Chapter 10
Sockeye Salmon of Chilko-Chilcotin, Fraser River, British Columbia, Canada

DENISSE JAUREGUI
WILDLIFE & CONSERVATION BIOLOGY
UNIVERSITY OF CALIFORNIA, DAVIS, CA95616
DJAUREGUI@UCDAVIS.EDU

Abstract
Sockeye Salmon (Oncorhynchus nerka) are a keystone species in the Chilko-Chilcotin River (CCR) ecosystem. The Chilcotin River is an important tributary to the Fraser River, the largest Sockeye salmon producing river in Canada and one of the most important in North America. Salmon have spawned in the Fraser River for thousands of years, and their annual spawning run have provided abundant harvests for aboriginals and, commercial fishers (Johnsen 2001).

Introduction

The objective of this study is to understand sockeye salmon using a model to review the interplay between abiotic habitat characteristics and ecological interactions. During the late summer and autumn along the Fraser River, female sockeye can be found depositing their eggs in gravel beds. After the eggs are laid they incubate over the winter until the fry emerge in spring and then proceed to migrate towards a nearby lake. Once in the lake the salmon stay growing and feeding for either a year or two within the lake, until the fry transform into smolts in the spring. The smolts then make their way to the sea where they will live their lives until it is time for them to migrate back and repeat the process. To understand this complex life cycle and the myriad of interactions that go along with it, a box and arrow diagram was created. This model, in addition to field data will provide a scientific basis for the complex interactions observed within the CCR ecosystem and focus on the life history of sockeye salmon. The model will also serve to inform regional management and research decisions as a specific reference for the current state of the system, especially concerning the potential for ecosystem change within the CCR.

Context
The purpose of this conceptual model is to examine the important linkages between habitat characteristics and the juvenile survival of sockeye salmon *(Onchorhynchus nerka*) within the CCR. The conceptual model has two parts: egg-fry survival and smolt-adult survival (see chapter 11). The first model assesses the factors influencing the egg-fry survival, while the second model examines those influencing smolt-adult survival. There are a number of environmental factors that can influence the

biology of sockeye salmon such as, substrate, water flow, dissolved oxygen, and temperature are known to be particularly important. Additionally, our model as a whole is interconnected and linked to several other sub-models. These include the tectonics model, glaciers model, geomorphology model, hydrology model, water quality model, invertebrates model, terrestrial plant communities model, terrestrial animals model, and resident fishes model (see chapter 1,2,3,4,5,6,7,8,9). The interdisciplinary approach used here is essential to address the complex life cycle of sockeye salmon. Only through integrative and interdisciplinary examination will it be possible to understand the complex interactions involved with the sockeye salmon life cycle.

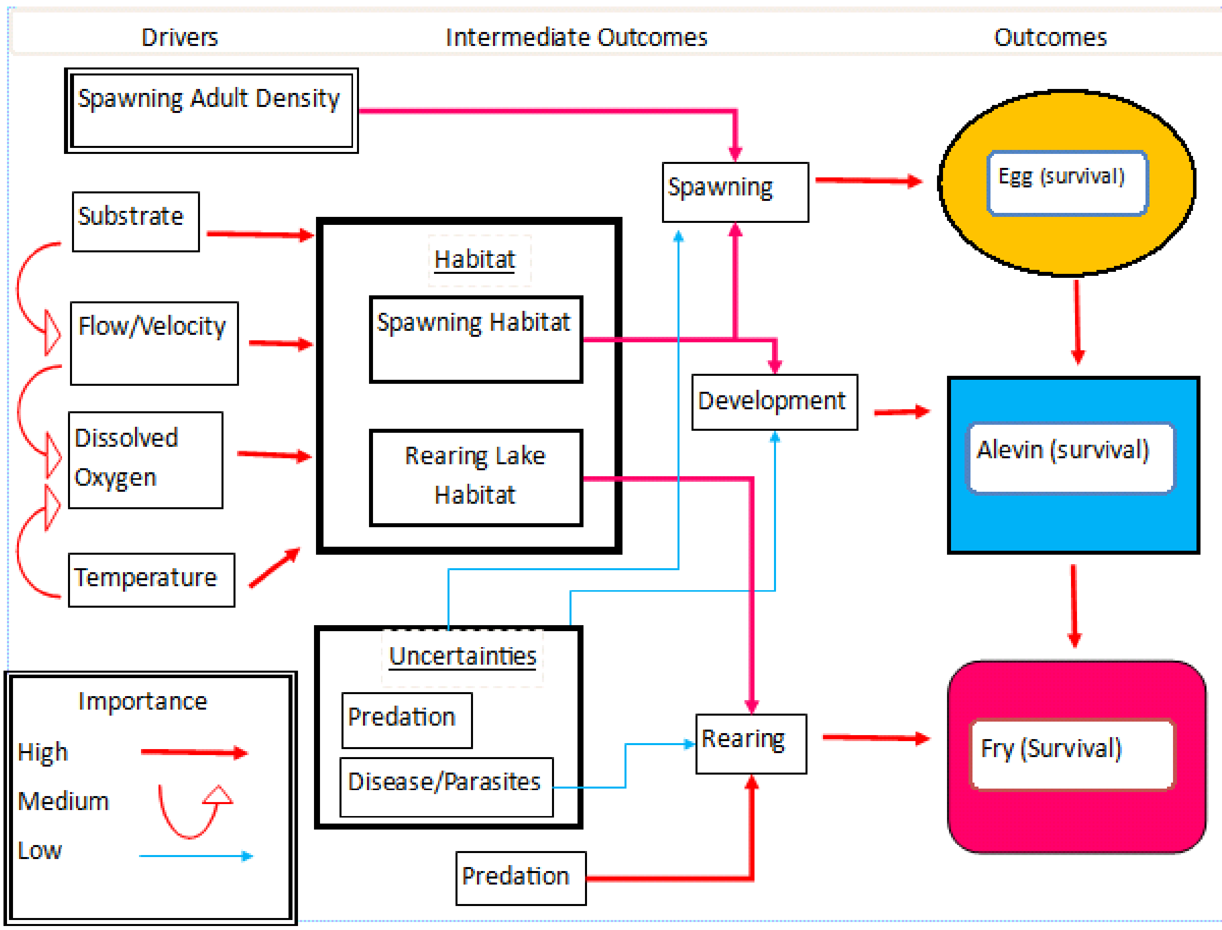

Figure 10.1 Egg-Fry Survival Model
In the present model: egg refers to the pre-hatching stage, alevin refers to the post-hatching stage, and fry refers to the stage beyond complete yolk absorption. The relationships among the drivers and their subsequent outcomes are discussed below. Red linear arrows represent linkages that are important, red curved arrows represent less important linkages and blue arrows are the least important that relatively less well-understood.

Drivers

Substrate

Substrate is a critical element in the sockeye salmon life cycle. Suitable gravel is a crucial component for successful spawning and subsequent egg-fry survival (Northern St'at'imc Fisheries 2008). Although adult sockeye utilize a variety of habitats for their benthic spawning sites, such as river, stream, lakeshore and springs, they generally select a habitat with medium to small sized gravel (Foerster 1968). Reiser and Bjornn (1979) listed gravel sizes from 1.3 to 10.2 cm in diameter as most suitable for sockeye salmon spawning. When the substrate is larger than the considered optimum this may reduce the ability of female salmon to excavate their redds during spawning (Northern St'at'imc Fisheries 2008). There is also a relationship between substrate and flow of oxygenated water. Ideally, the incubation substrate should not have a high proportion of fine sediment as this limits the intra-gravel water movement (Quinn et al. 1995). Drastic reductions in egg survival are observed in field and lab situations when the fine material constitutes more than about 15% by weight of the gravel mixture (Quinn 2005). Excessive fine sediments in the gravel can lower the survival of alevins and fry by clogging their gills and hindering their emergence (Reiser and Bjornn 1979). Substrate is a critical component of the alevin lifecycle because after hatching they seek refuge in interstitial spaces between gravels. Their yolk sac makes movement slow, so they avoid high velocities and rely on the surrounding gravel to facilitate movement.

Flow/Velocity effect

The reliance on the natural flow regime permeates into every phase of sockeye life cycle. Fortunately to this date, the CCR system remains unimpaired without any dams and continues to be a major producer of sockeye salmon in the Fraser River system (Roos 1991). When flows increase, more and more gravel is covered and becomes available for spawning, but as flows continue to increase, velocities in some areas can become too high for spawning (Reiser and Bjornn 1979). As eggs, sockeye need enough flow through the redd to provide oxygen and carry away waste products (Quinn, 2005). Sockeye tend to spawn in areas that experience water velocities around 21-101cm^3/s (Reiser and Bjornn 1979). During high flows, eggs are vulnerable to scour and predators (Quinn 2005). High velocities also present alveins with similar difficulties. A study by Brannon (1965) reveals mortality is greatest among alevins held in high velocities. For Chilko Lake the majority of the spawning occurs at the outlet (Burgner 1991). Once the fry emerge they migrate upstream to enter the lake rearing area (Burgner 1991). Here, fry depend on stable water flow conditions as they actively swim from their spawning area to their rearing area.

Dissolved Oxygen

Dissolved oxygen is an important element of water quality that directly influences sockeye habitat. Sockeye salmon eggs require at least 5mg/L of dissolved oxygen for successful incubation (Reiser and Bjornn 1979). Dissolved oxygen demands of the embryos increase as they develop and reach a peak immediately before hatching (Quinn 2005). Low oxygen concentrations have been shown to affect the rate of development of sockeye salmon, through prolonging the time it takes to hatch (Brannon 1965).

Once the eggs have hatched, alevins can use their gills to pick up oxygen from their surroundings. In contrast to eggs, alveins can tolerate greater extremes by moving to areas of higher oxygen concentrations, and also by circulating water around themselves with their fins (Quinn 2005). There is also an interaction between the dissolved oxygen concentration and the water temperature. The availability of dissolved oxygen is controlled by water temperature as the capacity of water to hold oxygen decreases with increasing temperature.

Temperature

Water temperature is known to be a particularly important factor given its strong effects on energetics and growth. Generally, the optimum spawning temperatures of sockeye salmon range between 10.6 and 12.2°C, while incubation temperatures are between 4.4 and 13.3°C (Reiser and Bjornn, 1979). Each phase of the sockeye lifecycle is highly sensitive to temperature. Incubation above or below the optimum range may increase egg mortality and the frequency of deformed alevins (Murray and McPhail 1988). Egg incubation usually lasts 50-140 days and is primarily dependent on water temperature (Scott and Crossman 1973). Both temperature and its fluctuations are important determinants in the number of days required for incubation and emergence. When alevins are incubated within their optimal temperature range, yolk is converted to tissue with maximum efficiency (Weber Scannell 1992). Individual spawning populations have specific development rates that are related directly to the temperature regime of the spawning site (Figure 10.2) (Brannon 1987). Higher temperatures stimulate faster embryonic development. On average, Chilko sockeye experience a mean incubation temperature of 3.5°C (Figure 10.2). These differences in temperature are local adaptations that ensure that sockeye fry emerge in the spring at the optimal time to take advantage of the spring zooplankton bloom in their nursery lake (Brannon 1987).

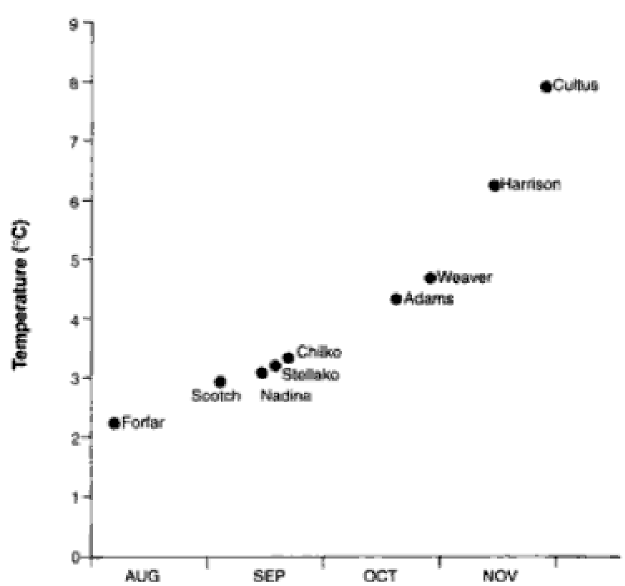

Figure 10.2 Spawning times and mean incubation temperatures of nine Fraser River sockeye stocks from (Brannon 1987). In general Sockeye salmon spawn in late summer and early fall.

Spawning Adult Density

The survival from egg to fry is density dependent for many salmonid populations, especially sockeye that spawn at high densities (Quinn 2005). Competition among spawning females for spawning sites is a common result of high spawning densities. Crowding on the spawning grounds can result in repeated excavations of the same gravel by subsequent females and can cause heavy egg mortality (Krogius and Krokhin 1948). As with other salmonid species, sockeye eggs are vulnerable to physical disturbances during the incubation state (Quinn 2005). Ultimately, the extent of competition varies with adult density and the availability of suitable spawning habitat (Essington et al. 2000).

Intermediates

Habitat

The availability of quality habitat for sockeye salmon is driven by an array of factors, including the physical elements of the habitat (substrate, flow, dissolved oxygen, temperature). Like many fish, sockeye salmon require specific ranges of appropriate substrate, water flow, temperature and dissolved oxygen. Sockeye spend approximately the first half of their life cycle in the freshwater environment. The remainder of the life cycle is spent foraging in estuarine and marine waters of the Pacific Ocean (see Chapter 11). Within the CCR system the majority of spawning occurs at the Chilko lake outlet as this is an ideal spawning habitat. The probability of a habitat being selected for spawning will be the greatest where substrate is between 1.3 to 10.2cm, water velocity does not exceed $101cm^3/s$, dissolved oxygen makes up no less than 5mg/l , and intragravel temperatures are between 4.4 and 13.3°C. Habitats outside of these optimum ranges are less likely to be used by spawners. After spawning the eggs remain in the gravel redd and incubate over the winter until the fry emerge in spring and then proceed to migrate towards a nearby lake. Chilko Lake is the primary rearing lake habitat for sockeye within the CCR system (Quinn 2005). The rearing lake habitat is also influenced by the physical drivers of the CCR and in particular by temperature and flow. Lake temperature and flow drive the productivity of rearing habitat and influence the rearing quality of the lake. Most sockeye fry stay in a lake to feed and grow for one year, with about 25% surviving (Roos 1991) to become seaward migrating smolts (see chapter 11). survival. Sockeye salmon spend an extensive time in freshwater and so the quality of the habitat will directly limit the egg-to-fry survival.

Spawning

Spawning occurs in areas of gravel bottom where there is sufficient oxygenated waterflow through the gravel as these are important habitat elements for spawning. The number of eggs per female increases directly with length, and on average each female sockeye lays about 3500 eggs in the gravel (Quinn 2005). In addition to having advantages related to fecundity, larger females are more successful at competing for redd sites. Sockeye generally spawn at high densities and the crowding on the spawning grounds can lead to competition among females for redd sites. The larger females can construct deeper redds and as a result are presumably more resistant to disturbances by the other females. In summary a females ability to prevail the disturbances brought forth by the high spawning densites and attain a redd site with all the habitat elements will affect spawning success.

Development

Successful development is dependent on the physical elements of the spawning habitat. Alevin requires specific substrate, flow, dissolved oxygen and temperatures during their intragravel development. As a whole, these drivers directly influence the development of alevin by providing the optimal habitat for development. During this intragravel phase alevins are attached to their yolk sac and require suitable gravel as this optimizes the yolk energy for development. The gravel becomes a safe haven from sweeping velocities, thus minimizing the energy depleted on metabolic demands. Flowing water is also important as it helps deliver oxygen to the developing alevein. Temperature plays a vital role as well through regulatory the rate of development of the alevins.

Rearing

Rearing success is directly linked to fry survival. Sockeye fry within the CCR system migrate upstream and spend one full year rearing in the Chilko lake. The variation in rearing success among lakes is primarily related to the availability of food, as well as the lake's temperature. Water temperature and zooplankton availability are prevailing factors controlling growth of sockeye fry in lakes and consequently survival. During this phase, successful rearing will depend on the food availability to help achieve optimal growth. In order to meet the energy demands rearing sockeye salmon commonly display diel vertical migrations in lakes (Quinn 2005). Growth is a product of temperature and food availability. The optimal temperature for rearing varies greatly among habitats in relation food availability. In most rearing habitats the lake environment is oligotrophic and so the optimal temperature is not a high value. High temperatures have high energy demands, and most oligotrophic lakes cannot deliver this level productivity. The environmental conditions experienced during the rearing phase directly affect the fitness at later life stages.

Predation

Predator studies suggest that most of the mortality following emergence is due to predation by other fishes. Fry are highly vulnerable to predation as they emerge and migrate to the rearing lake habitat (Burgner 1991). The degree of predation varies among systems according to the fish assemblage present. In general predatory fishes include trout, charrs, and cottids (see chapter 9) (Burgner 1991). Studies on predation by Dolly Varden on sockeye fry indicate that this species is a primary predator in Chilko Lake (Roos 1991). In general this period is a very crucial stage, one in which mortality from predation is very high and can be extensive.

Outcomes

Eggs

The survival of sockeye eggs is driven by many factors, including the physical elements of the spawning habitat (substrate, flow, dissolved oxygen, temperature) and disturbances brought on by the dense spawning. Losses during incubation are generally influenced by the degree of crowding during spawning and by environmental conditions (Burgner 1991). Given the sensitive state of the eggs, high densities of spawning adults can affect spawning success and in consequence the survival of the eggs. The degree to which density will affect spawning is going to depend on the availability of spawning habitat. Female salmon select and compete among themselves for the best sites. The availability of suitable habitat is controlled by characteristics such as substrate size, flow, dissolved oxygen and temperature. Aside from shaping the spawning habitat these drivers also influence each other. Substrate alone limits intra-gravel flow of oxygenated water through the redd and increasing temperature limits the level of dissolved oxygen. This is a fundamental phase of the life cycle because the great majority of lifetime mortality generally takes place during the period of incubation in the gravel and much of that is related to features of the spawning site (Quinn 2005).

Alevin Survival

Like many fish, sockeye hatch from the egg with the yolk sac still attached. Over the next few months, alveins continue to grow using the nutrients provided by the yolk sac. Unlike eggs, alevins have means of compensating for sub-optimal environmental factors such as decreased water flow, and low oxygen levels, but they are not impervious to poor substrate environments. After hatching, alevins can breathe with their gills and can also move. These adaptations allow alevins to pick up oxygen more efficiently and if conditions become unfavorable move to more favorable conditions. However when the spawning habitat lacks appropriate substrate this directly constrains alevin development. During development alevins bury themselves among the substrate and depend on this to maximize the efficiency of their yolk. Without suitable gravel the energy from the yolk is altered as more of it is used for active swimming and less is available for development. Once more we see the physical elements impact the state of the spawning habitat except here, the state of the spawning habitat will determine the development success of the alevin. Taken as a whole, the single greatest contributor to the alevin phase will certainly be the number of eggs that survive the transition phase.

Fry survival

After emerging from the gravel sockeye fry depend on their rearing lake habitat and its intrinsic rearing productivity. During this lake residence, fry are considered to be food-limited as most lakes are usually oligotrophic (Quinn 2005). The productivity of the rearing lake habitat is important because this is directly related to the availability of food. The availability of food in the rearing lake habitat ultimately determines the rearing success and consequently survival of sockeye fry. In the nursery lakes of British Columbia, the common zooplankton prey for sockeye fry includes Cladocera (Bosmina and Daphnia) and copepods (Cyclops and Epischura) (Foerster 1968). The availability of these important food items are driven by the quality of rearing habitat which is primarily related to factors like lake temperature. At Chilko lake, recorded fluctuations in fry growth have been directly correlated to the temperatures during lake residence (Quinn 2005). After a year of rearing in the lake habitat, fry take their chances at sea (see chapter 11).

Uncertainties

The role of disease and parasites on sockeye salmon has not received nearly enough as much attention as it should. Studies on agents of mortality tend to focus on the attributes of the habitat while the role of disease in natural populations is relatively less well-understood. The average survival from egg deposition up to emergence is generally estimated on the basis of the physical elements of the habitat (substrate, flow, dissolved oxygen, temperature) including disturbances brought on by the dense spawning. Diseases and parasites certainly do exist; the infectious hematopoietic necrosis virus (IHNV) is a common virus that affects salmon but in particular sockeye (Quinn 2005). The prevalence in nature is not completely known but major outbreaks have occurred. The first confirmed outbreak in the wild occurred at Chilko Lake among the fish of the 1972 brood (Williams and Amend 1976). The IHNV severely reduced the survival during the egg-to-fry stage of the life cycle to a low 3.8% (Williams and Amend 1976). The exact pathway of transmission is not well-understood; what is known is that it affects salmon during the egg-to-fry stage.

Predation on eggs and alevins is also a less-well understood interaction. The physical and chemical factors shaping the affecting the spawning habitat, are generally thought as the most important mortality factors. Many observations have been made on the feeding activities of predatory fishes on eggs while sockeye spawn (Burgner 1991). However in most cases it was concluded that the majority of the eggs eaten were those dislodged during spawning. Aside from the vulnerability to predation brought on by the disturbance, disturbed eggs in general have a low chance of survival (Foerster 1968).In general losses due to predation have not been quantified for sockeye eggs or embryos.

Summary

There is a delicate balance between productivity of a species and its environment. At each stage of egg-to-fry cycle the environment played a critical role in governing survival. Both the rearing and spawning habitat were ultimately driven by substrate, flow, dissolved oxygen, and temperature. Aside from the important linkages to the habitat these drivers also influenced one another. This model is important in the fact that it allows us to view drivers, the intermediates, and the outcomes of the early freshwater life cycle of sockeye salmon. Sockeye salmon spend an extensive time in freshwater and so the quality of the habitat will directly limit the egg-to-fry survival. Salmon are products of their environment and the model created plays a key part in helping to identify major influences.

Literature Cited

Brannon. E. (1965). The influence of physical factors on the development and weight of sockeye salmon, embryos and alevins. INT PACIFIC SALMON FISH COMM PROGR REP, ((12)), 1-26.

Brannon, E. (1987). "Mechanisms stabilizing salmonid fry emergence timing." Canadian Special Publication of Fisheries and Aquatic Sciences **96**: 120-124

Burgner R.L. (1991) Life history of sockeye salmon. Pp. 3–117 in C. Groot and L. Margolis, eds. *Pacific Salmon Life Histories*. University of British Columbia Press, Vancouver.

Essington, T.E., Quinn, T.P., and Ewert, V.E. 2000. Intra- and inter-specific competition and the reproductive success of sympatric Pacific salmon. Can. J. Fish. Aquat. Sci. 57(1): 205-213. Doi: 10. 1139/cjfas-57-1-205

Foerster, R.E. 1968. The sockeye salmon, Oncorhynchus nerka. Bull. Fish. Res. Board Can. 162. 422 pp.

Johnsen, D.B. 2001. Customary law, scientific knowledge, and fisheries management among northwest coast tribes. N.Y. Univ. Environ. Law J. 10: 1-69.

Murray, C. and J. McPhail (1988). "Effect of incubation temperature on the development of five species of Pacific salmon (ONcorhynchus) embryos and alevins: Canadian Journal of Zoology 66(1): 266-273.

Northern St'at'imc Fisheries, . "Rehabilitation of Sockeye Spawing gravel in the Gates Creek spawning channel." *BC Hydro Bridge Coastal Fish and Wildlife Restoration Program* (2008): 1-15. Web. 3 Jun 2011.

Quinn, T.P., Hendry, A.P., and Wetzel, L. A. 1995. The influence of life history tradeoffs and the size of incubation gravels on egg size variation in sockeye salmon (Oncorhynchus nerka).- Oikos 74: 425-438.

Reiser, D.W., and T.C. Bjornn. 1979. Habitat requirements of anadroumous salmonids. U.S. For. Serv., Pac. Northwest For. Range Exp. Stn. Gen. Tech. Rep. PNW-96. 54 pp.

Roos, J.F. 1991. The history of the International Pacific Salmon Fisheries Commission, 1937-1985. Pacific Salmon Commission Vancouver, B.C.

Scott, W.B., and E.j> Crossman. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184. 966 pp.

Weber Scannell, Dr. Phyllis K. "Influence of temperature on freshwater fishes: A literature review with emphasis on species in Alaska." *Alaska Department of Fish and Game* 91.1 (1992): 1-53. Web. 3 Jun 2011.

Williams, I.V., and D.F. Amends. 1976. Natural Epizootic of Infectious Hematopoietic Necrosis in Fry of Sockeye Salmon (Oncorhynchus nerka) at Chilko Lake, British Columbia. Journal of the Fisheries Research Board of Canada **33**(7): 1564-1567

(1976). "A Natural Epizootic of Infectious Hematopoietic Necrosis in Fry of Sockeye Salmon (Oncorhynchus nerka) at Chilko Lake, British Columbia." Journal of the Fisheries Research Board of Canada **33**(7): 1564-1567.