# Interactions Between Sockeye Salmon, Kokanee and Rainbow Trout in Quesnel Lake

## A Workshop on Planning for Future Research


Workshop Attendees (left to right): Rick Holmes, Eddy Carmack, John Morrison, Christian Guill, Svein Vagle, Brian Riddell, Ellen Petticrew, Rob Dolighan, Barbara Drossel, Michael Drossel, Tyler Weir, Sebastian Dale, Sam Albers, Jeremy Hume, Christoph Schmitt

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**Executive Summary and Recommendations:**

In September, 2011, fourteen researchers keenly interested in processes and production in interior sockeye salmon lakes, and specifically Quesnel Lake, British Columbia, met at the Elysia Lodge, overlooking Quesnel Lake to share data, discuss the present understanding of the lake ecosystem and to identify knowledge gaps and directions for future research on the lake. A significant portion of the workshop-discussion centered on a recently developed model for life cycle structuring of sockeye in Quesnel Lake.

Representatives from Fisheries and Oceans Canada (DFO), British Columbia's Ministry of Forests, Lands and Natural Resource Operations, University of Northern BC's Quesnel River Research Centre, the Technical University of Darmstadt (Germany) and the Pacific Salmon Foundation attended. Participants provided presentations indicating the data that are available in their agency/group on the Quesnel system and questions of interest which their work addressed. Several researchers who were invited were not able to attend but identified scientific papers of interest or provided questions for discussion.

Quantitative models developed to forecast population sizes already exist. These models depend on continuous input from empirical data, giving reasonable forecasts over a year or so. The life cycle structuring model that was presented at the meeting was developed by Christian Guill and Barbara Drossel (University of Darmstadt, Germany) (Guill et al. 2011) and is not such a forecasting model. This particular model serves the purpose of gaining mechanistic understanding of the causes of cyclic dominance and the effects of various factors, such as fishing, kokanee, etc., on population dynamics. One of the main goals of the meeting was to determine how available data on the lake can be used to test and expand this model to more accurately reflect the lake's food-web.

Also, there was significant discussion about what additional information is needed to develop this model into a practical and useful tool for research and resource management of interior salmon lakes. An interactive version of the model, provided by Carl Walters (UBC), was presented and used to numerically experiment with a range of predator-prey scenarios.

Given the social-ecological importance of Quesnel Lake and the complexity of questions challenging to its effective management, it is recommended that a multidisciplinary and multi-organizational research program is put in place to test hypotheses and develop the modeling and predictive tools needed by resource managers at multiple levels in order to better manage large lake ecosystems like Quesnel Lake in a sustainable and environmental fashion.

As a result of data review and model results, three ***central working hypotheses*** to guide ongoing and future research emerged from the workshop discussions:

1. The carrying capacity of Quesnel Lake is limited by overall nutrient supply and timing of local availability. How might this change as a result of climate change or other drivers?

2. Increased returns of sockeye to spawning grounds result in decreased kokanee abundance, which in turn, results in decreased production of rainbow trout, and visa versa.

3. Continued and focused observational studies integrated with an improved model, or set of models, will allow managers to better predict the effect on sockeye, kokanee, and rainbow trout abundances arising from changes in possible drivers, including: climate change, fishing pressure, stream modifications, precipitation rates, increased lake stratification, air and water pollution, lake dynamics associated with seiching and wind forcing, etc.

At the end of the workshop everyone was asked to consider what data collection/research they would be interested in working on over a five year period as well what they would like to see others doing within a larger collaborative five-year project. A request was also made for names (or areas of expertise) of other individuals who could be included or contacted regarding the larger project. Detailed responses are included in Appendix 1.

**Rationale for using Quesnel Lake as the focus of a watershed-lake food-web research program:**

Quesnel Lake is as a system well-suited for conducting a full-scale food-web modeling study. Many of the characteristics of the Quesnel ecosystem are widely applicable and there are a number of scientific and logistic conditions which generate a confluence of opportunity for studying Quesnel Lake, the “Queen of Lakes”.

This work will build on an existing two decades-long data set already available within DFO, the provincial government, UNBC, UBC and so on. All available data need to be cataloged, data gaps and monitoring procedures need to be defined and described and this information needs to be incorporated into suitable models, such as the Guill-Drossel Cyclic Dominance (GDCD) model (described below). However, it was also identified during the workshop that there is a need to expand the focus of this work to address full watershed-lake and food-web dynamics in the Quesnel system.

As noted, the information and knowledge base on Quesnel Lake is held by a large number of individuals located over a range of institutions and disciplines; this makes the interested researchers or “Great Group” interdisciplinary as well as intergenerational (see Fig.1 in Appendices). There is a strong economic as well as ecologic argument for pursuing the study of this system before most of this knowledge base is lost due to retirement and/or agency data burial.

The region has several resorts providing accommodation over the large land mass surrounding the lake as well as a university research station, UNBC's Quesnel River Research Centre (QRRC),that can support open water and tributary research. Laboratory and fish rearing facilities are also available at QRRC. Communication, via science outreach, between residents of the watershed and lake users has been underway over the past decade though QRRC which should enhance collaboration and support for future research from local stakeholders.

Quesnel Lake is an exceptional water body in being the world's deepest inland fjord lake and having distinctive physical processes which in turn regulate temperature regimes, mixing and nutrient dispersion, thereby controlling the biological responses. The inland salmon stocks are economically important for sport fishing, open water commercial fishing as well as for a relatively new First Nations proposal to obtain licenses for commercial fishing on the lake itself. Scientifically, fishing can be considered as another predator within the models allowing for estimates of its impact and sustainability. The lake is oligotrophic, thereby sequestering available nutrients rapidly for use in the food chain. A number of large tributaries delivering nutrients to the lake are available for research, some of which support salmon stocks and others that do not.

The lake itself is in a region where several other large lakes supporting sockeye have different configurations (e.g. Chilko salmon spawn downstream of the lake not upstream as here). Both the tributary conditions and the regional lake variations enhance natural experimental comparison. The lake is not truly pristine as its watershed has supported and continues to support a forest harvesting industry. As well, a growing mining sector in the province has identified development of copper-gold extraction in and around the watershed. This may be a very opportune time to begin a more intensive full lake study given the interest the BC government has in expansion of mining.

As indicated earlier a large data and knowledge base on the Quesnel Lake food-web is available - albeit dispersed among various agencies and institutions - and it is timely to follow up with collaborative research on these issues while the interested parties are still active researchers.

**The Guill-Drossel Cyclic Dominance Model:**

The trout/salmon/plankton foodweb is an example of a complex system that shows cyclic dominance, but also a variety of other dynamical patterns and bifurcations. The Guill-Drossel Cyclic Dominance Model (GDCD) is a simple three-species model that produces the phenomenon of cyclic dominance. The model includes population dynamics equations for sockeye, a predator (rainbow trout), and the zooplankton food of the sockeye fry in their nursery lake. The migration of the sockeye smolts to the ocean and spawning at age 3+ or 4+ is taken into account via the survival probability and average number of offspring. When the fry carrying capacity of the lake is large enough, the model shows cyclic dominance, i.e., a 4-year oscillation of the sockeye population, with the typical sequence of a dominant, a subdominant, and two weak years. When the carrying capacity is not large enough, this oscillation does not occur. A mathematical analysis of this model reveals that this phenomenon will occur whenever a few general conditions are satisfied; the precise mathematical formulation of the model may vary. These conditions are that the lake is large enough to support sufficiently large fry and predator populations, that the majority of sockeye return at age 3+ to spawn, and that the coupling between the predator and the sockeye fry is sufficiently strong that the dynamics of both species is affected by their interaction. When a control parameter, such as survival, competition strength or carrying capacity is varied, the model can undergo transitions to other types of dynamics, such as a period-2 oscillation or chaos. The parameter changes that may trigger such bifurcations may occur due to external influences such as climate, fisheries policies, or lake fertilization. Understanding the effect of these influences on the dynamics of the foodweb is of prime importance due to economic and conservational reasons. Evaluating the response to fisheries would allow an estimate of optimal fishing quotas that maximize sustainable gain. Evaluating the response to various types of perturbations – through numerical experimentation - will aid in the assessment of the risk they carry. The abstract of the Guill et al. (2011) paper and a weblink to it is included here as Appendix 2.

**Sockeye/Kokanee/Rainbow Interactions**

Rob Dolighan and Dale Sebastion (BC) led discussions regarding the effects of sockeye on the Quesnel system. Summaries of past work (1988-1994) on rainbow trout diet, analysed via stomach content, confirmed the importance of O. nerka in the Quesnel Lake foodchain. Age 1 and 2 kokanee were clearly the most important component in rainbow diet following non-dominant and subdominant sockeye runs, while sockeye fry were by far the most numerous in rainbow stomachs following a dominant sockeye run. However, because of body size to weight differences between sockeye and kokanee, the biomass of the lower numbers of age 1-2 kokanee eaten by rainbow was still significant in their diet. The most interesting and counter-intuitive result was that the mean total biomass of O+ nerka eaten declined as sockeye fry numbers in the lake increased. The lower stomach content biomass was due almost entirely to the lower numbers of age 1-2 kokanee eaten during dominant sockeye years, presumably due to the predators investing more energy in chasing the abundant but smaller sockeye fry. This appears to explain how rainbow growth can decline in the presence of high juvenile sockeye densities. Cyclic dominance in the sockeye population may further exasperate foraging problems for rainbow trout as the densities of O+ nerkids are typically very low in the off years. While confirmation of the data is required, it appears that the densities of total nerkids (following the kokanee collapse) ranged from approximately 20,000 to 30,000 per hectare in high years to under 500/ha in the off years. As such, the frequency of encountering prey may be reduced.

Although further work needs to be carried out, there appears to be a link between nerkid abundance and rainbow trout survival in Quesnel Lake: in a more controlled situation (kokanee spawning channels and annual fertilization programs) spawning populations of Gerrard rainbow in Kootenay Lake showed poor returns in 2001 to 2003 following significant declines in kokanee abundance. The declines in kokanee abundance in this case were apparently a direct effect of reduced nutrients

**Workshop Comments on the Model and Future Research:**

From the workshop suggestions for future research directions were made and circulated to both attendees and to other interested researchers to begin a discussion of potential collaborative opportunities. From this a set of working hypotheses were generated. The comments below incorporate both the workshop and subsequent email discussion.

1) C. S. (Buzz) Holling asked if there have been any efforts to validate the Guill-Drossel model. If not, what data and approaches would be needed?
2) John Morrison (DFO) provided a simple spreadsheet model that uses randomly generated numbers to simulate changes in cycles of a population. He suggests that his model generates the four year cycle noted in sockeye, and that if a random generator can do this we need to think carefully about how we describe biological behavior with other mathematical models. He calls his model "the lead (Pb) standard", suggesting that some alchemy, or possibly a Midas touch may be required to attain the gold!
3) Kim Hyatt, who was not in attendance but was involved in the email discussion, comments that it was an interesting narrative and perhaps one with several themes that require further exploration. For example, the seldom tested but still popular view is that fluxes of nutrients and energy provided by salmon returning to spawn shift the entire ecosystem to higher production levels. In this view, although within year or limited year impacts of higher sockeye abundance on kokanee and rainbow trout might be negative, the time weighted effect would be expected to result in higher production as lower trophic levels respond to higher nutrient loading over decades of time in Quesnel Lake and upper trophic level species like rainbow trout receive a late summer-fall energy subsidy in the form of an abundance of sockeye eggs associated with dominant year returns. Although both of these processes fall outside of the time frame and focus

of current results and analysis, they too require consideration along the path to eventually generating useful advice for resource managers attempting to balance multi-species management objectives. Kim indicated that while he is not familiar with the model presented at the workshop and/or the data available on Quesnel Lake he and Don McQueen have been undertaking bioenergetic approaches to determine the strength of competitive interactions among juvenile sockeye, juvenile kokanee, older age classes of kokanee and lake whitefish in Skaha Lake (BC) to test for impacts of re-introducing sockeye to the lake on resident fish. They have been impressed with the use of the bioenergetic approach and he suggested that if the zooplankton, sockeye and kokanee data sets for Quesnel Lake are of high enough quality (e.g. minimum of monthly samples and egg counts for zooplankton, bimonthly samples with size by age-class for sockeye and kokanee), bioenergetics based production-consumption analysis might provide additional insight into abundance and/or production thresholds at which species interactions would be intense enough to account for changes in fish growth, survival and production outcomes.

4) To address these issues, Sam Albers and Ellen Petticrew (UNBC) have been working on marine derived nutrient transfers in the Horsefly Basin of Quesnel Lake. As indicated by Hyatt above, an often cited, yet rarely tested, hypothesis is that the pulse of nutrients provided by returning salmon can shift freshwater nursery habitats to higher production levels. This hypothesis, however, remains contested and uncertain. For example, in high return years juvenile density dependence may restrict salmon-derived nutrient (SDN) productivity benefits for the next generation. Following these larger runs, however, adult carcass SDN loading may confer size and survival benefits to the next generation of juvenile salmon via increased nursery lake food web productivity. Currently SDN and productivity transfers from adults to juveniles, particularly the timing and magnitude, remain poorly understood. Spawning salmon, for example, modify both physical and biological riverine habitat in ways that potentially regulate SDN loading to nursery lakes. At high spawner densities salmon spawning and decay products can result in gravel bed nutrient sequestration and fewer SDNs transported to downstream nursery lakes thereby limiting lake productivity. These sequestered nutrients may be seasonally retained and exported during spring freshet, influencing subsequent temporal patterns of food web productivity for juvenile sockeye salmon. A project aimed to test the presumed relationship that SDNs transfer productivity to nursery lakes and subsequent generations of salmon over the complete yearly pattern of a snow melt dominated hydrograph is required. The objectives of this project being undertaken by Petticrew and Albers would be to determine the magnitude of SDN retention in spawning streams during high and low spawner densities, the spatio-temporal impacts on nursery lake productivity, and the implications of riverine SDN storage on the growth and survival of juvenile salmon.

*5)* Brian Riddell (PSF) suggested at the workshop that an inventory of the available Quesnel Lake data sets be undertaken as a first step in planning a larger study. This concern was brought forward again during post-workshop discussions as knowledge of the format, location and quality of the data sets is clearly required in the development of future proposed research (see 3 and 4 above).

**Our Potential *Central Hypotheses* for future testing**

1. *The carrying capacity of Quesnel Lake is limited by overall nutrient supply and timing of local availability. How might this change as a result of climate change or other drivers?*

2. *Analysis of recent data suggests that increased returns of sockeye to spawning grounds result in decreased kokanee abundance, which in turn, results in decreased production of rainbow trout, and visa versa.*

3. Continued and focused observational studies integrated with an improved model, or set of models, will allow managers to better predict the effect on sockeye, kokanee, and rainbow trout abundances arising from changes in possible drivers *including: climate change, fishing pressure, stream modifications, precipitation rates, increased lake stratification, air and water pollution, lake dynamics associated with seiching, wind forcing, circulation and mixing.*

**Where do we go from here?**

Christian Guill, Svein Vagle and John Morrison looking for future data in Quesnel Lake. September, 2011.

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