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FERTILIZATION EXPERIMENT
SUMMARY REPORT - 1999 to 2004**

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SUMMARY REPORT - 1999 to 2004**

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ABSTRACT

The Arrow Lakes food web has been influenced by several anthropogenic stressors during the past 45 years. These include the introduction of mysid shrimp (*Mysis relicta*) in 1968 and 1974 and the construction of large hydroelectric impoundments in 1969, 1973 and 1983. The construction of the impoundments affected the fish stocks in Upper and Lower Arrow lakes in several ways. The construction of Hugh Keenleyside Dam (1969) resulted in flooding that eliminated an estimated 30% of the available kokanee spawning habitat in Lower Arrow tributaries and at least 20% of spawning habitat in Upper Arrow tributaries. The Mica Dam (1973) contributed to water level fluctuations and blocked upstream migration of all fish species including kokanee. The Revelstoke Dam (1983) flooded 150 km of the mainstem Columbia River and 80 km of tributary streams which were used by kokanee, bull trout, rainbow trout and other species.

The construction of upstream dams also resulted in nutrient retention which ultimately reduced reservoir productivity. In Arrow Lakes Reservoir (ALR), nutrients settled out in the Revelstoke and Mica reservoirs, resulting in decreased productivity, a process known as oligotrophication. Kokanee are typically the first species to respond to oligotrophication resulting from aging impoundments.

To address the ultra-oligotrophic status of ALR, a bottom-up approach was taken with the addition of nutrients (nitrogen and phosphorus in the form of liquid fertilizer from 1999 to 2004). Two of the main objectives of the experiment were to replace lost nutrients as a result of upstream impoundments and restore productivity in Upper Arrow and to restore kokanee and other sport fish abundance in the reservoir.

The bottom-up approach to restoring kokanee in ALR has been successful by replacing nutrients lost as a result of upstream impoundments and has successfully restored the productivity of Upper Arrow. Primary production rates increased, the phytoplankton community responded with a shift in species and zooplankton biomass was more favourable for kokanee. With more productive lower trophic levels, the kokanee population increased in abundance and biomass, resulting in improved conditions for bull trout, one of ALR's piscivorous species.

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Introduction

Lake fertilization has been widely used in lakes and reservoirs throughout British Columbia and Alaska as a technique for improving sockeye and kokanee stocks (Stockner and MacIsaac 1996; Perrin et al. 2006; Ashley et al. 1999). Prior to fertilization, systems such as Arrow Lakes Reservoir, Kootenay Lake, Packers Lake, and Wahleach Reservoir were ultra-oligotrophic (Pieters et al. 1999; Ashley et al. 1999; Perrin et al. 2006; Mazumder and Edmundson 2002). An ultra-oligotrophic reservoir or lake has extremely low levels of nutrients, which results in low productivity and biomass at all subsequent trophic levels in the aquatic food web. To address the ultra-oligotrophic status of these systems, a bottom-up approach was taken with the addition of nutrients (nitrogen and phosphorus in the form of liquid fertilizer) to increase the production of *Daphnia*, a main food source for kokanee. Lake fertilization has been a successful technique used for both the enhancement and conservation of sockeye salmon populations (Hyatt et al. 2004). Fertilization has also been successful in restoring kokanee populations in lakes and reservoirs altered by hydroelectric construction (Ashley et al. 1999; Perrin et al. 2006).

In Arrow Lakes Reservoir (ALR), kokanee (*Oncorhynchus nerka*) are a keystone species, because they are a forage fish for predators such as bull trout (*Salvelinus confluentus*) and rainbow trout (*Oncorhynchus mykiss*). In the late 1980s and early 1990s, Upper and Lower Arrow tributary streams supported approximately 600,000 to 800,000 spawning kokanee, but the numbers declined to a low of 108,000 in 1997. As the number of kokanee decreased, there was no increase in size, an observation consistent with nutrient limited conditions (Pieters et al. 2003a). The decline in the kokanee population in ALR resulted in a two-year limnological study of the reservoir in 1997 and 1998. A fertilization program was then initiated in 1999 to try and restore kokanee populations by replacing nutrients lost from upstream impoundments. The project was modelled on the existing, successful Kootenay Lake fertilization project (Ashley et al. 1999; Wright et al. 2002; Schindler et al. 2006a).

This report presents a summary of six years of fertilization experiment data (1999 to 2004) with two years of pre-fertilization lower trophic data (1997 and 1998) and varying years of pre-fertilization kokanee data. Detailed history, methods, and results are documented in Pieters et al. 1998, 1999, 2000, 2003b, 2003c and Schindler et al. 2006b. Costs of the fertilization project are found in Appendix 1.

Study Area

Arrow Lakes Reservoir originally consisted of two lakes, Upper Arrow Lake and Lower Arrow Lake, which lie between the Selkirk and Monashee mountain ranges in southeastern British Columbia (50 °N and 118 °W). These lakes were changed into a reservoir when the Hugh Keenleyside Dam was constructed in 1969, flooding the narrow strip of land separating them (Fig. 1). There are two additional dams on the main tributary, the Columbia River, which flows into the north end of Upper Arrow. The Mica Dam was constructed in 1973 and the Revelstoke Dam in 1983. Both the Mica and Hugh

Keenleyside dams were constructed under the terms of the Columbia River Treaty and are operated for hydroelectric generation and flood control. These operations altered the hydrology of the lakes: the mean water level of the Arrow lakes rose by 12.6 m and mean water level variation doubled from 8 m to 15.5 m with peak variations of 20 m. Before impoundment, water levels remained near the low water level throughout the year with a brief peak in the spring. Reservoir operations also altered the hydrology of the Columbia River and changed the timing of its inflow to the reservoir. The spring peak flows were reduced and there is more variable flow throughout the year.

At full pool, ALR has a surface area of 464.5 km² at mean water level and a mean elevation of 342.4 m. Upper Arrow has six major tributaries and 25 minor tributaries, and Lower Arrow has four major tributaries and 26 minor tributaries. The ALR is 240 km in length, has a mean depth of 83 m, a maximum depth of 287 m and a mean width of 1.8 km (Pieters et al. 2003a).

Causes of Kokanee Decline

The construction of upstream impoundments affected the fish stocks in Upper and Lower Arrow lakes in several ways. The construction of Hugh Keenleyside Dam resulted in flooding that eliminated an estimated 30% of the available kokanee spawning habitat in Lower Arrow tributaries and at least 20% of spawning habitat in Upper Arrow tributaries (Andrusak, 1969; Sebastian et al 2000). The Mica Dam contributed to the water level fluctuations and blocked upstream migration of all fish species including kokanee. The Revelstoke Dam flooded 150 km of the mainstem Columbia River and 80 km of tributary streams which were used by kokanee, bull trout, rainbow trout and other species. The dam also blocked upstream passage to an estimated 500,000 kokanee spawners (Martin 1976). As compensation for some of the lost kokanee habitat resulting from dam construction, the Hill Creek spawning channel (capacity of 150,000 kokanee spawners) was completed in 1980.

The construction of upstream dams results in a boom-and-bust nutrient response (Horne and Goldman 1994; Ney 1996; Stockner et al. 2000). In other words, nutrient retention by upstream impoundments ultimately reduces reservoir productivity. In ALR, nutrients settled out in the Revelstoke and Mica reservoirs, resulting in decreased productivity, a process known as oligotrophication. Kokanee are typically the first species to respond to oligotrophication resulting from aging impoundments (Ney 1996), and the kokanee in ALR are no exception. The pre-impoundment annual escapement in the Upper and Lower Arrow lakes was estimated at 0.8 to 1.6 million kokanee by Sebastian et al (2000) using three different methods. The post-impoundment escapement declined as low as 108,000 kokanee.

In addition to the lost habitat and oligotrophication caused by impoundments, kokanee populations have been negatively affected by an exotic species. *Mysis relicta*, a small exotic crustacean, was introduced into ALR in mid-1968 and again in 1974 (Northcote, 1991; Sebastian et al. 2000). *M. relicta*, also referred to as mysid shrimp, was discovered

to be a major competitor for the zooplankton species (*Daphnia*) preferred as a food source by kokanee.

Additional Fish Stocks

As well as kokanee, ALR supports a variety of other fish species, including rainbow trout and bull trout. Based on work of Martin (1976) Lindsay (1977a and b) and Paish (1974) an estimated 1000 rainbow spawners and 4000 bull trout spawners were blocked by the Revelstoke Dam (Sebastian et al 2000). A stock of smaller-sized native rainbow trout also contributed to the ALR sport fishery. Lindsay and Seaton (1978) estimated losses of these smaller rainbow at 1250 spawners per year based on an estimated 30% loss of spawning and rearing habitat through flooding of Arrow Lakes tributaries. Production of small rainbow trout occurred at the Hill Creek Hatchery from 1983 to 2000. A bull trout stocking program began in 1981 at Wardner Hatchery and then Hill Creek Hatchery starting in 1983, but was discontinued in 1999 following an evaluation by Winsby and Stone (1996).

Gerrard rainbow trout were stocked into ALR from 1984 to 1997. The stock originated from Kootenay Lake and was introduced into ALR in an attempt to provide a sport fishery for the public. The stocking was discontinued in 1998 as a result of the decline in kokanee.

Methods

Study design

Prior to initiating nutrient additions to ALR, limnological information was collected for two years, 1997 and 1998, which were considered to be control years (Pieters et al. 1998, 1999). During these years, two extremes in climate were observed; 1997 was a year with high flow and 1998 was a year with low flow (Pieters et al. 1999).

The ALR fertilization experiment began in 1999 with four objectives:

1. To replace nutrients lost as a result of upstream impoundments and restore the productivity in Upper Arrow to pre-impoundment conditions;
2. To restore the abundance of kokanee and other sport fish through the continued application of appropriate quantities of fertilizer
3. To implement and document an appropriate monitoring program to provide the data necessary to evaluate the long-term response to fertilizer addition;
4. To evaluate the long-term response to fertilizer addition and make recommendations for future phases of enhancement works if required.

An adaptive management approach was applied to this experiment (Walters 1986).

Nutrient application

Nutrient additions to ALR were based on the successful Kootenay Lake fertilization experiment (Ashley et al. 1999; Wright et al. 2002). Total phosphorus loading was targeted at 274 mg/m² per season (Table 1). This loading rate was similar to that used for

Kootenay Lake and other nutrient addition experiments in British Columbia (Perrin et al. 2006).

Nutrients were added to ALR in the form of liquid fertilizer (ammonium polyphosphate 10-34-0 and urea ammonium nitrate 28-0-0). Nutrients were added from the end of April through the beginning of September from 1999-2003 and through mid-September in 2004. The total annual load was as follows:

- In 1999-2002: 52 metric tons of phosphorus and 232 metric tons of nitrogen;
- In 2003: 52 metric tons of phosphorus and 268 metric tons of nitrogen;
- In 2004: 39 metric tons of phosphorus and 278 metric tons of nitrogen.

The nutrient additions were applied to the north end of Upper Arrow from the DEV Galena ferry between Galena Bay and Shelter Bay. Details of additions for each year are described in a series of reports (Pieters et al. 2000, 2003b, 2003c; Schindler et al. 2006b).

The seasonal loading of fertilizer was intended to simulate pre-impoundment spring freshet conditions for phosphorus loading (following a natural hydrograph) and to compensate for biological uptake of dissolved inorganic nitrogen as the season progressed. Weekly nitrogen loading began with low rates in the spring and increased through the summer in an attempt to inhibit the growth of blue-green algae which can be associated with low N:P ratios (Pick and Lean 1987). The fertilizer N:P ratio was 0.67:1 (weight:weight) at the beginning of each season and was modified at three to four week intervals, with increases as follows:

- In 1999 to 2002: from 0.67:1 to 7.5:1;
- In 2003: from 0.67:1 to 9:1;
- In 2004: from 0.67:1 to 17:1.

Based on an area of 193 km², the fertilizer applications corresponded to a range of weekly phosphorus loading from fertilizer of 7.5 mg/m² to 22.5 mg/m² depending on the week of the application season in 1999 to 2003 and from 7.5 mg/m² to 20 mg/m² in 2004. The range of weekly nitrogen loading from fertilizer was 5 mg/m² to 135 mg/m² in 1999 to 2003 and from 5 mg/m² to 141 mg/m² in 2004 (Fig. 2).

Table 1. Total nitrogen (N) and phosphorus (P) loading rates (mg/m²) to Upper Arrow, before (1997 and 1998) and during (1999-2004) fertilizer applications. Nitrogen from natural sources is in the form of dissolved inorganic nitrogen (DIN; DIN = NH₃ + NO₃ + NO₂). Phosphorus from natural sources is in the form of total dissolved phosphorus (TDP).

Year	Load from fertilizer N (mg/m ²)	Load from fertilizer P (mg/m ²)	Load from natural sources * DIN (mg/m ²)	Load from natural sources * TDP (mg/m ²)
1997			14,457	390
1998			11,245	198
1999	1203	274	14,859	235
2000	1203	274	14,659	247
2001	1203	274	9,438	191
2002	1203	274	10,643	233
2003	1389	272	9,036	289
2004	1436	180	10,850	235

*1997-2003 data from Schindler et al. 2006b; 2004 data from Schindler, unpublished data

Physical limnology

Once every month from May to October in 1998 and from April to November in 1999 to 2004, water transparency, temperature, oxygen, and turbidity were measured at stations AR 1-8 (Fig. 1). A standard 22-cm diameter, black-and-white Secchi disk was used to measure water transparency. A HydroLab was used to take temperature, oxygen, and turbidity profiles at 1-m intervals from 0 to 50 m and at 5-m intervals from 50 to 100 m.

Water chemistry

Integrated water chemistry samples were collected monthly from May to October in 1998 and from April to November in 1999 to 2004 at all stations, AR1 – AR8 (Fig. 1). An integrated column of water was retrieved using a 2.54-cm (inner diameter) sampling tube; the column extended from 0 to 30 m in 1997-2003 and from 0 to 20 m in 2004. Discrete water samples at 2, 5, 10, 15, and 20 m were collected from June to October in 2003 and 2004 using a van Dorn sampling bottle (Ocean Test Equipment). At stations AR 1-3 and AR 6-8, a hypolimnion sample was also collected 5 m off the bottom using a van Dorn sampling bottle.

Water samples were shipped to PESC (Pacific Environmental Science Centre) from 1999 to 2001 and to Maxxam Analytics from 2002 to 2004. Analysis included orthophosphate (OP), total dissolved phosphorus (TDP), total phosphorus (TP), ammonia (NH₃), nitrate and nitrite (NO₃₊₂), and chlorophyll a (chl *a*). Samples for OP were field filtered and the filtrate sent for analysis. Chl *a* samples were filtered the same day as collection and the filters were sent frozen for analysis. All other analyses were done on whole water samples.

Water samples for nutrient analyses were taken in 1997 to 2004 from a few of the major streams and rivers flowing into ALR (details in Schindler et al. 2006b). The purpose of collecting this information was to determine nutrient loads to the reservoir from inflowing tributaries.

Phytoplankton

A single, depth integrated (0-20 m) sample from each of 8 monitoring stations (AR 1-8) along a north/south axis of ALR were obtained monthly coinciding with the water chemistry samples. Discrete samples were also collected as described in the methods for water chemistry. Each phytoplankton sample was preserved in acid Lugol's iodine and stored in the dark for one to four weeks until enumerated. Prior to quantitative enumeration, the samples were gently shaken for 60 seconds, carefully poured into 25 mL settling chambers, and allowed to settle for a minimum of 24 hours. Counts were done using a Carl Zeiss inverted phase-contrast plankton microscope. Counting followed a two-step process:

1. Microphytoplankton (20-200 μm) within 5-10 random fields were enumerated at 250X magnification.
2. Nanophytoplankton (2.0-20.0 μm) and picophytoplankton (0.2-2.0 μm) within or touching a 10-15 mm transect line were counted at 1560X magnification.

The microphytoplankton include diatoms (bacillariophytes), dinoflagellates (dinophytes), and filamentous blue-greens (cyanophytes). The nanophytoplankton include golden-brown flagellates (chrysophytes and cryptophytes) and green algae (chlorophytes), and the picophytoplankton include minute ($<2.0 \mu\text{m}$) blue-green cells (cyanophytes). In total, 250-300 cells were consistently enumerated in each sample to ensure statistical accuracy (Lund et al. 1958). The taxonomic reference was the compendium of Canter-Lund & Lund (1995). Calculations with the raw phytoplankton counts provided results of abundance and biomass (Pieters et al. 2003c, Schindler et al. 2006b, Stockner 2005).

Primary production

Primary production measurements were conducted at stations AR2 and AR7 at monthly intervals from April to October in 1998-2001. Water samples were collected at 0, 1, 2, 5, 10, 15, and 20 m using a van Dorn sampling bottle equipped with silicone tubing. Light penetration was also measured at each sampling station, using a Licor LI-185A quantum sensor and meter, at 1-m intervals from the surface to at least 1% of surface light (Pieters et al. 2003a).

Measurements of primary production were conducted using the methods of Steeman-Nielsen (1952). Samples were inoculated with 0.185 MBq (5 μCi) of $\text{NaH}_4^{14}\text{CO}_3$ New England Nuclear (NEC-086H) and incubated at the original sampling depths for 3-4 hours, depending on weather conditions. In 1998, the incubations were terminated by adding 1 mL of 37% formaldehyde solution to each bottle. The bottles were then transported to the University of British Columbia where each sample was filtered through a 0.45- μm cellulose nitrate filter (Pieters et al. 1999, 2000). In 1999-2001, the incubations were terminated by filtering each sample through a filter (filter size depended on the year) immediately after the incubation (Pieters et al. 2000, 2003b, 2003c).

Each filter was placed into a vial, and hydrochloric acid (200 μL of 0.5 N) was added to each one to eliminate the unincorporated inorganic $\text{NaH}_4^{14}\text{CO}_3$. Five mL of Ecolite

scintillation fluor was added to each vial, and they were then stored in the dark for 24 hours before being counted using a Beckman Model #LS 6500 liquid scintillation counter. Primary production was measured from the amount of ^{14}C incorporated into particulate organic carbon retained by the phytoplankton on the filter and was calculated according to Parsons et al. (1984).

Zooplankton

Zooplankton samples were collected monthly at six stations (AR 1-3, AR 6-8) from April to October in 1997-2001 and from April to November in 2002-2004. A Clarke-Bumpus sampler was used with a 153- μm mesh net. At each station, three replicate oblique tows were made from a depth of 40 m to 0 m at a boat speed of 1 m/s. The tow duration was 3 minutes, with approximately 2,500 L of water filtered per tow. The exact volume sampled was estimated from the revolutions counted with the Clarke-Bumpus flow meter. Samples were rinsed from a dolphin bucket through a 100- μm filter to remove excess lake water and were then preserved in 70% ethanol.

Zooplankton samples were analyzed for species density and biomass (estimated from empirical length-weight regressions, (McCauley 1984). Samples were re-suspended in tap water filtered through a 74- μm mesh and sub-sampled using a four-chambered Folsom-type plankton splitter. Splits were placed in gridded plastic petri dishes and stained with Rose Bengal to facilitate viewing with a Wild M3B dissecting microscope (at up to 400X magnification). For each replicate, organisms were identified to species level and counted until up to 200 organisms of the predominant species were recorded. If 150 organisms were counted by the end of a split, a new split was not started. The lengths of 30 organisms of each species were measured for use in biomass calculations using a mouse cursor on a live television image of each organism. Lengths were converted to biomass (μg dry-weight) using an empirical length-weight regression from McCauley (1984). Zooplankton species were identified with reference to Pennak's taxonomic keys (Pennak 1989), and Wilson's keys were also referred to for the identification of the calanoid copepods (Wilson 1959).

Mysid shrimp

Mysid shrimp were collected monthly from January to December, 1997-2004, at six stations (AR 1-3, AR 6-8). Sampling occurred at night, around the time of the new moon when possible, to decrease the chance of mysids seeing and avoiding the net. Mysids were also sampled at night because they are closer to the surface of the reservoir during darkness. Three vertical hauls were done at each station, with the boat stationary, using a 1- m^2 square-mouthed net with 1,000- μm primary mesh, 210- μm terminal mesh, and 100- μm bucket mesh. Two hauls were made in deep water (0.5 nautical miles west and east of lake centre) and one haul was made in shallow water near either the western or eastern shore. The net was raised from the lake bottom with a hydraulic winch at 0.3 m/s. The contents of the bucket were rinsed into a filter to remove excess lake water, and were then preserved in 100% denaturated alcohol (85% ethanol, 15% methanol).

Samples were analyzed for density and biomass (estimated from an empirical length-weight regression, Lasenby 1977), life history stage, and maturity (Reynolds and DeGraeve 1972). Results of density and biomass are shown in this report. Details of life history stage and

maturity are found in the series of reports already published. Samples were re-suspended in tap water filtered through a 74- μ m mesh filter, placed in a plastic petri dish, and viewed with a Wild M3B dissecting microscope at up to 160X magnification. All mysids in each sample were counted and had their life history stage and maturity identified. The body length (tip of rostrum to base of telson) of up to 30 individuals of each stage and maturity was measured for use in biomass calculations, using a mouse cursor on a live television image of each organism.

Kokanee

Escapement estimates

Kokanee escapements to most ALR streams have been estimated periodically since 1966 and annually since 1988 (Sebastian et al. 2000). Estimates were made from aerial surveys, with additional ground counts. The aerial estimates were subject to wide variation due to a number of variables including weather, tree cover, and flow conditions. Therefore, these escapement estimates serve only as indices of abundance, since budget limitations did not provide the opportunity to estimate total numbers through the area-under-the-curve (AUC) methodology (see Hill and Irvine 2001; Parken et al. 2003). The annual surveys focused on seven index streams plus Hill Creek, which together support the vast majority of spawning. Conversion of the aerial estimates to actual numbers was made using a factor of 1.5, derived from regression analysis of data from several spawning channels where peak and total cumulative counts were available. Total counts were conducted at fish fences located at Hill and Bridge spawning channels. Run timing generally occurs between late August and late September with the peak of spawning usually occurring during the third week of September.

Unfortunately, the surveys in 1993 and 1994 were incomplete with no escapement estimates made for the major index streams on the Lower Arrow. Similarly, no estimates were made in 2003 due to unavailability of helicopters, all of which were fighting forest fires. Because of these data gaps, some extrapolations were required for this report.

Biological data

Kokanee returning to the Hill and Bridge Creek spawning channels were enumerated annually since 1984 at Hill Creek and 1988 at Bridge Creek. using permanent fish fences. Redfish Consulting Ltd. (1999) has described the operation and performance of these channels in detail. At Hill Creek, the total number of fish in the system was estimated through a combination of the channel fence count and ground estimates of fish downstream of the channel. Kokanee at both channels were sub-sampled throughout the run at the lower channel fence site for length, sex ratio, fecundity, and egg retention. Annual egg deposition was estimated from the mean fecundity less egg retention, determined from dead fish samples taken within the channel over the spawning period.

Fry enumeration

Fry enumeration during the spring outmigration has been conducted annually since 1981. At Hill Creek, initial spring fry outmigration was usually determined by leaving a net at the lower end of the channel overnight. Once the outmigration had begun, fry sampling occurred every 2-5 nights, depending upon the rate of emergence. Nightly sampling

usually occurred during peak fry migration, with less frequent sampling on either side of the peak. Fry sampling consisted of placing three nets equidistant across the channel width to subsample the cross-section of the channel. Testing of these net subsampling locations has been conducted periodically to ensure representative sampling of the cross-sectional area. The percentage of stream width sampled was then applied across the entire width of the sampling site.

Fry sample nets were typically placed in the stream every hour, on the hour, from dusk to dawn. The amount of time sampled within each hour varied by the rate of fry emergence. Net fishing times usually varied from 1-20 minutes and were then adjusted for the hour. The number of fry passing by the sampling site per hour was extrapolated between hours and then added for all hours of darkness. If fishing ceased before dawn, a correction factor was applied to estimate the entire night's fry outmigration. The number of fry per night was arithmetically extrapolated for those evenings not sampled, and an estimate of total fry production was then determined by summing the estimates for the entire period of outmigration.

Total fry production estimates

Based on early work conducted at Hill Creek and several other natural streams (Redfish Consulting Ltd. 1999), a 5% survival rate was applied to lower Hill Creek when fry-to-adult survival rates were calculated. Total Hill Creek production was the sum of fry estimated out of the channel (described above) and the natural production from lower Hill Creek.

Tributary fry production estimates for all other streams were developed using expanded stream counts (described above), fecundity from the spawning channel, an assumed sex ratio of 1:1, and average egg-to-fry survival of 10% for natural streams. Correlations between late summer fry in the reservoir (acoustic estimate) and estimates of fry production from Hill Creek spawning channel and other tributary streams were examined firstly to determine if adult counts were sufficiently reliable to use for trend information, and secondly to determine if fertilization affected fry survival during the first summer.

Age determination

Numerous attempts have been made to accurately age kokanee spawners using either scales or otoliths. Results have been mixed and some uncertainty has persisted about age-at-maturity. However, over the years, the trawl samples have been aged using scales and then matched to the length-frequency modes generated by length-frequency histograms. Typically, the trawls have captured three groups of juvenile kokanee that are distinct in size from those in the spawning streams at the time of the trawl survey. There is little doubt that four age groups represent most kokanee, although there has been some variation in age-at-maturity that reflects the state of lake productivity.

Habitat area estimates

Habitat area estimates for surface area, limnetic area, and 5-m depth strata used in developing fish abundance estimates were interpreted from 1:40,000 Canadian Hydrographic Charts and adjusted for water surface elevation at the time of survey

(Appendix 1; Sebastian et al. 2004). Limnetic habitat for kokanee surveys was defined as habitat where water depth was greater than 20 m at the time of survey (Pennak 1964).

Trawl sampling

A standard trawl survey of the limnetic habitat (>20 m depth) in ALR has been conducted annually since 1989 during the moonless nights of September or October. The survey design and sampling techniques were consistent with the kokanee stock monitoring conducted by the province on other lakes and reservoirs in BC (Sebastian et al. 2000). Three trawl stations are located within each of the two main basins (Fig. 1) and three trawls were conducted at each station. Stepped-oblique trawls ensured a representative sample of fish was obtained from each depth strata where fish were observed on the echosounder. A 15-m-long beam trawl net with a 5-m² square opening was towed at 0.8 m/s. The net consisted of mesh panels graduated in size from 10 cm (stretched mesh) at the head bar to 0.6 cm at the cod end. The net was fished for 16 minutes over consecutive 5-m depth layers from beneath the observed fish layer to a few metres above the layer. The depth of the net was estimated from the cable angle and the length of cable deployed. A geographic positioning system (GPS) was used to determine distances travelled, boat speed, and trawl sample volumes.

Captured fish were kept on ice until processing the following morning. The species, fork length, weight, distinguishing marks (e.g., fin clips), scale code, and stage of maturity were recorded. The trawl surveys provided species verification for the acoustic surveys (described below), as well as an index of kokanee abundance, age structure, and size-at-age. Using length correction factors suggested by Sebastian et al. (1995), kokanee lengths were adjusted to an October 1 standard, enabling growth comparisons among years (Appendix 2; Sebastian et al. 2004).

Hydroacoustic surveys

Since 1989, complete night-time surveys of the limnetic habitat in ALR have been conducted during September or October, concurrent with the annual trawl sampling. Acoustic surveys were conducted for eighteen standard transects, ten in Upper Arrow and eight in Lower Arrow (Fig. 1). Navigation was by radar and 1:40,000 Canadian Hydrographic Service charts. All surveys were conducted using standard methods, as outlined in Sebastian et al. (1995), using a Simrad model EY200P operating at 70 kHz. The transducer was towed on a planer alongside the boat at a depth of 1.5 m, and data were collected continuously along survey lines at 1-2 pings/s while cruising at 2 m/s. False bottom echoes necessitated a slower ping rate (0.5-1.0 pings/s) for many of the transects. The data were converted to digital format and stored on a PC computer. The Simrad system was calibrated in the field at the beginning of each survey in both Upper and Lower Arrow.

The Simrad survey data were digitized and then analyzed using the Hydroacoustic Data Acquisition System (HADAS) program (version 3.98, Lindem 1991). The HADAS performed a function similar to manual counting to determine the number of targets per unit area by depth stratum. Habitat was stratified by 5-m depth layers and then further stratified into relatively homogeneous zones within each basin. Limnetic habitat strata

were adjusted based on the reservoir water level at the time of the survey. The HADAS analysis provided mean fish density in each transect and mean fish density in each basin. A statistical analysis based on Craig and Forbes (1969) gave fish size distribution. The size distribution was used to apportion the fish population into two size classes representing age 0 fish and age 1-3 fish.

Fork lengths of trawl-caught fish were converted to the acoustic scale using Love's (1977) empirical relation (Sebastian et al. 2004) and were compared to acoustic size distributions in order to verify the age cut-off for the two size groups. Since it was not possible to distinguish between age 1, 2, and 3 fish using acoustic data, the proportions of these age groups could only be based on trawl catches.

Results

Physical limnology and water chemistry

Maximum surface temperature of ALR varied during the years of study. The maximum surface temperature was 26 °C in 1998, 25 °C in 2001 (Pieters et al. 2003a), 22 °C in 2002, 23 °C in 2003 (Schindler et al. 2006b), and 24 °C in 2004 (E. Schindler, unpublished data). ALR was well oxygenated throughout the study years, consistent with an oligotrophic system (Pieters et al. 2003a; Schindler et al. 2006b; Schindler et al., unpublished data; Wetzel 2001).

Secchi depth, total phosphorus (TP), total dissolved phosphorus (TDP), dissolved inorganic nitrogen (DIN; $\text{DIN} = \text{NH}_3 + \text{NO}_3 + \text{NO}_2$), and chlorophyll *a* (chl *a*) for Upper and Lower Arrow are listed in Tables 2 and 3. These results indicate ALR was oligo-mesotrophic based on trophic classification (Wetzel 2001). Discrete-depth profiles from 2003 indicated the upper depths of the epilimnion became nitrogen deficient for a portion of the year (Fig. 3). Nitrate was less than 30 µg/L, which is considered a limiting concentration for nitrogen (Wetzel 2001). The discrete-depth results from 2004 were used in conjunction with phytoplankton results to adaptively manage the fertilizer applications throughout the season. This adjustment to fertilizer application resulted in nitrate concentrations greater than 30 µg/L in the upper depths of the epilimnion in 2004 (Fig. 3). Adequate nitrate is important to ensure growing conditions are favourable for “edible” phytoplankton.

Fertilization has not resulted in a significant change in phosphorus measurements compared to pre-fertilization, indicating that phytoplankton quickly use the added phosphorus (Stockner and MacIsaac 1996).

Table 2. Mean value (and range in parentheses) of Secchi depth and selected water chemistry parameters from Upper Arrow, April to November, 1997-2004. Water chemistry results were from the integrated 0-30 m sample (0-20 m sample in 2004).

Upper Arrow					
Year	Secchi (m)	TP (µg/L)	TDP (µg/L)	DIN (µg/L)	Chl <i>a</i> (µg/L)
1997	6.1 (2.1-16.7)	6.0 (2-14)	3.6 (2-8)	142 (114-205)	2.2 (0.8-8.6)
1998	10.0 (5.8-15.9)	2.7 (2-6)	2.0 (2-3)	136 (86-181)	1.5 (0.8-6.4)
1999	7.8 (3.4-14.9)	4.6 (2-8)	2.4 (2-4)	145 (115-174)	1.2 (0.2-4.3)
2000	7.0 (2.7-13.7)	5.0 (2-10)	2.4 (2-3)	155 (124-186)	1.7 (0.8-4.3)
2001	7.6 (2.1-16.1)	3.7 (2-12)	2.1 (2-4)	170 (92-258)	1.4 (0.8-4.3)
2002	8.0 (2.1-16.8)	2.8 (2-6)	3.2 (2-9)	148 (101-169)	2.8 (1.0-4.2)
2003	6.9 (2.7-15.9)	2.9 (2-8)	2.8 (2-7)	132 (75-174)	2.1 (0.5-7.3)
2004	6.7 (3.0-13.1)	3.1 (2-9)	2.4 (2-7)	122 (76-178)	2.1 (0.5-7.8)

Table 3. Mean value (and range in parentheses) of Secchi depth and selected water chemistry parameters from Lower Arrow, April to November, 1997-2004. Water chemistry results were from the integrated 0-30 m sample (0-20 m sample in 2004).

Lower Arrow					
Year	Secchi (m)	TP (µg/L)	TDP (µg/L)	DIN (µg/L)	Chla (µg/L)
1997	8.7 (3.7-20.4)	5.0 (2-9)	3.0 (2-6)	122 (97-150)	2.0 (0.8-3.2)
1998	8.7 (5.2-14.3)	3.5 (2-7)	2.4 (2-6)	118 (86-162)	1.2 (0.8-4.3)
1999	7.9 (4.0-12.5)	4.4 (2-7)	2.8 (2-6)	126 (98-215)	1.7 (0.2-6.4)
2000	7.5 (3.0-11.3)	5.2 (3-12)	2.4 (2-4)	124 (89-183)	1.8 (0.8-4.3)
2001	8.2 (5.2-12.2)	3.2 (2-8)	2.4 (2-5)	153 (72-225)	1.4 (0.2-3.2)
2002	6.9 (3.0-11.6)	2.9 (2-5)	3.4 (2-7)	113 (63-164)	2.7 (0.5-4.6)
2003	7.7 (3.0-14.6)	3.1 (2-9)	2.7 (2-7)	96 (44-196)	3.4 (0.5-8.9)
2004	7.8 (4.3-14.0)	3.1 (2-8)	2.6 (2-4)	98 (49-167)	2.5 (0.5-4.9)

Results from tributary samples were used to determine the input of nutrients from inflowing streams. Discharge and nutrient concentrations were used to determine the natural nutrient load to the reservoir in addition to the load applied with fertilizer (Table 1). The nitrogen to phosphorus (N:P) ratios varied between years; those years with lower flows and less dissolved inorganic nitrogen tended to have slightly lower N:P ratios than years with higher flow.

Phytoplankton

In all years, phytoplankton included diatoms (bacillariophytes), nanoflagellates (chrysophytes and cryptophytes), green algae (chlorophytes), dinoflagellates (dinophytes), and blue-green algae (cyanophytes). The biomass and percent composition of phytoplankton varied from year to year (Figs. 4 and 5).

The composition during the two pre-fertilization years was dominated by chrysophytes/cryptophytes, followed by diatoms and dinophytes. A small picocyanobacteria, *Synechococcus* sp., was dominant in 1997 and 1998. There were no spring or fall blooms of phytoplankton in 1997 and 1998 indicating typical oligotrophic conditions (Pieters et al. 1999).

In 1999, the species composition was similar to 1997 and 1998; *Synechococcus* and nanoflagellates continued to be dominant. During 2000, there were smaller populations of picoplankton (*Synechococcus* decreased), and there was an increase in the biomass of nanoflagellates with a moderate spring diatom population and large mid-summer to late autumn diatom populations. The year 2000 was the first where significant changes to community composition occurred (Pieters et al. 2003b).

Phytoplankton results from 2001 indicated that the largest populations occurred in the narrows of ALR (stations AR 4 and AR 5). Large populations of diatoms occurred at all stations in both Lower and Upper Arrow from July to October with a peak in September. This large response of diatoms had not been seen in fertilized or interior sub-alpine lakes before (Pieters et al. 2003a). Four new colonial species of diatoms appeared—*Diatoma elongatum*, *Fragilaria acus*, *F. crotonensis*, and *Asterionella formosa*. These results indicated that the reservoir was responding significantly to the fertilizer additions (Pieters et al. 2003c).

In 2002, the diatom populations did not respond as they did to the fertilizer additions in 2001. The biomass significantly decreased in Lower Arrow. In 2002, a new species of filamentous green alga (*Ulothrix elongatum*) contributed significantly to the biomass of Upper Arrow by mid-September, but it was rare in Lower Arrow (Fig. 4). The large colonial diatoms continued to be major contributors to biomass at all stations from July to October. There was a continued suppression of picocyanobacteria in the spring and early summer and a return to moderate populations of nanoflagellates in Upper Arrow. The large colonial diatoms were *Fragilaria crotonensis*, *F. acus*, *Diatoma elongatum*, and *Asterionella Formosa* (Schindler et al. 2006b).

During 2003, the diatom blooms occurred earlier in the season than they had in previous years. The filamentous green alga *Ulothrix* was a minimal component of the phytoplankton population, while *Fragilaria* spp. occurred in both Upper Arrow and Lower Arrow. There were larger populations of *Fragilaria* spp. in 2003 than in 2002. Nanoflagellates in 2003 were similar to 2001 (Schindler et al. 2006b).

During 2004 (the year of decreased fertilizer additions compared to the previous five years), diatoms and dinophytes were the major contributors, followed by chrysophytes/cryptophytes. In Lower Arrow, the biomass of inedible diatoms was similar in 2004 compared to 2003. In response to no nutrient additions for four weeks in July and early August 2004, diatom growth declined between the July and August sampling dates (Fig. 6) (Stockner 2005).

Primary production

Primary production rates were lower in Upper Arrow during the pre-fertilization years than during the fertilized years (Table 4). There was a significant increase in the daily rate of photosynthesis in Upper Arrow, the area of nutrient application.

Table 4. Mean daily primary production rates ($\text{mg C m}^{-2} \text{ d}^{-1}$) in Upper and Lower Arrow before fertilization (1998) and after fertilization (1999, 2000, and 2001).

Year	Upper Arrow	Lower Arrow
1998	132	132
1999	202	74
2000	190	59
2001	163	100

Nanoplankton (the preferred food source of herbivorous zooplankton) contributed the greatest to primary production rates in Upper Arrow and Lower Arrow in 2000, coinciding with the phytoplankton data, which showed an increase in the biomass of nanoflagellates (Pieters et al. 2003a). The size structure of the phytoplankton changed in 2001, according to the primary production data, with the contribution of nanoplankton decreasing and microplankton increasing. These results coincided with the phytoplankton results, which showed an increase in the microplankton *Fragilaria* spp.

Zooplankton

The zooplankton composition in ALR was dominated by copepods from April to June and by *Daphnia* spp. from July to October. The dominant copepods in ALR were *Diacyclops bicuspidatus*, *Epischura nevadensis*, and *Leptodiptomus ashlandi*. The major cladocerans in ALR were *Daphnia galeata*, *D. pulex*, *D. longispina*, *Bosmina longirostris*, and *Leptodora kindti*.

By density, copepods made up the majority of the zooplankton population in ALR. However, by biomass, *Daphnia* spp. were a significant portion of the zooplankton population (Fig. 7). *Daphnia* is the target species of zooplankton of the fertilization program as they are a preferred food source of kokanee.

Zooplankton biomass typically showed a trend of Upper Arrow being less productive than Lower Arrow (Fig. 8a). Nutrient additions in Upper Arrow resulted in initial increases in zooplankton biomass in Upper and Lower Arrow in 1999 and 2000, a decrease in 2001 and 2002, an increase in 2003 and a decrease in 2004. The zooplankton biomass decrease could be attributed to the increase in the number of kokanee and possible grazing pressure on the zooplankton population.

Zooplankton biomass was comprised mostly of *Daphnia* in all years except for 2004 where copepods dominated (Fig. 8 b,c). This could be attributed to the shift in phytoplankton population to large colonial diatoms, which are considered inedible by

zooplankton. Zooplankton results indicate that Lower Arrow benefited from nutrient application in Upper Arrow, especially in the year 2000.

Mysid shrimp

Mysids were more productive in Lower Arrow than Upper Arrow from 1997 to 2001, and the reverse occurred in 2002, 2003, and 2004 (Fig. 9). There was a slight decrease in biomass in 2004 compared to 2003. Mysid results to date indicate ALR has become more productive from nutrient addition.

Kokanee

Escapements

The limited historical data for index streams, illustrated in Figure 10, suggest that annual kokanee escapements to all ALR streams were >1 million. The pre-Revelstoke Dam estimate by Martin (1976) of 0.5 million spawners upstream of Revelstoke has been used for the years 1966, 1969, 1974, and 1978 to show that large numbers of kokanee spawned throughout the system with a large portion using tributaries of the Upper Columbia River upstream of the Revelstoke Dam. Most recent escapements approximated historical numbers, although it should be noted that the 2003 data has been estimated based on average escapements from 1999-2002 because the index streams were not enumerated in 2003. It is also quite evident that a precipitous decline occurred during most of the 1990s due to nutrient depletion caused by nutrient retention by upstream reservoirs (Pieters et al. 2000).

From 1988-2004, Hill Creek was a major kokanee producer within ALR with escapements often exceeding 200,000 (Fig. 11). The vast majority of these kokanee were due to construction of a spawning channel that was completed in 1980. Significant increases in spawners became apparent four years later (large egg plants in 1981 and 1982 accounted for most of the increase). Escapements to Hill Creek rose sharply during the late 1980s to a level of >300,000 and then fell to <50,000 in the late 1990s (Fig. 12). Spawner numbers began to increase again in 1999, and in 2004 the total was ~286,000.

Since Hill Creek spawners were counted manually using the same methods over time, a direct comparison can be made between six years before fertilization and six years after. The mean number prior to fertilization was 108,151(1993-1998) compared to 169,444 (1999-2004). In other words, there has been a 57% increase in numbers since fertilization. The impact of lake fertilization on kokanee is even more apparent when the acoustics data are analyzed (see below).

Biological data

Most biological data has been collected from Hill Creek spawners although a good data set is also available from the Bridge Creek spawning channel from 1990-2003 (data on file, Ministry of Environment, Nelson BC). Here, comparisons are provided for spawner length and fecundity between pre-fertilization years (1993-1998) and fertilization years (1999-2004). Caution is necessary with these analyses since kokanee densities in the reservoir greatly influence these biological attributes.

The mean lengths of Hill Creek spawners were quite stable through the 1980s to the mid-1990s with females averaging ~23 cm and ranging from ~19-27 cm (Fig. 13). As the number of kokanee declined during the mid-1990s, length increased with both males and females exceeding 30 cm in 1999 and 2000 (Fig. 13). Since then, mean length of both sexes has been decreasing and in 2004 the mean was 20.2 cm, the smallest size recorded in 22 years. The decrease in length corresponds to the rapid rebuilding in kokanee numbers during the 2000s (Figs. 10, 13). Nonetheless, the mean size of females over the six years prior to fertilization was 22.8 cm (s.d. 1.9) while it was 24.4 cm (s.d. 4.50) from 1999-2004. In other words, the mean length has increased with fertilization.

Fecundity directly reflects numbers of kokanee in the reservoir. Mean fecundity over 22 years has been 277 eggs/female with a low of 173 (1996) and a high of 469 (2000). High fecundities in the early 1980s (Fig. 13) most likely reflect a density-growth response to lower numbers of kokanee due to blocking of the Columbia River during Revelstoke Dam construction. Fecundity declined during the mid-1990s despite low kokanee numbers signalling serious problems with reservoir productivity. Fecundity rose sharply with the onset of fertilization (1999 and 2000) but has gradually declined since 2000 as the in-lake population increased. The fecundity in 2004 was 189, the third lowest statistic in 22 years.

Mean fecundity during the six years prior to fertilization was 277 eggs/female (s.d. 52) but and from 1999-2004 the mean fecundity was 313 eggs/female (s.d. 116). These data are somewhat meaningless without reference to the in-lake populations and the density growth responses associated with decreasing and increasing levels of productivity (see below).

Fry production

Kokanee fry production from Hill Creek spawning channel has had a considerable influence over ALR kokanee production. Shortly after completion of the channel, monitoring of kokanee fry production began (1982) and except for 1984, a good record is on file of total annual production. The average production over 22 years has been 3.53 million with a low recorded in 2004 of 0.17 million and a high in 2001 of 8.89 million (Fig. 14). Fry production generally tracked fecundity with a one-year lag. For example, the decline in fry numbers in 2003 can be traced to the significant decline in fecundity in 2002 (Figs. 13, 14). The severe decline of fry production at Hill Creek in 2004, however, was due to a complete production failure at the spawning channel for undetermined reasons. Except for 2004, egg-to-fry survival rates were quite consistent, averaging 37.3% (Fig. 14).

Mean fry production during the six years prior to fertilization was 2.55 million compared to 4.53 million during the last six years, including the near total failure of production in 2004. The lower fry production in 2003 and 2004 will likely mean far lower escapements in 2006 and beyond.

Estimates of fry production from Hill Creek (spawning channel and stream) and all other tributaries were compared with late summer fry estimates (Table 5). Both Hill Creek

production and theoretical tributary fry production from spawner counts correlated reasonably well with late summer fry abundance estimates in the reservoir from acoustic surveys (Figs. 15a, b). A ‘best fit’ was achieved by combining the fry estimates from streams and Hill Creek and suggests a fairly good relationship between total annual fry production in spring and late summer fry abundance in the reservoir by fall (Fig. 15c). These simple analyses suggest that escapement estimates, as crude as they seem, provide reasonable time series data on trends in stream production. They also confirm that fry production from the Hill Creek spawning channel provides a significant contribution to total fry production in ALR.

Table 5. Estimated fry production from Hill Creek spawning channel and from all other tributaries compared with late summer fry abundance in Arrow Lakes Reservoir (acoustic estimate).

Fry year	Hill Creek fry migration ¹ (millions)	Estimated fry from tributaries ² (millions)	Total fry from all sources ³ (millions)	Late summer fry abundance ⁴ (millions)
1992	2.87	4.41	8.02	2.70
1993	3.00	2.02	5.90	2.96
1994	3.43	3.46	8.01	4.22
1995	2.22	5.45	8.25	2.62
1996	0.68	2.57	3.67	1.90
1997	0.69	1.58	2.28	1.31
1998	0.93	0.34	1.44	2.71
1999	0.86	2.49	3.46	3.87
2000	3.72	6.35	10.25	9.56
2001	8.46	7.32	16.21	15.44
2002	8.32	9.89	18.32	13.38
2003	3.93	4.83	8.93	4.94
2004	0.06	5.83	6.00	4.62

1. Fry count from Hill Creek spawning channel

2. Derived from escapement estimates and fecundity assuming 1:1 sex ratio and 10% egg-to-fry survival

3. Sum of channel and tributaries plus non-channel production from Hill Creek

4. Hydroacoustic estimate of age-0-sized fish in ALR.

Size-at-age

Kokanee mean size-at-age, measured as length, from trawl sampling provides valuable information on growth rates at different life stages. When examined in the context of fish abundance, it can provide a measure of how productive the rearing conditions are for kokanee. Very low densities combined with small kokanee length at all ages in 1996 and 1997 confirmed that productivity must have declined to very low levels in ALR (Figs. 16, 17). Kokanee growth of all age classes began to improve in 1998 under low density conditions and increased rapidly in 1999 as numbers began to build following initial lake fertilization. Spawner lengths and fecundity peaked in 2000 following two years of strong growth in the newly fertilized regime and relatively low densities of age 1-3 fish (Figs. 13, 18). The decline in growth from 2001 to 2004 occurred concurrently with a building of the population, particularly the age 1-3 component which has higher demands on the

food supply than age 0 fish. Increased growth of various age groups in the late 1990s and early 2000s cannot be attributed entirely to fertilization since there were also density-dependent influences.

Age-at-maturity

Age data have been obtained by a number of methods, with the most reliable considered to be trawl length-frequency analyses backed up with scale interpretation. These age determinations have been matched to limited age analysis from Hill Creek spawners to round out the composition of all age groups and their mean lengths-at-age. Since lake fertilization, changes in the age composition of spawners have been observed between years and also between basins in the same year. Prior to lake fertilization, the vast majority of mature fish were age 3+, as determined through a combination of length-frequency analysis, scale reading, and limited otolith aging (Sebastian et al. 2000). Some independent verification of these age interpretations came from limited mark-and-recapture of fed fry from the spawning channel in 1977-78 (Sebastian et al. 2000).

Accelerated growth rates of the 1997-2001 year classes evidently resulted in a shift in the dominant age at maturity from 3 year olds to a mix of ages 2s and 3s. By 2000, a significant shift in age-at-maturity of Hill Creek spawners had occurred, and the 2000 and 2001 length-frequency data of the spawners illustrated bimodal length frequencies (Andrusak 2004). The 2001 age data determined from the Hill Creek kokanee otoliths also confirmed what the length-frequency distribution suggested. Of 253 otoliths interpreted from the 2001 sample, 49% were 2 year olds, 51% were 3 year olds, and one fish was a 4 year old. By 2003, the predominant age was again 3 year old fish based on an independent contractors' analysis and the size-at-age data from the trawl samples. In 2004, the age-at-maturity was again predominately 3 year olds.

There has been very little age determination for Lower Arrow kokanee because data are quite sparse. There does appear to be some differences in age-at-maturity between the two basins as determined by Sebastian et al. (2003). As noted above, age-at-maturity of Upper Arrow kokanee (Hill Creek) in recent years seems to have changed from 3 year olds to age 2 year olds with a shift back to predominately 3 year olds (Table 6). In contrast, the Lower Arrow fish appear to be more of a mix of ages 2s and 3s supported by Sebastian et al.'s (2003) observation that there was more overlap in size of trawl-caught 2s and 3s. A few otoliths aged from a small sample (n=39) of Octopus and Deer creek spawners collected in 2003 also suggested a mix of age 2s and 3s (Table 6).

Table 6. Age composition (%) of Upper and Lower Arrow kokanee spawners, 1999-2004.

	Year	% Age 2s	% Age 3s	% Age 4s	Sample size
Upper Arrow					
Hill Creek	1999	20	73	7	182
	2000	52	46	2	194
	2001	49	51	<1	253
	2002	10	90		N/A
	2003	5	95		N/A
	2004	No ages	100		N/A
Lower Arrow					
Octopus Creek	1999	22	66	11	53
	2000	7	90	3	29
	2001	9.5	86	4.5	21
	2002	41	59	0	22
	2003	95		5	20
Deer Creek	2003	16	84		19

*N/A = not available; data from Ministry of Environment files, Nelson BC

Abundance and biomass

Hydroacoustic and trawl surveys have been conducted using the same equipment and analyses since 1991. Data from the surveys suggested the total abundance of kokanee in ALR remained fairly static at 3-5 million prior to fertilization (Fig. 18). In 1999, kokanee numbers began a fairly rapid increase, and by 2001 and 2002 they reached 20 million fish. The 2003 data indicated a decline to just under 12 million kokanee followed by a further decline in 2004 to ~7.5 million, which was still higher than the pre-fertilization estimates. The 2003 decline was mostly due to lower fry production from both Hill Creek and other tributaries and can be traced to reductions in growth and fecundity as populations adjusted to higher densities in the reservoir. The 2004 decline was primarily due to production problems at the Hill Creek channel in 2003, which resulted in a near total fry failure from the spawning channel. There tended to be more kokanee in Upper Arrow compared to Lower Arrow (Fig. 17).

The acoustics data can be separated by size into age 0s and ages 1-3s. Despite high fry production from Hill Creek during the pre-fertilization years (Fig. 14), often >4 million, the acoustic estimates of fry for the entire reservoir remained very low (Fig. 18). Once fertilization began, total fry estimates via acoustics increased dramatically, exceeding 15 million in 2001. This peak in fry numbers coincided with peak production at Hill Creek, another indication of the importance of Hill Creek to the entire reservoir. The pattern of increased numbers after fertilization also occurred for the 1-3 year old fish. The results to date has been much larger escapements to Hill Creek (and other streams) since fertilization began (Fig. 12).

Kokanee biomass estimates have been made for the entire reservoir based on estimated numbers from acoustics and on the weights of trawl-captured fish of 0-3 year olds . The annual pelagic area of the reservoir, determined at the time of trawl survey, was then used to determine the biomass per hectare. The mean kokanee biomass prior to fertilization (1993-1998) was estimated at 4.0 kg/ha whereas the post-fertilization biomass was 15.9 kg/ha, a four-fold difference (Fig. 19).

Discussion

ALR suffered from the cumulative impacts of impoundment by Hugh Keenleyside Dam and by the formation of upstream reservoirs (Pieters et al. 1999, 2000). The result was a decline in productivity at all trophic levels, including the kokanee population, which is a key species that several predators depend on. Kokanee escapements approached one million in the 1960s and 1970s, and they then began to decline. The Hill Creek spawning channel was constructed in the early 1980s in an effort to replace ~0.5 million kokanee estimated to be lost annually when the Revelstoke Dam blocked access to key spawning areas. During the late 1980s, Hill Creek did experience large escapements, but the target of 0.5 million spawners has yet to be achieved in Upper Arrow (Sebastian et al. 2000). Despite continued high fry production from Hill Creek in the early 1990s, escapements began to decline not only at Hill Creek but also at all other major spawning streams. The low point of <100,000 spawners for the entire system in 1997 was a clear signal that lake carrying capacity had diminished. The cause of the poor carrying capacity was believed to be nutrient impoverishment as a result of nutrient trapping in the upstream reservoirs (Pieters et al. 2003a). Nutrient additions began in 1999 in an attempt to reverse the downward trend in kokanee numbers.

Nutrient application has not resulted in a significant change in phosphorus measurements in ALR compared to pre-fertilization, indicating that phytoplankton quickly use the added nutrients. Lower trophic levels in ALR responded to nutrient additions. The phytoplankton responded in abundance and composition; the composition in 2003 and 2004 was not as favourable for zooplankton as in the earlier years of nutrient addition. The zooplankton composition showed an initial *Daphnia* increase and then a decline. There is a possibility that the *Daphnia* decline is actually due to increased grazing pressure.

The shift in phytoplankton species and size to nanoplankton resulted in an increase in *Daphnia* biomass. The decrease in *Daphnia* biomass in 2002 can be attributed to grazing effects by the increased kokanee population. The increase in zooplankton biomass in Lower Arrow in 2003 can be attributed to decreased pressure from grazing kokanee.

The mysid shrimp population in ALR also responded to the nutrient additions, initially in both basins and more recently only in Upper Arrow. Mysid shrimp were introduced to ALR in 1968 as a food source for rainbow trout. It was later concluded that mysids compete with kokanee for zooplankton as a food source. Therefore, a potential confounding factor with the experimental fertilization of ALR was the possibility of increasing the number of mysids. Indeed, Walters et al.(1991) indicated that fertilization

of Kootenay Lake would result in increased mysid production, and kokanee would continue to decline. However, results to date in Kootenay Lake indicate that kokanee populations have actually increased as a result of nutrient addition, and mysids have not increased significantly (Ashley et al. 1999; Wright et al. 2002, Schindler et al. 2006a). A similar result has been observed in ALR. Mysids responded positively to the nutrient additions, but their increase does not appear to have inhibited the kokanee response. In fact, as in Kootenay Lake, the ALR kokanee population has benefited from the nutrient additions.

There are four lines of evidence that suggest lake fertilization has had a strong, positive impact on kokanee production in ALR since it began in 1999:

1. Increased spawner returns

The most obvious change to the kokanee population has been the observed increase in spawner escapements over the last six consecutive years (1999-2004). Returns of close to 1 million spawners in 2003 and 2004 were the highest in thirty years. Hill Creek spawner numbers have increased from <50,000 prior to fertilization to between 100,000 and 286,000 in the 2000s.

2. Increased abundance of juvenile kokanee

Abundance estimates of juvenile kokanee (all ages in ALR), made from hydroacoustic surveys over fourteen consecutive years, provide the most compelling evidence of the influence of fertilization on the kokanee population. The total number of juveniles in ALR prior to fertilization was <5 million, and the number increased to ~20 million by 2001-2002.

The decline in fry abundance in 2003 (age 0) in ALR can be traced to growth response and lower fecundity as the numbers of age 1-3 year old fish peaked in the reservoir. The further decline in fry numbers in 2004 is mainly attributed to production problems at Hill Creek spawning channel.

3. Density-dependent growth responses

In 1998, prior to fertilization, individual kokanee began to show a growth response as a result of extremely low densities of kokanee in the reservoir. During the first two years of fertilization (1999 and 2000), individual kokanee in all age classes showed increased growth rates as population numbers doubled. This result provides additional evidence that both primary (phytoplankton) and secondary (zooplankton) levels of production had changed as a result of fertilization. Kokanee growth leveled off and then declined with a second doubling of the population size during the third and fourth years (2001 and 2002) of fertilization.

A similar trend is evident in spawner size and fecundity, both of which were high during the first three years of fertilization. Once the population had built to a peak by the fourth year, spawner size and fecundity returned to more typical values for this population. Nonetheless, overall potential egg deposition remained high due to the large number of spawners returning. This type of pattern—rapid initial growth followed by a density-

dependent reduction in growth and fecundity as populations equilibrate to new growth conditions—has been observed twice during the Kootenay Lake experiment (see below).

4. In-lake biomass of kokanee

The impact of fertilization on kokanee can best be quantified by calculating the mean biomass density before and after nutrient addition. Mean biomass prior to nutrient addition (1993-1998) was 4.0 kg/ha, whereas from 1999-2004 mean biomass has been 15.9 kg/ha, a four-fold increase. In addition, indirect evidence of increased in-lake kokanee biomass comes from angling information, which, albeit anecdotal, suggested that both the number and size of bull trout in ALR had increased by 2004. These large fish are very dependent on the kokanee food supply (Arndt 2004), so it appears that they have benefited from a greater abundance of kokanee.

Further evidence in support of fertilization can be seen by comparing the responses observed to date on ALR with the Kootenay Lake fertilization experiment. The kokanee population in Kootenay Lake expanded from <10 million to ~35 million after only two years of lake fertilization (which began in 1992; Fig. 20). There was also an immediate response in growth rates and fecundity, which increased sharply at first and then declined as kokanee numbers and biomass peaked. Further evidence of the impact of nutrient additions in Kootenay Lake came from the decline in kokanee numbers following a 50% reduction in fertilizer levels from 1997-2000 (Andrusak 2004; Sebastian et al. 2003). When the fertilizer was increased again in 2001, kokanee abundance and biomass returned to higher levels. The spawner returns to Meadow Creek on the Kootenay system also mirrored the fertilizer reduction and reinstatement, but they showed a lag time consistent with the average number of spawners (Fig. 21).

Conclusion

The bottom-up approach to restoring kokanee in ALR has been successful, and the objectives of the ALR fertilization experiment have been met. Namely, the fertilization has successfully replaced nutrients lost as a result of upstream impoundments and has successfully restored the productivity of Upper Arrow. Primary production rates increased, and the phytoplankton community responded with a shift in species, and zooplankton biomass was more favourable for kokanee. With more productive lower trophic levels, the kokanee population increased in abundance and biomass, resulting in improved conditions for bull trout, one of ALR's piscivorous species. The monitoring program has been valuable in assessing the effects of nutrient additions throughout the food web and should continue to sample all trophic levels to gain a true picture of the conditions in ALR.

It's important to emphasize that fertilization alone is insufficient to restore kokanee populations. Also key is adequate spawning habitat, which is provided in large part by operation of the Hill Creek spawning channel. The spawning channel supplies a significant portion of the fry required to fully use the increased productive capacity of Upper Arrow.

Nutrient applications in the form of liquid fertilizer need to continue on ALR in order to maintain the reservoir's carrying capacity. A change in application method was

implemented in 2005 in order to dispense nutrients over a larger distance with less frequent additions (i.e fertilizer was dispensed once a week instead of several times a week). The MV Shelter Bay ferry was used to dispense fertilizer over a 15 km distance in Upper Arrow and results to date have been positive. Continued use of this application method is recommended.

The ALR fertilization experiment needs to continue with an adaptive management approach in order to assess any necessary changes to nutrient application that will favour growing conditions for zooplankton which are important for favourable growing conditions for kokanee.

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Figure 1. Arrow Lakes Reservoir sampling stations and locations.

P loading to Upper Arrow

N loading to Upper Arrow

Figure 2. Total weekly phosphorus (P) and nitrogen (N) loading to Upper Arrow from fertilizer, 1999. All other years (2000 – 2003) were similar except during 2004 where fertilizer was not added for a total of four weeks in July and early August.

Figure 3. Discrete-depth profiles of nitrate-nitrogen from station AR2, 2003 and 2004.

Figure 4. Monthly average phytoplankton biomass 1998 to 2004 (April to October in 1998 to 2002 and April to November in 2003 and 2004) in Upper and Lower Arrow.

Figure 5. Percent composition by phytoplankton class in Upper and Lower Arrow 1998 to 2004.

Figure 6. Phytoplankton abundance and biomass results from discrete-depth profiles collected in 2004.

Figure 7. Percent composition of zooplankton in Upper Arrow and Lower Arrow 1997-2004.

Figure 8. Seasonal average biomass of zooplankton in Upper and Lower Arrow (top); seasonal biomass of zooplankton in Upper Arrow (middle) and Lower Arrow (bottom), 1997-2004.

Figure 9. Annual average density (top) and biomass (bottom) of *Mysis relicta*, 1997- in 2004, Upper Arrow and Lower Arrow.

Figure 10. Historical estimates for all index streams including Hill creek, 1966 – 2004. Upper Columbia tributary spawner numbers determined by Martin (1979) illustrates probable numbers prior to Revelstoke Dam. Notes: in three years, aerial surveys could not be conducted and data are shown with hatched bars. In 1993 and 1994 index stream data were estimated using the previous four-year average; similarly the 2003 data have been constructed from actual Hill Creek data plus the previous four-year average for the index streams.

Figure 11. Relative contribution of Hill Creek spawners vs. spawners estimated in the major index streams throughout the basin. Note: Major index streams were not enumerated in 1993, 1994 and 2003.

Figure 12. Kokanee escapements to Hill Creek before spawning channel production (pre-1984) and, before and after experimental fertilization.

Figure 13. Mean length (cm) of male and female Hill Creek kokanee spawners and mean fecundity (eggs/female).

Figure 14. Estimates of total fry production from Hill Creek spawning channel and natural streams 1980s to 2000s. Natural stream production assumed egg-to-fry survival of 5%.

Figure 15. Comparison of late summer fry abundance estimates from hydroacoustic surveys with a) measured spawning channel fry production, b) estimated total tributary fry production and c) combined channel and stream fry production.

Figure 16. Mean length-at-age of a) trawl-captured kokanee from Upper Arrow and mean length of spawners measured at the Hill Creek spawning channel, and b) mean length-at-age for trawl-captured kokanee from Lower Arrow. Note: trawl-captured fish lengths all adjusted to October 1st.

Figure 17. Kokanee abundance estimates (all ages) for Arrow Lakes Reservoir (combined upper and lower basins), and for Upper and Lower Arrow from annual fall acoustic surveys, 1991 – 2004. Note that the vertical axis has a different scale in each panel.

Figure 18. Kokanee abundance trends for age 0+ and age 1-3+ fish from fall hydroacoustic surveys, 1993 – 2004.

Figure 19. Estimates of total kokanee biomass for Arrow Lakes Reservoir based on fall trawl survey data, 1993-2004. All ages have been combined.

Figure 20. Abundance of kokanee (all ages) determined by hydroacoustic surveys in Kootenay Lake, 1985-2005.

Figure 21. Annual estimates of kokanee spawners in Meadow Creek, 1964 – 2005. Note: 1964 – 1968 data from Acara (1970, unpubl. MS).

Appendix 1. Costs of Arrow Lakes Fertilization Project – 1999 to 2004 (does not include in-kind contributions).

Year	Amount spent on ALR fertilization project (includes CPC and MoE contributions)
1999	\$730,850
2000	\$790,452
2001	\$799,930
2002	\$686,590
2003	\$627,120
2004	\$665,761