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Review of recent and proposed Okanagan Sockeye Salmon (*Oncorhynchus nerka*) fry introductions to Skaha and Okanagan lakes: history, uncertainties, and implications

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The Columbia River Basin supports a Sockeye Salmon (*Oncorhynchus nerka*) aggregate that is composed of three Sockeye Salmon populations. Anadromous Sockeye Salmon and freshwater-resident kokanee are two ecotypes within *Oncorhynchus nerka* that occur frequently as sympatric paired populations sharing a common nursery (juvenile-rearing) lake. Okanagan Lake currently provides no access to Sockeye Salmon but contains shore- and stream-spawning kokanee that display limited morphological and genetic differentiation and may constitute incipient ecotypes. This work was initiated to determine the potential risks, impacts and uncertainties associated with variable scale introductions of Sockeye Salmon fry into Okanagan Lake – through bioenergetics or food-web disruption, pathogen transfer, or genetic impacts.

Based on results from an introduction experiment in a nearby lake (Skaha Lake), and data from nearby lakes (acknowledging differences in lake size, depth, and productivity, and scaled to account for *O. nerka* proportion of total pelagic fish biomass), the impact of Sockeye Salmon fry introductions on Okanagan Lake and especially its' populations of resident kokanee salmon were considered. Sockeye Salmon fry introductions, across the range of abundance currently proposed for Okanagan Lake, are considered unlikely to induce detectable changes to pelagic food-webs (i.e. phytoplankton and zooplankton), or to sensitive aquatic biota (all ages and size classes of pelagic fish) within Okanagan Lake.

The transfer of bacterial, parasitic, and viral pathogens to the watershed from hatchery-origin Sockeye Salmon fry were considered as part of the impact evaluation. Due to their capacity to spread from mother to offspring, viruses such as infectious pancreatic necrosis virus (IPNV) and infectious hematopoietic necrosis virus (IHNV) were noted of concern. Nevertheless, based on results from the Skaha Lake introduction, and the use of egg disinfection and containment procedures employed by the applicant, the potential transfer risk of these pathogens is low, as no detection of IPNV, IHNV or other cell culture replicating agents has occurred in fry since the inception of the hatchery program in 2003.

Genetically distinct ecotypes may arise within a species when there is more than one selective niche to occupy in the environment and there exists within the species sufficient genetic diversity to respond to the divergent selective forces through an adaptive process of ecotype development (Wellborn and Langerhans 2015). The process of ecotype development and maintenance is not always stable and irreversible, especially in the face of environmental change. Little genetic impact on the kokanee populations, including ecotype formation and persistence or degradation, would be expected to result from a one-time introduction of 750,000 Okanagan Sockeye Salmon fry to the lake, while an ongoing release of between 0.75 and 3.5 million Okanagan Sockeye and kokanee in Okanagan Lake; the results of which cannot be predicted.

1. INTRODUCTION

The Columbia River Basin supports a Sockeye Salmon (*Oncorhynchus nerka*) aggregate that is composed of three Sockeye Salmon populations including: the Okanagan population from British Columbia (BC), Canada, the Wenatchee Lake population from Washington State, and a small population from Redfish Lake in Idaho that is listed under the United States Endangered Species Act (ESA). On average, over the most recent decade, the Okanagan population has accounted for greater than 80% of all Sockeye Salmon returning to the Columbia Basin. Historically, the Columbia River supported substantial US commercial, Treaty Tribal, non-treaty, and Canadian First Nations fisheries. Sockeye Salmon production drastically declined during the mid- to late-20th century resulting in sporadic openings of commercial fisheries after 1972, as well as significant reductions to First Nations fisheries for the next 35 years.

In 2004, the Okanagan Nation Alliance (ONA) began introducing hatchery-origin Sockeye fry to rear in Skaha Lake, as part of a collaborative, 12-year project ("Skaha Re-introduction Project") to inform future introductions of Sockeye to Okanagan Lake. The ONA has more than a decade of experience in hatchery propagation and Sockeye Salmon fry introductions (2004-present) by virtue of their Skaha Lake Sockeye Salmon re-introduction program, including the completion of a 3-year disease and ecological risk assessment in advance of the program's initiation (2000-2002). The disease risk assessment focused on the likelihood of introducing new or extending the range of known pathogens and specifically identified five pathogens of concern relating to the re-introduction program. The broader ecological risk assessment considered potential impacts of newly introduced Sockeye Salmon fry on resident fish populations and other aquatic biota. Observational data to assess both disease and other ecological impacts have been gathered on an ongoing basis by the ONA and subjected to annual review by the three-party (ONA, DFO, BC-FLNRO) Canadian Okanagan Basin Technical Working Group since the program's inception (Alexander and Hyatt eds. 2015).

The ONA has applied to release up to 750 000 Sockeye Salmon fry into Okanagan Lake in 2017, and has indicated that their hatchery facility has the capacity to rear 7 million fry, with maximum single-year introductions estimated at 3.5 million fry. To provide a recommendation regarding whether or not to authorize the release application, a joint Federal-Provincial Introductions and Transfers Committee (ITC) requires science advice on potential ecosystem disruption, pathogen transfer, or genetic interference impacts associated with the proposed release.

2. BACKGROUND

One or more ecotypes of Sockeye Salmon that either complete their entire life cycle in freshwater (i.e. kokanee salmon), or fresh and marine waters (i.e. sea-run Sockeye Salmon), represent the most abundant limnetic fish species rearing in three of the Okanagan Valley's largest lakes (Okanagan, Skaha and Osoyoos lakes) (Figure 1). Introduced Lake Whitefish (*Coregonus clupeaformis*) and native Rainbow Trout (*Oncorhynchus mykiss*) also occupy offshore waters of these lakes in much smaller numbers. Although not identical, the pelagic fish communities and supporting food webs that characterize the open waters of Osoyoos, Skaha and Okanagan lakes are similar (Northcote et al. 1972; Andrusak et al. 2002). All age classes of Sockeye Salmon, kokanee and Lake Whitefish occupying these lakes are principally zooplankton feeders. In contrast, young Rainbow Trout depend on small aquatic invertebrates and plankton for food as juveniles but become piscivorous, consuming kokanee and/or Sockeye Salmon in offshore waters as larger, older age classes (Scott and Crossman 1973, Parkinson et al. 1989). A non-native species of freshwater shrimp (*Mysis diluviana*) has become the



dominant macroinvertebrate in the limnetic zone of all three lakes since its intentional introduction into Okanagan Lake by B.C. biologists in the late 1960's (Andrusak et al. 2002).

Figure 1. Okanagan River map. Map Source: Hyatt et al. 2003.

EVALUATION OF THE EVIDENCE THAT SOCKEYE SALMON HAVE BEEN A HISTORIC PART OF THE OKANAGAN LAKE ECOSYSTEM

Okanagan Sockeye Salmon are the last, self-sustaining, anadromous salmon population of more than a dozen salmon populations that historically returned on an annual basis to Canadian waters through the Columbia River (Fryer 1995, Hyatt and Rankin 1999). Prior to, and extending into, the period of European settlement in the Okanagan valley, an important First Nations fishery for Sockeye Salmon, Chinook Salmon and kokanee salmon is known to have existed at Okanagan Falls immediately downstream of Skaha Lake (Bouchard and Kennedy 1975). The potential range of salmon distribution is a source of uncertainty; some historical narratives suggest that Okanagan Falls represented the upstream terminus of salmon distribution in the Okanagan; while oral testimonials from Okanagan Nation Alliance (ONA) suggest that anadromous salmon, including Sockeye Salmon, were known to occur upstream of Okanagan

Falls in Skaha and Okanagan lakes prior to the development of dams and irrigation system works that blocked access by salmon, beginning in the late 1800s to early 1900s.

Based on the recognition that a large, natural origin population of lake and stream spawning kokanee has been present in Okanagan Lake since before the arrival of European settlers (Rae 2005), and that natural kokanee populations develop from anadromous Sockeye Salmon colonization (references in Burgner 1991), it is evident that Sockeye Salmon colonized Okanagan Lake although the historic period in which the colonization occurred is unknown. Although there is no overwhelming evidence for the presence of a major Sockeye Salmon population occupying Okanagan Lake within the past 100-150 years (roughly the period of historic European occupation), as noted above there are oral testimonials from the ONA to suggest anadromous salmon, including Sockeye Salmon, were known to occur upstream of Okanagan Falls. Based on consideration of Okanagan Sockeye Salmon size and swimming performance, and Okanagan Falls step heights, derived from examination of historic photographs, it is likely that Okanagan Falls would not have constituted an absolute barrier to ascent by anadromous Sockeye Salmon (Shepherd 1996). As Okanagan Falls represents the only potential hydraulic barrier to free passage by salmon between the Columbia River and Okanagan Lake, it is unlikely that anadromous salmon were entirely absent from the system until after impassable dams were built in the early 1900s in support of irrigation works coincident with European settlement in the Okanagan valley (Rae 2005). Historical pre-dam photos from the early 1900s (e.g. Wilson 2011) do provide evidence for a kokanee population harvested by First Nations in Okanagan Lake, as well as abundant large Rainbow trout that may have depended on abundant large kokanee for forage (Parkinson et al. 1989).

3. ANALYSIS AND RESPONSE

POTENTIAL IMPACTS TO STRUCTURE AND FUNCTION OF EXISTING FOOD WEBS, OR DETECTABLE PRODUCTION OUTCOMES FOR SENSITIVE AQUATIC BIOTA

Although not identical, the pelagic fish communities and supporting food webs that characterize the open waters of Osoyoos, Skaha, and Okanagan lakes are similar (Northcote et al. 1972, Andrusak et al. 2002). All three of the planktivorous fish species that rear in the offshore waters of the subject lakes exhibit variable levels of diet overlap that change seasonally and developmentally (Hyatt et al 2015a, 2015b) and could theoretically engage in competition for food. However, the extent to which such interactions will emerge depends not only on food-web and fish population structure in a given lake but also on the intrinsic production potential of the lake and its associated capacity to support growth and survival of pelagic fish such as Sockeye and kokanee Salmon.

It is beyond the scope of the current report to undertake quantitative analysis of the entire suite of factors likely to be involved in controlling annual to seasonal production variations from plankton to pelagic fish in the valley bottom lakes of the Okanagan. However, limnological variables such as total phosphorus, Secchi transparency and chlorophyll-a may be used as effective, high level indicators of lake or reservoir trophic state that affects fish production, biomass and yield (see references in Carlson 1977, Rieman and Myers 1992); these indicators have been used in studies of nutrient poor lakes (4 to 45 µg P per liter) to examine associations among kokanee abundance, growth and size at age. Observations of these same types of associations in the three Okanagan valley lakes (Table 1) are used here as the basis for initial inferences about the relative productive capacity of these lakes and the potential for occurrence of strong or weak interactions between hatchery-origin Sockeye Salmon fry and resident kokanee given potential future introductions of the former to Okanagan Lake.

Observations of mean lake depth, spring (June) phosphorus concentration, mean summer chlorophyll, Secchi depth, mean abundance of cladoceran prey and Mysis sp. all exhibit values (Table 1) to suggest that Osoyoos Lake is likely more productive than either Skaha or Okanagan Lake. The latter two lakes may be relatively close in overall productivity, i.e. Skaha Lake has slightly higher phosphorus concentrations in June (7.7 vs 6 ug per liter) but Okanagan Lake maintains higher mean chlorophyll levels (2.5 vs 1.81 ug per liter) and higher Secchi values (mean of 6.9 vs 5.3 m) through the growing season. Average summer densities of Mysis sp. are not especially informative other than to suggest that populations of this introduced species are well established in all three lakes (Table 1). The average biomass of fish maintained in the pelagic zone of these lakes is consistent with an inference of highest to lowest fish production potential occurring in Osoyoos, then Skaha and finally Okanagan Lake (column 3 of Table 2b) in accordance with the general observation that phosphorus is the nutrient most commonly limiting production at all trophic levels in many BC lakes (Hyatt and Stockner 1985, Hyatt et al. 2004). However, the average biomass of fish currently maintained in a given lake does not invariably represent its' maximum carrying capacity or production potential to support populations of O. nerka. For example, although the average biomass of pelagic fish carried into the fall over nine years of observation in Osoyoos Lake is 26 kg per ha, the mean value over the most recent five years of observation has been sustained at an average of more than 35 kg per ha as adult sockeye escapement and subsequent sockeye fry recruitment have more than doubled without any appreciable accompanying changes in nutrient loading or zooplankton production (Hyatt and Rankin 1999, Hyatt et al. 2015a, Hyatt et al. 2018). This result suggests the pelagic fish production potential in all three lakes may be closer to the upper end of the currently observed range of values (Table 2b, column 4) than to the all-year mean of pelagic biomass, where the latter is constrained by a variety of factors that limit sufficient fry recruitment to test the upper end of a lake's productive capacity to support fish.

Observations of Sockeye Salmon Abundance, Growth, and Survival in Osoyoos Lake

Numerous studies to examine variations in O. nerka abundance, growth and survival in a wide range of lakes and reservoirs have provided evidence that their growth and survival are likely to decrease as in-lake abundance increases (see references in Rieman and Myers 1992 and Hyatt et al. 2011). Hyatt and Rankin (1999) combined both historic and new survey data on Osoyoos Lake O. nerka abundance and determined that although there was an effect of increasing sockeye fry abundance on their subsequent growth, virtually all of the scope for impacts of increased fry abundance on growth to age-1 was exhausted once sockeye fry reached abundance levels greater than 1500 per ha. Nine additional years of systematic monitoring of O. nerka growth and survival to abundance levels in excess of 7000 fry per ha have confirmed the absence of strong density effects on either growth or survival, once fry populations increased above an abundance threshold of roughly 1500 fry per ha (i.e. about 4.5 kg per ha by fall) in Osoyoos Lake (Fig. 2.7 in Alexander and Hyatt 2015, Hyatt et al. 2015a, Hyatt et al. 2018). These findings appear to be in agreement with those of Rieman and Myers (1992) and Beauchamp et al. (1995) that strong density dependent interactions within O. nerka (kokanee) populations in oligotrophic lakes are principally driven by older kokanee (ages 2 and 3) but not fry or yearlings. They concluded that intraspecific competition probably increases with age and size of fish and is unlikely to be important among age-0 or age-1 kokanee at densities of < 1000 fish per ha.

The absence of evidence for strong growth suppression of age-0 Sockeye fry at much higher abundance levels (i.e. up to 7000 per ha) in Osoyoos Lake than the 1000 fish per ha threshold suggested by Rieman and Myers in their studies of kokanee populations may be a consequence of the relatively low abundance of older, larger fish (principally kokanee and Lake Whitefish) in

the Osoyoos Lake pelagic fish population. O. nerka age-0 fish dominate the pelagic fish community by numbers in all of these lakes. However, older, larger fish still routinely make up the majority of the biomass of pelagic fish in these lakes and are likely to be the most important competitors of juvenile Sockeye and kokanee to the extent that they share the same food sources. This would appear to be the case even in Osovoos Lake where older, larger planktivorous fish still make up 66% (Table 2b, column 7) of pelagic fish biomass (e.g. see Hyatt et al. 2018 for bioenergetics-based analysis of the relative magnitude of zooplankton consumption by age-0 Sockeye fry, older and larger fish and mysids). Because older, larger fish make up a smaller portion of the pelagic fish biomass in Osoyoos Lake (66.4%) than in either Skaha (92.2%) or Okanagan (93.7%) lakes (see Table 2, column 7 and text below) this may allow Osoyoos Lake to support much higher O. nerka age-0 fry abundances than Skaha and Osyoos Lake without exhibiting strong intraspecific competition for food. However, it also suggests, consistent with the results of Rieman and Myers, that the strongest intraspecific, and by inference, interspecific competitive interactions are most likely to occur between larger and older age classes of planktivores rather than among fry in situations where all are sharing a common food source.

Sockeye Salmon and Kokanee Abundance, Growth, and Survival in Skaha Lake

At their highest abundance levels in recent years, age-0 Sockeye Salmon in Osoyoos Lake not only dominate the pelagic fish community numerically but also can occasionally dominate pelagic fish biomass because recruitment of both kokanee and Lake Whitefish to Osoyoos Lake is sporadic (Hyatt et al 2015a). Thus, Osoyoos Lake observations are limited as a basis for clarifying uncertainties about the full range of potential interactions between age-0 Sockeye Salmon and other pelagic fish; including more complicated, age and size-structured populations of kokanee. The experimental introduction of hatchery-origin Sockeye fry into Skaha Lake was designed to more clearly address these uncertainties and to provide a basis for anticipating future impacts of Sockeve introductions in the much larger Okanagan Lake system. A monitoring and evaluation program has provided more than a decade of seasonal to annual observations of: water chemistry, zooplankton production, pelagic fish community structure, growth, and survival of introduced hatchery and wild-origin O. nerka (Hyatt et al 2015b), as well as summary results (McQueen et al. 2014, Alexander and Hyatt eds. 2015). Observed and potential impacts of Sockeye Salmon fry introductions on the food-web and pelagic fish community of Skaha Lake are briefly summarized below as a basis for anticipating possible impacts of future Sockeye Salmon fry introductions on the kokanee population and the pelagic food-web of Okanagan Lake.

Skaha Lake *O. nerka* fry, comprised of wild-origin kokanee and hatchery-origin Sockeye Salmon fry, although still dominant numerically (Table 2a, column 5), make up a smaller proportion (7.8%) of the total biomass of pelagic fish than was the case in Osoyoos Lake. Older and larger kokanee, plus much smaller numbers of Lake Whitefish, account for greater than 92% of pelagic fish biomass in Skaha Lake (Table 2b, column 7). Further, because all ages and sizes of *O. nerka* and Lake Whitefish exhibit diet overlap (i.e. all consume significant quantities of *Daphnia* spp.), the greatest potential for competitive interactions exists wherein large fish compete with each other and with *O. nerka* fry. There is less likelihood for strong competitive interactions between Sockeye Salmon fry and kokanee fry based on the relative biomass and inferred consumption of zooplankton prey. Bioenergetics-based analysis of zooplankton production, fish production and fish consumption of zooplankton in Skaha Lake (McQueen et al. 2014, p. 49) indicated that for the 8 years examined:

(i) rates of zooplankton consumption by fish and mysids together seldom exceeded rates of zooplankton production,

- (ii) Mysis consumed more zooplankton than all of the fish combined, and
- (iii) age-0 hatchery-origin Sockeye Salmon consumed only 2-5% of the total zooplankton consumed by all pelagic fish and mysids together.

These results further suggest that both intraspecific and interspecific competitive interactions are likely to be most intense among larger, older pelagic fish as well as between fish and mysids. Based on the proportion of total zooplankton consumed by Sockeye Salmon, there would appear to be little potential for Sockeye Salmon fry to influence either the structure of the Skaha Lake pelagic food web; or the growth or survival of each other, kokanee fry, older age classes of fish, or mysids even though all four classes of planktivores exploit some common zooplankton taxa.

Analyses of empirical observations of annual variations in abundance, growth, size and survival of various categories of pelagic fish (i.e. Sockeye Salmon fry, kokanee fry, larger-older kokanee) generally support the inferences above (see results in McQueen et al 2014, Alexander and Hyatt 2015). For example, Sockeye Salmon and kokanee fry appear to grow at similar rates and achieve similar year-end sizes (near 9.5 and 7.0 cm in length respectively) regardless of their abundance variations among the eight years of record (Fig. 2.12a of Alexander and Hyatt 2015). However, two growth and abundance metrics suggest potential competitive interactions: (1) the appearance of a significant decrease in mean kokanee length from pre to post Sockeye Salmon additions, (2) a significant association between declining age-0 Sockeye Salmon fry winter weight and initial stocking density (Fig. 2.12c of Alexander and Hyatt 2015). The sockeye winter weight relationship is heavily influenced by a single observation at the lowest level of Sockeye Salmon fry stocking abundance and was not corroborated by any parallel associations between subsequent, mean growing season abundance of either Sockeye Salmon or kokanee and their resultant fall or winter weights (Figure 2.12b in Alexander and Hyatt 2015). Single point estimates of kokanee size between summer and fall in 5 years prior to any Sockeye Salmon introductions are available (Figure 2.15 in Alexander and Hyatt 2015). These data suggest that in the presence of Sockeye Salmon fry, kokanee are roughly 0.5 cm (~8%) smaller in length in summer than when Sockeve Salmon are absent. However, this size difference largely disappears by winter as the sizes of kokanee from all years converge near a length of 7 cm (see Figure 2.12a and Figure 2.15 in Alexander and Hyatt, 2015).

Evidence that bottom-up processes (e.g. river flushing) control the biomass of plankton, rather than fish predation, supports the observation that growth of Sockeye Salmon and kokanee fry are unlikely to be limited through any intense competition for zooplankton prey. Recent observations by McQueen et al. (Fig. 8 in McQueen et al. 2014) suggest an inverse relation between average seasonal discharge of the Okanagan River and the mean biomass of zooplankton (excluding Mysis) maintained in Osoyoos (r=0.74, P<0.01, n=8) and Skaha (r=0.58, p=0.01, n=8) lakes through the spring-fall production interval. During eight years of monitoring, zooplankton biomass in both lakes fluctuated from a low average of about 70 µg per liter (as dry wt) in higher discharge years (> 30 cms) to a high average biomass of 155 µg per liter in lower discharge years (<10 cms). However, there is no indication that removal, through flushing actions by the Okanagan River, of more than 50% of zooplankton prey in both lakes exerted any detectable negative impacts on fry growth which reinforces the theory that O. nerka fry are not generally engaged in intense density dependent, competition for food. By contrast, there is evidence that mean seasonal biomass of zooplankton in Osoyoos Lake is significantly associated with increased survival of Sockeye Salmon fry there (Hyatt et al. 2018). Because it is the Okanagan River, rather than fish, that controls annual variations in zooplankton abundance in both Osoyoos and Skaha lakes, the observed association between variations of zooplankton biomass and O. nerka survival is a consequence of a bottom-up impact of the river on both

zooplankton and fish, and does not constitute evidence that *O. nerka* fry are either controlling or competing for limited supplies of zooplankton prey in these lakes.

The observations of weak to non-existent competitive interactions between Sockeye Salmon and kokanee fry-of-the-year contrast with much stronger evidence for density dependent impacts of larger and older Skaha system kokanee on their own size at maturity (Figure 2.14, P. Askey unpublished data in Alexander and Hyatt 2015) as well as on the size that kokanee fry achieve in Skaha Lake going into the winter of their first year (Figure 2.16 in Alexander and Hyatt 2015). In the latter case, winter weights of kokanee fry appear to decline from almost 5 g to less than 3.5 g as aggregate abundance of age 1-3 year-old kokanee increased from roughly 100 per ha to 350 per ha (i.e. from 4.5 to 11.2 kg per ha). Also, given Skaha kokanee annual escapements in excess of 40,000 adults, kokanee size at maturity is relatively constant at 25-26 cm in length. However, at escapements below 15,000, average adult size exceeds 31 cm and the shape of the density dependent relationship conforms to the decaying exponential form that Rieman and Myers (1992) and Askey (2016) identified as characteristic of several kokanee populations (including Okanagan Lake).

Larger and older (ages 1-3) kokanee affect not only their own size at maturity but also appear to affect winter weights of their own fry in Skaha Lake. The potential for competition between older and larger kokanee with O. nerka fry would be even greater except that larger, older fish rely on consumption of Mysis while fry rely on Daphnia as the largest proportions of their diet by weight. Further, bioenergetics-based modeling analysis (McQueen et al 2014) indicates that large fish in Skaha Lake have the potential to drive down seasonal abundance of mysids sufficiently to cause competition for this food source. However, there is no evidence that fish consistently deplete Daphnia as the common zooplankton prey that all age classes of pelagic fish share (McQueen et al. 2014), so the scope for strong competition to emerge between older kokanee and age-0 fry of O. nerka in Skaha Lake appears to be moderated by the presence of Mysis. The Skaha kokanee population has maintained higher abundance levels (all-year average > 30,000 mature adults) during the 2004-2015 interval of Sockeye Salmon fry introductions to Skaha Lake, than during the more than two-decade, "control" interval (all-year average <10,000 mature adults) prior to Sockeye Salmon fry introductions (Figure 2 in Webster 2015), However, the inter-decadal level of recruitment variability exhibited by this kokanee population, in the absence of Sockeye, is significantly greater than the variation observed during Sockeye fry introduction years. Consequently, a declining trend in the most recent observations of adult kokanee present as fry during Sockeye introductions does not constitute statistically significant evidence for or against the existence of competitive interactions between hatchery-origin Sockeye Salmon fry and kokanee.

The relevance of observations of Sockeye Salmon and kokanee interactions to date at Skaha Lake to the ONA proposal for future introductions of variable numbers of Sockeye Salmon fry into Okanagan Lake will be addressed further below. Currently, the Canadian Okanagan Basin Technical Working Group's (COBTWG) perspective is that there is "no compelling evidence of serious impacts of Sockeye Salmon fry introductions (maximum numbers in excess of 800 per ha) to Skaha Lake on kokanee growth, survival, production or life history attributes" (p. 109 in Alexander and Hyatt 2015).

Observations of Kokanee Abundance, Growth, and Survival in Okanagan Lake

During the interval spanning three decades from the early 1970's to the late 1990's the kokanee population in Okanagan Lake exhibited a precipitous decline from peak numbers of adult spawners of nearly 1,000,000 fish to an observed, four-year average of fewer than 25,000 adults during 1995-1998 (Askey and Johnston 2013). Consequently from 1996-2007, BC Fisheries, with funding from the BC Habitat Conservation Trust, launched the Okanagan Lake

Action Plan (OLAP), which included an annual program of scientific investigations into the causes of the decline in the kokanee populations. Results of these investigations have been published as a series of Fisheries Project Reports by the BC Ministry of Environment. The final report in this series (Andrusak et al. 2008) not only provides observations from 2006 and 2007 as the final years of OLAP study, but also the historic range of observations on physical, chemical and biological characteristics of Okanagan Lake. Thus, the 2008 report by Andrusak et al. has been used as the principal source of information summarized here. In addition, BC-MOE personnel provided access to unpublished observations from the following data sources:

- acoustic-and trawl based sampling of total abundance and biological traits (age, size-atage) of the kokanee population rearing in Okanagan Lake between 1988-2013 (Tyler Weir, BC-MOE)
- (ii) fall surveys of adult kokanee numbers spawning on Okanagan Lake beaches and tributary streams between 1992-2016 (Tara White, BCMOE).

Review of the survey methods used by BC-MOE crews to gather these data indicate that observations assembled on physical, chemical and biological characteristics of the Okanagan Lake ecosystem permit comparison to those already summarized above for Osoyoos and Skaha Lake aquatic ecosystems.

The age and size structure of the pelagic fish community in Okanagan Lake is similar to that described earlier for Skaha Lake. In Okanagan Lake *O. nerka* fry comprise 65% of all pelagic fish by number versus 66.5 % in Skaha Lake (Table 2a, column 5). By contrast they only make up 6.3% of pelagic fish biomass (i.e. similar to the 7.8% observed for Skaha Lake), with the remaining 94.7% comprised principally of older, larger kokanee (Table 2b, column 7). Therefore, the size and biomass spectra of the pelagic fish communities in Osoyoos, Skaha, and Okanagan lakes all support the inference that competition among *O. nerka* fry-of-the-year is likely weak to non-existent while both intraspecific and interspecific competition will be potentially greatest between older, larger pelagic fish (e.g kokanee and/or Lake Whitefish) which, depending on dietary overlap and prey production, may induce negligible to serious effects on *O. nerka* fry growth and survival.

There is little information on the seasonal diets of the various size and age classes of Okanagan Lake kokanee (Askey and Andrusak 2008) but what little information does exist suggests their dietary habits may be similar to the well documented dietary habits of comparable size classes of Sockeye Salmon and kokanee from either Osoyoos or Skaha lakes (Hyatt et al. 2015a, 2015b, 2018). Results from the latter two lakes indicate that *Daphnia* spp. and the large copepod *Epischura* sp. generally dominate the diet of Sockeye Salmon and kokanee fry both numerically and by weight, which is consistent with the limited observations of dietary habits of Okanagan kokanee fry. By contrast, Askey and Andrusak (2008) noted that although all kokanee consumed *Daphnia* spp. and *Epischura, Mysis* represented the largest component of the larger (> 8 cm in length) older (age 1 and 2) Okanagan kokanee diet by weight even though *Mysis* made up less than 1% of their dietary items by number. This observation was for a single seasonal time period (fall), but is consistent with the results of McQueen et al (2014) and Hyatt et al. (2015a and b) on the dominance of *Mysis* by weight in the diets of larger, older *O. nerka* sampled from Osoyoos and especially Skaha lakes.

Given the similarity in the overall abundance, age, and size-structure, and the apparent similarity in dietary habits of the Okanagan and Skaha Lake kokanee populations, it appears that Okanagan Lake kokanee fry, and potentially introduced Sockeye Salmon fry, are unlikely to exert much if any controlling influence on their zooplankton prey, as appears to be the case in Skaha Lake. Examination of current (1988-2013) relationships between weight of age-0 kokanee at the time of fall surveys and either their own abundance variations (Figure 2a, this report) or the total biomass of all kokanee older than age-0 (Figure 2b, this report) in Okanagan Lake indicates an absence of any continuous influence of either fry density or kokanee biomass on fall fry weight across a relatively wide range of values. As was the case for age-0 Sockeye Salmon fry in Osoyoos Lake, there is some evidence for increased growth performance by age-0 fry if either their densities or pelagic fish biomass drop below a lower threshold (e.g. <100 fry per ha and/or < 5 kg per ha). However, above these thresholds, growth variations remain virtually unresponsive to fry abundance or kokanee biomass increases out to the highest values recorded to date (Figure 2a and b, this report).

The relatively constant growth performance of age-0 kokanee across a wide range in pelagic fish abundance is inconsistent with a hypothesis of continuous increase in competition for zooplankton prey as the pelagic fish population expands or contracts except at its' lowermost limits. However, larger and older fish in combination with a relatively large population of Okanagan Lake *Mysis* (Table 1) may have impacts on their common zooplankton prey to impact growth and survival of kokanee. At this time, the linkage between seasonal to annual production variations of zooplankton prey and their potential associations with growth or survival of all size and age classes of Okanagan Lake kokanee remains unclear.

Several decades after their introduction to Okanagan Lake in 1966, mysids have clearly become a major consumer of the zooplankton forage base in Okanagan. Skaha and Osovoos lakes, impacting food web structure (Schindler et al 2012) and production outcomes of other species (McQueen et al 2014), however the specific role of mysids in each lake system may still be unclear. To date, the common assumption has been that the dominant impact of "invasive" mysids here and elsewhere has been as competitors with kokanee (Northcote 1991, Andrusak et al 2002) and Sockeye Salmon fry (Hyatt et al. 2005) in lakes where both O. nerka and mysids occur. Thus, OLAP biologists proposed that competition between invasive mysid shrimp and kokanee for limited zooplankton resources precipitated population declines in both ecotypes (i.e. shore-spawners and stream-spawners) of kokanee in Okanagan Lake (Walters 1995, Ashley et al. 1999. Walters and Korman in Andrusak et al. 2004. Andrusak et al. 2006). However, new observations that Mysis have also become a major source of forage for older and larger age classes of kokanee (McQueen et al 2014, Hyatt et al 2015b, Askey and Andrusak 2008) suggest that interactions among kokanee and mysids may be more complicated than this. The recovery of one of the kokanee ecotypes within the past 10 years from fewer than 25, 000 to an average of 165,000 shore spawning adults (range 78,000-304,860), absent any major decline in the abundance of mysid shrimp, may indicate that the introduction and subsequent large increase in population of mysid shrimp has not entirely constrained the potential for Okanagan Lake kokanee to increase, despite possible competition for common zooplankton prey.

Potential for within-lake interactions between Okanagan Lake kokanee and introduced Sockeye Salmon across a range of abundance

The Okanagan Nation Alliance has requested authorization to introduce up to 750,000 Sockeye Salmon fry into Okanagan Lake in the spring of 2017. It is also anticipated that requests to introduce larger numbers (upwards of 3.5 million) of hatchery-origin Sockeye Salmon fry may be made in subsequent years. Information presented above is considered along with projections of what an assumed abundance range of Sockeye Salmon fry (750,000-3,500,000) may represent as single to multi-year impact events affecting the pelagic food-web or resident populations of fish in Okanagan Lake.

Because Okanagan Lake is more than 30 times the size of either Osoyoos or Skaha lakes, the potential impact of a given Sockeye Salmon fry introduction on the Okanagan Lake ecosystem has been scaled to a set of common units (e.g. no's. per ha, kg per ha, Table 3) for applicable

comparison of results from Skaha Lake Sockeye Salmon fry introductions to projections of impacts in Okanagan Lake.

The proposal to introduce 750,000 hatchery-origin Sockeye Salmon fry in 2017 equates to an in-lake abundance of at most 30.2 Sockeye Salmon fry per ha in Okanagan Lake (i.e. assumes only 24,828 ha of pelagic area waters are occupied out of a total lake area of 35,008). These would represent approximately 10% of the all-year mean of kokanee fry abundance (i.e. a 1:10 ratio of Sockeye Salmon to kokanee by numbers) and just 1.08 % of the all-year mean of Okanagan Lake pelagic fish biomass (Table 3) identified through acoustic-and-trawl based methods by BC-MOE (BC-FLNRO unpublished data). The total fall fry of wild kokanee and hatchery Sockeye Salmon in Skaha Lake (which includes both hatchery released Sockeye Salmon, as well as Sockeye Salmon fry produced by Sockeye Salmon adults spawning in the wild) have ranged from a low of 156 to a high of 800 fry per ha by numbers and 0.44 to 2.94 kg of fry per ha by weight (Table 4). From 2004-2012, the ratios of Sockeye Salmon fry to kokanee fry numbers have been as low as 1:10 and as high as 1:1.25. These ratios shift if expressed as resultant biomass because hatchery-origin, Sockeye Salmon fry are larger than kokanee fry at the time of introduction and maintain this size differential (McQueen et al. 2014) such that by fall the biomass ratios are as low as 1:3.4 where kokanee fry make up most of the biomass, and as high as 11.6:1 where Sockeye Salmon comprise most of the aggregate fry biomass in Skaha Lake (Table 4). Despite these wide ranges in total summer fry abundance, total fall fry biomass and fluctuating ratios of Sockeye Salmon fry to kokanee ratios, no compelling evidence for strong food-web impacts (e.g. fry-induced reductions in primary prey) or competition between Sockeye Salmon and kokanee fry has emerged from analysis of a decade of Skaha Sockeye Salmon introduction results.

Based on the assumption of similar productivity levels between Okanagan and Skaha lakes supported by index values listed in Table 1, it is unlikely that the introduction of 30 Sockeye Salmon fry per ha to potentially interact with an all-year average of 242 kokanee fry per ha (most recent 10-year average from BC-MOE, unpublished data) in Okanagan Lake will exert anything more than a minor impact on either growth or survival of Okanagan kokanee fry. In addition, due to their relatively small sizes at first introduction, Sockeye Salmon fry will generally make up only a small fraction of the total biomass of the vertebrate planktivores in lakes such as Skaha (Hyatt et al 2015b) and Okanagan (e.g. about 1% of fall biomass of all Okanagan pelagic fish, Table 3, column 7); where older and much larger kokanee and/or Lake Whitefish account for most of the fish biomass and therefore generate greater cropping pressure on the zooplankton forage base (McQueen et al. 2014). It is anticipated that the majority of the introduced Sockeye Salmon fry would migrate seaward in the spring of the following year; consequently there would be little ongoing, within-lake impact of these fish on Okanagan foodwebs, kokanee, or even larger but rarer Rainbow Trout at older ages.

Empirical data and observations specifically from Okanagan Lake provide further support for this conclusion. Observations in the fall of 2016 indicated a spawning population of 127,849 adult kokanee throughout Okanagan Lake, and associated streams. Production of kokanee fry from the 2016 escapement is predicted to result in recruitment of approximately 5.6 million fall fry (i.e. 226 per ha) to Okanagan Lake in 2017 (Figure 3, this report). The potential addition of 750,000 Sockeye Salmon fry represents at most the addition of 30 fall fry to predicted fall fry abundance (Figure 2a, this report). Consequently, the Sockeye fry introduction proposed for 2017 would appear to have little potential to shift fry abundance sufficiently to generate detectable impacts on the growth of kokanee fry. Due to their relatively small sizes at first introduction (1.49g wet wt, based on current mean weights of hatchery-origin Sockeye fry introduced to Skaha Lake), Sockeye fry will generally make up only a small fraction of the total biomass of the vertebrate planktivores in lakes such as Skaha (Hyatt et al 2015b) and

Okanagan (e.g. about 1% of fall biomass of all Okanagan pelagic fish, Table 3, column 7) where older and much larger kokanee and/or Lake Whitefish account for most of the fish biomass and therefore generate greater cropping pressure on the zooplankton forage base (McQueen et al. 2014). Assuming Sockeye fry would quadruple their 1g weight at introduction by the fall of the year, the specific addition of 750,000 Sockeye Salmon fry in 2017 could add, at most 0.18 kg per ha to the fall biomass of pelagic fish other than kokanee fry. Consequently, the Sockeye fry introduction proposed for 2017 would also appear to have little potential to shift pelagic fish biomass sufficiently to generate detectable impacts on the growth of kokanee fry (Figure 2b, this report).

Summary analyses of variations in the total abundance of Okanagan Lake kokanee fry and variations in abundance at subsequent ages (Table 5) indicate there are statistically significant associations between age-0 kokanee and the subsequent abundances of age-1 and age-2 kokanee in Okanagan Lake. However, annual variations in kokanee fry are not significantly associated with annual variations in either the abundance of age-3 kokanee present in the offshore waters of Okanagan Lake or of total numbers of adults spawning in streams and shore locations. The absence of a persistent, significant relationship between age-0 kokanee and subsequent abundance of age-3 kokanee in-lake may be attributable to the lower resolution of acoustic-and-trawl survey methods to reliably estimate the abundance of these larger, older fish. However, low resolution observations cannot account for the absence of a significant association between large variations in age-0 kokanee and subsequent variations in total numbers of spawning adults, the vast majority of which also spawn at age-3 (Askey and Johnston 2013). Thus although annual variations in recruitment of kokanee fry to Okanagan Lake are affected significantly by variations in adult abundance (Figure 3, this report), variations in adult abundance are not significantly influenced by a wide range of variations in fry abundance (i.e. 2 million to 8.4 million). Consequently, there appears to be little scope for the introduction of 750,000 Sockeye fry to influence recruitment of adult kokanee in Okanagan Lake even if Sockeye fry were to have a significant impact on survival of kokanee fry within their first summer of lake rearing.

Similar conclusions would appear to apply to spring Sockeye Salmon introductions to Okanagan Lake of at least 3,500,000 fry which would represent an addition of 141 fry per ha by numbers, an average of 36% of the total fall abundance of all *O. nerka* fry (i.e. Sockeye Salmon plus kokanee) and <6% of the projected fall biomass of all pelagic fish in Okanagan Lake (Table 3, column 7). These values remain below or slightly above the all-year mean values, and far below the maximum values, for Sockeye Salmon fry numbers or biomass introduced into Skaha Lake without evidence of any major impacts on the Skaha Lake food-web or its lake-resident kokanee.

Uncertainties Raised by Studies of Food Webs, Sockeye Salmon, and Kokanee in Other Lakes

Observations from studies of food webs, annual variations in *O. nerka* abundance, and associated changes in *O. nerka* growth, survival, and population trends in two other large British Columbia lakes (Quesnel Lake and Kootenay Lake) are potentially relevant to clarifying whether sockeye fry introductions proposed for Okanagan Lake are likely to have significant impacts on food webs or resident fish in that lake.

Quesnel Lake, like Okanagan Lake, is large (20,700 ha), has a moderately long water resident time (10.8 years), mean growing season concentrations of 3.0 ug of P per liter, a resident kokanee population and, like Okanagan and Skaha lakes, is classified as an oligotrophic lake (Dolighan et al. 2012). However, Quesnel Lake likely has a lower average productivity than either Skaha or Okanagan lakes given that it has a cooler average summer thermal regime, its

production is considered to be strongly P limited (Hume et al. 1996), and it has lower average P values than lakes in the Okanagan. Quesnel Lake food webs also differ from Okanagan Lake in other respects given the absence of mysids, the presence of sympatric populations of both Sockeye and kokanee Salmon, and an abundant population of piscivorous fish that includes Rainbow Trout (*Oncorhynchus mykiss*) and Lake Trout (*Salvelinus malma*) where the latter are absent from Okanagan Lake (Dolighan et al. 2012). Notwithstanding these differences, of principal relevance here are whether observations from Quesnel Lake provide evidence of density dependent growth or survival interactions for fry of Sockeye and kokanee Salmon and, if so, what we may conclude about likely outcomes of potential for interactions between Sockeye Salmon and kokanee fry in Okanagan Lake.

Time series observations from Quesnel Lake indicate that there is no detectable effect of a very wide range of adult escapement (and implicitly of fry abundance) on the size that O. nerka attain as summer fry, but that fall fry size does decrease logarithmically with increasing spawner abundance (P,0.05, r²=0.45; Figure 23A in Dolighan et al. 2012). However, the significance of this negative exponential relation for fall fry depends largely on a single data point where abundance of effective female spawners dropped below 30, 000 fish and subsequent fall fry reached a size of 9-10g. Further inspection of these data indicates that virtually all of the scope for increased growth exists at abundance levels below 50, 000 effective female spawners and that the size of both summer and fall fry is relatively "flat" and unresponsive to changes in fall fry abundance between roughly 7000 to 1, 000, 000 effective female spawners. The latter range of spawners equates to a range of <200 to >4000 frv per ha (estimated from data in Fig. 23 A and B of Dolighan et al. 2012). These authors also provided evidence that the total biomass of older age classes of pelagic kokanee underwent a rapid decline between 2001 and 2002 from 5.3 to 1.9 kg per ha in association with the largest sockeye escapement on record which resulted in total fall fry biomass on the order of 6.5 kg per ha. Total biomass of older age kokanee then returned to 4-5 kg per ha during 2008 and 2009 when sockeye fall fry biomass declined to less than 1 kg per ha. The relevance of these observations to anticipating impacts of Sockeye Salmon fry introductions on Okanagan Lake kokanee are as follows. First, because Okanagan Lake is at least as productive as Quesnel Lake, it is unlikely that the introduction of between 30-140 fall fry sockeye equivalents to Okanagan Lake will influence either kokanee growth or survival as noted earlier in this report. Similarly, the addition of 30-140 Sockeye fall fry equivalents at 5g per capita will add, at most, 0.15-0.70 kg per ha to the biomass of all O. nerka fry in Okanagan Lake. Biomass additions, resulting from Sockeye Salmon fry introductions, when added to the maximum observed biomass of 0.7 kg per ha of kokanee as fall fry (Figure 2a in the current report), results in an estimated range of O. nerka fall fry biomass in Okanagan Lake of between 0.85 and 1.40 kg per ha. This range of fry biomass is close to the crudely determined threshold in Quesnel Lake at which kokanee populations appear to be sustained without impact (i.e. < 1.0 kg per ha) from interspecific competition with wild Sockeye fry and is far below the pelagic fry biomass values suggested to have resulted in kokanee salmon population declines there (i.e. roughly 6.5 kg per ha).

Kootenay Lake provides yet another large lake source of evidence to examine the relative influence of annual variations in *O. nerka* (in this case strictly kokanee) fry recruitment on their own growth and survival or the influence of larger, older age-classes of con-specifics (Bassett et al. 2016). In Kootenay Lake, fall fry weight over a 22 year interval (1992-2013) exhibited no significant associations across a range of abundance variation from 185-817 fry per ha and across a range of pelagic kokanee biomass variations (i.e. sum of age 1, 2 and 3 kokanee) from 3.25-18.59 kg per ha (K. Hyatt, unpublished analysis of observations from Appendix 8 of Bassett et al. 2016). Similarly, fall fry abundance in Kootenay Lake varied in direct proportion to Meadow Creek spawner abundance (y=1.068x - 0.193, $r^2=0.84$, n=23) indicating an absence of density-dependent survival as in-lake fry abundance varied between <5 million fry to >30 million

fry (i.e. 129-848 per ha). However, Bassett et al. did suggest that density dependent growth and survival responses must have occurred at some point in the full life cycle of the 2009 and 2010 kokanee fry cohorts in association with the unusually cool and wet springs that occurred in 2011 and 2012 such that the maturing kokanee declined to their lowest sizes on record during 2011-2012. Subsequent to this, Kootenay Lake kokanee exhibited an unprecedented population crash to only 2 % of their long term average abundance from 1954 to present. Of relevance, Bassett et al. (2016) note this occurred "at some point in the life cycle"; as direct evidence suggests that the density dependent growth and survival reductions did not occur during the first year of life for the 2009 and 2010 kokanee fry cohorts - which exhibited fall fry size and abundance levels well within the all-year ranges observed during the 1992-2013 interval in Kootenay Lake.

The sharp declines in Kootenay Lake kokanee population numbers and total biomass were also observed in Arrow and Okanagan lakes at the same time coincident with back to back years of abnormally cold and wet spring conditions in 2011 and 2012. Bassett et al. (2016) concluded that a common set of regional environmental drivers that were unfavourable to kokanee production in 2011 and 2012 were the likely ultimate source for population declines in these three systems in spite of some basic differences among them (e.g. including relative abundance and identity of predators, fertilized versus unfertilized status, presence or absence of sockeye fry as competitors). Consequently, observations from Kootenay Lake kokanee assessments suggest, as noted earlier with respect to Okanagan and Skaha Lake results, that outcomes of intraspecific and interspecific competitive interactions within or between populations of Sockeye and kokanee Salmon are unlikely to have been controlled by variations in the abundance, growth or survival of age-0 fry across the range of abundance for which observations have been obtained to date.

Decades of detailed observations of interactions among food-webs, age-0 Sockeye Salmon, and kokanee in three Okanagan valley lakes have been considered here to draw inferences about the likelihood of negative impacts of Sockeve fry introductions proposed for Okanagan Lake. Although the weight of evidence from these observations suggests a low likelihood of strong negative impacts, a range of uncertainties remain regarding the ultimate controls on fish production in these lakes. For example, the relatively shallow depths of Osoyoos and Skaha lakes could lead to divergent outcomes for interactions between planktivorous pelagic fish and mysids (Whall and Lasenby 2009, Schoen et al. 2015). Whall and Lasenby (2009) presented limited evidence that production of Mysis sp. in relatively shallow Kalamalka Lake relied to a greater extent on a high level of zooplankton consumption while production of Mysis sp. in the much deeper Okanagan Lake depended to a greater extent on consumption of both phytoplankton and zooplankton as food. These authors concluded that mysids in Okanagan Lake were not consistently feeding at the same trophic level as kokanee indicating that there may have been less competition for food between mysids and kokanee in this lake than previously thought. Schoen et al. (2015) proposed that a lake's depth and thermal structure will influence species interactions such that smaller, shallower lakes will exhibit stronger top-down control than larger deeper systems. From this perspective, Schoen et al. proposed a deep water refuge hypothesis and provided supporting evidence that mysids were more vulnerable to fish (i.e. Lake Trout) predation in shallower water than in extremely deep waters. If this is generally the case, then previous observations that mysids in Skaha Lake are very important in the diet of older age classes of kokanee may not apply to Okanagan Lake. However, limited observations indicate that older, larger (>8 cm fork length) kokanee in Okanagan Lake do utilize mysids as a food source to a larger extent than previously recognized (Askey and Andrusak 2008) which adds to the uncertainty of the role of interspecific competition between mysids and kokanee in controlling populations of the latter. The dual role that mysids obviously play in Osoyoos and Skaha lakes as both competitors and as prey of kokanee and/or Sockeve salmon may differ in

Okanagan Lake. However, the role of mysids in Okanagan Lake cannot be clarified further in the absence of representative, seasonal sampling of mysids and all age and size classes of Okanagan Lake kokanee to quantify the contributions of various classes of biota to mysid and kokanee diets there.

Moore and Schindler (2004) noted that anadromous salmon not only import nutrients to freshwater ecosystems but also export nutrients in association with seaward migrations of salmon smolts that leave freshwater on an annual basis. In a related study, Selbie et al. (2011) provided evidence that introductions of Sockeye salmon fry into Tuya Lake, B. C. resulted in reductions in the availability of key nutrients (N and P) that control epilimnetic production from spring through fall. Further analysis indicated that epilimnial nutrient losses due to export by migrating smolts were minor relative to total epilimnial nutrient loads and so could not account for the magnitude of growing season nutrient losses. These authors concluded that epilimnial nutrient reductions during summer were most likely related to the establishment of a zooplankton eating population of pelagic fish, previously absent in Tuya Lake, and enhanced transport of nutrients from the epilimnion to hypolimnian through sedimentation of fecal matter. Export of nutrients from Okanagan Lake by Sockeye salmon smolts and from its epilimnion in summer through increased fecal sedimentation from incremental additions of pelagic planktivores will occur in association with Sockeye fry introductions should these take place. However, the magnitude of losses from both sources will be expected to scale to the biomass of juvenile Sockeye Salmon during lake rearing and lake exit which, as noted above, is certain to represent a small portion of either the annual nutrient load present at the beginning of the growing season in the epilmnion (Table 1) or the biomass of all pelagic fish (Table 2) mediating nutrient transport within Okanagan Lake.

Summary of Key Evidence for Anticipating Impacts of Hatchery-origin Sockeye Fry Introductions on Okanagan Lake Kokanee and Pelagic Food Webs

- Sockeye fry stocking rates in Skaha Lake during the past 12 years have exceeded the range of values required to anticipate the full range of potential within-lake impacts of Sockeye fry introductions proposed for Okanagan Lake.
- Sockeye Salmon fry and all age groups of kokanee share the same zooplankton taxa as food; consequently, interspecific and intraspecific competitive interactions are potentially a concern.
- More than a decade of bioenergetics, fish population and food-web assessments of outcomes of Sockeye fry introductions to Skaha Lake have been executed with oversight from the Canadian Okanagan Basin Technical Working Group (COBTWG) to inform future introductions to Okanagan Lake (Alexander and Hyatt eds, 2015).

Bioenergetics and Food-web Assessments for Evidence of Impacts

- In lakes that support populations of kokanee, juvenile Sockeye Salmon or mixtures of both, *O. nerka* fry commonly dominate the pelagic fish communities by number (e.g. 65-85% in Osoyoos, Skaha and Okanagan Lakes) but make up a much smaller proportion of the biomass totals of pelagic fish (e.g. only 6.3-7.8% in Skaha and Okanagan lakes).
- The similarity of lake productivities (all are considered oligotrophic, Table 1), zooplankton species composition, age, species, biomass structure and diets of the pelagic fish community in Skaha and Okanagan lakes (Table 2) indicate that, from a bioenergetics perspective, pressure exerted by age-0 fry on their forage base will scale to their biomass representation in their respective pelagic fish communities.

- Bioenergetics analyses based on more than a decade of detailed field observations of current ranges of zooplankton production, pelagic fish abundance and size in Skaha and Osoyoos lakes (McQueen et al. 2014, Hyatt et al. 2018) indicate that larger and older pelagic fish consume >90% of the common zooplankton prey used by all pelagic fish while Sockeye and kokanee fry consistently consume less than 8%. Consequently, there is significant potential for strong competitive interactions between older, larger kokanee and *O. nerka* fry, but little potential for intraspecific or interspecific competition among age-0 fry.
- Introductions of up to 3.5 million Sockeye fry proposed for Okanagan Lake are estimated to comprise incremental additions of a maximum of 5% to the all-year mean of pelagic fish biomass there. Because impacts on the zooplankton forage base will undoubtedly scale to the biomass of introduced Sockeye fry, as revealed by bioenergetics analyses of the role of *O. nerka* fry in Osyoos and Skaha lakes, it is unlikely that the proposed range of sockeye fry introductions to Okanagan Lake will exert a detectable influence on either that lake's foodweb or its pelagic fish.

Fish Population Assessments for Evidence of Impacts

- Demonstrations of statistically significant associations between increasing fish abundance and decreasing growth or survival of various classes of fish (species, age groups, etc.) are generally considered as evidence for the occurrence of competitive interactions within or between species in a given lake community.
- Multi-trophic level assessments of interactions between introduced Sockeye fry, kokanee and food-webs in Skaha Lake have identified minor consequences for kokanee growth and no direct evidence of impacts on kokanee fry survival or Skaha Lake food webs over the 12 year duration of studies there.
- Analysis of decadal-scale data sets from all of the lakes considered in the current report does suggest a frequent, but statistically variable, occurrence of a density dependent growth pattern in fall fry and subsequent yearling size with increases in fry abundance (see Fig. 2a in the current report for Okanagan Lake, Fig. 2.7 in Alexander and Hyatt 2015 for Osoyoos Lake, Fig. 5 of Hume et al. 1996 for Shuswap, Quesnel and Chilko lakes).
- The common form of this fall fry or yearling size to abundance relation is that of a negative exponential relationship such that little, if any, density dependence of fall fry or yearling size occurs across the full range of fry abundance within which Sockeye and kokanee Salmon populations are normally managed, including the kokanee population in Okanagan Lake.
- Density dependent growth compensation may occur in Okanagan Lake kokanee fry, but if so, it appears to exist only at extremely low fry abundance (i.e. < 2.8 million fall fry or <110 per ha, Fig. 2a, this report) associated with critically low population levels of adults (i.e. a system total of fewer than 20,000 versus a system average near 150,000 adult spawners, Fig. 3).
- Current and projected kokanee fry abundances in Okanagan Lake are within the range where much larger, incremental changes in fry abundance (Fig. 2a, this report) or pelagic fish biomass (Fig. 2b, this report) than represented by the proposed Sockeye fry introductions would be required to generate a detectable impact on seasonal growth of kokanee fry or other components of the pelagic fish community.
- There is evidence that recruitment of kokanee fry to the fall of the year exhibits a density dependent association with increasing numbers of spawning adults such that total abundance generally fluctuates between a maximum of 4.6-8.8 million fall fry at escapement levels in excess of 100,000 adults (Fig. 3, this report).

- These observations indicate that kokanee fry are subject to a survival bottleneck somewhere between the egg-incubation and fall fry stages of development but currently available evidence is insufficient to reliably identify whether this is a spawning ground or within lake limitation on fall fry production.
- Despite these observations, there appears to be no strong association between large annual variations in kokanee fall fry numbers and subsequent adult recruitment derived from their fall fry cohorts (Table 5) which may indicate that annual variations in adult kokanee are controlled by additional within lake interactions (e.g. among larger, older age classes of pelagic fish or between pelagic fish and mysids).
- Regardless, given the limited range of incremental abundance (30 per ha) and biomass (0.18 kg per ha) that the proposed Sockeye Salmon fry introduction in 2017 represents relative to existing kokanee fry numbers and pelagic fish biomass already present in Okanagan Lake (200-250 per ha and 9-11 kg per ha, Fig. 2a and 2 b, this report), Sockeye fry are unlikely to exert a detectable impact on critical competitive interactions involving growth or survival of age-0 kokanee even if such interactions currently exist.

Summary of Remaining Uncertainties About Okanagan Lake Kokanee and Pelagic Food Webs

- General production indices suggest that Okanagan, Skaha and Osoyoos all currently qualify as oligotrophic lakes. However, they are not identical and the exact level of production differences among these lakes along with precisely determined differences in the upper limits on their carrying capacities for pelagic fish remain poorly defined.
- The general level of productivity of Okanagan Lake has been variously described as N limited, P limited or N and P co-limited dependent on the particular span of years in which observations of nutrient and phytoplankton dynamics have been considered. Consequently, the true influence of these nutrients or their changing N:P on production and the rapidity with which production state changes may occur in Okanagan Lake given its relatively long water residence time (>50 years) remain uncertain.
- Older age classes of kokanee are likely to represent the principal source of competition for zooplankton prey with age-0 kokanee in Okanagan Lake. However, the magnitude of this potential intraspecific competitive interaction remains uncertain in the absence of reliable observations of: the productivity of key zooplankton taxa serving as prey, seasonal abundance and growth of all ages of kokanee and the seasonal utilization of zooplankton taxa by the various size, age and/or developmental stages of pelagic fish and mysids in Okanagan Lake.
- There is some evidence that the role of *Mysis diluviana* in inducing the dramatic decline of kokanee in the 1980's has been overstated (i.e. they may utilize phytoplankton as food to a greater extent than originally thought, they may serve as a prey source for older kokanee contrary to earlier assumptions). Consequently, the status of *Mysis diluviana* as the principal driver of historic changes in Okanagan Lake kokanee abundance declines in the 1980-1995 interval remains uncertain absent reliable observations of annual rates of zooplankton production and consumption of key zooplankton taxa by the various groups of pelagic predators (i.e. kokanee fry, older kokanee, Lake Whitefish, *Mysis* sp.).
- Several papers as well as theoretical considerations suggest that a lake's size, depth and productivity differences will influence outcomes of fish and food web interactions. To the extent possible, application of results from Osoyoos and especially Skaha Lake to infer impacts of future introductions of Sockeye fry on the Okanagan Lake system have been

scaled to account for these differences. However, differences in production and energy flow among these systems are still imperfectly resolved.

- Current evidence from Okanagan Lake is insufficient to reliably identify whether a bottleneck for survival of Okanagan kokanee is a spawning ground or within-lake limitation on production of fall fry (as per Fig. 3).
- Most of the analyses of decadal-scale, annual observations of relationships within and between pelagic fish and their aquatic food-webs in all lakes considered in the current document implicitly assume that impacts of long-term climate change may be ignored as a driver of nutrient dynamics, lake productivity and fish population dynamics. Although this assumption is likely warranted at a decadal time scale it becomes increasingly suspect as time series observations move ever closer to a centennial time scale.

POTENTIAL IMPACTS DUE TO GENETIC INTROGRESSION AND RESIDUALIZATION

Kokanee, anadromous Sockeye Salmon and residual Sockeye Salmon (non-anadromous offspring of anadromous Sockeye Salmon) are all ecotypes of a single species, *Oncorhynchus nerka* (Ricker 1940). Evolutionarily, anadromous Sockeye Salmon colonize newly-available freshwater habitat and, in some locations, give rise to residual non-migrating individuals and self-sustaining freshwater resident kokanee populations. Just as anadromous Sockeye populations generate residual individuals, kokanee populations can generate anadromous individuals (Nichols et al. 2016) and, potentially, revert to anadromy if they arose recently from landlocked Sockeye Salmon (Godbout et al. 2011). The level of genetic differentiation between sympatric Sockeye Salmon and kokanee populations is variable (Wood et al. 2008); both ecotypes can be maintained in some locations in spite of considerable gene flow between them, presumably as the result of divergent selection (Craig and Foote 2001, Wood et al. 2008). Thus, both genetic differentiation and phenotypic plasticity underlie the ecotypic diversity observed in this species.

Ecotype Formation and Persistence

In salmonids and other organisms, novel phenotypes may arise within a single population through phenotypic plasticity (ecological expansion) that occurs when some individuals within a population become capable of exploiting resources that had been hitherto unavailable (Shedd et al. 2015). Alternately, novel phenotypes may arise through development of a new population or ecotype (ecological speciation) formed as a result of genetic adaptation to exploit newly available resources (i.e. a new niche) that exerts novel natural selection on the pre-existing population. Under these circumstances, the new population is characterized by restricted genetic interchange with the original population as it becomes adapted to utilization of the new resources (Wellborn and Langerhans 2015). In some cases, ecological expansion (individual response within a population) may precede ecological speciation (development of a second population).

According to Wellborn and Langerhans (2015), ecological speciation can be expected to occur when two conditions are met; (i) the presence of more than one environmental niche, each with sufficiently distinct characteristics to drive differential selection for resource exploitation and (ii) sufficient genetic diversity within a population to respond to new selective forces through the process of genetic adaptation. The process of ecotype development and maintenance is not stable and irreversible, especially in the face of environmental change (Wellborn and Langerhans 2015). After initial formation, ecotypes may fail to evolve barriers to mating and thus not develop into highly distinctive populations. Even after divergent populations are

established, they may revert to higher levels of interbreeding or complete panmixia (random interbreeding) if environmental alteration relaxes or alters the selective forces that were responsible for the initial divergence (Wellborn and Langerhans 2015, Taylor et al. 2006).

Okanagan Lake Kokanee Background Information

There is no clear point of distinction (in terms of genetic differentiation) between a single population exhibiting ecological expansion and two populations containing distinctive ecotypes until reproductive isolation is clearly established (Hendry 2009). The Okanagan Lake shore- and stream-spawning kokanee display limited morphological differentiation and are not consistently genetically distinct at neutral genetic loci, but carry distinctive mitochondrial DNA haplotype frequencies and nuclear DNA allele frequencies at some loci of presumed adaptive significance (Taylor et al. 1997, Winans et al. 2003, Lemay and Russello 2015). This indicates that fish arising from the two spawning habitats are not reproductively isolated but instead fall somewhere along a spectrum of differentiation that characterizes the transition of a single population into two separate populations; Okanagan Lake kokanee may be either members of a single population or members of two incipient or developing ecotypes.

Okanagan Lake is a large lake with numerous tributaries and shore spawning locations available to *O. nerka*. The presence of two incipient ecotypes in Okanagan Lake kokanee indicates the existence of some level of ecological opportunity (multiple environmental niches) within the extant Okanagan Lake system, but the low level of genetic differentiation between the two kokanee ecotypes may indicate that these niches are not sufficiently different to drive rapid adaptation and reproductive isolation, or that previous environmental perturbations (e.g. the construction of dams, spawning channels, long-term introduction of Kootenay Lake kokanee, hatchery supplementation of Okanagan kokanee, altered seasonal flow in many regulated streams, introduction of *Mysis diluviana*) have disrupted the process of differentiation between the ecotypes. Alternately, existing genetic diversity within the current kokanee populations may limit the degree of adaptation and reproductive isolation (Wellborn and Langerhans 2015). Thus, the current trajectory of Okanagan Lake kokanee ecotype evolution (stable, increasing or decreasing genetic differentiation) is not known.

Kokanee eyed eggs and fry of Kootenay Lake origin have been transplanted into Okanagan Lake since the 1920s (Andrusak et al. 2000). Kootenay Lake contains genetically diverse kokanee populations in its North and West Arms, including both stream- and shore-spawners (Lemay and Russello 2012). Approximately 1.5 million eggs/fry were transplanted from West Arm Kootenay Lake locations into Okanagan Lake and its' tributaries during the 1920s and 1930s, whereas 2.1 million were transplanted from North Arm Kootenay Lake locations between 1941 and 1951. Between 1970 and 1991, over 2.0 million Kootenay Lake eggs and fry were transplanted into Okanagan Lake and hatchery supplementation of Okanagan Lake Mission Creek kokanee was also undertaken, with over 3.6 million eyed eggs and fry released over two decades (Andrusak et al. 2000).

No assessment of the genetic impacts of the Kootenay Lake transplants or the hatchery supplementation of Okanagan Lake kokanee (primarily the stream-type ecotype) on the Okanagan Lake ecotypes has been made. Kootenay Lake kokanee are genetically distinct from Okanagan Lake kokanee (Iwamoto et al. 2012), indicating that introgression from the Kootenay introductions, to the extent that it occurred, was limited for much of the genome. However, one of the genes (TAP2) with significant allele frequency differentiation between the two Okanagan ecotypes also distinguished Kootenay Lake stream and shore spawners (Frazer and Russello 2013). The shared genetic variants at the TAP2 gene may reflect the shared evolutionary history of Kootenay and Okanagan *O. nerka* populations as suggested by Frazer and Russello

(2013), but it is also possible that the Kootenay Lake kokanee transplants were the source of genetic variation, such as a TAP2 variant, that initiated or facilitated the process of ecotypic differentiation in Okanagan Lake. Ecotypic differentiation arising as recently as the 1920s would certainly be expected to have produced the incipient level of differentiation observed between the Okanagan Lake ecotypes. Alternately, the long-term introductions of Kootenay Lake kokanee into Okanagan Lake may have resulted in little or no introgression into, and little genetic impact on the genetic diversity in, Okanagan Lake kokanee. This would indicate that the Okanagan Lake kokanee possess some resilience to introgression from closely related *O. nerka* individuals, such as Kootenay kokanee and Okanagan Sockeye.

The Canadian Okanagan River Sockeye Salmon population, for which the spawning habitat is the Okanagan River between Skaha and Osoyoos lakes below McIntyre Dam, is the source of brood fish for a hatchery program (McQueen et al. 2013). The nursery lake for this population is Osoyoos Lake (i.e. the fry migrate downstream into Osoyoos Lake for rearing). Osoyoos Lake kokanee also spawn in this portion of the Okanagan River and here the sympatric native kokanee and Sockeye populations maintain genetic differentiation through differences in spawn timing, location, or mate choice (or some combination thereof). Only occasional kokanee-Sockeye hybrids are detected in Okanagan River adult spawner or Osoyoos Lake juvenile samples.

Re-introduction of the hatchery Sockeye Salmon fry into Skaha Lake, which hosts a kokanee population genetically similar to the kokanee of Okanagan Lake, began in 2004. The release site of hatchery fry has been the Okanagan River between Skaha and Okanagan lakes. This portion of the river, commonly referred to as 'Penticton Channel', is highly modified and provides suitable spawning habitat in a limited area surrounding the mouth of the Shingle Creek tributary. All or a large portion of the juvenile Sockeye released from Penticton Channel migrate downstream and rear in Skaha Lake.

Once access to Skaha Lake was available to adult Sockeye Salmon on their return migration (due to high water conditions and McIntyre Dam modification), the introduced Okanagan River Sockeye Salmon returned with high fidelity through Skaha Lake to their release site in Penticton Channel, even though they swam through the natal spawning ground of their parents (downstream of Skaha Lake) to do so. Large numbers of adult Sockeye Salmon gained access to the limited spawning habitat in Penticton Channel and their presence resulted in a rapid increase in hybridization between the ecotypes (Veale and Russello 2016). The proportion of hybrid Sockeye-kokanee genotypes rose from under 5% to 15% among underyearling *O. nerka* in Skaha Lake within 4 years of adult Sockeye Salmon return to the spawning ground release site (Veale and Russello 2016). In 2016, four individuals identified genetically as Sockeye Salmon among 81 adult *O. nerka* carcasses sampled on the spawning grounds were phenotypically (length and age) classified as freshwater resident individuals; likely constituting residual Sockeye Salmon that matured within the Canadian freshwater Okanagan River system (Paul Askey, personal communication).

The evolutionary outcome of the high and rapid level of introgression of Sockeye Salmon genes into the Skaha Lake kokanee population will be established over time; Veale and Russello (2016) suggested that while 'genetic swamping' or complete admixture of Sockeye Salmon into the kokanee population was possible, extinction or loss of the kokanee population was unlikely. The rapid introgression of Sockeye Salmon genes into the Skaha Lake kokanee population, and initial observations of some level of hybrid survival to maturity, are consistent with the suggestion that freshwater resident salmonid populations are particularly susceptible to introgression from intraspecific introductions, likely because of higher fitness of hybrids in freshwater resident populations than in anadromous populations (Utter 2000).

Genetic Impacts of Introductions of Okanagan River Sockeye Salmon Juveniles

A. Impacts on Okanagan Lake Kokanee

There is currently no natural access to Okanagan Lake available for adult Sockeye Salmon although juvenile emigration from the lake is possible. If adult Sockeye Salmon are not provided access to Okanagan Lake upon their return migration, the limited presence of mature Sockeye Salmon individuals in Okanagan Lake (only those that arise through residualism) and multitude of spawning habitats available for use are likely to influence the course and timing of evolutionary outcomes. It is possible, but not certain, that anadromous Sockeye Salmon and one or both kokanee ecotypes would co-exist in Okanagan Lake if Okanagan River Sockeye Salmon were introduced into the lake on an ongoing basis. The closely related Sockeye Salmon and kokanee that co-exist in many large lake systems and maintain some level of genetic and demographic independence typically develop naturally, with the presence of Sockeye Salmon believed to give rise to the subsequent development of kokanee. The genetic outcomes of the re-introduction of Sockeye Salmon into a lake containing closely related kokanee that have undergone incipient ecotypic divergence cannot be reliably predicted as outbreeding of one or both ecotypes of Okanagan kokanee with Okanagan Sockeye Salmon may increase or decrease their fitness (Utter 2001, McClelland and Naish 2007).

A one-time introduction in spring 2017 to Okanagan Lake of 750,000 Sockeye Salmon fry may give rise to residual mature Sockeye Salmon in the Lake in 2020. These Sockeye Salmon would have no natal habitat in the Lake to return to for spawning; they could return to spawning habitats in the vicinity of their release site or to more suitable spawning habitats available elsewhere in the lake. If the Sockeye Salmon spawned successfully, there would be a high probability that some or all of them would hybridize with kokanee using the same spawning habitats. However, the small number of Sockeye Salmon relative to kokanee abundance in the lake, the availability of multiple spawning sites, and the likelihood that most of the Sockeye Salmon and/or hybrid progeny would leave the lake as smolts, would preclude extensive or ongoing interbreeding of Sockeye Salmon and kokanee.

It is not possible to predict the genetic impact of ongoing introductions of between 750,000 to 3.5 million Sockeye Salmon fry for ten years or more on the kokanee ecotypes, but short-term outcomes that seem likely range from negligible (the apparent outcome of ongoing introductions of Kootenay Lake kokanee juveniles) to significant introgression from Sockeye Salmon into one or both kokanee ecotypes (the observed outcome when Okanagan Sockeye Salmon adults gained access to Skaha Lake spawning grounds). The presence of additional genetic diversity from Sockeye Salmon in the total *O. nerka* spawning population of Okanagan Lake could provide the genetic material to allow either further divergence or complete interbreeding of the existing two kokanee ecotypes. Less likely is the possible development of a reproductively isolated novel kokanee ecotype. The long term (evolutionary) outcome of significant introgression of Sockeye Salmon genes into the Okanagan Lake kokanee could affect (increase or decrease) both the number of *O. nerka* ecotypes that are maintained in the Lake and the overall fitness of *O. nerka* in the Lake.

In summary, the process of ecological speciation that gives rise to multiple ecotypes within salmonid fishes likely depends both upon the genetic diversity present and introduced to the original population as well as the number of distinct ecological niches available within the environment to support distinctive ecotypes. *O. nerka* populations frequently contain sufficient diversity to enable ecotype formation and Okanagan Lake may provide multiple niches for utilization by distinctive anadromous and/or resident *O. nerka* ecotypes. Ecotype formation is greatly influenced by environmental conditions and perturbations and is not an irreversible evolutionary process. Hybridization of Sockeye Salmon and kokanee and the introgression of

Sockeye Salmon genes into the existing kokanee populations can be expected to occur if mature Sockeye Salmon are present in Okanagan Lake. The evolutionary outcome of ongoing hybridization resulting from multiyear introductions of Sockeye Salmon fry in terms of the fitness of *O. nerka* within Okanagan Lake, and the number of anadromous and/or resident ecotypes that subsequently develop, cannot be predicted.

B. Impacts on Other Canadian Okanagan River O. nerka Populations

Adult Sockeye Salmon that return from Okanagan River Sockeye Salmon fry released into Okanagan Lake can be expected to attempt to home with fidelity to Okanagan Lake release and rearing sites as they have done in Skaha Lake/Penticton Channel. Flow control structures at the south end of Okanagan Lake from which the Okanagan River drains the lake currently preclude lake access for returning Sockeye Salmon. Sockeye Salmon released in Okanagan Lake may be harvested on their return migration through the Columbia drainage in the United States or Canada (in Skaha and/or Osoyoos lakes). Returning adults not removed by harvest can be expected to aggregate downstream of Okanagan Lake in Penticton Channel. From here, they may disperse downstream into the Skaha Sockeye Salmon - kokanee spawning aggregate near the Shingle Creek inlet in Penticton Channel. Additional Sockeye Salmon spawning in this location would likely increase the rate of introgression of Sockeye Salmon genes into the Skaha Lake kokanee population. Some obstructed fish may travel further downstream through Skaha Lake into the Okanagan River between Skaha and Osoyoos lakes. In this river portion, the Sockeye Salmon would be expected to interbreed with the Okanagan River Sockeye Salmon population from which their parents originated, with minimal genetic consequences, as the hatchery fish are genetically diverse and not highly domesticated (McQueen et al. 2013, Veale and Russello 2016).

POTENTIAL FOR PATHOGEN TRANSFERS OR RANGE EXPANSION

The Okanagan Nation Alliance (ONA) conducted a 3-year disease risk assessment from 2000-2002 as part of the 12-year experimental re-introduction of Sockeye Salmon (*Onchorynchus nerka*) into Skaha Lake (Evelyn and Lawrence 2003). The risk assessment focused on the likelihood of introducing new or extending the range of known pathogens, and specifically identified five pathogens to be concerned with in the re-introduction program. The five pathogens investigated were: infectious pancreatic necrosis virus (IPNV), infectious hematopoietic necrosis virus IHNV, erythrocytic inclusion body virus (EIBV), *Myxobolus cerebralis*, and *Ceratomyxa shasta*. To assess pathogen translocation potential through Sockeye Salmon re-introduction, fish captured above Okanagan Falls Dam and below McIntyre Dam were analyzed for each of the five pathogens annually over the 3 year risk assessment period. At the completion of the analysis, it was determined that fish populations above and below locations of high population abundance of anadromous Sockeye Salmon did not differ with respect to the five pathogens, and thus it was concluded that the transfer of disease agents of concern posed a low risk of introduction into Skaha Lake (Kieser & Harrower 2003).

As Skaha Lake and Okanagan Lake are hydrographically connected, and likely shared historical exchanges between fish populations given the absence of any substantive hydraulic barriers following deglaciation of the Okanagan valley, it would be expected that these lakes would also be equivalent in pathogen diversity and occurrence. Consequently, the results of Kieser and Harrower (2003) are of direct relevance in evaluating potential pathogen impacts due to the introduction of Sockeye Salmon fry to Okanagan Lake. Nevertheless it's important to acknowledge that the scope of Kieser and Harrower's assessment considered introductions of both Sockeye Salmon fry and adult life stages to Skaha Lake. Thus the discussion below focuses solely on the introduction of Sockeye Salmon fry and the potential of introducing new or extending the range of known pathogens into Okanagan Lake.

In terms of pathogen risk due specifically to Sockeye Salmon fry introductions, viruses such as IHNV and IPNV are of concern due to their capacity to be transmitted vertically (mother-to-child infection) and cause disease in fry. Currently IPNV is not known to exist in British Columbia, but has been detected in Washington State, and would be considered a new pathogen introduction to the Okanagan watershed. Conversely, IHNV is present throughout the Okanagan watershed yet introduction of a non-native strain would be of concern. Consequently, to mitigate the risk of virus diseases in Sockeye Salmon fry, the Okanagan Nation Hatchery implements egg collection and disinfection procedures based on avoidance and containment practices, as prescribed in the Alaska Sockeye Salmon Culture Manual (McDaniel et al. 1994). Since the inception of the hatchery enhancement of Okanagan Sockeye Salmon, annual diagnostic testing of fry for virus infection has confirmed the absence of IHNV, IPNV, or any other cell culture replicating agent. Additionally, it is noteworthy that the lack of IHNV infection of hatchery fry resulted despite high prevalence of IHNV (upwards of 85%) in adult broodstock, further supporting the effectiveness of the hatchery egg disinfection procedures.

As part of the experimental re-introduction of Sockeye Salmon into Skaha Lake, fish health screening conducted on spawning adult Okanagan Sockeye Salmon revealed the presence of the myxosporean parasite *Parvicapsula minibicornis*. The parasite was first described in Fraser river Sockeye Salmon (Kent et al. 1997) where it has been associated with significant pre-spawning mortalities (Raverty et al. 2000, Bradford et al. 2010). It is not known whether the parasite occurs in fish above McIntyre Dam. However, it is known that this parasite is not transmitted via salmonid eggs and therefore is of minimal risk of spreading through the introduction of Sockeye Salmon fry. Moreover, this parasitic infection occurs only when fish are exposed to infectious stages of the parasite that are released from certain polychaete worms found in specific benthic zones not present in a hatchery environment. Similarly the parasitic pathogens *Myxobolus cerebralis* and *Ceratomyxa shasta* are of low risk of being introduced with Sockeye Salmon fry as they too are not transmitted through eggs, and infectious stages of the parasite require a polychaete worm host.

As an additional determinate of health status of hatchery Sockeye Salmon, consideration should be given towards the requirements of the Fish Stocking Aquaculture License issued under the authority of the *Fisheries Act*. Currently, Okanagan Nation Aquatic Enterprises Ltd holds a valid aquaculture license for the cultivation of Sockeye Salmon at the ONA hatchery located in Penticton, BC. In order to comply with license requirements, the hatchery must notify their Fish Health Veterinarian (FHV) immediately if there is suspicion or evidence of a fish health event and/or mortality event. Further if the disease suspected is among those listed by the National Aquatic Animal Health Program, it is required under the Health of Animals Act to inform the Canadian Food Inspection Agency. On suspicion of infectious disease, surveillance must be increased, the FHV consulted and samples must be submitted to a FHV-approved diagnostic laboratory for diagnosis if required. Additionally, if fish are to be transferred, the stock to be moved must not show any signs of clinical disease and if mortalities have occurred, they must not exceed 1% per day due to any infectious diseases, for any four consecutive day period during the rearing period. Lastly, fish can also not be transferred if any of the hatchery fish stock is known to have had any of the following diseases:

- Infectious Hematopoietic Necrosis (IHN) (causative agent: Infectious hematopoietic necrosis virus (rhabdovirus)
- Infectious Pancreatic Necrosis (IPN) (causative agent: Infectious pancreatic necrosis virus (birnavirus)
- Viral Hemorrhagic Septicemia (VHS) European Strain (causative agent: Viral hemorrhagic septicemia virus (rhabdovirus)

- Infectious Salmon Anemia (ISA) (causative agent: Infectious salmon anemia virus (orthomyxovirus)
- Oncorhynchus masou Virus Disease (OMV) (causative agent: Oncorhynchus masou virus (herpes virus)
- Any filterable agent causing cytopathic effects in tissue culture other than the above.
- Whirling disease (causative agent: *Myxobolus cerebralis*)
- Cold Water Vibriosis (Hitra disease) (causative agent: *Vibrio salmonicida*)

Therefore by complying with license conditions, multiple safeguards have been established to mitigate risk of disease in hatchery origin Sockeye Salmon fry. Collectively, these measures along with rigorous egg collection and disinfection procedures implemented by the hatchery, minimize the risk that the proposed introduction of Sockeye Salmon fry into Okanagan Lake would introduce new or extend the range of known pathogens to fish in this portion of the Okanagan basin. Overall, the introduction of 750,000 fry (spring 2017) or ongoing introductions of between 350,000 to 3.5 million fry (i.e. annually from 2017-2026) hatchery origin Sockeye Salmon fry into Okanagan Lake is of low risk of spreading new or extending the range of known pathogens to this portion of the watershed.

4. SOURCES OF UNCERTAINTY

Based on the information provided above, the potential impacts of the proposed introduction of hatchery-origin Sockeye Salmon fry on the food-webs and resident fish populations of Okanagan Lake are not anticipated to be either immediate (i.e. occur in association with a single year of fry introduction) or of large magnitude. However, uncertainties regarding the ultimate impact of a multi-year series of Sockeye Salmon fry introductions remain. These include:

- Identification of the upper limit to the carrying capacity of Okanagan Lake for the production of pelagic fish.
- The actual rates of growth and survival of Sockeye Salmon fry following introduction and the subsequent magnitude of smolt and anadromous adult salmon production from Okanagan Lake.
- The actual range of annual production of residual adult Sockeye Salmon that would be derived from a given abundance of introduced Sockeye Salmon fry.
- The location(s) of preferred spawning sites that residual Sockeye Salmon adults would come to occupy among those currently available in the Okanagan Lake system and the level of interbreeding and genetic introgression with kokanee ecotypes that would emerge as a consequence.

The complex interaction of additional factors that will continue to control production variations of the two kokanee ecotypes in the Okanagan Lake system with or without introductions of Sockeye Salmon fry remain largely unresolved including:

- The role of *Mysis* in influencing historic to current recruitment success of Okanagan kokanee given new evidence that they are part of a trophic triangle in which they function as both potential competitors and as potential food sources for various size and age classes of kokanee in Okanagan Lake.
- The extent to which the older, larger classes of pelagic fish may control growth and survival of kokanee fry in Okanagan Lake.

- The extent to which pelagic fish and *Mysis* in Okanagan Lake control population and production levels of their zooplankton prey and whether this results in outcomes such that growth and survival of kokanee fry are acutely food limited.
- The origins of the two Okanagan Lake kokanee ecotypes, their current levels of reproductive isolation, and the status of these ecotypes as either a single interbreeding population exhibiting phenotypic divergence or as two separate populations that could be either genetically diverging or converging.
- The extent to which the current abundance of the larger-bodied, stream spawning ecotype of kokanee is controlled by historic to recent stream habitat alterations.

5. CONCLUSIONS

Introductions of a proposed range of between 750 000 and 3.5 million hatchery-origin Sockeye Salmon fry into Okanagan Lake represent relatively small incremental additions to either the average numbers of pelagic kokanee fry or biomass of other pelagic fish currently present in Okanagan Lake. However, as noted above, there are several uncertainties associated with the potential impacts should the introductions continue beyond a single year.

Key potential risks of the proposed action include genetic introgression with the kokanee stream-spawners and potential hybridization. The potential for disease transfer, or food web interactions (i.e. phytoplankton and zooplankton), or impacts to sensitive aquatic biota (all ages and size classes of pelagic fish within Okanagan Lake). is currently considered low based on available information. However, cumulative impacts that may potentially exacerbate the current limiting factors for kokanee populations in Okanagan Lake have not been explored for this review.

Sockeye Salmon fry stocking rates for which detailed monitoring and evaluation have been carried out at Skaha Lake have already exceeded the range of values of Sockeye Salmon fry introductions proposed for Okanagan Lake. Examination of the potential impact of this range of Sockeye Salmon fry additions within the context of existing annual variations in Okanagan Lake kokanee fry abundance and growth; or fry survival and recruitment of mature kokanee; indicates that Sockeye Salmon fry introductions are unlikely to have major ecological impacts on resident kokanee or the pelagic fish community.

Examples from similar lake systems in British Columbia do not provide specific evidence of density dependent growth or survival across the range of fry abundance variation within which these populations are normally managed; these results may illustrate stochastic effects that may warrant further consideration.

Hybridization of Sockeye Salmon and kokanee, and the introgression of Sockeye Salmon genes into the existing kokanee populations can be expected to occur if mature Sockeye Salmon are present in Okanagan Lake. Because anadromous adult Sockeye Salmon will not have access to Okanagan Lake, genetic introgression would depend on interbreeding between residual adult Sockeye Salmon (that may originate from introduced Sockeye fry) and adults of the two Okanagan Lake kokanee ecotypes.

The process of ecotype development and maintenance is not always stable and irreversible, especially in the face of environmental change. Okanagan Lake has experienced extensive environmental perturbation over the past 100 years and the evolutionary trajectory of the stream and shore spawning kokanee ecotypes (stable, increasing or decreasing genetic differentiation) is not known.

Genetically distinctive kokanee eggs and fry from another Upper Columbia River lake (Kootenay Lake) were repeatedly transplanted into Okanagan Lake between 1920 and 1991, but little or no genetic introgression of Kootenay kokanee genes into Okanagan Lake kokanee has been observed in limited genetic analysis of recent samples of Okanagan Lake kokanee. In contrast, the recent re-introduction of the hatchery-reared Sockeye Salmon into Skaha Lake, which hosts a kokanee population genetically similar to the kokanee of Okanagan Lake, resulted in a rapid increase in hybridization between the Sockeye and kokanee ecotypes. The high level of Sockeye introgression into the resident Skaha Lake kokanee population will likely result initially in complete genetic admixture of the two populations in Skaha Lake kokanee, although the longterm evolutionary outcome on the two ecotypes is unknown (Veale and Russello 2016).

The contrasting genetic outcomes observed from the introduction of Kootenay Lake kokanee into Okanagan Lake on native kokanee (little or no genetic introgression) and Okanagan River Sockeye Salmon into Skaha Lake on native kokanee (extensive introgression) indicates that Okanagan Lake kokanee may show some resilience, but are likely not immune, to introgression from related Upper Columbia drainage Sockeye Salmon populations. Little genetic impact on the kokanee populations, including ecotype formation and persistence or degradation, would be expected to result from a one-time introduction of 750,000 Okanagan Sockeye fry to the lake, given the apparently limited impact of repeated Meadow Creek kokanee introductions.

The ongoing release of between 0.75 and 3.5 million Okanagan Sockeye fry would be expected to result in hybridization between residual Sockeye and kokanee in Okanagan Lake, given the observed hybridization between Sockeye and kokanee in Penticton channel (Skaha Lake population). The level of introgression from Sockeye into the kokanee population(s) that would ultimately result and the number of *O. nerka* ecotypes that would develop and persist in Okanagan Lake cannot be predicted.

The introduction of 750,000 fry (spring 2017) or ongoing introductions of between 350,000 to 3.5 million (i.e. annually from 2017-2026) hatchery-origin Sockeye Salmon fry into Okanagan Lake is of low risk of spreading new or extending the range of known pathogens to this portion of the watershed.

The Okanagan Nation Alliance (ONA) conducted a 3-year disease risk assessment from 2000-2002 as part of the 12-year experimental re-introduction of Sockeye Salmon (*Onchorynchus nerka*) into Skaha Lake (Evelyn and Lawrence 2003). At the completion of the analysis, it was determined that fish populations above and below locations of high population abundance of anadromous Sockeye Salmon did not differ with respect to the five pathogens and thus it was concluded that the transfer of disease agents of concern posed a low risk of introduction into Skaha Lake from the transfer of either fry or adults.

Since the inception of the hatchery enhancement of Okanagan Sockeye Salmon, annual diagnostic testing of fry for virus infection have revealed the absence of IHNV, IPNV, or any other cell culture replicating agent. The lack of IHNV infection of hatchery fry resulted despite high prevalence of IHNV (upwards of 85%) in adult broodstock.

Fish Stocking Aquaculture License requirements, coupled with rigorous egg collection and disinfection procedures implemented by the hatchery, minimize the risk that the proposed introduction of Sockeye Salmon fry into Okanagan Lake would introduce new or extend the range of known pathogens to fish in this portion of the Okanagan basin. Overall, the introduction of 750,000 fry (spring 2017) or ongoing introductions of between 350,000 to 3.5 million (i.e. annually from 2017-2026) hatchery-origin, Sockeye Salmon fry into Okanagan Lake

is of low risk of spreading new or extending the range of known pathogens to this portion of the watershed.

A monitoring and evaluation program that provides valuable information, and ensures early detection and mitigation of potential impacts, would help form the basis for a rigorous adaptive management approach to the potential introduction of Sockeye Salmon fry into Okanagan Lake. It is possible that the current monitoring and evaluation program for Skaha Lake can be supplemented with new elements to provide information to either verify or revise projections of Sockeye Salmon impacts on the Okanagan Lake food-web and its resident fish.

6. TABLES

Table 1. Comparison of mean values of potential "production parameters" for Osoyoos, Skaha and Okanagan lakes.

Osoyoos

Value	Depth (m)	Water residence time (yrs)	Total P in June	Mean of summer Chl-a (ug/L)	Secchi depth (m)	Cladocera (#/m²)	<i>Mysis</i> sp. (all year summer mean density)	Data Source
Mean	14.0	<1	10.0	3.26	3.19	1,980	173	Hyatt et al. 2015a
Range	0-63	-	7.0 - 14.0	1.1 - 5.4	1.0-4.4	960-2640	132-223	-
n	na	-	5	30	30	90	8 yrs*	-

Skaha

Value	Depth (m)	Water residence time (yrs)	Total P in June	Mean of summer Chl-a (ug/L)	Secchi depth (m)	Cladocera (#/m²)	<i>Mysis</i> sp. (all year summer mean density)	Data Source
Mean	26.0	<1	7.7	1.81	5.33	1,990	99	Hyatt et al. 2015b
Range	0-57	-	6.0-9.6	0.7 - 3.6	2.3-7.3	1790-2530	69-176	-
n	na	-	5	30	64	93	9 yrs	-

Okanagan

Value	Depth (m)	Water residence time (yrs)	Total P in June	Mean of summer Chl-a (ug/L)	Secchi depth (m)	Cladocera (#/m²)	<i>Mysis</i> sp. (all year summer mean density)	Data Source
Mean	75.0	>60	6.0	2.5	6.86	1,333	360	Andrusak et al. 2008,
Range	0-242	-	2.0-12.0	1.2 - 5.7	3.5-10.7	666-2000	257-552	BC-MOE January 2006
n	na	-	11	na	61	na	9 yrs	-

*Note: 2011 *Mysis* abundance has been excluded from the Osoyoos Lake summary due to the 2010 Testalinden slide which caused a recruitment failure in 2011. Total abundance for *Mysis* in 2011 reached only 27 animals/m² (Hyatt et al. 2018).

Table 2. Contributions of sockeye and kokanee age-0 "nerkids" to pelagic fish communities of subject lakes as either proportion by (a) numbers or (b) weight.

a) Contribution by #s

	Lake Years	Pelagic fish: x#/ha	Range	% Age 0	Range	% Age > 0	Range	n	Source
Osoyoos	2005-2013	3,811	1300-8500	88.0	68-100	12.0	0.2-32	9	2018.
Skaha	2005-2013	424	198-618	66.5	54-87	33.5	13-46	9	Hyatt et al 2015b. Andrusak et al. 2008, BC-
Okanagan	1988-2010	358	125-548	65.0	57-83	35.0	17-51	23	FLNRO.

(b) Contribution by weight

	Lake Years	Pelagic fish: x kg/ha	Range	% Age 0	Range	% Age > 0	Range	n	Source
Osoyoos	2005-2013	26.00	13.5-43.5	33.6	12.0-51.7	66.4	48.3- 88.0 85.5-	9	Ayatt et al 2015a, Ayatt et al. 2018.
Skaha	2005-2013	20.2	14.6-24.2	7.8	3.4-14.5	92.2	96.6 85.0-	9	Hyatt et al 2015b. Andrusak et al. 2008. BC-
Okanagan	1988-2010	8.99	2.8-21.3	6.31	3.2-15.4	93.7	97.0	23	FLNRO.

# hatchery Sockeye fry	#/ha	Est. spring mean hatchery fry biomass (hg/ha)	Est. fall mean hatchery fry biomass (hg/ha)	Low end of range (kg/ha)	High end of range (kg/ha)	Fall Sockeye fry biomass as % of mean of all OKL pelagics	Fall Sockeye fry biomass as % mean numbers of all nerkid fry
5.000	0.2	0.000	0.00	0.00	0.00	0.01	0.08
10,000	0.4	0.001	0.00	0.00	0.00	0.01	0.15
20.000	0.8	0.001	0.00	0.00	0.00	0.03	0.31
40,000	1.6	0.002	0.01	0.00	0.01	0.06	0.61
100.000	4.0	0.006	0.01	0.01	0.02	0.14	1.51
200.000	8.1	0.011	0.03	0.02	0.04	0.29	2.98
400,000	16.1	0.023	0.05	0.04	0.09	0.57	5.79
750.000	30.2	0.042	0.10	0.07	0.16	1.08	10.34
1,500,000	60.4	0.085	0.19	0.14	0.33	2.15	18.74
3.000.000	120.8	0.169	0.39	0.28	0.65	4.30	31.56
3,500,000	140.9	0.198	0.45	0.33	0.76	5.01	38.86

Table 3. Potential contributions of hatchery origin sockeye fry by numbers and as a proportion of the average biomass of all pelagic fish in Okanagan Lake across a range of hatchery fry stocking levels.

Assumes hatchery-origin fry are the same weight (mean=1.49 g) as hatchery fry introduced into Skaha Lake.
 Assumes sockeye fry weigh 1.49 g at introduction and then grow to mean of 3.2g as at Skaha by Sept census.

Note 3.2 g is the mean of 9 years of observations at Skaha where growth rates are likely faster than in Okanagan L.

³ Applies observed mean abundance of age-0 kokanee pop. in Ok-lake of 262 per ha over past 23 years.

Lake Year	Hatchery Sockeye fry at intro (#/ha)	Hatchery Sockeye fry at intro (kg/ha)	Sockeye fall fry (#/ha)	Sockeye fall fry (kg/ha)	Kokanee fall fry (#/ha)	Kokanee fall fry (kg/ha)	Total Age- 0 fall fry (#/ha)	Total Age- 0 fall fry (kg/ha)	Sockeye fry as % of total fall fry
2004	622	0.62	301	2.38	99	0.56	400	2.94	75.25
2005	709	1.49	100	0.41	148	0.27	248	0.68	40.32
2006	761	1.29	154	1.00	112	0.20	266	1.20	57.89
2007	457	0.78	41	0.22	115	0.22	156	0.44	26.28
2008	827	0.91	152	0.81	318	0.64	470	1.44	32.34
2009	231	0.39	88	0.47	85	0.16	173	0.63	50.87
2010	462	0.51	203	0.91	225	0.27	428	1.18	47.43
2011	0	0	634	1.97	166	0.17	800	2.13	79.25
2012	0	0	33	0.16	261	0.55	294	0.70	11.22
Ave	-	0.86	190	0.92	170	0.34	359	1.26	46.76

Table 4. Contributions of hatchery origin Sockeye Salmon by numbers and as proportion of all age-0 nerkids in Skaha Lake by lake-year.

Table 5. Summary of associations between annual variations in age-0 kokanee abundance and their observed abundance at subsequent ages in either Okanagan Lake or as total adults in terminal spawning areas. Values for age 0-3 kokanee abundances are expressed in millions while those of adult spawners are in thousands.

Sibling Associations	r ²	р	n
age-1 = 0.28 (age-0) + 0.02	0.68	<0.01	23
age-2 = 0.22 (age-0) - 0.05	0.44	<0.05	23
age-3 = 21.03 (age-0) + 116.96	0.03	n.s.	20
spawners = 7.13 (age-0) + 99.80	0.04	n.s.	23



Figure 2. Relationships between fall size (g wet wt) of kokanee fry in Okanagan Lake and (a) total abundance of kokanee fry (numbers per ha) or (b) biomass of all kokanee older than age-0. Data include fall fry production from brood years 1988-2013 inclusive (BC-FLNRO data courtesy of Tara White and Tyler Weir). Circular points indicate values expected by the fall of 2017 based on projections of fall fry abundance in panel a, derived from data in Figure 3, and fall biomass in panel b, based on the 2001-2010 average abundance of age 1-3 kokanee vs their biomass (data not shown).



Figure 3. Total number of kokanee fry present in Okanagan Lake in the fall of year n+1 as a function of the total number of spawning adults in the fall of year n. The circular data point represents the number of kokanee fry expected to be present in the fall of 2017 based on a total of 127,849 adult kokanee observed spawning in streams and on beaches of the Okanagan Lake system in the fall of 2016. Data include fall fry production from brood years 1988-2013 inclusive (BC-FLNRO data courtesy of Tara White and Tyler Weir).

6.REFERENCES CITED

- Alexander, C. A. D. and K. D. Hyatt (eds) 2015. Proceedings of the Peer Review Workshop for the Okanagan Sockeye Re-introduction Experiment, Final Draft. Summary report to the Okanagan Nation Alliance and Canadian Okanagan Basin Technical Working Group. 125 p. Available from the Okanagan Nation Alliance, 101-3535 Old Okanagan Highway, Westbank, B. C. V4T 3L7.
- Andrusak, H., D. Sebastian, I. McGregor, S. Matthews, D. Smith, K. Ashley, S. Pollard, G. Scholten, J. Stockner, P. Ward, R. Kirk, D. Lasenby, J. Webster, J. Whall, G. Wilson and H. Yassien. 2000. Okanagan Lake action plan year 4 (1999) report. Province of British Columbia, Fisheries Project Report No. 83.
- Andrusak, H., S. Matthews, I. McGregor, K. Ashley, G. Wilson, L. Vidmanic, J. Stockner, D. Sebastian, G. Scholten, P. Woodruff, D. Cassidy, J. Webster, M. Gaboury, P. Slaney, G. Lawrence, W. K. Oldham, B. Janz and J. Mitchell. 2002. Okanagan Lake Action Plan report for year 7 (2003). Province of British Columbia, Fisheries Project Report No. 106. Fisheries Management Branch, Ministry of Water, Land and Air Protection, Province of British Columbia.
- Andrusak, H., S. Maththews, I. McGregor, K. Ashley, R. Rae, A. Wilson, D. Sebastian, G. Scholten, P. Woodruff, D. L. Vidmanic, J. Stockner, G. Wilson, B. Janz, J. Webster, H. Wright, C. Walters and J. Korman 2004. Okanagan Lake Action Plan Year 8 (2003) Report. Province of British Columbia, Fisheries Project Report No. 108. Fisheries Management Branch, Ministry of Water Land and Air Protection, Province of British Columbia.
- Andrusak, H., S. Matthews, A. Wilson, G. Andrusak, J. Webster, D. Sebastain, G. Scholten, P. Woodruff, R. Rae, L. Vidmanic, J. Stockner 2006. Okanagan Lake Action Plan Year 10 (2005) Report. Province of British Columbia, Fisheries Project Report No. 115. Ecosystems Branch, Ministry of Environment, Province of British Columbia.
- Andrusak, H., G. Andrusak, S. Matthews, A. Wilson, T. White, P. Askey, D. Sebastain, G. Scholten, P. Woodruff, J. Webster, L. Vidmanic, J. Stockner 2008. Okanagan Lake Action Plan Years 11 (2006) and 12 (2007) Report. Province of British Columbia, Fisheries Project Report No. 123, Ecosystems Branch, Ministry of Environment, Province of British Columbia.
- Ashley, K. I., B. Shepherd, D. Sebastian, S. Mattews, L. Vidmanic, P. Ward, H. Yassien, L. McEachern, H. Andrusak, D. Lasenby, J. Quirt, J. Whall, E. Tayloer, A. Kuiper, P. M. Troffe, C. Wong, G. Scholten, M. Zimmerman, P. Epp, V. Jensen, and R. Finnegan. 1999. Okanagan Lake Action Plan Year 3 (1998-99) Report. Province of British Columbia, Fisheries Project Report No. 78. Fisheries Management Branch, Ministry of Fisheries, Province of British Columbia.
- Askey, P. and H. Andrusak. 2008. Okanagan Lake kokanee food habits- Do mysids (*Mysis relicta*) contribute to the kokanee diet. Pp 237-246 in Andrusak, H., G. Andrusak, S. Matthews, A. Wilson, T. White, P. Askey, D. Sebastain, G. Scholten, P. Woodruff, J. Webster, L. Vidmanic, J. Stockner 2008. Okanagan Lake Action Plan Years 11 (2006) and 12 (2007) Report. Province of British Columbia, Fisheries Project Report No. 123, Ecosystems Branch, Ministry of Environment, Province of British Columbia.

- Askey, P.J. and Johnston, N.T., 2013. Self-regulation of the Okanagan Lake kokanee recreational fishery: Dynamic angler effort response to varying fish abundance and productivity. *North American Journal of Fisheries Management*, 33(5), pp.926-939.
- Askey, P.J., 2016. Managing Dynamic Fisheries with Static Regulations: an Assessment of Size-Graded Bag Limits for Recreational Kokanee Fisheries. *North American Journal of Fisheries Management*, *36*(2), pp.241-253.
- Bassett, M., E. U. Schindler, D. Johner, T. Weir, D. Sebastian, L. Vidmanic and K. I. Ashley. 2016. Kootenay Lake restoration program year 22 (North Arm) and year 10 (South Arm) (2013) report. Fisheries Project Report No. RD. 149.
- Beauchamp, D. A., M. G. Larivierre and G. L. Thomas. 1995. Evaluation of competition and predation as limits to juvenile kokanee and Sockeye Salmon production in Lake Ozette, Washington. N. Am. J. Fish. Manage, 15:193-207, DOI:10.1577/1548-8675(1995)015<0193:EOCAPA>2.3.CO:2
- Bouchard, R. and D. I. D. Kennedy. 1975. Utilization of fish by the Colville Indian people. Unpublished Ms of the British Columbia Indian Language Project, Victoria, B. C.
- Bradford, M. J., J. Lovy, D. A. Patterson, D. G. Speare, W. R. Bennett, A. R. Stobbart, and C. P. Tovey. 2010. *Parvicapsula minibicornis* infections in gill and kidney and the premature mortality of adult sockeye salmon (*Oncorhynchus nerka*) from Cultus Lake, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, 2010, 67(4): 673-683. (Accessed January 15, 2018)
- Burgner, R. L. 1991. urg, University of British Columbia Press, Vancouver.
- Carlson, R. E. 1977. A trophic state index for lakes. Limnol. Oceanogr. 22:361-369.
- Craig, J.K. and C.J. Foote. 2001. Countergradient variation and secondary sexual color: phenotypic convergence promotes genetic divergence in carotenoid use between sympatric anadromous and nonanadromous morphs of sockeye salmon (*Oncorhynchus nerka*). Evolution 55: 380-391.
- Dolighan, R. B., T. Weir, D. Sebastian, J. Hume and K. Shortreed. 2012. Interactions between sockeye salmon, kokanee and piscivorous rainbow trout populations in Quesnel Lake, British Columbia. Stock Management Report No. 39. Province of British Columbia.
- Evelyn, T. and S. Lawrence. 2003. OBJECTIVE 1 Disease Risk Assessment. Contribution No. 1 to an evaluation of an experimental re-introduction of sockeye salmon into Skaha Lake year 3 of 3. Presented to Colville Confederated Tribes. 78 pp.
- Frazer, KK, and Russello, MA. 2013. Lack of parallel genetic patterns underlying the repeated ecological divergence of beach and stream-spawning Kokanee salmon. Journal of Evolutionary Biology 26: 2606–2621.
- Fryer, J. K. 1995. Columbia Basin Sockeye Salmon: Causes of their past declines, factors contributing to their present low abundance, and future outlook. PhD Thesis, University of Washington, Seattle.
- Godbout, L., C.C. Wood, R.E. Withler, S. Latham, R.J. Nelson, L. Wetzel, R. Barnett-Johnson, M.J. Grove, A.K. Schmitt and K.D. McKeegan. 2011. Sockeye Salmon (*Oncorhynchus nerka*) return after an absence of nearly 90 years: A case of reversion to anadromy. Canadian Journal of Fisheries and Aquatic Sciences 68: 1590–1602.
- Hendry, A.P. 2009. Ecological speciation! Or the lack thereof? Can. J. Fish. Aquat. Sci. 66: 1383–1398.

- Hume, J. M. B., K. S. Shortreed and K. Morton. 1996. Juvenile sockeye rearing capacity of three lakes in the Fraser River system. Can. J. Fish. Aquat. Sci. 53:719-733.
- Hyatt, K.D., and Stockner, J.G. 1985. Responses of sockeye salmon (*Oncorhynchus nerka*) to fertilization of British Columbia coastal lakes. Can. J. Fish. Aquat. Sci. **42**: 320–331.
- Hyatt K. D. and D. P. Rankin. 1999. A habitat based evaluation of Okanagan Sockeye Salmon objectives. PSARC Working Paper S99-18. Canada Department of Fisheries and Oceans, Pacific Science Advisory Review Committee, Pacific Biological Station, Nanaimo, BC.
- Hyatt, Kim D., Margot M. Stockwell and D. Paul Rankin. 2003. Impact and adaptation responses of Okanagan River Sockeye Salmon (*Oncorhynchus nerka*) to climate variation and change effects during freshwater migration: Stock restoration and fisheries management implications. Can. Water Res. Journal 28: 689-711.
- Hyatt, K. D., D. J.McQueen, K. S. Shortreed and D. P. Rankin.2004. Sockeye salmon (*Oncorhynchus nerka*) nursery lake fertilization. Review and summary of results. Environ. Rev. 12:133-162.
- Hyatt, Kim D., Charles Ramcharan, Donald J. McQueen and Karen L. Cooper. 2005. Trophic triangles and competition among vertebrate (*Oncorhynchus nerka, Gasterosteus aculeatus*) and invertebrate (*NeoMysis mercedis*) planktivores in Muriel Lake, British Columbia, Canada. Ecoscience 12(1): 11-26.
- Hyatt, K. D., D. J. McQueen, D. P. Rankin, and E. Demers. 2011. Density dependent growth in juvenile sockeye salmon (*Oncorhynchus nerka*). Open Fish Sci. J. 4:49-61
- Hyatt, K. D., D. J. McQueen, D. P. Rankin, M. M. Stockwell, H. Wright, S. Lawrence and A. Stevens. 2015a. Methods and summary data for limnology and food-web structure in Osoyoos Lake, B. C. (2005-2013). Can. Dat. Rep. Fish. Aquat. Sci. No. 1258, 71p.
- Hyatt, K. D., D. J. McQueen, D. P. Rankin, M. M. Stockwell, H. Wright, S. Lawrence and A. Stevens. 2015b. Methods and summary data for limnology and food-web structure in Skaha Lake, B. C. (2005-2013). Can. Dat. Rep. Fish. Aquat. Sci. No. 1259, 76p.
- Hyatt, K. D., D. J. McQueen, A. D. Ogden 2018. Have invasive mysids (*Mysis diluviana*) altered the capacity of Osoyoos Lake to produce Sockeye Salmon (*Oncorhynchus nerka*)? Open Fish. Sci. J. [online serial] 11: 3-28.
- Iwamoto, E. M., J. M. Myers and R. G. Gustafson. 2012. Resurrecting an extinct salmon evolutionarily significant unit: archived scales, historical DNA and implications for restoration. Molecular Ecology 21: 1567-1582.
- Kent, M. L., D. J. Whitaker, and S. C. Dawe. 1997. *Parvicapsula minibicornis* n. sp. (Myxozoa, Myxosporea) from the kidney of sockeye salmon (*Oncorhynchus nerka*) from British Columbia, Canada. Journal of Parasitology 83:1153–1156.
- Kieser, D. and Harrower, B. 2003. Aquatic organism risk analysis: Reintroduction of Sockeye Salmon (*Oncorhynchus nerka*) to Skaha Lake, British Columbia. Prepared for the British Columbia Introductions & Transfers Committee.
- Lemay, MA and MA Russello. 2012. Neutral loci reveal population structure by geography, not ecotype, in Kootenay Lake Kokanee. North American Journal of Fisheries Management 32: 282-291. Doi: 0.1080/02755947.2012.676383.
- Lemay, MA and MA Russello. 2015. Genetic evidence for ecological divergence in Kokanee salmon. Molecular Ecology 24: 798-811. Doi: 10.1111/mec.13066.

- McClelland, E.K. and K.A. Naish. 2007. What is the fitness outcome of crossing unrelated fish populations? A meta-analysis and an evaluation of future research directions. Conservation Genetics 8: 397–416.
- McDaniel, T. R., K. M. Pratt, T. R. Meyers, T. D. Ellison, J. E. Follett, and J. A. Burke. 1994. Alaska Sockeye Salmon Culture Manual. Special Publication No. 6., Alaska Department of Fish and Game, Commercial Fisheries Management Division, Juneau, Alaska, 99802-5526.
- McQueen, D., Hyatt, K. D., Stockwell, M., Wright, H., Bussanich, R., and Stevens, A. 2013. Evaluation of the experimental introduction of Sockeye Salmon *(Oncorhynchus nerka)* into Skaha Lake and assessment of Sockeye rearing in Osoyoos Lake: Okanagan Aquatic Enterprises Ltd, Westbank, BC.
- McQueen, D., K. Hyatt, H. Wright, R. Bussanich, A. Stevens, M. Stockwell, P. Rankin. 2014. Evaluation of the experimental introduction of Sockeye Salmon (*Oncorhynchus nerka*) into Skaha Lake and Sockeye rearing in Osoyoos Lake: Synthesis of the first 8 years. Okanagan Nationa Alliance Report for the Canadian Okanagan Basin Technical Working Group. 66p.
- Moore, J.W., and D. E. Schindler 2004. Nutrient export from freshwater ecosystems by anadromous salmon (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 61(9): 1582–1589. doi:10.1139/f04-103.
- Nichols, K.M., C.C. Kozfkay and S.R. Narum. 2016. Genomic signatures among *Oncorhynchus nerka* ecotypes to inform conservation and management of endangered Sockeye Salmon. Evolutionary Applications 2016: 1–16.
- Northcote, T. G., G. Halsey and S. J. MacDonald. 1972. Fish as indicators of water quality in the Okanagan Basin lakes, British Columbia. Report No. 22, Canada-B.C. Okanagan Basin Agreement.
- Northcote, T. G. 1991. Success, problems and control of introduced mysid populations in lake and reservoirs *in* T. Nesler and E. Bergusen eds. Mysids in Fisheries, Am. Fish. Soc. Symp. No. 9.
- Parkinson, E.A., Hume, J.M. and Dolighan, R., 1989. *Size selective predation by rainbow trout on two lacustrine Oncorhynchus nerka populations*. Province of British Columbia, Ministry of Environment.
- Rae, R. 2005. The state of fish and fish habitat in the Okanagan and Similkameen basins. Prepared for the Canadian Okanagan Basin Technical Working Group (COBTWG), Westbank, B. C. 110 p. Available from the COBTWG Secretariat, Westbank, B. C.
- Raverty, S., D. Kieser, J. Bagshaw, and S. St-Hilaire. 2000. Renal infestation with *Parvicapsula minibicornis* in wild sockeye salmon from the Harrison and Adams rivers in British Columbia. Canadian Veterinary Journal 41:317–318.
- Ribble, C. and Stitt, T. 2016. Okanagan River Sockeye Epidemiology Project: Final Report. Prepared for Okanagan Nation Aquatic Enterprises Ltd and Department of Fisheries and Oceans Canada. Available upon request from the authors at Vancouver Island University, Department of Biology, Nanaimo, BC
- Rieman, B. E. and D. L. Myers. 1992. Influence of fish density and relative productivity on growth of kokanee in ten oligotrophic lakes and reservoirs in Idaho. Trans. Am. Fish. Soc. 121: 178-191.
- Ricker, W.E. 1940. On the origin of kokanee, a fresh-water type of sockeye salmon. Transactions Roy. Soc. Canada 34:121-135.

- Schindler, D.E., Carter, J.L., Francis, T.B., Lisi, P.J., Askey, P.J., and Sebastian, D.C. 2012. *Mysis* in the Okanagan Lake food web: A time-series analysis of interaction strengths in an invaded plankton community. Aquat. Ecol. 46: 215–227. doi:10.1007/s10452-012-9393-0.
- Schoen, E.R., Beauchamp, D.A., Buettner, A.R. and Overman, N.C., 2015. Temperature and depth mediate resource competition and apparent competition between Mysis diluviana and kokanee. *Ecological Applications*, *25*(7), pp.1962-1975.
- Scott, W. B. and E. J. Crossman. 1973. Freshwater Fishes of Canada. Bulletin 184, Fisheries Research Board of Canada, Ottawa, Canada. 966p.
- Selbie, D. T., J. N. Sweetman, P. Etherton, K. D. Hyatt, D. P. Rankin, B. P. Finney and J. P. Smol. 2011. Climate change modulates structured and functional lake ecosystem responses to introduced anadromous salmon. Can. J. Fish. Aquat. Sci. 68: 675-692.
- Shedd, K.R., F.A. von Hippel, J.J. Willacker, T.R. Hamon, O.L. Schlei, J.K. Wenburg, J.L. Miller, and S.A. Pavey. 2015. Ecological release leads to novel ontogenetic diet shift in kokanee (*Oncorhynchus nerka*). Can. J. Fish. Aquat. Sci. 72: 1718–1730.
- Shepherd, B. 1996. "History Mystery" Solved! Draft report of B. C. Environment, Okanagan Subregion Fisheries Section, 3547 Skaha Lake Road, Penticton, B. C.
- Taylor, EB, Harvey, S, Pollard, S, and Volpe J. 1997. Postglacial genetic differentiation of reproductive ecotypes of Kokanee Oncorhynchus nerka in Okanagan Lake, British Columbia. Molecular Ecology 6, 503-517.
- Taylor, E.B., J.W.Boughman, M. Groenenboom, M. Sniatynski, D. Schluter. and J.L. Gow.
 2006. Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. Molecular Ecology 15: 343–355.
- Utter, F. 2000. Patterns of subspecific anthropogenic introgression in two salmonid genera. Reviews in Fish Biology and Fisheries. 10: 265-279.
- Utter, FM. 2001. Patterns of subspecific anthropogenic introgression in two salmonid genera. Reviews in Fish Biology and Fisheries 10: 265–279.
- Veale A.J., M.A. Russello. 2016. Sockeye salmon repatriation leads to population reestablishment and rapid introgression with native kokanee. Evolutionary Applications. 9: 1301-1311.
- Walters, C. J. 1995. Model for kokanee populations responses to changes in lake carrying capacity. Contract report to the Fisheries Research and Development Section, Fisheries Branch, Province of BC. 5 pp.
- Wellborn, G.A. and R.B. Langerhans. 2015. Ecological opportunity and the adaptive diversification of lineages. Ecology and Evolution 5: 176-195.
- Whall, J. D. and D. C. Lasenby. 2009. Differences in the trophic role of *Mysis diluviana* in two intermontane lakes. Aquatic Biology 5: 2818-292.
- Wilson, B. 2011. Okanagan-Similkameen Fisheries. Archivos: Quarterly Journal of the Okanagan Archive Trust Society Volume 2, Issue 1. 23pp.
- Winans, GA, Pollard, S and Kuligowski, DR. 2003. Two reproductive life history types of Kokanee, *Oncorhynchus nerka*, exhibit multivariate morphometric and protein genetic differentiation. Environmental Biology of Fishes 77: 87–100.

- Webster, J. 2015. Enumeration and biological sampling of stream spawning kokanee from the Okanagan basin's main lakes, 2014. Report prepared by Chara Consulting for B.C. Ministry of Forests, Lands and Natural resource Operations, Feb 2015, Penticton, B.C.
- Wood, CC, Bickham, JW, Nelson, RJ, Foote, CJ and Patton, JC. 2008. Recurrent evolution of life history ecotypes in Sockeye Salmon: implications for conservation and future evolution. Evolutionary Applications 1: 207-221.