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

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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.

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1. 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 the 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 in to 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 suboptimal oxygen conditions.

2. Methods

2.1. Field methods

2.1.1. 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 ∼7800 m² of accessible habitat during the spawning season and the side pond and beaver pond provide an additional ∼800 m² and 4000 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.

2.1.2. Stream surveys

From 1962 to 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 (Fig. 1). To avoid double counting, dead fish are removed from the stream and tossed at least 3 m beyond the bank. Starting in 1992, in addition to counting live and dead fish daily, survey teams also recorded