Potential effects of Spawning Enhancement on Wild Babine Sockeye: a Review

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Part I: Narrative

Do artificial spawning channels negatively affect wild salmon?

Abstract

Artificial propagation is an important tool for increasing the harvest of exploited fish, and restoring depressed wild populations. A spawning channel is one propagation technique often considered benign, yet its potential to adversely impact wild salmon has been poorly assessed. Given recent prompts by the Marine Stewardship Council and an independent science review panel to assess the potential effects of channel-enhanced fish on wild populations, my intention here is to review the relevant literature, and offer suggestions of key research questions aimed at addressing current knowledge gaps. Several negative ecological effects for wild stocks due to spawning channels are evident from Canada's largest sockeye salmon (*Oncorhynchus nerka*) producing lake. Increased production of spawning channel fish since the 1970s has intermittently altered prey communities, and reduced the average weight of juveniles leaving the nursery lake. Marine survival rates decline with increasing numbers of emigrating juveniles. High harvest rates targeted at channel-produced salmon appears to have contributed to the decline of less productive stocks. Finally, pathogen transmission may be more likely to occur when channel-produced fish densities are high. Targeted research is required to fully evaluate the sustainability of wild and channel-produced salmon.

Introduction

Fish are generally considered natural resources to be utilized by humans (Hutchings and Fraser 2008); consequently, numerous fish populations around the world are heavily exploited and in decline (Worm et al. 2006). Artificial propagation (enhancement) has become an important tool for increasing the harvest of exploited fish species, and augmenting or restoring depressed wild

populations (Ford et al. 2002). Enhancement programs have been applied to a variety of commercially-important species, such as sturgeon, flounder, and cod, although they have been used most extensively with anadromous salmonids (Hilborn and Winton 1993; Neff et al. 2011).

North America hosts the largest number of enhancement programs for salmonids (*Oncorhynchus* spp.; Paquet et al. 2011). Although salmon enhancement has been highly effective at producing fish for harvest, it remains unclear whether these programs are a benefit, or an impediment, to the recovery of depressed wild populations (Chilcote et al. 2011). For example, enhancement has been successful for some populations at high risk of extinction (e.g., Snucins et al. 1995; Brannon et al. 2004), but there has generally been low success at restoring less endangered populations (Griffith et al. 1989; Fischer and Lindenmayer 2000; Neff et al. 2011). Adding to the discourse is a growing body of evidence that suggests some types of salmon enhancement, such as hatcheries, may have unintended consequences for wild populations. The release of large numbers of hatchery-produced salmon have been implicated in negative genetic and ecological interactions that may lower wild salmon productivity and abundance (Hindar et al. 1991; Nickleson 2003; Araki et al. 2007; Ruggerone et al. 2010). Moreover, large-scale hatchery programs have effectively replaced wild salmon with hatchery salmon in many areas of the Pacific (Kostow 2009).

Much less understood are the potential negative effects of salmon produced from artificial spawning channels on wild salmon. A spawning channel is a manufactured stream built to simulate a natural salmon river using regulated flow, gravel size, and spawner density (Hilborn

1992a; Figure 1). Unlike hatcheries that incubate fish eggs and rear juveniles under artificial conditions, spawning channels enable sexual selection based on phenotypic differences during spawning, which significantly decreases the chance of negative genetic effects on adjacent wild populations (Kynard et al. 2011). But ecological interactions between enhanced and wild salmon are inevitable, and impacts may be most severe for species with numerous overlapping life-history phases, such as sockeye (*O. nerka*), that spend one to two years in freshwater before ocean rearing.

There have been several prompts lately to assess whether artificial spawning channels negatively impact wild salmon. For example, the recent certification of a commercial sockeye fishery in Canada as *sustainable* by the Marine Stewardship Council (MSC) is conditional "...until a peer-reviewed assessment of the impact of production from spawning channels on wild sockeye stocks has been completed..." (MSC 2010). A report by the Skeena Independent Science Review Panel similarly recommended a formal assessment of the impact of enhanced stocks on wild stocks within the same Canadian sockeye salmon system (Walters et al. 2008). Given these calls to improve our understanding, my intention here is to investigate whether artificial spawning channels negatively impact wild salmon, and offer suggestions of key research questions aimed at addressing current knowledge gaps. I focus on the managed spawning channel system for sockeye salmon of Canada's Skeena watershed, and discuss the broader implications for wild salmon conservation.

Skeena River Sockeye Salmon

Babine-Nilkitkwa is the largest sockeye salmon producing lake system in Canada, and it forms one of the major drainage basins in the Skeena River watershed (Figure 2). Babine Lake flows into the upper Babine River and Nilkitkwa Lake before adjoining the lower Babine River and Skeena River. Skeena sockeye salmon have been subjected to over-fishing and habitat alteration for more than 100 years (Gottesfeld and Rabnett 2008); all known populations declined in the early part of the last century, and the majority of nursery lakes now produce sockeye salmon below their estimated potential production due to reduced spawners (Cox-Rogers et al. 2004). Investigations during the 1950s suggested that spawning capacity was limiting sockeye salmon production in Babine Lake (Johnston 1958). These investigations led directly to the inception of three spawning channels on the two major lake tributaries, located at Fulton River (two channels) and Pinkut Creek (one channel). The first spawning channel was operational in 1967, with all channels in full operation by 1971; the first significant returns of enhanced sockeye salmon occurred in 1975 (Wood et al. 1998; Cox-Rogers and Spilsted 2012).

Sockeye salmon typically spawn in streams adjacent to Babine Lake during the fall, but also in shoreline areas of the lake, and emerging fry migrate to the lake in spring to rear for one year. Babine Lake consists of one primary sockeye salmon rearing area (the Main Arm), and three smaller rearing areas (North, Morrison, and Hagan Arms). Fry from spawning channels are thought to rear in the Main Arm together with many wild Babine Lake tributary fry (McDonald 1969), but no recent investigations have been performed to substantiate this. Wild fry from the upper and lower Babine Rivers, and tributaries to Nilkitkwa Lake and Babine Lake's North Arm, rear mostly in Nilkitkwa Lake and the North Arm (Wood et al. 1998). Smolts from these

populations typically migrate to sea one to two weeks before those that rear in Babine Lake's Main Arm (Cox-Rogers and Spilsted 2012). A mark-recapture program to count smolts emigrating from Babine Lake occurred between 1951 and 2002, which provides a rich dataset for biological evaluations.

Freshwater Rearing

Average annual fry abundance in Babine Lake's Main Arm increased from 56 million (1950-1966) to 185 million (1967-2010) due to spawning channel production (McDonald and Hume 1984; Wood et al. 1998; Cox-Rogers and Spilsted 2012). The rearing capacity of the Main Arm is estimated at 219 million fry according to Shortreed and Morton (2000), and has been exceeded in terms of numbers of fry in 11 of 43 years post-enhancement. Importantly, this estimate assumes that lake productivity is constant, which it may not be. Annual fry densities have similarly increased from less than 1,260 fry/ha to 3,940 fry/ha, and have exceeded 6,000 fry/ha in some years post-enhancement (Johnson 1958; Wood et al. 1998; Hume and MacLellan 2000). Densities of sockeye salmon fry in smaller lakes of the Skeena watershed range from 77 fry/ha to 1,994 fry/ha, with most lakes hosting less than 500 fry/ha (Shortreed et al. 1998).

Sockeye salmon fry selectively graze on large cladocerans, and will feed almost exclusively on *Daphnia* when available (Narver 1970; Goodlad et al. 1974; Hume *et al*. 1996; Shortreed et al. 1998). The total estimated biomass of *Daphnia* in Babine Lake is low relative to other interior nursery lakes (Shortreed and Morton 2000). During years when fry densities in Babine Lake were exceptionally high, abundance of large-bodied zooplankton prey and total prey biomass

declined significantly (Rankin 1977). Overwinter growth of fry has also been shown to slow in high fry density years, with subsequent declines in smolt production (West 1978; McDonald and Hume 1984). High grazing pressure can shift prey communities from large-bodied cladocerans to less productive species (Brooks and Dodson 1965; Goodlad et al. 1974; Kyle et al. 1988), and lake rearing capacity may be compromised when grazing pressure is high and sustained over consecutive years (Cox-Rogers and Spilsted 2012). Sockeye salmon densities of >500 fry/ha have had a detectable effect on community composition and prey biomass in nursery lakes elsewhere in British Columbia (Hume et al. 1996).

However, seven years of data assembled from several studies before and after enhancement in Babine Lake showed a non-significant decline in *Daphnia* abundance as smolt numbers increased (Shortreed and Morton 2000). Although fry densities were as high or higher than those reported by Rankin (1977) in 12 of the 25 years post-enhancement examined by Shortreed and Morton (2000), annual fry production may have been variable enough over the time series to maintain prey-community structure. More recently, fry densities in Babine Lake have been sustained at high levels, which may be contributing to the current decline in juvenile production of both wild and enhanced sockeye salmon (Cox-Rogers and Spilsted 2012). Unfortunately, the cessation of the smolt count program has meant that there is no recent evidence of such density-dependent effects. Further work is needed to determine whether food-web perturbations are occurring, and if so, whether wild sockeye salmon populations are negatively impacted.

There is no evidence to suggest that the average size of fry has declined since spawning channel enhancement (McDonald and Hume 1984; Hume and MacLellan 2000). Fry-to-smolt survival appears unrelated to fry density in most years (McDonald and Hume 1984; Macdonald et al. 1987; West and Mason 1987), and may actually have increased (Wood et al. 1998; Cox-Rogers and Spilsted 2012). Furthermore, fry-to-smolt survival rates in the Main Arm have been higher than average during some years when smolt production exceeded Babine Lake's estimated maximum potential (Cox-Rogers and Spilsted 2012), although data quality is suspect (Wood et al. 1998). Accordingly, numerous authors have concluded that the carrying capacity of Babine Lake's Main Arm has not been exceeded as a result of spawning channel production (Macdonald et al. 1987; West and Mason 1987; Wood et al. 1998; Shortreed and Morton 2000; Hume and MacLellan 2000; Cox-Rogers and Spilsted 2012). Conversely, in some nursery lakes of the adjacent Fraser watershed, the size and survival rates of sockeye salmon fry has declined during years of higher than average fry densities (Hume et al. 1996).

In contrast to Babine Lake's Main Arm, Nilkitkwa Lake and the North Arm show strong signs of rearing limitation. Fry-to-smolt survival has declined as fry densities increased (Cox-Rogers and Spilsted 2012). Average fry recruitment to Nilkitkwa Lake and the North Arm is thought to have declined post-enhancement because of a reduction in the number of returning wild spawners, and an underlying assumption that enhanced fry rear only in Babine Lake's Main Arm. But there is some evidence to suggest that a proportion of enhanced fry may rear in southern sections of the North Arm (see Hume and MacLellan 2000). Given the large decline in sockeye salmon populations that spawn in the upper and lower Babine River, and rear in Nilkitkwa Lake and the

North Arm, it may be timely to investigate whether enhanced fry disperse into these rearing areas and interact with wild fry, as inter-basin and inter-lake migrations by fry occur elsewhere (Hartman and Burgner 1972).

One potential benefit of the spawning channels for fry is the 38% increase in phosphorus due to nutrients from enhanced spawner carcasses (Shortreed and Morton 2000). These nutrients are believed to have contributed to an increase in the photosynthetic rate and biomass of phytoplankton in the Main Arm, which has likely resulted in a subsequent increase in zooplankton prey for fry. If so, enhanced spawners may serve to reduce or negate any negative influence that large fry inputs into the Main Arm might otherwise have had. Alternatively, the large increase in macrophyte densities observed in Nilkitkwa Lake post-enhancement, which could be the result of increased nutrients from enhanced spawner carcasses, is thought to have had a negative influence on rearing fry. For example, increased macrophytes may have improved refuge sites for predators in Nilkitkwa Lake, and/or decreased water quality for fry (Cox-Rogers and Spilsted 2012). Research is needed to determine whether the increase in macrophyte densities in Nilkitkwa Lake are caused by increased nutrients, which in turn might influence fry survival, and whether similar processes are occurring in the North Arm.

The increase in abundance of enhanced fry in Babine Lake is associated with a significant decrease in the average size of smolts leaving the lake (Macdonald et al. 1987; Wood et al. 1998; Hume and MacLellan 2000; Figure 3). During the post-enhancement years of 1972 to 1983, the mean length and weight of smolts declined, particularly for main basin stocks (Macdonald et al.

1987). Forty-five years of data from 1950 to 1995 also showed a significant decrease in smolt mass with increasing fry density in Babine Lake (Hume and MacLellan 2000). A reduction in size with increasing numbers of fry is consistent with earlier predictions (Johnson 1965). It is unclear whether the size reduction of smolts post-enhancement is related to prey quality and abundance, or whether an additional or alternative factor is of influence. A native parasite common to sockeye salmon in Babine Lake, *Eubothrium salvelini*, can significantly reduce the size of its host (Dombroski 1955; Smith 1973; Boyce 1979). Thus, the reported average size reduction of smolts following channel enhancement prompts the question as to whether the prevalence or virulence of *Eubothrium salvelini* has increased with increasing fry abundance. Pathogen infection of wild populations often amplifies when host populations are concentrated into dense aggregations (McCallum and Dobson 1995; Daszak et al. 2000; Krkosek et al. 2011).

Marine Residence

Density-dependent effects likely influence the marine survival of Babine Lake sockeye salmon. Larger smolt outputs in the years since channel-enhancement has increased the number of adults returning to Babine Lake, but the relationship is not linear (Peterman 1982; McDonald and Hume 1984; Wood et al. 1998; Wood 2008; Cox-Rogers and Spilsted 2012; Figure 4a). A smaller proportion of smolts survive as smolt numbers increase, with survival rates at high smolt abundance estimated to be one-quarter of those at low abundance (Walters et al. 2008; Figure 4b), and smaller smolt size may be a factor. A clear relationship between smolt length and subsequent marine survival has been shown within cohorts for Babine sockeye salmon (Macdonald et al. 1987), but not between cohorts. Data for sockeye salmon from Chilko Lake in

the Fraser watershed also show a direct relationship between size of smolts and survival (Henderson and Cass 1991). Furthermore, results for other salmon stocks show that the smaller the smolt population, the larger the average body size, and the higher the subsequent marine survival (Foerster 1954). But because Babine Lake smolts remain large or are larger than sockeye salmon from several other productive interior lakes of British Columbia (Wood et al. 1998; Hume and MacLellan 2000), several authors have concluded that size-related mortality may be negligible given the small changes observed (West and Mason 1987; Cox-Rogers and Spilsted 2012). Many factors influence survival, and further work is needed to determine whether smolt size is a factor in the marine survival of wild Babine sockeye salmon.

Most sockeye salmon marine mortality is thought to occur during early residence. An increase in the numerical and functional responses of predators to larger smolt outputs may partly be responsible for reduced marine survival (Peterman 1978, 1982; McDonald and Hume 1984). Predators normally operating on the low end of their functional response curves are capable of causing higher mortality on larger prey populations (Peterman and Gatto 1978). Larger numbers of smolts leaving Babine Lake may increase the numerical response of predators (Elson 1962; Nickleson 2003), which could negatively influence sockeye salmon smolts from other lake systems of the Skeena (i.e., non-Babine) if the latter's seaward migration coincides with enhanced smolts (Hilborn 1992b; Walters et al. 2008). Pathogens may also lower marine survival rates. For example, juvenile sockeye salmon in Babine Lake infected with *Eubothrium salvelini* show a reduced ability to adapt to sea water (Boyce and Clarke 1983). Regardless of the mortality agent, further work is needed to determine whether predation and/or parasite infection

is enhanced under varying levels of smolt abundance, and how survival rates for wild Skeena sockeye salmon are influenced by density-dependent effects. This could be achieved by a large-scale perturbation experiment that decreases the annual number of enhanced-smolts, followed by a smolt-health monitoring program, as has been suggested (Peterman 1991).

Returning Adults

Excessive harvest rates on mixtures of enhanced and wild fish have contributed to the decline in the number of wild Skeena sockeye salmon returning to spawn. The average abundance of wild sockeye salmon returning to tributaries of Babine Lake had declined considerably before the onset of enhancement, but the decline was more pronounced once spawning channels became operational. Other wild Skeena sockeye salmon stocks also showed steeper declines in the average number of returning spawners during the post-enhancement period, and the continuation of intense fishing pressure targeted at abundant channel-enhanced fish is at least partly responsible (West and Mason 1987; Wood et al. 1998; Walters et al. 2008; Wood 2008). The separation of wild and enhanced populations into run-timing groups (early, middle, and late) provides some supporting evidence of overfishing effects on wild fish. Sockeye salmon that return to the Skeena River accompanied by channel-enhanced Babine stocks (i.e., middle-run) have shown an average decline of more than 50% since enhancement, whereas early-run groups have been less affected (Wood et al. 1998; Walters et al. 2008; Cox-Rogers and Spilsted 2012). Late-season fishing in years when sockeye salmon returns are unexpectedly large may also have had an effect on wild late-run populations (i.e., upper and lower Babine River; Walters et al. 2008). Complicating the issue, however, is the fact that wild late-run fish have experienced a

long-term decline post-enhancement even with reduced harvest rates (Cox-Rogers and Spilsted 2012), and the cause remains unclear. There is evidence of a broader-scale decrease in density-corrected sockeye salmon productivity (adult recruits per spawner) along Canada's west coast (Peterman and Dorner 2011), which may partly explain the recent overall decline in abundance of Skeena sockeye salmon. A robust quantitative analysis is needed to address whether the current harvest rates targeted at enhanced fish are contributing to the decline in abundance of wild Skeena sockeye salmon.

Disease outbreaks among enhanced sockeye salmon returning to Babine Lake may have exposed wild stocks to potentially harmful pathogens. A notable example is when a heavy infection of the parasite, *Ichthyophthirius multifiliis*, caused severe pre-spawning mortality for enhanced sockeye salmon in 1994, 1995, and 1997 (Traxler et al. 1998; Wood et al. 1998). Although this parasite is common to salmon and other fishes, and disease outbreaks have occurred at salmon hatcheries and spawning channels elsewhere, there had been no previous reports of epizootics of this particular parasite in wild salmon (Traxler et al. 1998). Because the infective stage of the parasite is viable for only a few days, epizootics are more likely to occur where host densities are high (Trazler et al. 1998). Enhanced sockeye salmon are believed to have contracted the parasite from resident fish in Babine Lake, but the disease proliferated when enhanced fish remained for weeks in high densities below the spawning channels. This high host-density scenario may have exposed wild populations to elevated parasite levels. Stocks that mingle with enhanced fish prior to spawning, or that spawn in alluvial fans at the outlet of the enhanced channels may have been at risk. Wild sockeye salmon from two populations situated between spawning channel systems

were found to host high levels of the parasite during the 1995 outbreak, although no significant pre-spawning losses were reported (Traxler et al. 1998). Further work is needed to examine whether pathogens, such as *Ichthyophthirius multifiliis*, or *Eubothrium salvelini* (mentioned above), could be more prevalent and cause higher mortality at increasing levels of enhanced fish abundance.

Future Prospects

Wild Skeena sockeye salmon have experienced some negative ecological effects from spawning channels (Table 1). The estimated maximum carrying capacity of Babine Lake's Main Arm has been exceeded in 25% of the years post-enhancement, and most of the current capacity is being used by enhanced fry, not wild fry (Cox-Rogers and Spilsted 2012). Importantly, further increases in fry recruitment beyond Babine Lake's maximum capacity may not result in additional smolt production (Shortreed and Morton 2000). Even if smolt production for wild stocks is increased, subsequent marine survival rates would likely be less than at lower smolt abundance; thus, further increases in wild smolts may not necessarily produce more wild adult spawners. This defines one of the challenges facing the recovery of many wild Babine sockeye salmon stocks that are currently below historic abundance. A total reduction in the number of smolts leaving Babine Lake may help wild stocks. For example, reducing the smolt output by one-half is predicted to increase the marine survival rate by 34%, and result in the same percentage increase in returning adults (Walters et al. 2008). Admittedly, this calculation ignores the influence of larger-scale oceanographic factors on marine survival. But unlike ocean conditions, resource managers can control (to a degree) the production of enhanced fry in Babine

Lake, and an effective way to reduce fry numbers is by limiting the number of sockeye salmon returning to spawning channels.

Selective harvesting of enhanced fish could serve as a conservation measure to help wild stocks. The development of the Babine Lake spawning channels has greatly increased the chance of overfishing wild sockeye salmon in non-selective mixed-stock fisheries (Hilborn 1992b; Walters et al. 2008; Wood 2008). Because channel spawners tend to produce more offspring per parent than wild spawners, harvest rates have been excessive for other Skeena sockeye salmon whose run-timing overlaps with returns of enhanced Babine fish (Walters et al. 2008). Indeed, the mixed-stock harvest of wild and enhanced fish challenges the conservation of salmon diversity in the Skeena watershed (Wood 2008). Conversely, fishing restrictions that were applied to protect less productive Skeena stocks have often resulted in enhanced spawner escapements far in excess of spawning ground capacity (Shortreed et al. 1998). Excess enhanced spawners are restricted from accessing spawning channels by weir closures, and their expulsion to Babine Lake may have unintended genetic and/or ecological consequences for wild stocks. A terminal fishery that targets enhanced Babine sockeye salmon is one way that will undoubtedly alleviate pressure on wild stocks while maintaining some of the economic benefits of harvesting salmon (Healey 2009; Darimont et al. 2010), but only if traditional mixed-stock fisheries are reduced. One such fishery now targets spawning channel fish in Babine Lake (Taylor and Dickie 2009), but it remains supplemental to the commercial mixed-stock fishery.

Measurable effects of abundant enhanced fish on wild stocks remain limited despite many

decades of scientific research. The cessation of the Babine Lake smolt-count program in 2002

has weakened our ability to detect any more recent or future ecological effects on wild stocks,

and ultimately may challenge recovery efforts. Targeted research initiatives are required to more

fully understand the impacts of spawning channels on wild salmon. The reintroduction of the

smolt-count program should be considered a high priority because it would provide smolt

abundance and condition information critical to management decisions. Additionally, Canada's

Wild Salmon Policy (WSP) calls for a "biological risk assessment framework" to evaluate the

risks that salmon hatchery production may have on wild salmon (WSP 2005). Although this

framework remains incomplete, I urge Fisheries and Oceans Canada, the agency responsible for

salmon management in British Columbia, to extend their risk assessment to include artificial

spawning channels. Importantly, others have duly noted the need for a thorough evaluation of the

merits and risks of continued operation of spawning channels on Babine Lake (Walters et al.

2008).

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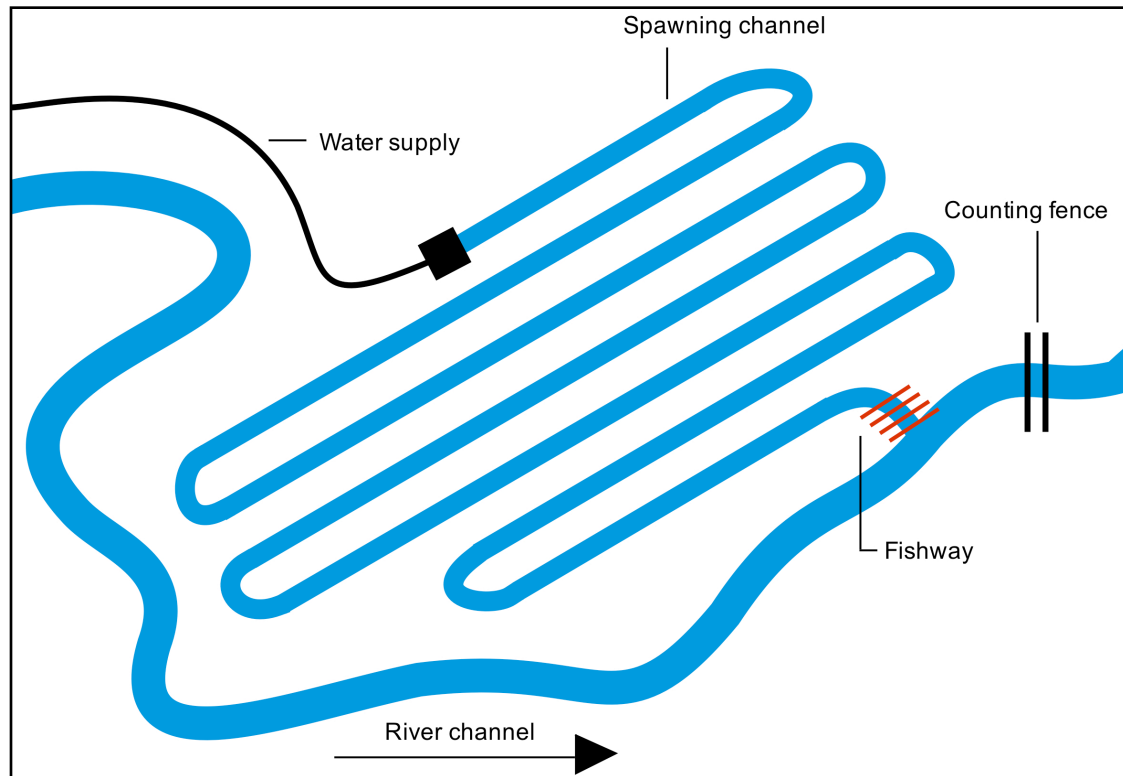Watson. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787-790.

Figure 1. A common artificial spawning channel used in Canada. Spawning salmon migrate upriver, are enumerated at a counting fence, and enter the spawning channels through a fishway; river flow is depicted by an arrow. Water is supplied to the spawning channels from an upriver reservoir.
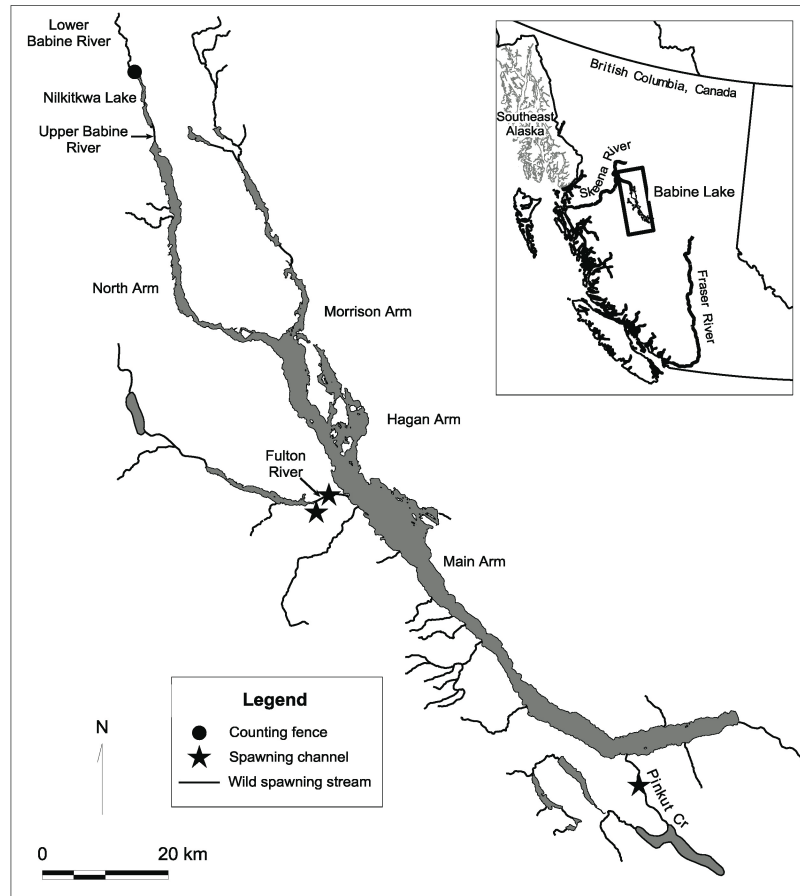
Figure 2. Map of Babine Lake, which includes the enhanced spawning channels at Fulton River and Pinkut Creek, and locations of wild sockeye spawning creeks. Adapted from West and Mason (1987).
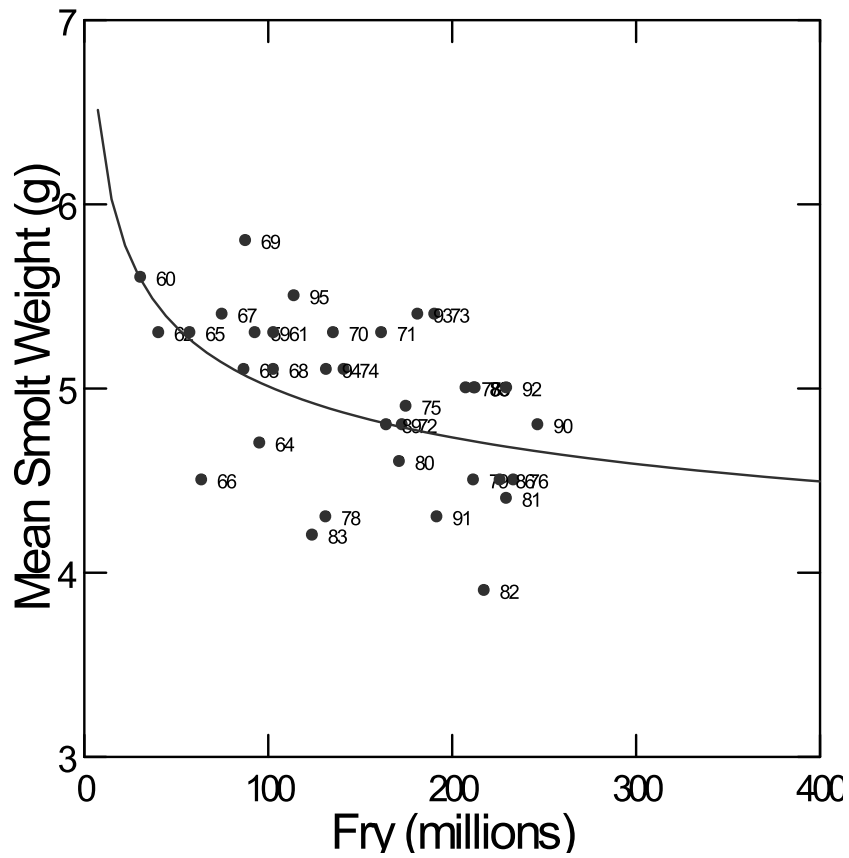
Figure 3. Relationship between mean smolt weight (in grams) versus brood year fry recruitment to Babine Lake Main Arm during 1960-1995; lines fitted as a Power Function after Wood *et al*. (1998). Adapted from Cox-Rogers and Spilsted (2012).
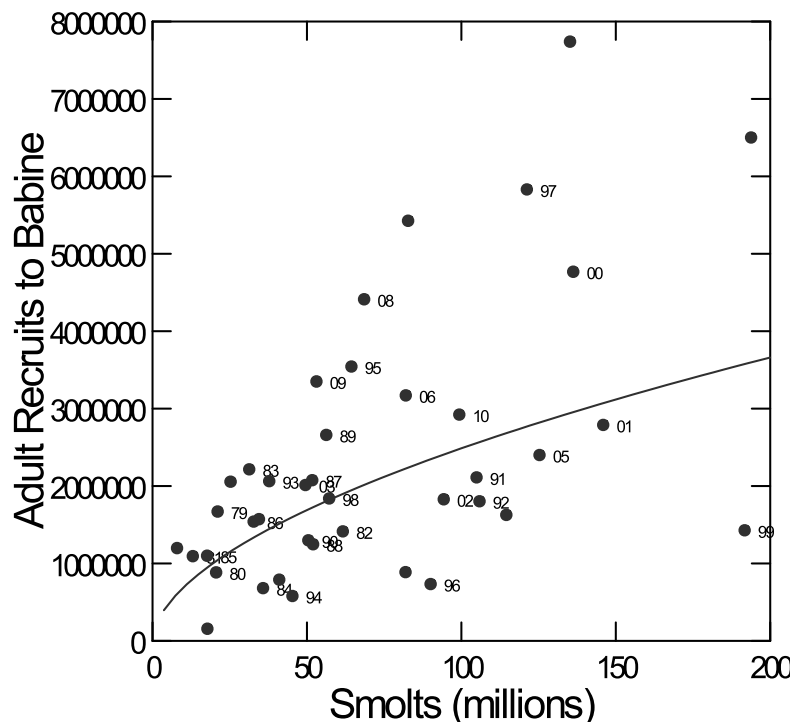
Figure 4a. Relationship between brood year adult recruitment (age 3, 4, and 5) versus numbers of smolts for all Babine/Nilkitkwa Lake sockeye during 1959-2000; lines fitted as a Power Function. Adapted from Cox-Rogers and Spilsted (2012).

Figure 4b. Relationship between smolt to adult survival (%) versus numbers of smolts for all Babine/Nilkitkwa Lake sockeye during 1959-2000; lines fitted as a Power Function. Adapted from Cox-Rogers and Spilsted (2012).
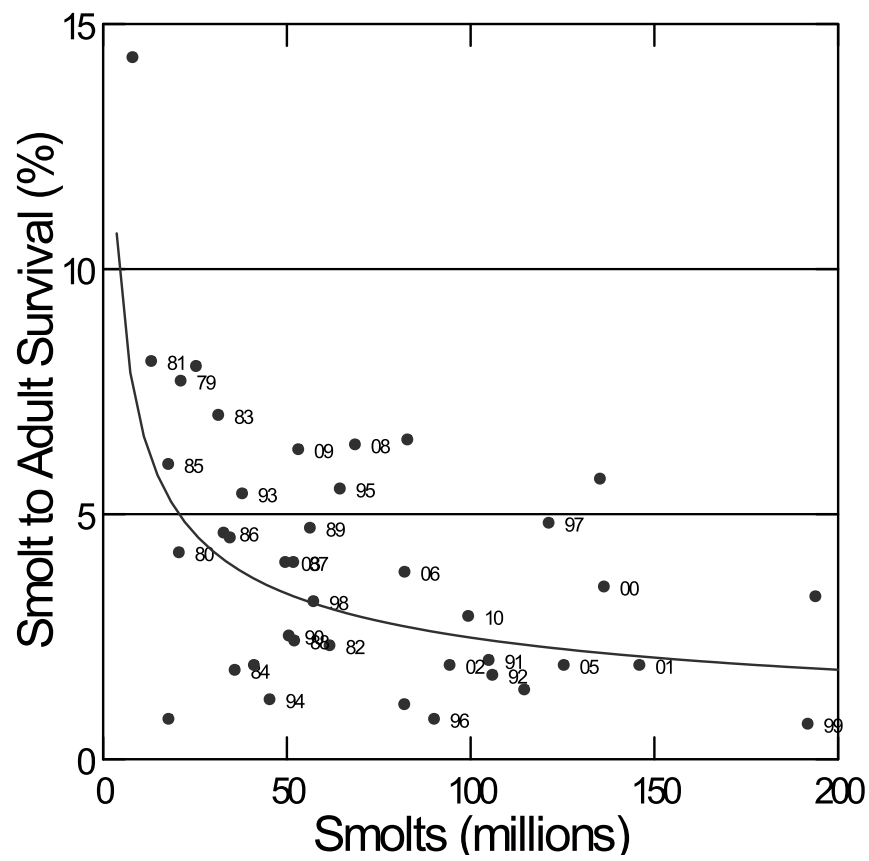
Part II: Synopsis of Relevant Literature

Babine Lake is one of the most intensively studied sockeye salmon nursery lakes in the world. Numerous limnological investigations have been carried out to determine the potential impact of increased escapements on wild sockeye (i.e., Stockner and Shortreed 1975, Rankin 1977, McDonald and Hume 1984, West and Mason 1987, Shortreed and Morton 2000), while several others have attempted to examine the effect of enhancement on juvenile sockeye populations (i.e., McDonald 1969, Peterman 1982, Macdonald et al. 1987, West and Larkin 1987, West and Mason 1987, Wood et al. 1998, Hume and McLellan 2000, Wood 2008, Cox-Rogers and Spilsted 2012). Finally, Levy and Hall (1985) provide a detailed review of juvenile sockeye ecology in Babine Lake. The following is a synopsis of the relevant literature (to my knowledge) that highlights the potential effects of spawning enhancement on wild sockeye stocks of the Babine watershed. I further include the abstract and points of relevance for each literature entry, and divide the publications into four sections based on overarching potential effects of enhanced production on wild populations:

1) Resource Limitation/Competition
2) Reduced Marine Survival
3) Increased Fishing Pressure
4) Disease Transmission

Resource Limitation/Competition

McDonald, J.G. 1969. Distribution, growth, and survival of sockeye fry (*Oncorhynchus nerka*) produced in natural and artificial stream environments. Journal of the Fisheries Research Board of Canada 26: 229-267.

A comparative study was made at Babine Lake, British Columbia, of the distribution, growth, and survival of sockeye salmon fry resulting from the same parental stock but reared in natural and artificial streams. Fry produced from natural spawning in the Fulton River and from eyed eggs planted in an adjacent artificial spawning channel were marked distinctively, released and later recovered in the lake nursery area and at the lake outlet at time of seaward migration. Both groups dispersed rapidly and widely into the main lake basin and apparently mixed extensively with sockeye produced from other main lake tributaries. Lake distribution of marked fish, and the underyearling population as a whole, was not uniform nor static and the fish were concentrated in different lake areas at different times of their first growing season. River and channel fry were comparable in mean length at time of release but subsequently channel fish were smaller. Their smaller size appeared to result from late lake entry and a slower rate of growth for a short period thereafter. Over most of the growing period (June 25-October 25) rates of growth in length were similar (instantaneous daily rates of 0.00687 and 0.00737). No significant difference in survival rates of the two groups could be detected for the first 5 months of lake residence. Production of age 1 seaward migrants was less for river fish than for channel fish but no significance was attached to the small difference observed. These findings are discussed with respect to a fish-cultural scheme which is aimed at increasing adult production by making fuller use of the lake's capacity to rear young sockeye.

Relevance -

• Fulton River sockeye fry (spawning channel and river type) were found to disperse widely throughout Babine Lake, with a non-uniform distribution. This is contrary to the earlier prediction that sockeye fry did not disperse and thus much of the lake was underutilized (Johnson 1958); this earlier hypothesis led directly to the inception of the spawning channels.

• Fry from enhanced spawning channels mix extensively with other [wild] stocks, with different stocks forming a single large population (within different areas of the lake) that share a common lake nursery area.

• Survival rates were similar between enhanced channel fry and non-enhanced river fry within Fulton River.

Stockner, J.G., and Shortreed, K.R.S. 1975. Phytoplankton succession and primary production in Babine Lake, British Columbia. Journal of the Fisheries Research Board of Canada 32: 2413-2427.

Ten stations located in six zones (sub-basins) were sampled biweekly from May to October 1973 to detect possible regional differences in production in this large, 155 km long, dystrophic lake. The spring bloom occurred in all zones while a fall bloom occurred only in Zones 5 and 6. Carbon assimilation showed two peaks in south basin zones, but only one (spring) at zones north of Topley Landing. Seasonal variation in phytoplankton numbers and volume, seston, and chlorophyll a followed a pattern similar to that noted for primary production. Mean production was 100 mg C.m.$^{-2}$ day^{-1} in Zones l-4, but was 145 in Zones 5 and 6. Annual production was estimated at 25 g C $\cdot$ m^{-2} in the north basin and 40 in the south basin. Reasons for the regional disparities are discussed, with greatest significance given to regional variations in mixed layer depth, surface inflows (loading), and basin mean depth. The development and sustainment of the autumnal bloom of Tabellaria fenestrata is thought to be one of the principal factors responsible for greater production in the south basin. An estimated 0.05g TP $\cdot$ m^{-2} enters the lake yearly. This can vary depending on the return of adult sockeye salmon (Oncorhynchus nerka), whose carcasses contribute up to 20% of the total. An estimated 30% is lost via the Babine River, and it is speculated that of the remaining 70%, most is lost to the sediments. Phosphate limitation is implied as a chief factor limiting primary production in the north basin stations, but not in the south basin. On the basis of total phosphorus load the lake is classed as oligotrophic, but in terms of annual production and its humic stained waters it is more correctly considered mixotrophic.

Relevance -
• Based on 1973 estimates, Babine is considered more productive than many well-studied sockeye-producing lakes in Alaska and British Columbia. The majority of the total phosphorus input to Babine came from the major tributaries (notably the Fulton River), with salmon carcasses contributing 19% to the total phosphorus load.

• 70-80% of the lake's surface nutrient load is received in the middle and south basins of Babine lake. Accordingly, zooplankton densities are greatest in the south basin (south of Topley Landing), and this regional production disparity has likely occurred for decades.

Rankin, D.P. 1977. Increased predation by juvenile sockeye salmon (*Oncorhynchus nerka*) relative to changes in macrozooplankton abundance in Babine Lake, British Columbia. MSc. thesis, Department of Zoology. University of British Columbia, Vancouver, B.C. 101p.

A two year study was initiated in 1973 to examine effects of substantial (3.8 fold; from a 1962-66 mean of 39 million to about 150 million in 1973 and 1974) increases in sockeye (Oncorhynchus nerka) fry numbers on zooplankton abundance in Babine Lake. Several lake areas and stations were sampled for zooplankton bimonthly from May to October during 1973 and 1974 and compared to data gathered between 1958 and 1962 prior to a large scale enhancement program for sockeye stocks. Zooplankton biomass had decreased up to 70% in some areas of the lake during 1973 but only 40% in 1974. Decreases in numbers were also evident. Although seasonal changes in fry diet followed changes in zooplankton species abundance, feeding was selective.

The less abundant but larger forms, Daphnia and Heterocope together comprised 70% of the diet during summer, while Cyclops and Diaptomus formed the bulk (87%) of the diet in late fall. Significant decreases in Daphnia and Diaptomus abundance and increases in nauplii early copepodite abundance had occurred by 1973. The increased 1974   zooplankton abundance relative to 1973   was attributed to decreased mid-summer fry numbers in the lake. Field data suggested low Diaptomus numbers contributed to much higher fry mortality (about double in 1974) compared to 1973.

Relevance -
• Average zooplankton biomass decreased 60% in 1973 and 40% in 1974 compared to the average zooplankton abundance before enhancement (1958-1962); the decrease was attributed to the significant increase in fry numbers post-enhancement, and prolonged concentrated predation on zooplankton in certain areas of Babine Lake.

• Area 1 of Babine Lake in particular (immediately south of Morrison Arm) experienced a 70% reduction in zooplankton biomass during 1973 compared to 1958-1962 average. It was hypothesized that because Area 1 historically supported low primary productivity and associated zooplankton biomass, the area was simply unable to support increased fry densities observed post-enhancement.

• The larger zooplankton biomass of 1974 compared to 1973 was attributed to heavy fry mortality in the former year. The numbers of fry entering Babine Lake in both years were similar, but the fry-smolt mortality rate in 1974 was more than double that in 1973, and mortality likely occurred early in the season due to food shortages of preferred prey in the area of the lake where fry were congregating. Greater parasite infection by *Eubothrium salvelini* may also have affected survival.

• Results also showed a significant decrease in large bodied zooplankton prey (*Cyclops* and *Diaptomus* - 50%; *Daphnia* - 80%), which was attributed to the selective removal of these species by the increased number of juvenile sockeye post-enhancement. A predicted consequence includes compensatory feeding on smaller prey and reduced growth of sockeye fry [smolts].

West, C.J. 1978. A review of the Babine Lake Development Project 1961-1977. Fisheries Marine Service Technical Report 812.
In 1962, the Babine Lake Development Project was initiated to provide additional sockeye fry, in order to utilize the rearing capacity of the Babine Lake basin. Two spawning channels were constructed at Fulton River and one at Pinkut Creek, with partial river-flow control facilities at each location. Production expectations of Fulton Channel No. 1 have been exceeded. The major producer of sockeye fry is Fulton Channel No. 2. Low egg-to-fry survivals have been experienced in the original Pinkut Creek spawning channel, due to technical difficulties. This channel has recently been rebuilt on improved specifications. Density-dependent factors have prevented increased fry production in Fulton River and Pinkut Creek. Benefits of partial flow are derived

from the insurance of maintained spawning and incubation flows and tempered spring freshets. The viability of spawning channel fry is comparable to that of natural fry, and increased fry outputs are followed by increased number of smolts. When large numbers of fry are produced, however, the smolt output has been found to be less than anticipated. Reasons for this loss are discussed.

Relevance -
• Increased fry outputs during 1968-1971 resulted in greater numbers of smolts leaving Babine Lake; however, smolt production then declined over the subsequent 2 years in response to increased fry production. Explanations for the smolt decline include: increased predators, food limitations, and increased parasite infection. The author concludes that either the carrying capacity of Babine Lake had been reached, or smolt density-dependent regulating mechanisms were occurring in Babine Lake.

Beacham, T.D., and McDonald, J.G. 1982. Some aspects of food and growth of fish species in Babine lake, British Columbia. Fisheries Research Board of canada Technical Report 1057: 23p.
Food preferences and growth rates of various fish species in Babine Lake were analyzed. Kokanee fed primarily on plankton and insects, with no fish recorded in the diet. Insects were generally the most significant component of the diet of rainbow trout, although fish could account for over 40% of the volume of stomach contents of rainbows over 25cm fork length. For these large rainbows, the proportion of insects consumed declined from July through October. Fish formed the major component of the diet of lake trout. Plankton and insects were the main foods of redside shiners. Analysis of instantaneous growth rates indicated that they were greater than 0.20 for rainbow trout until age 9 and for lake trout until age 7. There was no evidence to indicate that increased production of sockeye salmon fry by means of artificial spawning channels increased the relative contribution of sockeye fry to the diet of piscivorous fishes.

Relevance -
• The data did not suggest any substantial change in the proportion of fish in the summer and fall diet of rainbow trout and lake trout when sockeye fry abundance was greatly increased post-enhancement, although no investigation was undertaken to examine whether a numerical response (i.e., increase in predator numbers) had occurred.

McDonald, J.G., and Hume, J.M. 1984. Babine lake sockeye salmon (*Oncorhynchus nerka*) enhancement program: Testing some major assumptions. Canadian Journal of Fisheries and Aquatic Sciences 41: 70–92.
The objective of the Babine Lake sockeye salmon (Oncorhynchus nerka) enhancement project was to increase fry outputs (and thus, smolt outputs and adult returns) by expanding and improving available spawning beds through the use of artificial spawning channels and related water flow control facilities. The project proceeded on four basic assumptions: (1) the artificial

spawning channels would prove an effective means of producing sockeye fry, (2) the fry produced would be as viable as those produced from natural spawning beds, (3) the lake nursery area had the capacity to support larger juvenile populations, and (4) increased smolt outputs would result in increased adult returns. A before and after study has allowed these assumptions to be tested. Egg-to-fry survival in the channels was close to 40%, as expected. Comparisons of wild and channel-produced fry did not reveal any substantial difference in their distribution, growth, and survival in the lake. Increases in the abundance of fry were followed by corresponding increases in the abundance of underyearlings in the Bake and seaward migrating smolts. No significant change in the average size of the juveniles or their survival in the lake could be detected when population size increased. While the assumptions regarding juvenile production were found to be generally valid, adult returns did not meet expectations. This was due largely to the lack of response to increased smolt outputs from even-numbered brood years. Some options for future management are offered.

Relevance -
• Average annual fry outputs from enhanced spawning channels increased significantly from 43.2 million (1961-67) to 152.9 million (1970-76), a 3.5-fold increase; the main lake as a whole increased three-fold post-enhancement. Despite this increase, fry remained at least comparable in size post-enhancement with no significant change in the mean size of smolts.

• The authors caution that although they did not observe any reduction in size and survival rate of fry (which suggests that the main lake nursery is capable of supporting the larger post-enhancement populations), in years when juveniles were relatively large in size and number, overwinter growth tended to be slowed (which suggests that the overwinter carrying capacity of the lake may have been approached).

• Larger fry outputs had increased the number of returning adults, but the relationship was non-linear. The authors considered several factors that may reduce marine survival (the most probable life-history stage of increased mortality), one of which was the presence and abundance of *Eubothrium salvelini,* an internal parasite commonly found in Babine sockeye smolts.

• The authors conclude by stating, "current practice of attaining large brood stocks and smolt outputs from both even and odd years has not provided the expected increase in adult returns and shows little promise of doing so in the future. Returning to entirely natural production is one strategy that could be considered but one that would probably be politically unacceptable and possibly biologically unrealistic".

West C.J., and Larkin, P.A. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 44: 712-721.
Otolith - body length relations and back-calculation procedures were used to test the hypothesis that mortality of juvenile sockeye salmon (Oncorhynchus nerka) in Babine Lake, British

Columbia, is size selective. Samples of the 4,978 brood of sockeye were collected as fry from spawning tributaries as juveniles in the main basin, and as smolts at the outlet. Total otolith length was chosen as the most useful otolith dimension for back-calculation of fork length at emergence. Sockeye from the various tributaries show different fork length - otolith length relationships necessitating a weighting procedure for comparisons involving samples of mixed stocks from the lake. Instantaneous daily growth rate and ln fork length during the early lake-rearing period were significantly correlated. Smaller juveniles grew more slowly than larger individuals in mid-July, and a hierarchy of sizes was maintained. The distributions of total otolith length at emergence for fry, surviving juveniles, and smolts indicate selective mortality of fish with smaller otoliths, hence of small size at emergence. Survivals from the lower and upper halves of the initial total otolith length distribution were 8.9 and 63.6%, respectively. Comparable estimates for back-calculated fork lengths at emergence were 27.2 and 43.4%. Size-selective mortality is most intense in the late summer and early autumn, and may be associated with predation and parasitism.

Relevance -
• Sockeye fry that emerge small tend to stay in the lower end of the size distribution and become progressively smaller compared with larger individuals; these fish eventually experience selective mortality, which is most intense in the latter part of the summer and in early autumn.

• The proximate causes of mortality are presumably size related, such as predation, or condition related, such as disease and parasitism. Size-related mortality may be induced by parasitism of the cestode, *Eubothrium salvelini*. The susceptibility of fry to infection by the parasite declines sharply as fork length of fry increases (Boyce 1974). Larger and faster growing fry move quickly through this size range, and hence may be less prone to debilitating effects of the parasite. Although infected juveniles may survive to the smolt stage, in laboratory conditions they are less able to cope with stress and exhibit reduced growth, swimming performance, and survival (Boyce and Yamada 1977; Boyce 1979; Boyce and Clarke 1983). Indirect effects on juvenile sockeye quality could cause mortality from other sources (Smith 1973), and higher predation rates on the smaller and less vigorous parasitized fish within Babine lake are equally probable.

West, C.J., and Mason, J.C. 1987. Evaluation of sockeye salmon *(Oncorhynchus nerka)* **production from the Babine Lake Development Project.** *In* **Sockeye salmon** *(Oncorhynchus nerka)* **population biology and future management (Smith, H.D., Margolis, L., and Wood, C.C.,** *eds.***). Canadian Special Publication of Fisheries and Aquatic Sciences 96: pp. 176-190.**
The Babine Lake Development Project (BLDP) was initiated in 1962 and consists of three spawning channels on the Fulton River and Pinkut Creek systems, and associated river flow control works. The BLDP is intended to increase the number of sockeye salmon fry (O. nerka) rearing in the main basin of Babine Lake and ultimately, to increase the adult returns and commercial catch. A paucity of spawning area had been previously identified as the main factor limiting Babine sockeye production. Mean fecundity of BLDP stocks ranged from 3000 to 3500

eggs per female and was best estimated from body length. Length-independent, inter-annual variation in fecundity was related to the last year of ocean life. Egg retention and other spawning failures increased with female spawner density but did not exceed 3% over a wide range of densities. Egg to fry survival averaged 46% in the channels and 21% in the rivers, and was most affected by female spawning density. Efficiency of hydraulic sampling was 63% and the time course of pre-hatch mortality was nearly constant at a rate of 0.4-0.6%. Fry production remained efficient at densities as high as one female per 1.25m² of spawning area, the relationship becoming asymptotic at approximately twice that density. The relationship between numbers of main basin smolt and BLDP fry is linear through high levels of production, with fry-to-smolt survival averaging 42.9% over 21 years. Adult returns of Fulton and Pinkut origin have increased nearly four-fold since the inception of the BLDP, and are now in excess of 1 M fish annually. Of these, an average of 825 800 are taken in Canadian and U.S. fisheries combined. Commercial landings (741 700/yr) of BLDP sockeye are worth more than $ 6.2 M/yr (1985 Canadian dollars). This amounts to a benefit:cost ratio of 3.02:1, applying a 10% discount rate. History of adult production from the BLDP is compared with abundance trends of non-enhanced stocks of Skeena sockeye.

Relevance -

• The authors found that the relationship between numbers of main basin smolts and enhanced fry was linear through high levels of production. Enhanced fry production averaged 130 million (68% of total Babine fry during 1970-1985), which exceeded the target design of 100 million. The persistent linear relationship between fry and smolt production in the main basin suggests that there is no compensatory mortality mechanism serving to reduce fry-to-smolt survival even at high levels, and that the rearing capacity of Babine Lake has not been exceeded.

• The authors discuss the possible role of decreasing smolt size and decreased marine survival reported by Macdonald et al. 1987 (described above), but suggest that mortality is likely negligible given the small changes in smolt size. Regardless of fact, the authors suggest that because smolt biomass is increasing in Babine Lake as a result of the enhanced spawning channels, it may be more profitable to accept reduced survivals [of wild Skeena sockeye stocks] in favor of increasing overall returns.

• Although overall annual returns of Babine sockeye had doubled during 1958-1985, annual returns to Babine River and small Babine tributaries decreased by 22% and 28%, respectively. Of the non-Babine stocks, early runs had declined by 56%, likely due to intense fishing pressure during 1973-1976 (although these stocks had started to decline in the 1950s as noted by Larkin and McDonald 1968). It is hypothesized that one reason for the decline in Babine River sockeye may partly be due to interception fisheries during the harvest of Babine pink salmon.

Hume, J.M., and MacLellan, S.G. 2000. An assessment of the juvenile sockeye salmon (*Oncorhynchus nerka*) populations of Babine Lake. Canadian Technical Report of Fisheries and Aquatic Sciences 2327: 37 p.

Juvenile sockeye salmon (Oncorhynchus nerka) rearing in Babine Lake were re-examined 22 years after the initiation of the Babine Lake Development Project (BLDP). Abundance, distribution, size, and species composition of the limnetic fish populations, including juvenile sockeye salmon, were determined by hydroacoustic and midwater trawl surveys in the autumn of 1993 and the summer and fall of 1994 and 1995 and compared to results collected before and shortly after the start of the BDLP. Our objectives were to look for: 1) changes in the abundance of juvenile sockeye relative to spawning numbers; 2) changes in the utilization of the available nursery area; and 3) the effects of increased population size and density on the size and growth of juvenile sockeye. Abundance of fall sockeye fry ranged from 52.0•106 (1,400 fry/ha) in the fall of 1993 to ~16.5 •106 (455 fry/ha) in the autumns of 1994 and 1995. While the acoustic estimates appeared to be valid estimates of abundance, they were considerably lower than the smolt estimates from the same brood years. The dispersal and subsequent distribution of juvenile sockeye fry was similar to that found in the years before and immediately after the start of the BLDP. The size and growth rate of juvenile sockeye was similar to the earlier years and did not vary with density over the ranges studied. Our study found that Babine Lake has not reached nor exceeded its rearing capacity for juvenile sockeye salmon.

Relevance -
• Fry densities in Babine Lake during the fall were within the range of other smaller Skeena sockeye rearing lakes (which were believed to be well below the rearing capacity), and fall fry densities were considerably smaller than some lakes of the Fraser (Quesnel Lake and Shuswap Lake).

• Despite the four-fold increase in fry recruitment post-enhancement, the authors did not detect a change in summer or fall fry size or growth rate (an indication that food was not a limiting factor in Babine Lake); reduced fall fry size had been observed in Quesnel Lake and Shuswap Lake during years of higher fry densities.

• Using 45 years of Babine Lake smolt size data, the authors found a small but statistically significant decrease in smolt size with increasing fry density. Although the average smolt size had decreased post-enhancement, it was argued that Babine smolts remained as large or larger than many other coastal BC lakes, and 0.5g larger at similar densities than those from Chilko Lake on the Fraser River. However, smolt-to-adult survival has been attributed to smolt size for many other sockeye stocks (Henderson and Cass 1991; Koenings et al. 1993; Bradford et al. 2000), but this may be negated during years of favorable ocean conditions (Wood et al. 1998).

Shortreed, K.S., and Morton, K.F. 2000. An assessment of the limnological status and productive capacity of Babine Lake, 25 years after the inception of the Babine Lake Development Project. Canadian Technical Report of Fisheries and Aquatic Sciences 2316.
Construction of spawning channels in the late 1960's during the Babine Lake Development Program (BLDP) has resulted in increased sockeye escapements and fry densities in most years

from the early 1970's to the present. In 1994 and 1995 we carried out a limnological study of Babine Lake to determine its current trophic status and rearing capacity for juvenile sockeye salmon (Oncorhynchus nerka). We investigated the effect of the increased escapements and fry densities on lake physics, chemistry, lower trophic levels, and sockeye diet by comparing our data with similar data collected before (Johnson 1961, 1964) and shortly after (Stockner and Shortreed 1975; Rankin 1977) the inception of the BLDP . Current spring overturn total phosphorus concentrations (5-9 µg/L), seasonal average chlorophyll concentrations (1.9-2.5 µg/L), and bacteria numbers (<1.7x106/mL) indicate the lake is in the middle to upper range of oligotrophy. The average C:N:P ratio was 314:31:1, indicating that the lake was P-limited. Total phosphorus loading has increased approximately 38% from estimates prior to enhancement, primarily because of increased sockeye escapements (i.e. nutrients from carcasses). Seasonal daily photosynthetic rates were 125 mg C·m-2·d-1 in 1994 and 155 mg C·m-2·d-1 in 1995, higher than the 1973 average of 100 mg C·m-2·d-1. Daphnia were the dominant prey item of juvenile sockeye both before BLDP and during our study. However, in our study grazing pressure on the zooplankton community (inferred from fall fry densities and smolt numbers) was much lower than in most years after BLDP and was similar to years before BLDP. Available evidence indicates that despite consistently higher fry densities as a result of BLDP, Babine Lake remains a quality nursery area for juvenile sockeye and its rearing capacity has not been exceeded. However, evidence from 1973 diets suggests that some of the higher post-BLDP fry recruitments have neared or reached the lake's rearing capacity and that further increases in fry recruitment would not result in additional smolt production.

Relevance -
• Babine Lake hosted a favorable physical environment for juvenile sockeye, similar to that found in other large BC sockeye nursery lakes such as Francois, Quesnel, and Takla. Although the lake is believed to be in the middle-to-upper range of oligotrophy (nutrient limited), the total phosphorus input increased 38% from estimates prior to enhancement (the increase primarily the result of increased sockeye escapements (i.e., carcass nutrients).

• Total estimated biomass of *Daphnia* (the dominant prey for sockeye fry) is low relative to other interior nursery lakes, and comprises a much smaller proportion of juvenile sockeye diet.

• Neither fry size in the fall, nor growth rate, showed any significant change over previous years; nor did fry size or growth show any relationship to increased spawner abundances. Despite consistently higher fry densities as a result of enhancement, the authors conclude that Babine Lake's rearing capacity has not been exceeded and remains a quality nursery area for sockeye (although some past fry recruitments neared or reached the lake's rearing capacity, and further increases in fry recruitment may not result in additional smolt production).

Reduced Marine Survival

Peterman, R.M. 1978. Testing for density-dependent marine survival in Pacific salmonids. Journal of the Fisheries Research Board of Canada 35: 1434-1450.

Marine survival data for several different salmonid stocks were reviewed to determine whether there was significant density-dependent survival occurring in the ocean. Four classes of interaction were examined: (1) within-cohorts, (2) between-cohorts, (3) between stocks on the same or nearby rivers, and (4) between stocks of distant rivers. Results of statistical tests indicate that some stocks do not produce an increase in adult returns with increased smolt abundance, and that marine survival rate of other stocks is affected by abundance of other cohorts or stocks. Only a few stocks exhibit these density-dependent relations, but given present data, it is impossible to predict the frequency of occurrence of such limiting processes in future enhanced stocks. Salmonid enhancement planning is discussed in the context of this uncertainty and experimental enhancement projects are suggested that aim to obtain information about marine survival processes as well as additional catches.

Relevance -
• There is evidence of density-dependent marine survival. Data for Babine Lake sockeye show a smaller proportion of smolts survive as numbers increase. It is uncertain whether this is due to increased predation, pathogen transmission, or food-deprivation during the initial 15 months of marine life. The data are also suggestive of between-stock interactions with pink salmon.

Peterman, R.M. 1982. Nonlinear relation between smolt and adults in Babine Lake sockeye salmon (*Oncorhynchus nerka*) and implications for other salmon populations. Canadian Journal of Fisheries and Aquatic Sciences 39: 904–913.

Data on sampling variability in smolt abundance for Babine Lake sockeye salmon (Oncorhynchus nerka) are combined with a previous analysis to calculate a more accurate estimate of the degree of nonlinearity in the relation between smelts and adults. Results indicate significant within-stock nonlinear mortality, large variability in mortality which tends to obscure any smolt-to-adult relation. or both. Analysis of age structure data identifies the first 15 mo of marine life as the period when most of this nonlinear or relation-masking mortality occurs. I also calculate the amount of smolt measurement error below which other salmon stocks are classed as having nonlinear marine survival. A distinct separation between even and odd brood year marine survival of Babine Lake sockeye suggests interactions with pink salmon. Juvenile pink salmon (0. gorbuscha) abundances correlate positively with residuals in Babine Lake sockeye survival for the same seaward migration year. This suggests a depensatory mortality effect which occurs later in the marine life stage than the possible within-population compensatory effect. Depensation is plausible because the size of pink fry equals that of sockeye smolts by August in coastal waters, permitting mutual swamping of predators. The paper concludes with implications for further enhancement.

Relevance -
• Results showed that adult returns of Babine Lake sockeye are not significantly increased by increased smolt abundance post-enhancement, and that most of the mortality likely occurs during the first 15 months of marine life (not as fry in Babine Lake).

• Marine survival rates decreased with increasing smolt production (survival rates at high smolt abundances are roughly one-quarter of those at low abundance). Possible causal mechanisms of mortality include: increased competition for food, enhanced numerical and functional responses of predators, and increased prevalence of diseases.

• Results also show a positive relation between sockeye smolt survival and abundance of juvenile pink salmon entering the ocean in the same year; the hypothesis being that single predator species, such as seals and large fish, could potentially be swamped by large combined populations, resulting in higher sockeye salmon survival. Given this, it is plausible that larger sockeye smolt populations (post-enhancement) entering the ocean may act in a similar fashion to buffer predator-induced mortality. However, the author considers that any within-population density dependence occurs during downstream migration or in early marine life before pink juveniles overlap sockeye in physical distribution.

Macdonald, P.D.M., Smith, H.D., and Jantz, L. 1987. The utility of Babine smolt enumerations in management of Babine and other Skeena River sockeye salmon (*Oncorhynchus nerka*) stocks. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management (Smith, H.D., Margolis, L., and Wood, C.C., *eds*.). Canadian Special Publication of Fisheries and Aquatic Sciences 96: pp. 280-295.

Pre-season forecasts of the numbers of adult sockeye salmon (Oncorhynchus nerka) returning to the Skeena River have utilized estimates of the number of seaward-migrating juveniles (smolts) leaving Babine Lake, the primary nursery area. These forecasts have often been unsatisfactory. Using data on production, catch, and escapement for brood years 1943-1984 (including smolt data for brood years 1959-1983), we study the forecasting problem in two different ways: forecasting the accumulated return (over several calendar years) of fish from a given brood year, and forecasting the total return (which includes components from several brood years) in a given calendar year. Peterman's (1982a) observation of highly variable smolt-to-adult survival is confirmed, but the pattern of odd/even year differences he found appears to have been disrupted in recent years. The relationships which predict future returns from a given brood year are much less well-defined than those that predict total return in a given calendar year. Stepwise regression analysis shows that the best pre-season forecast of total return in a given calendar year is one based on the number of jacks (3 yr-old males) returning in the previous year and the number of smolts migrating to the ocean 3 years previously. Since the onset of the Babine Lake Development Project, the average return has increased by a million fish per year, but the variability in the return has has also increased to the point where returns have become impossible to predict from these data series alone. This variability may be related to a decrease in the average size of migrating smolts. There is not much that could be done to improve the smolt enumeration field operation that would be cost-effective: variable marine survival is a major source of uncertainty in the forecasts.

Relevance -

• There was a statistically significant decline in both length and weight of early and late run smolts since 1971 (the year all spawning channels were operational); likely due to the rising production of enhanced fry, and associated food resource challenges in Babine lake.

• There was no evidence of density dependent mortality between the fry and smolt stage, implying that fry densities between pre/post-enhancement (1961-1982) had not yet exceeded the carrying capacity of Babine Lake.

• There is concern that smaller smolts might suffer increased mortality during their first year at sea, and some evidence to show higher mortality among the smaller smolts in a given brood. The authors conclude that, "there should be clear targets for fry production which will maximize returns by balancing gains in smolt numbers against their declining size and reduced marine survival".

Fishing Pressure

Larkin, P.A., and McDonald, J. 1968. Factors in the population biology of the sockeye salmon of the Skeena River. Journal of Animal Ecology 37: 229-258.

Relevance -
• Non-Babine escapement during 1946-1948 period (considered historical) accounted for roughly 30% of the total sockeye escapement, decreasing to 7% by 1963, which suggested that non-Babine stocks were showing clear signs of decline pre-enhancement. Strong selective harvesting of larger fish (age-class 5s over 4s) is considered as a possibility for the non-Babine sockeye declines: non-Babine sockeye tended to be of the age-class 5 and 6, whereas Babine sockeye tended to be age-class 4 and 5.

Wood, C.C., Rutherford, D.T., Bailey, D., and Jakubowski, M. 1998. Assessment of sockeye salmon production in Babine Lake, British Columbia with forecast for 1998. Canadian Technical Report of Fisheries and Aquatic Sciences 2241: 50 p.

The Babine-Nilkitkwa lake system is the largest natural lake in British Columbia (500 km^2). It also supports the largest sockeye salmon (Oncorhynchus nerka) population in Canada, a total adult stock that has averaged over 4 million annually since 1990. This report provides a comprehensive assessment o f sockeye production from the Babine-Nilkitkwa system in that it brings together, for the first time in many years, recently compiled information on trends in spawning escapements by run timing group, fry recruitment, smolt production, adult returns, harvest rate, and surplus production from Babine Lake Development Project (BLDP) facilities. Exploitation rate on Skeena River sockeye has increased over the last decade, averaging 68% since 1990, and exceeding 70% in 1996 and 1997. Recent escapements to enhanced sites in

Babine Lake have exceeded spawning requirements such that over a third of the Babine fence count has been surplus produced by the BLDP. Enhanced fry now account for about 90% of fry recruitment to the main basin. As expected, increased fry and smolt production has increased adult returns although the relationship between adult returns and smolt abundance is non-linear. Available data indicate that further increases in adult returns could be expected by increasing smolt production, and that fry recruitment is still below levels required to yield maximum smolt biomass. However, pre-spawning mortality at the BLDP sites in 1994 and 1995 caused by parasitic infections has significantly reduced fry recruitment and smolt production. Near record low smolt production and jack returns from the 1993 brood, together with near record low smolt production and age 4 returns from the 1994 brood, provide clear signals that adult returns in 1998 and 1999 will be much lower than in recent years. The smolt forecast model indicates a 75% chance that adult returns to the Skeena River in 1998 will exceed 820,000 sockeye, and a 50% chance that returns will exceed 1,420,000 sockeye.

Relevance -
• Enhanced fry now account for 95% of total fry recruitment to Babine Lake, and the increased recruitment is thought not to have caused a detectable reduction in fry-to-smolt survival in Babine Lake. However, increasing density of juveniles in Babine Lake has been associated with a steady decrease in average smolt size, and this may be attributed to density dependence. Within Babine Lake, escapements to the unenhanced streams began to decline shortly after the first enhanced sockeye salmon returned, suggesting that increased exploitation rates on enhanced returns caused the decline.

• Increased fry and smolt production has increased aggregate adult returns, although the relationship between adult returns and smolt abundance is non-linear. Infection by white spot disease caused high pre-spawning mortality at both enhancement sites in 1994, 1995, and 1997, which may have been responsible for subsequently low production of smolts; however, fry-to-smolt survival had been below average and declining since the 1993 brood year, suggesting some other agent of mortality may be responsible (such as density-dependence).

Hilborn, R. 1992. Hatcheries and the future of salmon in the northwest. Fisheries 17: 5-8.
Artificial propagation is often seen as a way to maintain and increase or augment fish stocks that have suffered from habitat loss and overexploitation. Large-scale hatchery programs for salmonids in the Pacific Northwest have largely failed to provide the anticipated benefits; rather than benefiting the salmon populations, these programs may pose the greatest single threat to the long-term maintenance of salmonids. Fisheries scientists, by promoting hatchery technology and giving hatchery tours, have misled the public into thinking that hatcheries are necessary and can truly compensate for habitat loss. I argue that hatchery programs that attempt to add additional fish to existing healthy wild stocks are ill advised and highly dangerous.

Relevance -

• The increased numbers of fish by enhancement has typically justified subsequent harvest rates to be higher than they would otherwise have been, resulting in the over-harvest of wild salmon. Harvest rates on enhanced stocks have at times been matched to the potential productivity of enhanced stocks, causing wild stocks to be overfished.

• Hilborn illustrates another problem with a specific example of Skeena sockeye from work performed by McDonald and Hume 1984 (described in detail above). The more sockeye smolts that outmigrated from Babine Lake to the ocean, the smaller the proportion that survived their marine life. A major effect of this change is that the wild sockeye runs have declined. It is presumed that the non-Babine sockeye populations of the Skeena are equally affected by the resulting competition, as salmon compete for food and space in fresh water and ocean environments, and Hilborn cautioned that as we increase artificial production, enhanced fish will compete with wild fish, and the survival of wild fish will decrease.

Walters, C.J., Lichatowich, J.A., Peterman, R.M., and Reynolds, J.D. 2008. Report of the Skeena Independent Science Review Panel. A report to the Canadian Department of Fisheries and Oceans and the British Columbia Ministry of the Environment. May 15, 2008, 144 p.

Relevance -
• This report reviewed the management, status, and conservations concerns of Skeena salmonids. It describes how the development of the Fulton and Pinkut sockeye spawning channels greatly increased the chance of overfishing wild stocks in mixed-stock fisheries due to the higher productivity of enhanced stocks.

• Escapements of both early and mid-timing wild Babine sockeye declined as abundance of enhanced fish increased, suggesting competition in the lake between wild and enhanced sockeye juveniles. Data on marine survival rates of Babine smolts add to the concern about wild sockeye populations. There is an inverse relation between smolt abundance and marine survival rate (adult returns per smolt); although no smolt data exist for non-Babine sockeye, these data suggest that wild smolts, which migrate to sea with enhanced smolts, have likely faced similar reductions in survival rate when total smolt abundance is high.

• Disease problems with enhanced stocks during the 1990s greatly reduced freshwater survival rates, and smolt output has been extremely low in 5 of the last 8 years of associated data (up to 2000), which raised concerns about the long-term sustainability of channel production. Increasing smolt abundance through enhancement by 100% from 50 to 100 million, had only increased adult abundance by 57% from 2.3 to 3.6 million.

• If conservation objectives of the Wild Salmon Policy are focusing on concerns about wild Skeena sockeye, then reduced smolt output from Babine Lake would help those stocks. For example, a reduction of smolt output by half from 130 million to 65 million fish would increase

the marine survival rate by 34% (from ~ 4%), also leading to the same percentage increase in wild adult abundance.

Wood, C.C. 2008. Managing biodiversity of Pacific salmon: lessons from the Skeena River sockeye salmon fishery in British Columbia. *In* Reconciling Fisheries with Conservation, Volumes 1 and 2 (Neilson, J., Dodson, J.J., Friedland, K., Musick, J., and Verspoor, E. *eds*.). American Fisheries Society Symposium 49: 349-364.

Mixed-stock harvest of wild and artificially propagated (enhanced) salmon stocks greatly complicates the conservation of salmon diversity and nowhere is this more evident than in the fisheries for sockeye salmon (Oncorhynchus nerka) in the Skeena River, British Columbia, Canada. The total catch and production of sockeye salmon from the Skeena River has set record high levels over the last decade after a century of intensive commercial fishing. However, both species and stock diversity decreased significantly over the course of the fishery. Species diversity has largely been restored through conservation action, but many individual populations remain at very low abundance. Fishery managers have struggled to find an acceptable trade-off between extracting economic benefits from enhanced stocks while protecting less productive wild stocks from extinction. Recent policies promise to provide explicit limits to these trade-offs based on stewardship ethics and conservation principles.

Relevance -
• Salmon enhancement activities have had adverse effects on wild populations, with the greatest impact attributed to excessive harvest rate on mixtures of enhanced and wild fish. Enhancement of sockeye within the context of mixed-stock fisheries is incompatible with the conservation of wild salmon diversity.

• The diversity of Skeena sockeye has changed dramatically post-enhancement. Between 1950 and 1998, the non-Babine proportion of the Skeena sockeye salmon escapement declined from 30% to 4% using nominal visual estimates, or from about 40% to 7% after doubling visual estimates relative to the Babine fence count to allow for underestimation. It is unknown what effect this has for Skeena sockeye as a whole.

• The relationship between smolt production and adult returns is not linear; smolt survival appears to decline with increasing smolt abundance, presumably because of density-dependent ecological interactions (as discussed in Peterman 1978, 1982; McDonald and Hume 1984; Wood et al. 1998).

Cox-Rogers, S., and Spilsted, B. 2011. Update Assessment of Sockeye Salmon Production from Babine Lake, British Columbia. Canadian Technical Report of Fisheries and Aquatic Sciences 2956

Wood et al. (1998) provided the last formal assessment of sockeye production from Babine Lake using production data spanning the 1950-1996 return years (1950-1991 brood years). This

update adds 14 more years to the data series (1950-2010 return years, 1950-2005 brood years) and provides an overview of the monitoring methods used to assess Babine Lake sockeye production. Three distinct yet overlapped sockeye "runs" return to Babine Lake each year: early- timed, mid-timed, and late-timed. Babine Lake sockeye were enhanced in the late 1960's, which saw spawning channels and flow controls established on two of the mid-timed Babine Lake spawning tributaries located at Pinkut Creek and Fulton River. Approximately 90% of all Skeena River sockeye are now from Babine Lake, and of these, an average 75% are enhanced fish from Pinkut Creek and Fulton River. Skeena River sockeye returns (catch plus escapement) increased substantially after Babine Lake enhancement and continued to do so throughout the 1980's and through most of the 1990's as sockeye returns to Babine Lake increased. Since the early 2000's, Skeena River sockeye returns have declined to lower levels coincident with a recent decline in Babine Lake production. Escapements to enhanced Pinkut Creek and Fulton River continue to exceed spawning requirements, even with the recent declines in total production. Escapements to the unenhanced late-runs exhibit a long-term declining trend which was not evident in the last assessment conducted in the mid 1990's. Late-timed escapements have been much lower than historic in recent years. Escapements to the early-timed and mid-timed unenhanced runs have also been very low in recent years. Fry production from Pinkut Creek and Fulton River continues to account for ~90% of fry and smolt recruitment to the Main Arm of Babine Lake; yet total fry recruitment to the Main Arm still appears to be below maximum rearing capacity. North Arm/Nilkitkwa Lake fry and smolt production was on a declining trend prior to cessation of the last brood year assessed, consistent with reduced numbers of late-run spawners. It is currently unclear how freshwater and/or marine survival variation may be influencing recent Babine Lake brood year recruitment. Reduced adult returns the past decade could be due to fewer smolts leaving Babine Lake, fewer smolts surviving as adults in the ocean, or some combination of both. Several mechanisms affecting freshwater and marine survival have been proposed, but data are lacking to make a proper assessment. Future research may help address some of the concerns.

Relevance -
- Update to Wood et al.'s (1998) assessment of sockeye production from Babine Lake, adding 14 additional years to the data series (1950-2010 return years, 1950-2005 brood years).

- Skeena River sockeye returns have declined to lower levels since the early 2000s, coincident with a recent decline in Babine Lake production. Not clear whether the decline in productivity is due to reduced carrying capacity in Babine Lake, reduced marine survival, or a combination of these.

- Late-run Babine sockeye (i.e., lower and upper Babine River) show the largest long-term decline, with North Arm/Nilkitkwa Lake fry and smolt production on a declining trend prior to cessation of the last brood year assessed, consistent with reduced numbers of late-run spawners.

Disease Transmission

Traxler, G.S., Richard, J., and MacDonald, T.E. 1998. *Ichthyophthirius multifiliis* (Ich) epizootics in spawning sockeye salmon in British Columbia, Canada. Journal of Aquatic Animal Health 10: 143–151.

Epizootics of Ichthyophthirius multifiliis occurred in adult prespawning and spawning sockeye salmon Oncorhynchus nerka during the 1994 and 1995 spawning seasons in the Skeena River watershed in northern British Columbia, Canada. Exceedingly high mortalities occurred at Fulton River and in three spawning channels adjacent to Babine Lake. During these 2 years, the infection and subsequent death of prespawning adults resulted in an estimated 153.6 million fewer sockeye salmon fry produced from Fulton River and the three spawning channels adjacent to Babine Lake than the historical average. Resident fish were the most likely source of the parasite in the watershed because several species were found with light infections of I. multifiliis. Transmission of the parasite to anadromous sockeye salmon was enhanced by the high density of fish held below the spawning grounds for days or weeks prior to moving into the spawning channel. This is the first report of an epizootic of ichthyophthiriasis in wild spawning salmon.

Relevance -

• Disease outbreaks occurred in spawning sockeye at all three spawning channels over consecutive years, causing high pre-spawning mortality for diseased fish. Enhanced sockeye contracted the parasite from resident fish in Babine Lake, and the disease proliferated when enhanced sockeye were held in high densities below spawning channel weirs. Epizootics caused by this parasite have occurred at spawning channels elsewhere (i.e., tributaries to the Fraser River).

• Twin Creek, Pierre Creek, Morrison River, and Babine River all hosted high prevalence levels of the parasite during the 1995 outbreak (though infection intensities were considered low, and significant pre-spawning mortality was not observed).

Knowledge Gaps

Competition/Resource Limitation

Sockeye fry are thought to disperse widely in a non-uniform distribution throughout Babine

Lake, and particular stocks appear to utilize different regions at different times (McDonald

1969). Although annual production of Babine Lake in its entirety is considered sufficient to

support the increased number of sockeye fry post-enhancement (Stockner and Shortreed 1975; Macdonald et al. 1987; West and Mason 1987; Hume and McLellan 2000; Shortreed and Morton 2000), zooplankton biomass had decreased dramatically for some regions in the years immediately following enhanced fry production (Rankin 1977). For example, the area immediately south of Morrison Arm (Area 1) experienced a 70% reduction in zooplankton biomass during 1973 compared to 1958-1962 average, and the area adjacent to the Fulton River (Area 2) experienced a 40% decline in 1974 compared to the pre-enhancement average. Both Areas 1 and 2 have historically hosted lower zooplankton densities than the southern region of Babine Lake (Stockner and Shortreed 1975); these areas have also seen increases in fry densities post-enhancement (Hume and McLellan 2000). The question remains as to whether food shortages occur for some stocks in particular areas of Babine Lake, and how wild sockeye fry utilize the lake in relation to enhanced stocks.

Marine Survival

Although fry survival rates within Babine Lake appear to have remained unchanged under increasing fry densities post-enhancement (McDonald and Hume 1984; West and Mason 1987; Shortreed and Morton 2000), average smolt size has decreased (Macdonald et al. 1987; Wood et al. 1998; Hume and McLellan 2000). Marine survival rates have also decreased with increasing smolt production (Peterman 1978, 1982), and the smaller size of smolts post-enhancement may be a factor. Data for Chilko sockeye show a direct relationship between size of sockeye smolts and survival (Henderson and Cass 1991), and results for other salmonid stocks show that the smaller the smolt population, the larger the average body size, and the higher the subsequent

marine survival (Foerster 1954; Ricker 1962). This size-related mechanism may directly apply to wild Babine sockeye smolts if their size is influenced by enhanced smolt production. It has further been argued that predators normally operating on the low end of their functional response curves are capable of causing high mortality on larger prey populations (Peterman and Gatto 1978), and that larger smolt numbers may increase the functional response of predators (Elson 1962); both of which may influence wild Babine and non-Babine sockeye alike. Regardless of the causal mechanism, the question remains as to whether there is clear evidence of density dependent marine mortality (i.e., do marine survival rates decrease under increasing smolt abundances?) as Peterman (1982) suggested.

Fishing Pressure

The rise in production of enhanced Babine sockeye has greatly increased the chance of overfishing wild sockeye in nonselective mixed-stock fisheries (Hilborn 1992; Walters et al. 2008; Wood 2008). In fact, the greatest impact of salmon enhancement has been attributed to the excessive harvest rates on mixtures of enhanced and wild fish (Meffe 1992; Wood 2008). Despite the strong correlation, a robust quantitative analysis is needed to address the potential severity of the associated decline in wild stocks due to enhanced sockeye.

Disease Transmission

Several disease outbreaks have occurred in sockeye from Babine Lake. White spot disease caused severe pre-spawning mortality for enhanced sockeye stocks in 1994, 1995, and 1997 (Traxler et al. 1998; Wood et al. 1998), and wild sockeye from Twin Creek, Pierre Creek,

Morrison River, and Babine River all hosted high prevalence levels of the parasite during the 1995 outbreak. Although pathogen transmission is difficult to detect, it typically involves artificial reservoirs of host populations in high densities (Daszak et al. 2000). The containment of sockeye for several weeks in high densities below artificial spawning channels enabled the proliferation and transmission of white spot disease in Babine Lake (Traxler et al. 1998). This scenario places wild Babine sockeye populations at potential risk of pathogen transmission from enhanced stocks, particularly for lake spawning populations that may utilize alluvial fans of Fulton River and Pinkut Creek, or other wild stocks that mingle with enhanced fish prior to spawning. *Eubothrium salvelini* is a common intestinal parasite of juvenile sockeye contracted in freshwater (Smith 1973; Boyce 1974). Infected juveniles show reductions in growth, swimming performance, adaptation to salt water, and survival (Boyce 1979; Boyce and Clarke 1983), as well as increased susceptibility to zinc (a heavy metal in Babine Lake thought to have increased as a result of intensive copper mining; Boyce and Behrens Yamada 1977). There has not been an investigation to determine whether the prevalence of *E. salvelini* has increased post-enhancement, though it remains an important question. Perhaps the most pertinent question is whether larger smolt and/or adult densities result in higher rates of transmission of mortality agents (i.e., white spot disease, *E. salvelini*, or others)? It has been suggested that diseases could be more prevalent and cause higher mortality at high fish abundance, but very little documentation on these variables exists (Peterman 1982).

Further Citations

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