Locks arrival timing as May temperature at Race Rocks was included in all of the highest weighted models. Environmental variables were not included in the highly weighted Baker River models. However, pairwise comparisons of the time series found that run timing of sockeye past the

Ballard Locks was moderately correlated with the initiation of the Baker Lake sockeye run ($r = 0.58$; Table 4.4). This may reflect a shared marine environmental influence on both populations.

In contrast to the ambiguous model selection results for the Ballard Locks and Baker River arrival timing, timing trends in Cedar River run timing were best explained by a single class of models: those including two separate linear trends, and the cumulative increase in Cedar River flow during September (Figure 4.3a). Model 4b received over 80% of the AIC weight, while model 4d which also included average autumn Lake Washington surface temperature received the remaining weight. In both of these models and the other two including multiple linear trends, the break year was consistently identified as 1993 (Table 4.3). Examination of coefficients from model 4b shows that from 1969 through 1993 higher September flow increases were associated with earlier run timing, but that since 1994 this influence has been greatly reduced (Figure 4.3b). Conversely, after accounting for environmental change (i.e. a decreasing pattern in September flow; Figure 4.5) no significant temporal trend is apparent prior to 1994, but since then median timing has become earlier at a rate of 1.26 days per year (Figure 4.3c; Table 4.5). Consistent with previous analysis (Newell et al. 2007), run timing was not highly correlated between the Ballard Locks and Cedar River ($r = 0.30$; Table 4.4). Taken together, these findings suggest that observed changes in Cedar River run timing since 1994 reflect either a population-specific trait change, or response to a localized environmental process not included in our analysis.

Heritability of spawning timing in Cedar River sockeye

Our regression analysis of standardized offspring and parent spawning timing resulted in separate estimates of realized heritability of this trait in Cedar River sockeye salmon returning at

age-4 and age-5. For age-4 returns h^2 was estimated to be 0.86 (95% CI: 0.62 – 1.1) and 0.79 (95% CI: 0.5 – 1.08) for age-5 returns. Compared with published estimates of h^2 for salmonid spawning timing these estimates are rather high, though not unprecedented (Dickerson et al. 2005; Crozier et al. 2011; Abadía-Cardoso et al. 2013). Nevertheless, we used these estimates with some caution, and considered a broad range of h^2 in our sensitivity analysis.

Artificial selection on run timing

The selectivity of hatchery operations on run timing varied in strength and direction between years, but in most years favored earlier spawning fish (Figure 4.4). Using the point estimates in Table 4.1 for each parameter, hatchery spawning occurred on average 3.9 days earlier than natural spawning each year. Accounting for the egg-to-fry survival advantage of hatchery-spawned adults, the average selection differential was -3.2 days, and the average expected trait change was -0.95, -1.6 and -2.6 days per generation for h^2 values of 0.3, 0.5, and 0.83, respectively. The change in spawning timing between 1991 and 2015 resulting from artificial selection can be approximated by multiplying the average expected trait change (excluding those spawned in 2012-2015 for which adults have not yet returned, and any selection will not be realized in offspring timing) by the average number of generations that have experienced artificial selection during this period (5.25 assuming a 4-year generation time). Given low, medium and high estimates of heritability, the cumulative effect of artificial selection on spawning timing is estimated to be -5.6, -9.8 and -16.2 days, respectively.

Our Monte Carlo sensitivity analysis allowed us to explore variability in these estimates given uncertainties in model parameters. Figure 4.5 shows the frequency distributions of artificially-induced change in spawning timing between 1991 and 2105 given the ranges of

parameter values shown in Table 4.1. Regardless of heritability level, more than 90% of parameters combinations resulted in advancing spawning timing. The frequency distributions of the Monte Carlo output were centered on -3.9, -6.5 and -10.8 days for low, medium and high heritability. Plotting the Monte Carlo output against values of each model parameter allowed us to examine their relative influence. In general, the model output was most sensitive to stream life and the delay between arrival and spawning, while higher values for heritability and the hatchery survival advantage tended to amplify the variability of the model output. The effects of each parameter on expected change in spawning timing are shown in Figure 4.6. The observed change in Cedar River arrival timing between 1991 and 2015 is more than -20 days. A change of this magnitude resulting solely from artificial selection is unlikely unless heritability of spawning timing is indeed quite high in this population; while 13.7% of parameter combinations produced a shift toward earlier spawning at least this large when $h^2 = 0.83$, the proportion fell to 0.3% and 0% in the medium and low heritability scenarios.

DISCUSSION

The reproductive phenology of Cedar River sockeye salmon has changed markedly over the past five decades. Between 1969 and 1993 river entry and spawning by sockeye salmon became generally later, a pattern that may be partly explained by a shift toward lower late-summer flows in the Cedar River. In the early 1990s the pattern changed substantially, and from 1994 through 2015 the date of median spawning advanced by over three weeks. Our comparative analysis of trends in homeward migration and spawning timing indicated that watershed-specific processes are likely responsible for the majority of observed change because the timing of freshwater entry has remained relatively stable, and little change was observed in the phenology

of the Baker Lake origin population. Although trends in the Cedar River flow regime explain much of the variation in spawning timing up until the early 1990s, the shift toward earlier spawning that has occurred since is not well explained by environmental conditions. However, the observed shift towards earlier spawning began approximately coincident with initiation of hatchery supplementation. Analysis of hatchery operations relative to the phenology of natural spawners indicates that artificial selection for earlier spawning has occurred in the past, and depending on the heritability of the trait, can explain a substantial proportion of the observed advance in spawning timing since the mid-1990s. These findings collectively provide strong evidence that even in an integrated hatchery population, artificial selection on timing can induce population-level changes in phenology.

Although there is strong evidence that artificial selection on reproductive phenology has occurred, it is not clear that this alone can explain the dramatic advance in Cedar River sockeye spawning timing since the 1990s. Our evolutionary model and sensitivity analysis demonstrated that if heritability is close to our estimate of 0.8, then certain combinations of plausible stream life parameters can produce advances in spawning timing of greater than three weeks given observed patterns of hatchery selection. We use this heritability estimate with some caution as it is high compared with previous studies, though not improbably so. At the moderate heritability level ($h^2 = 0.5$), both our best estimates of model parameters and the central tendency of Monte Carlo output suggest that the effect of artificial selection has been more modest – on the order of 7 to 10 days – and far less than the observed change of around three weeks. It is possible that the additional change in phenology is the result of altered temperature or flow regimes resulting from climate warming. However, our analysis of likely environmental covariates of timing failed to support this hypothesis. On the contrary, prior to the influence of hatchery supplementation

some aspects of Cedar River flow and Lake Washington temperature were well correlated with run timing, and the trend toward later spawning between 1969 and 1993 was generally consistent with a pattern of warming autumn water temperatures and decline in September freshets. Since 1994, however, these relationships have broken down; likely as a result of the effect of artificial selection on phenology. Furthermore, both theory (Quinn, 2005), and previous studies of sockeye salmon populations responding to climate change (Kovach et al. 2015) indicate that spawning should occur later in response to warming waters; the opposite of the pattern observed since 1994 in the Cedar River. Thus, while these results do not preclude the effect of other environmental factors, our findings suggest that some other, unobserved process may be occurring. A number of factors may contribute to this remaining, unaccounted for change in timing.

The spawning timing phenotype that is ultimately observable (i.e. median spawning date in the population) emerges from a series complex and interrelated evolutionary, behavioral and physiological processes. In our study population spawning timing appears independent of ocean processes because, although marine environmental factors do influence the timing of arrival in freshwater, a long delay before spawning combined with a lack of relationship between lake and river entry timing appears to decouple migratory and reproductive processes (Newell et al. 2007). Thus, Cedar River sockeye spawning timing appears to be determined by an underlying, genetic predisposition combined with plastic response to flow, and possibly temperature conditions in the lake and river. Spawning timing can also covary with fish attributes such as size, age, and spawning location, so long-term changes in these traits may influence observable spawning timing (McPhee and Quinn 1998; Carlson and Rich Jr. 2004). Finally, because sockeye salmon cease feeding prior to freshwater entry, a fixed energy budget is available once the fish

are in Lake Washington. Though understudied, it has been previously suggested that early upstream migration in sockeye salmon may occur if energy reserves are atypically low (Lapointe et al. 2003). Energy availability can in turn be influenced by many factors including temperatures experienced during migration and staging, or by pathogens. Despite uncertainty regarding the influence of these additional processes in the Cedar River population, given the substantial selection differentials we observed and high estimated heritability of spawning date in our study population, we are confident in our conclusion that unintended artificial selection in the hatchery has contributed substantially to the trend toward earlier spawning.

Although we are unable to directly test the fitness effects of altered reproductive phenology in Cedar River sockeye, several pieces of evidence suggest that artificial selection for early spawning may be maladaptive in this population. First, juvenile sockeye that enter Lake Washington from the Cedar River later in the spring on average experience a survival advantage over the earlier migrants of their cohort (Hovel 2015). This is presumably because later migrants are more likely to experience a ‘match’ with favorable growth conditions during the vulnerable period shortly after lake entry (Cushing 1990). Because sockeye salmon spawn during a descending portion of the seasonal temperature cycle, the impact of earlier spawning is amplified in emerging juveniles. This is because embryonic development in salmonids is strongly influenced by *cumulative* temperature experienced, and earlier spawning exposes embryos to warmer water temperatures (Murray and McPhail 1988). Given the average temperature regime of the Cedar River, a one week shift in median spawning from mid- to early-October results in an over two week advance in median emergence timing; the impact of any artificial selection on spawning timing is therefore amplified substantially in terms of juvenile phenology. Combined with the relative survival advantage for later lake entry by juveniles, disruption of offspring

trophic dynamics seems a plausible fitness cost of artificial selection for earlier spawning in this population. And while spring lake processes – and therefore optimal juvenile entry timing – are also advancing in response to climate change (Winder and Schindler 2004), the rate of change in spawning timing since the 1990s has far exceeded the rate of environmental change.

The second mechanism by which artificial selection for earlier spawning may reduce fitness is through increased exposure of spawners to dangerously high water temperatures. Lake Washington sockeye salmon enter the lake prior to peak summer temperatures, holding in the cooler hypolimnion of the lake through the summer and then entering the river and spawning in the cooler fall months (Newell and Quinn 2005). Although the highest temperatures experienced likely occur during passage through the ship canal shortly after initial entry in to freshwater, temperature tolerance is typically higher in migrants than in fully mature spawners (Bjornn and Reiser 1991). In recent years, unexplained mortality has been observed in natural spawners and in hatchery broodstock. Pre-spawning mortality (PSM) such as this occurs in many salmon populations (Bowerman et al. 2016), but has been rare in the Cedar River (Ames 2006). The causes of PSM vary, but in many cases elevated temperatures increase the likelihood of failed spawning (Bowerman et al. 2017). It is possible that earlier migration, combined with a general pattern of warming in Lake Washington is driving an increase in the rate of PSM. Within-season patterns of PSM further support this notion, as the earliest migrating fish have typically experienced the highest rates of failed spawning (West Fork Environmental, 2017). In either case, if earlier spawning is indeed associated with lower fitness, then artificial selection on this trait will result in a larger proportion of the population spawning during less favorable times, which would be consistent with the pattern of declining abundance despite hatchery supplementation.

Artificial propagation may be necessary when demographic risks to a population's viability are substantial, and in the case of Pacific salmon, has sustained fisheries in cases where habitat loss reduced capacity for natural production (Naish et al. 2007; Flagg 2015). However, our findings add to a growing body of evidence documenting the inherent challenges in sustainable supplementation of fish populations (Frankham 2008; Baskett and Waples 2013). Hatcheries can reduce genetic diversity (Waters et al. 2015; Berejikian and Van Doornik 2018), impose artificial selection (Quinn et al. 2002; McLean et al. 2005), and may disrupt processes of natural selection and adaptive evolution (Waples et al. 2009). While substantial efforts are underway to improve the genetic management of hatcheries in some regions (Moberg et al. 2005; McGarvey and Johnston 2011; Flagg 2015), the results presented here demonstrate that even when best practices are followed, unanticipated impacts on supplemented populations may occur. Our findings further highlight that phenology can be particularly sensitive to artificial selection during artificial propagation. Because flexibility in the timing of migration and reproduction may represent one of the most effective pathways for salmon populations to adapt to climate change (Bradshaw and Holzapfel 2008), hatchery and fisheries management should strive to maintain diversity in these traits (Tillotson and Quinn 2018). Furthermore, consideration should be given to how forces of natural selection, such as warming waters or changing flow regimes, might interact with hatchery operations to ultimately shape patterns of selection on supplemented populations.

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TABLES

Table 4.1. Candidate trend models for median run timing

ID#	Break Point?	Environ. Covariate	Formula
1a	No	N/A	$\sim \alpha$
1b	No	1	$\sim \alpha + \beta E_1$
1c	No	2	$\sim \alpha + \beta E_2$
1d	No	Both	$\sim \alpha + \beta_1 E_1 + \beta_2 E_2$
2a	Yes	N/A	$\sim \alpha + \beta R$
2b	Yes	1	$\sim \alpha + \beta_1 E_1 + \beta_2 R + \beta_3 E_1 * R$
2c	Yes	2	$\sim \alpha + \beta_1 E_2 + \beta_2 R + \beta_3 E_2 * R$
2d	Yes	Both	$\sim \alpha + \beta_1 E_1 + \beta_2 E_2 + \beta_3 R + \beta_4 E_1 * R + \beta_5 E_2 * R$
3a	No	N/A	$\sim \alpha + \beta Y$
3b	No	1	$\sim \alpha + \beta_1 Y + \beta_2 E_1$
3c	No	2	$\sim \alpha + \beta_1 Y + \beta_2 E_2$
3d	No	Both	$\sim \alpha + \beta_1 Y + \beta_2 E_1 + \beta_3 E_2$
4a	Yes	N/A	$\sim \alpha + \beta_1 R + \beta_2 Y + \beta_3 R * Y$
4b	Yes	1	$\sim \alpha + \beta_1 R + \beta_2 Y + \beta_3 E_1 + \beta_4 R * Y + \beta_5 R * E_1$
4c	Yes	2	$\sim \alpha + \beta_1 R + \beta_2 Y + \beta_3 E_2 + \beta_4 R * Y + \beta_5 R * E_2$
4d	Yes	Both	$\sim \alpha + \beta_1 R + \beta_2 Y + \beta_3 E_1 + \beta_4 E_2 + \beta_5 R * Y + \beta_6 R * E_1 + \beta_7 R * E_2$

α – Intercept. β_x – Regression coefficients. E_1 – Best environmental predictor of timing identified using OLS regression (for Cedar River, natural logarithm of cumulative September flow increase. For Baker River and Ballard locks, mean May temperature at Race Rocks, BC). E_2 – Second best environmental predictor of timing (for Cedar River, mean autumn surface temperature in Lake Washington. For Baker River and Ballard locks, mean July temperature at Race Rocks, BC). R – A categorical regime variable distinguishing between periods before and after an estimated break point. Y – Year, capturing residual temporal trends after accounting for environmental change.

Table 4.2. Summary of Cedar River sockeye arrival model parameters

Parameter	Monte Carlo Range	Point estimate
Initial stream-life	14 – 22 d	18 d
Final stream-life	50 – 100% Initial	11 d
Mean stream-life	Calculated	14.5 d
Stream-life trend	-4 – 0 d	-2 d
Spawning delay	5 – 11 d	8 d
Hatchery egg-to-fry %	Calculated	93%
Natural egg-to-fry %	Calculated	17%
Hatchery advantage	0.6 – 0.95	0.83
Heritability	Fixed	0.25, 0.5, 0.83

Table 4.3. Summary of model comparisons for temporal trends in run timing

ID#	<u>Baker River</u>			<u>Ballard Locks</u>			<u>Cedar River</u>		
	AIC	AIC _w	Break	AIC	AIC _w	Break	AIC	AIC _w	Break
1a	311.51	0.11	N/A	266.13	0.01	N/A	319.86	0.00	N/A
1b	313.20	0.05	N/A	263.26	0.04	N/A	301.52	0.00	N/A
1c	312.42	0.07	N/A	266.59	0.01	N/A	315.11	0.00	N/A
1d	313.93	0.03	N/A	264.20	0.03	N/A	302.67	0.00	N/A
2a	<u>310.22</u>	<u>0.20</u>	<u>1996</u>	262.90	0.05	2007	310.07	0.00	1979
2b	313.52	0.04	1996	260.05	0.20	1995	292.03	0.00	2004
2c	314.18	0.03	1996	264.03	0.03	2007	295.11	0.00	2010
2d	313.19	0.05	1989	263.92	0.03	1995	383.37	0.00	2008
3a	311.31	0.12	N/A	267.11	0.01	N/A	321.02	0.00	N/A
3b	313.14	0.05	N/A	<u>259.63</u>	<u>0.25</u>	<u>N/A</u>	303.51	0.00	N/A
3c	313.29	0.04	N/A	264.86	0.02	N/A	317.04	0.00	N/A
3d	314.55	0.02	N/A	261.39	0.11	N/A	304.44	0.00	N/A
4a	311.27	0.12	1997	263.13	0.04	1994	284.42	0.00	1993
4b	313.95	0.03	1997	261.10	0.12	2013	<u>272.00</u>	<u>0.82</u>	<u>1993</u>
4c	314.73	0.02	1997	267.76	0.01	1994	287.30	0.00	1993
4d	314.54	0.02	1997	263.16	0.04	2014	275.00	0.18	1993

Table 4.4. Pairwise comparisons between run timing metrics at three locations

	Year	Baker Lake				Cedar River				Ballard Locks		
		10%	50%	90%	Duration	10%	50%	90%	Duration	10%	50%	90%
Baker 10%	0.22											
Baker 50%	0.20	0.76										
Baker 90%	0.45	0.67	0.69									
Baker dur.	0.39	-0.05	0.21	0.71								
Cedar 10%	0.48	0.14	0.05	0.25	0.21							
Cedar 50%	0.07	0.16	0.07	0.08	-0.04	0.78						
Cedar 90%	-0.31	0.12	0.07	-0.08	-0.23	0.33	0.85					
Cedar dur.	-0.66	0.00	0.02	-0.28	-0.38	-0.48	0.17	0.67				
Locks 10%	-0.18	0.51	0.25	0.18	-0.26	0.04	0.28	0.38	0.31			
Locks 50%	-0.15	0.58	0.26	0.23	-0.26	0.08	0.30	0.39	0.30	0.88		
Locks 90%	-0.01	0.53	0.28	0.33	-0.07	0.33	0.48	0.45	0.15	0.71	0.87	
Locks dur.	0.20	0.16	0.10	0.26	0.20	0.41	0.35	0.19	-0.15	-0.17	0.19	0.57

Reported values are Pearson correlation coefficients (r). 10, 50 and 90% – Run completion percentiles. Duration – calculated as the difference between 90% and 10% completion dates.

Table 4.5. Summary of best-fit Cedar River trend model coefficients

Variable	1969 - 1993		1994 - 2015	
	Coefficient	p -value	Coefficient	p -value
ln(Sep. flow increase)	-8.80	<0.001	-0.86	0.01
Year	0.25	0.335	-1.26	<0.001

$F = 22.75$ on 5 and 36 degrees of freedom. $R^2 = 0.72$, $p < 0.001$

FIGURES

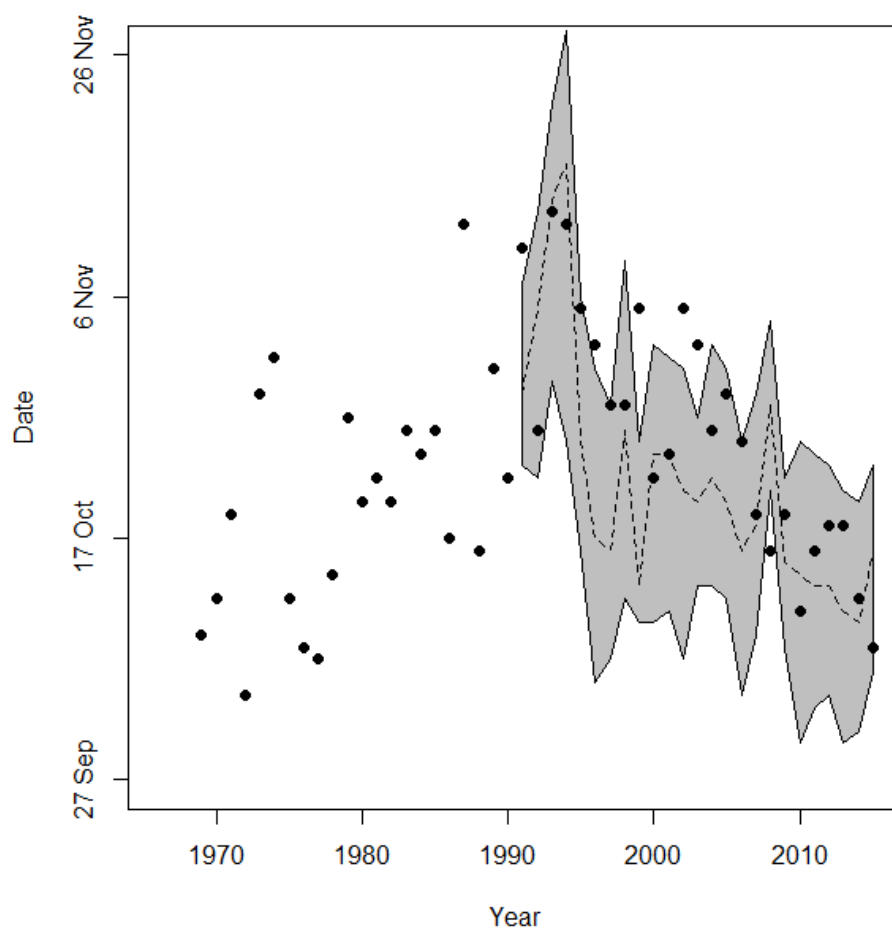


Figure 4.1. Dates of natural and hatchery Cedar River sockeye salmon spawning, 1969-2015. Points show median date of natural spawning, dashed line shows median date of hatchery spawning; the shaded area spans 25% to 75% completion dates of hatchery spawning.

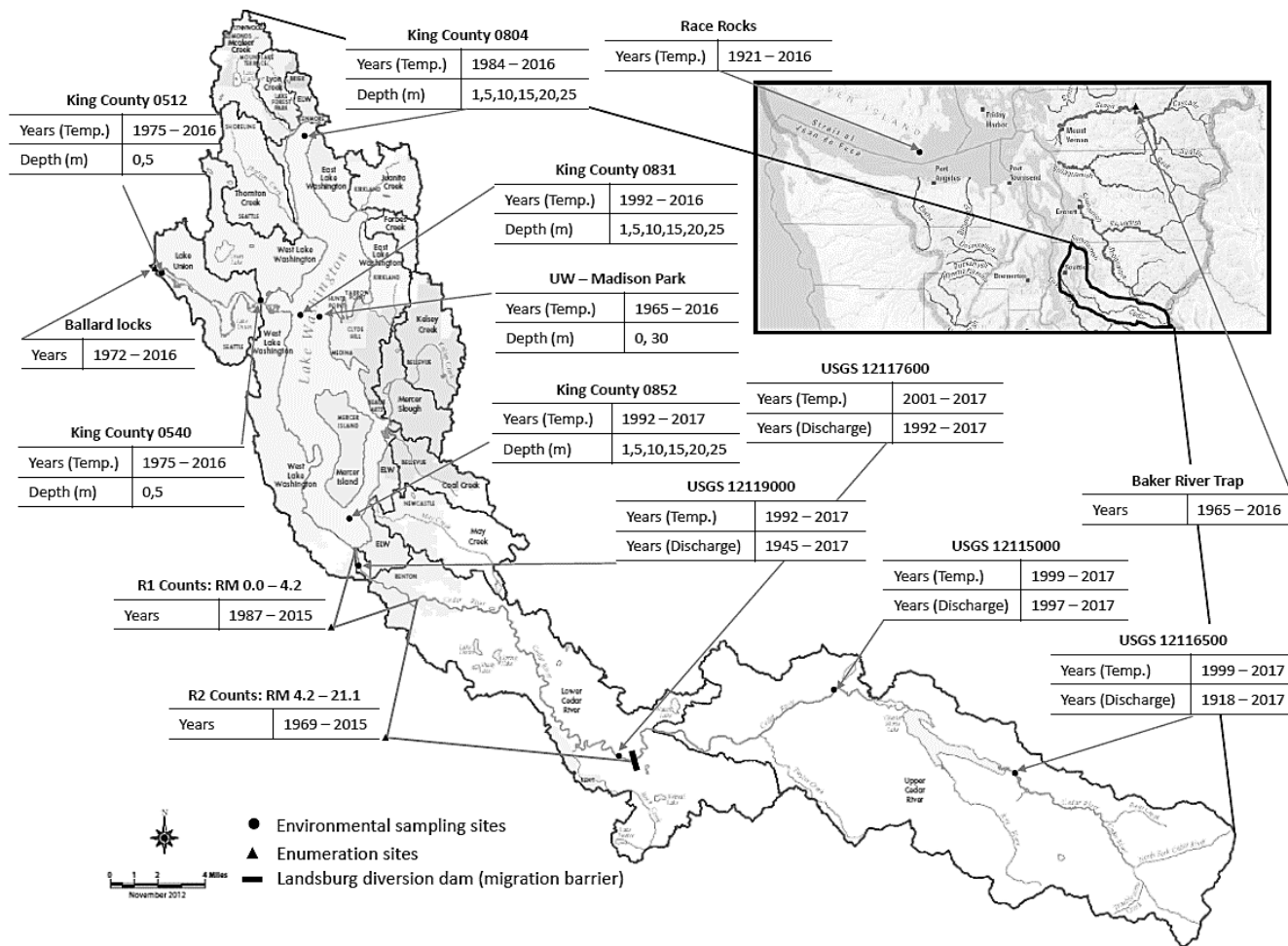


Figure 4.2. Cedar River watershed showing all sampling locations and summaries of data availability.

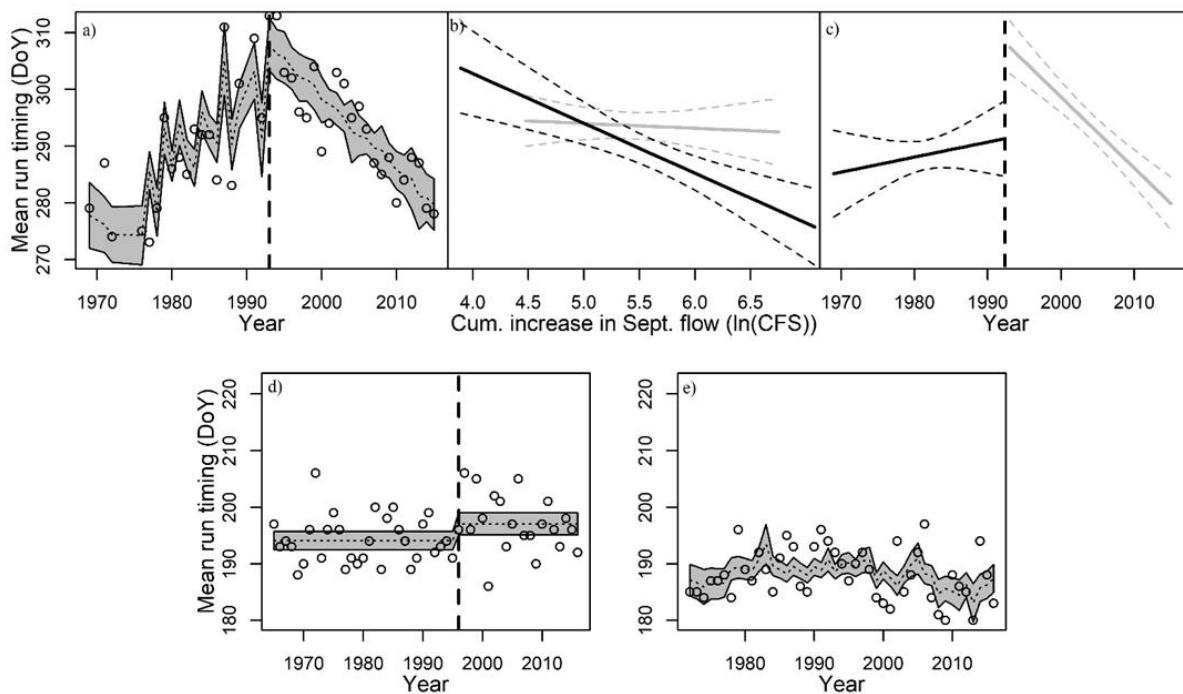


Figure 4.3. Fits and partial dependency plots for AIC-selected trend models. Panels a), d) and e) show model-predicted trends in median run timing dates for Cedar River, Baker River and Ballard Locks, respectively. Shaded areas show 95% confidence intervals and open circles show observed values. Panel b) shows the partial dependency of Cedar River run timing on river flow before 1993 (in black) and after (in gray). Panel c) shows residual temporal trends for the same periods after accounting for the influence of flow. If included in the model, vertical dashed lines indicate break years. In partial dependency plots dashed lines show 95% confidence intervals. y-axes for all plots show equal ranges to facilitate comparison of trend magnitude between panels.

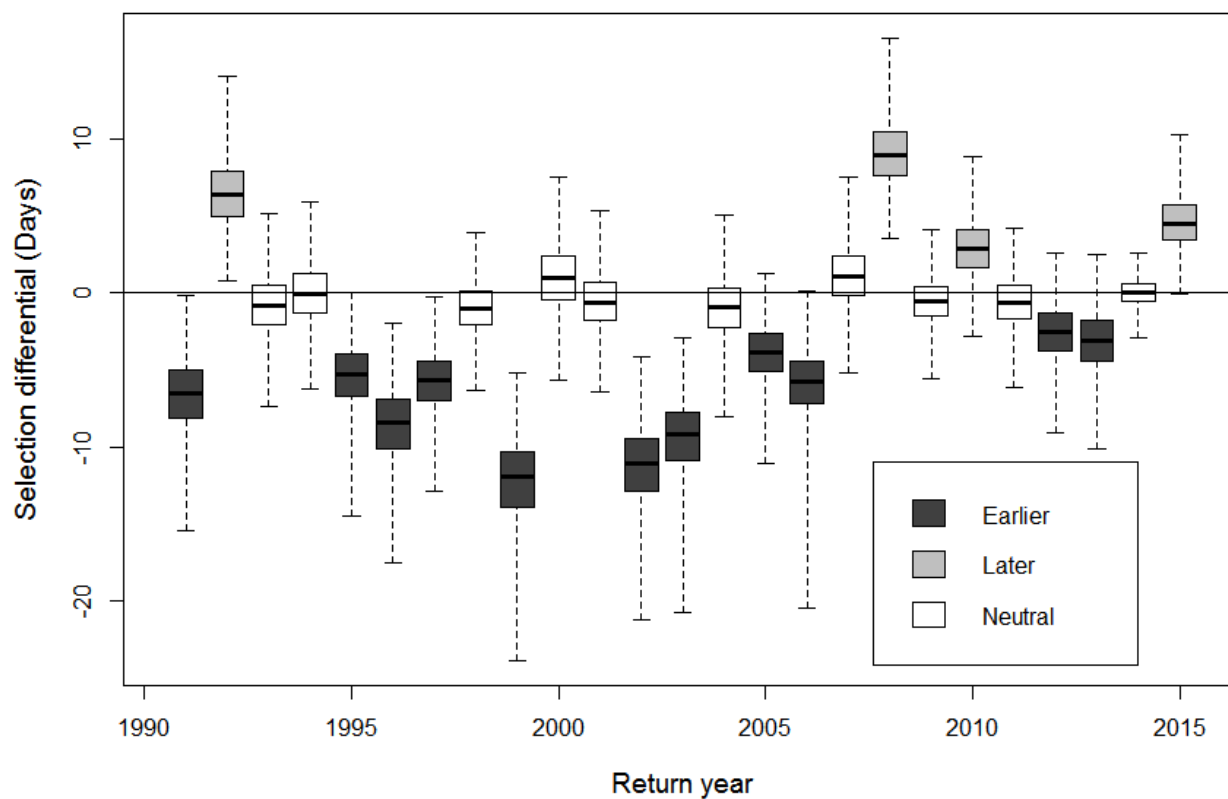


Figure 4.4. Boxplots of annual selection differentials on spawn timing. Heavy lines show medians, boxed areas show interquartile ranges (IQR), and whiskers show full range of Monte Carlo output. Boxes are shaded based on the position of the IQR relative to zero.

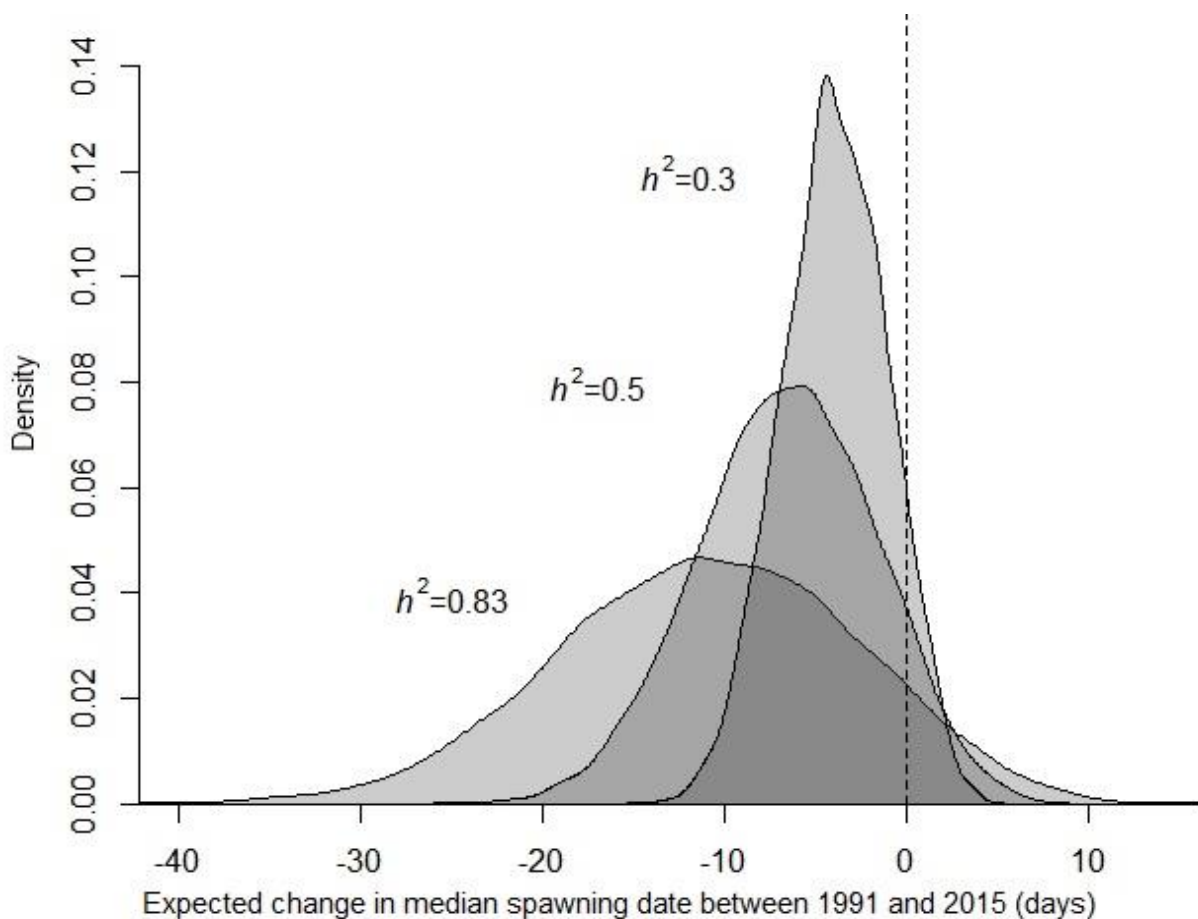


Figure 4.5. Distributions of expected change in median spawning date based on 10,000 Monte Carlo simulations at three levels of heritability. Distributions of expected change in median spawning date based on 10,000 Monte Carlo simulations at three levels of heritability. Vertical dashed line shows zero expected change, negative values indicate an expected change toward earlier spawning.

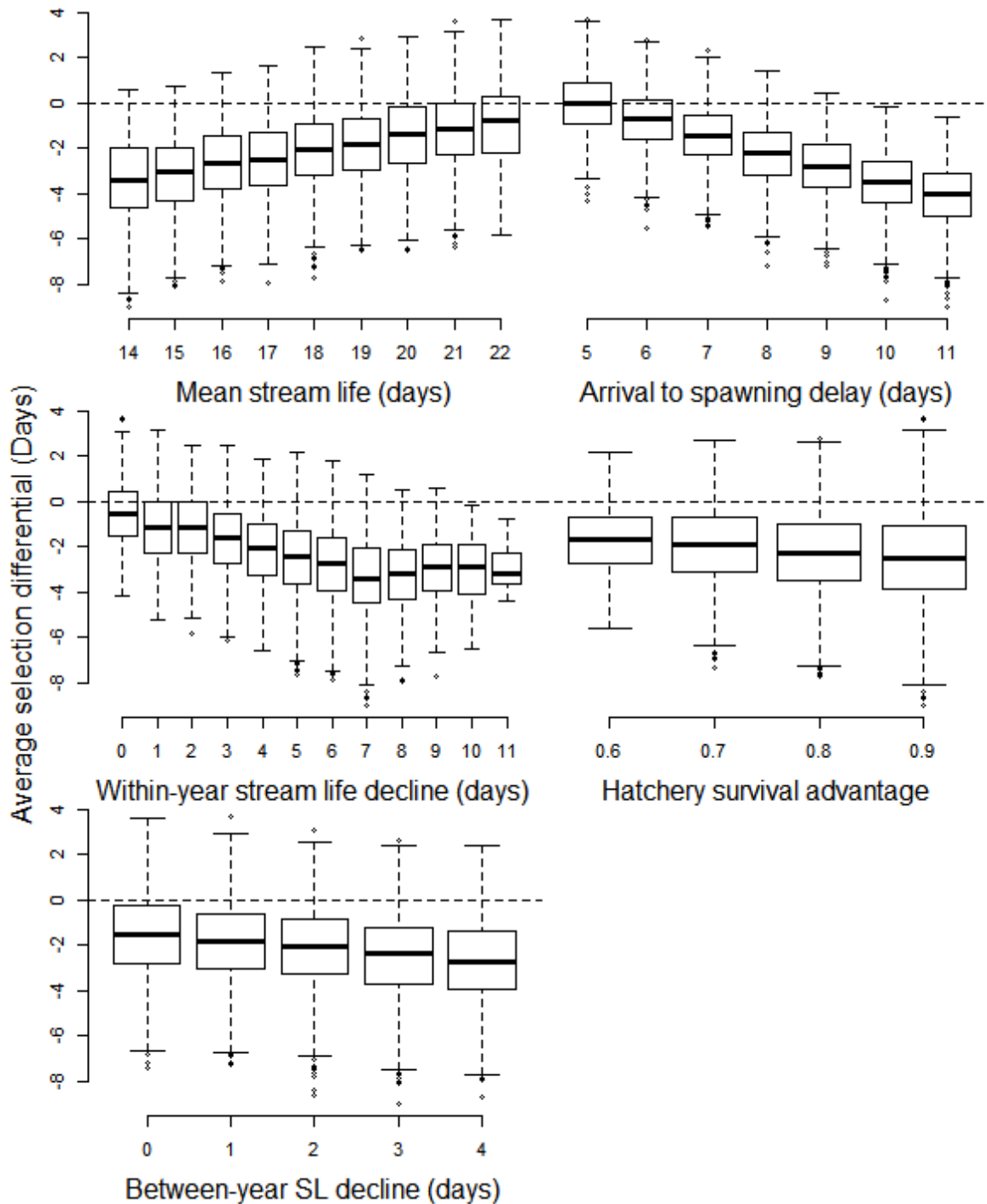


Figure 4.6. Sensitivity of Cedar River sockeye arrivals model to parameter values. Boxplots of the distribution of model outputs given each parameter value. Heavy bars show medians, boxes show the interquartile range, whiskers show the overall range and open circles show outliers.

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