American Fisheries Society Symposium 34:177–196, 2003

Restoration of Kokanee Salmon in the Arrow Lakes Reservoir, British Columbia: Preliminary Results of a Fertilization Experiment

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Abstract.—The Upper and Lower Arrow lakes have undergone major anthropogenic changes. Dams were built below (Grand Coulee 1942), at the outlet (Keenleyside 1967), and above (Mica 1973 and Revelstoke 1983) the Arrow Lakes, and *Mysis relicta* were introduced in 1968. The reservoirs created behind the upstream dams act as nutrient traps, reducing the already naturally low levels of nutrients in the Arrow Lakes Reservoir. The objective of nutrient additions to the Arrow Lakes Reservoir was to replace nutrients trapped upstream and was driven by rapidly declining stocks of kokanee, a native land-locked sockeye salmon *Oncorhynchus nerka* and keystone species of this aquatic ecosystem. In the late 1980s and early 1990s, Upper and Lower Arrow tributaries supported between 600,000–800,000 kokanee salmon spawners, but the numbers declined steadily through the 1990s to a low of 97,000 in 1997. As the number of kokanee decreased, no increase in size was observed, consistent with nutrient-limited conditions. Unlike its neighbor, Kootenay Lake, which is one of the most studied in British Columbia, the Arrow Lakes Reservoir had received little limnological attention. After an initial study of the limnology and trophic status in 1997 and 1998, a 5-year fertilization experiment was initiated in 1999 with seasonally adjusted nutrient (phosphorus and nitrogen) additions to the Upper Arrow Reservoir, in an effort to restore historic kokanee populations. Preliminary data from the first two years of fertilization, 1999 and 2000, show positive and encouraging trends in primary productivity, phytoplankton succession, zooplankton biomass, and the number, size, and fecundity of kokanee spawners. No significant changes have been observed in the water quality parameters measured, consistent with immediate utilization of nutrients in an oligotrophic system.

Introduction

A fundamental problem occupying the center of limnological attention over the past 40 years has been the excess supply of nutrients or eutrophication (e.g., Vallentyne 1974; Schindler 1974; Vollenweider 1976). However, the opposite, namely a reduction in nutrient supply or oligotrophication, is being recognized as a companion problem (Ney 1996; Stockner et al. 2000). Oligotrophication can result from the trapping of nutrients behind upstream impoundments or from the blockage of the anadromous nutrient pump by overfishing or downstream dams (Stockner and MacIsaac 1996; Cederholm et al. 2000). Large water level variation in reservoirs has been implicated in nutrient loss by enhanced transport of littoral nutrients to the profundal sediments (Milbrink and Holmgren 1981), and large changes to the pattern of the seasonal hydrograph may also affect nutrient pathways.

The Arrow Lakes Reservoir, part of the Columbia River system (Figures 1 and 2), exemplifies the process of oligotrophication, having undergone major anthropogenic changes. Prior to dam construction, anadromous runs of chinook salmon, sockeye salmon, and steelhead trout were found in and above the Arrow Lakes (Sebastian et al. 2000). This anadromous nutrient pump to the upper Columbia was blocked by the Grand Coulee Dam, built on the Columbia River in the late 1930s. The Upper and Lower Arrow lakes were converted to a large reservoir with the completion of the Keenleyside Dam at the outlet of the Lower Arrow Lake in 1967. This increased the mean water level of the resulting Arrow Lakes Reservoir by 12.6 m and flooded both the narrows between the Upper and Lower Arrow lakes and the river between Beaton Arm and Revelstoke (Figure 3). In 1973 and 1983, the Mica and Revelstoke dams were completed on the Columbia River above the Arrow Reservoir (Figures 1, 2). Operation of these dams for flood control and hydroelectric generation changed the timing of the Columbia River inflow to the Arrow Lakes Reservoir. Another major perturbation was the introduction of *Mysis relicta* in 1968 (Lasenby et al. 1986), a small, exotic crustacean that is a highly effective competitor for the zooplankton species preferred as a food source by kokanee.

Dramatically declining kokanee numbers, with no compensating density-driven increase in size, resulted in a two-year baseline study of the trophic status of the Arrow Lakes Reservoir in 1997 and 1998 (Pieters et al. 1998, 1999). Kokanee *Oncorhynchus nerka* spend their entire life cycle in the lake and are one of the keystone species within the ecosystem, supporting large piscivorous sport fish such as rainbow trout *Oncorhynchus mykiss*, white sturgeon *Acipenser transmontanus*, and bull trout *Salvelinus confluentus*. In the late 1980s to the early 1990s, Upper and Lower Arrow tributary streams supported spawning populations of 600,000–800,000 kokanee, but the

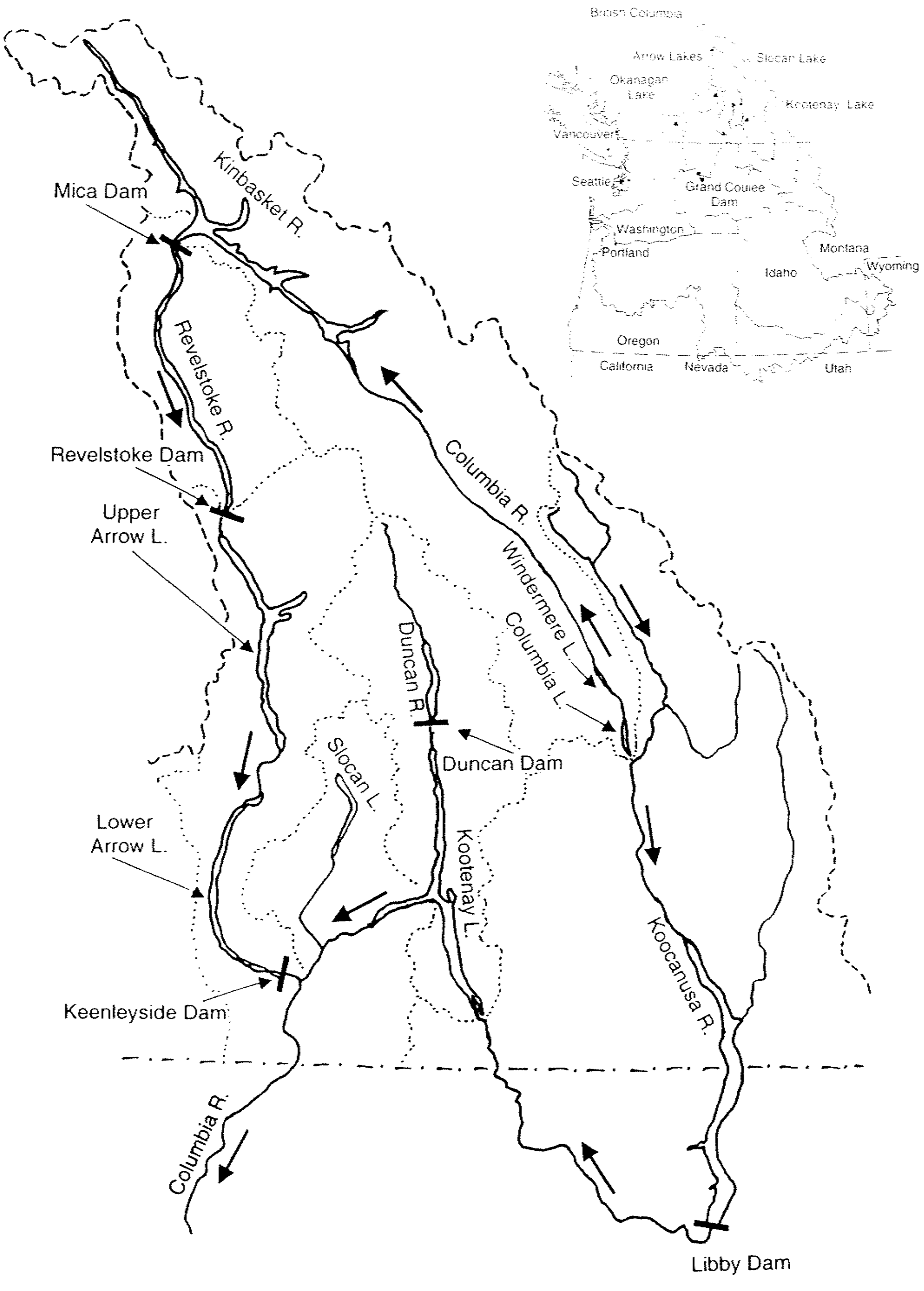

FIGURE 1. Upper Columbia River. Inset: Columbia River drainage. The source water of the Columbia River at Columbia Lake flows northwest into the Kinbasket Reservoir. At Mica Dam, the Columbia River turns south, flowing through Revelstoke Reservoir and into the north end of the Upper Arrow Lakes Reservoir. The outflow at the south end of Upper Arrow passes through a shallow, formerly riverine, narrows and then through the Lower Arrow Lakes Reservoir.

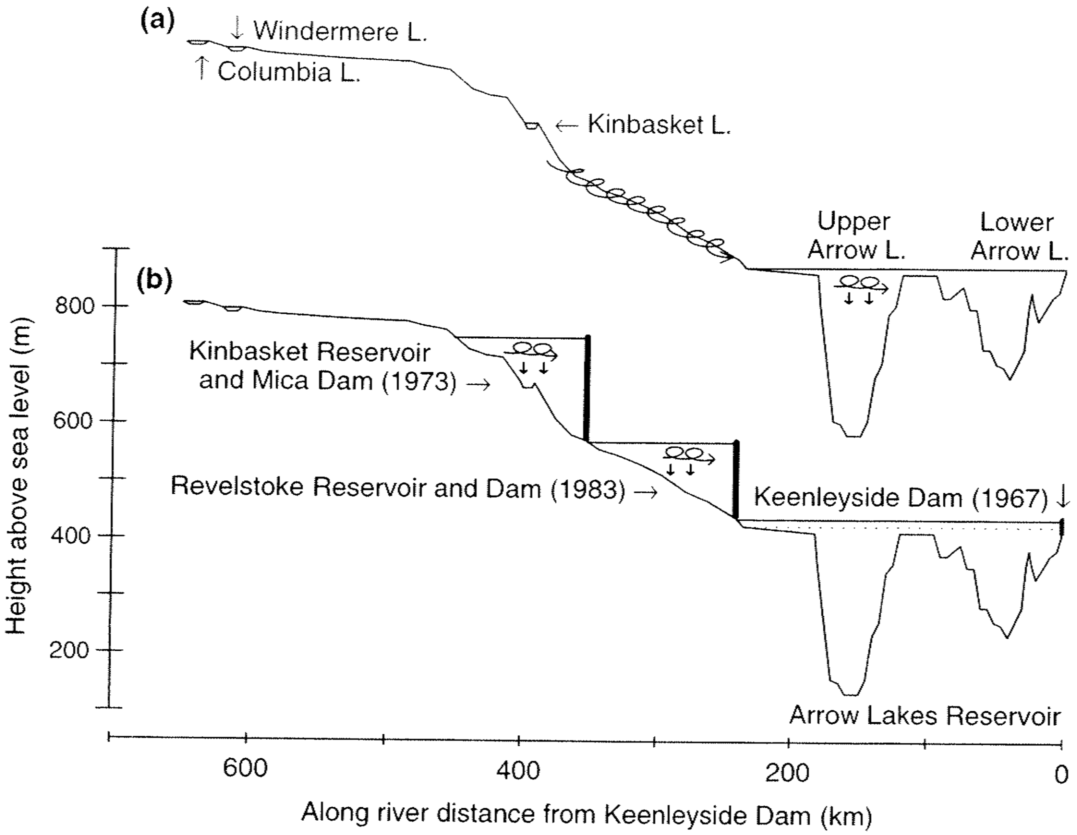

FIGURE 2. Elevation of the Upper Columbia River (a) before and (b) after construction of impoundments.

numbers declined steadily through the 1990s to a low of 97,000 in 1997. In response to these rapidly declining kokanee stocks, experimental fertilization of the Arrow Lakes Reservoir was initiated to replace nutrients lost in the upstream impoundments. A five-year fertilization experiment was started in 1999, modeled on the adaptive management approach used for Kootenay Lake (Ashley et al. 1997, 1999a, 1999b). Summarized here are the results of two years of baseline monitoring (1997, 1998) and the preliminary results of the first two years of the fertilization experiment (1999, 2000).

The first objective of this paper is to describe the Arrow Lakes Reservoir and to assess its trophic status. Large aquatic ecosystems such as the Arrow Lakes Reservoir are sustained by complex physical, chemical, and biological interactions. These include, among many others, the physical role of river inflows to deliver nutrients to the euphotic zone, the adsorption of nutrients to sinking particulates, the recycling of nutrients in the microbial food web, and the transfer of nutrient-limited productivity through the traditional food web of phytoplankton, zooplankton, plankti-vorous fishes, and the large piscivores. Because of these interactions, it is unwise to base an assessment of the trophic status of an aquatic system on any given trophic level. With this in mind, a variety of data are reported here to assess the trophic status of the Arrow Lakes Reservoir.

The second objective is to describe the fertilization experiment and the initial response of the system to the nutrient additions. Two controls are considered, both with limitations. First, the untreated years, 1997 and 1998, act as a control. As will be discussed, two extremes in climate were observed in these years, pointing to the problem of interannual variability inherent in both this short two-year control record and the short two-year record of fertilization described here. The only long-term record on the Arrow Lakes Reservoir is that for kokanee salmon,

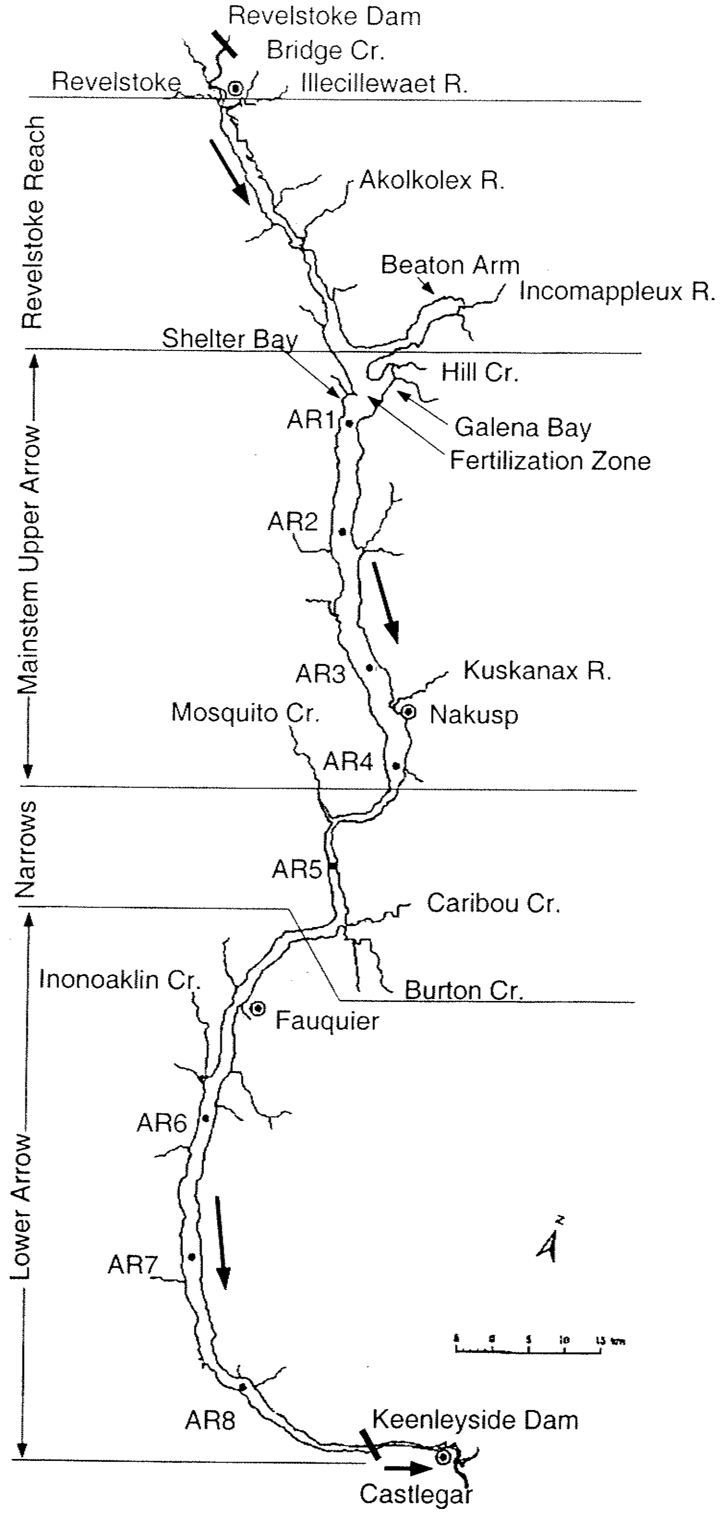

FIGURE 3. Arrow Lakes Reservoir with sampling stations AR1–8.

which has shown a steady decline through the 1990s. The second control is the Lower Arrow Reservoir. However, the Lower Arrow is downstream of the fertilization zone at the top of the Upper Arrow and may benefit from nutrient additions as the residence time of the top 50 m of the main-stem Upper Arrow is approximately two months. The absence of an ideal control is inherent in large-scale experiments of this type.

Background

The Columbia River drains from seven states of the United States and the southeastern corner of British Columbia, Canada (Figure 1). In the Canadian component, the terrain is mountainous, dominated by deep valleys trending north to south, in which five large natural lakes are found: Okanagan, Upper and Lower Arrow, Slocan, and Kootenay. These lakes occupy long, narrow, deep, steep-sided, and glacially carved basins. While representing only 5% of the Columbia River's total drainage area, the discharge from the Arrow Lakes Reservoir contributes 16% of the total flow. The Arrow Lakes Reservoir has a length of 240 km, a mean width of 1.8 km, and a mean and maximum depth of 83 and 287 m, respectively. With a surface area of 465 km^2 at mean water level, the Arrow Lakes Reservoir represents one of the largest to undergo experimental fertilization.

The elevation of the Columbia River above the Arrow Lakes outlet is shown in Figure 2. Before the construction of upstream dams, nutrients would spiral through the riverine sections. While these nutrients might be utilized in the river, they would nevertheless be recycled as they moved downstream. The river-borne nutrients would then contribute to productivity in the Upper and Lower Arrow lakes, which were two separate basins connected by a riverine narrows (Figure 2a). With the construction of upstream dams, nutrients are now utilized in the upstream impoundments, and most settle to the impoundment sediments, thereby reducing the available nutrients to the Arrow Lakes Reservoir. In effect, the potential for productivity is moved upstream.

The construction of an upstream dam results in a 'boom and bust' nutrient response (Horne and Goldman 1994; Ney 1996; Stockner et al. 2000). On filling the impoundment, the decomposition of organic materials in the basin releases a pulse of nutrients that can last 5–10 years. However, after this period, the impoundment acts as a settling basin, where entering nutrients are used and sedimented rather than being passed for downstream use. Both the Mica Dam (1973) and, more recently, the Revelstoke Dam (1983) were built above the oligotrophic Arrow Lakes Reservoir. These resulted in a marked reduction in the naturally low level of nutrients in the Arrow Lakes Reservoir.

Methods

Methods are only briefly summarized here. For greater detail see Pieters et al. (1998, 1999, 2000, 2001).

Fertilizer Application

From late April to early September, in 1999 and 2000, 1,060 t (metric tons) of agricultural grade fertilizer were applied to the north end of Upper Arrow between Galena Bay and Shelter Bay (Figure 3), 5 km above the first sampling station (AR1). Fertilizer was dispensed from the Ministry of Transportation and Highways' ferry, the *DEV* Galena. This diesel electric ferry (Figure 4a) is 50 m long, has a draft of 2.4 m, and is powered by two Voith-Schnieder cycloidial propellers with 1.6 m blades. A truck and tank were driven onto the ferry and connected to a 3.6 m diffuser pipe (with 0.6 cm holes every 30 cm) bolted to the side of the ferry. Once away from shore, fertilizer was pumped through the diffuser into the propeller wash (Figure 4). Approximately 3,900 L of fertilizer were delivered per trip, with 2–15 trips per day and a total of ~215 trips from April to September.

The fertilizer consisted of a seasonally adjusted blend of liquid ammonium polyphosphate (10–34–0; % by weight equivalent of N-P_2O_5-K_2O) and urea-ammonium nitrate (28–0–0; % by weight equivalent of N-P_2O_5-K_2O; 14% urea N, 7% ammonium N and 7% nitrate N). This delivered 52.8 t of phosphorus and 232 t of nitrogen per year. The seasonal loading and timing of the fertilizer application (Figure 5) was modeled on the Kootenay Lake fertilization experiment (Ashley et al. 1997, 1999a, 1999b). Phosphorus additions followed the preimpoundment freshet flow pattern, increasing to early June and then declining. The ratio of nitrogen (N) to phosphorus (P) is critical to prevent blooms of undesirable blue-

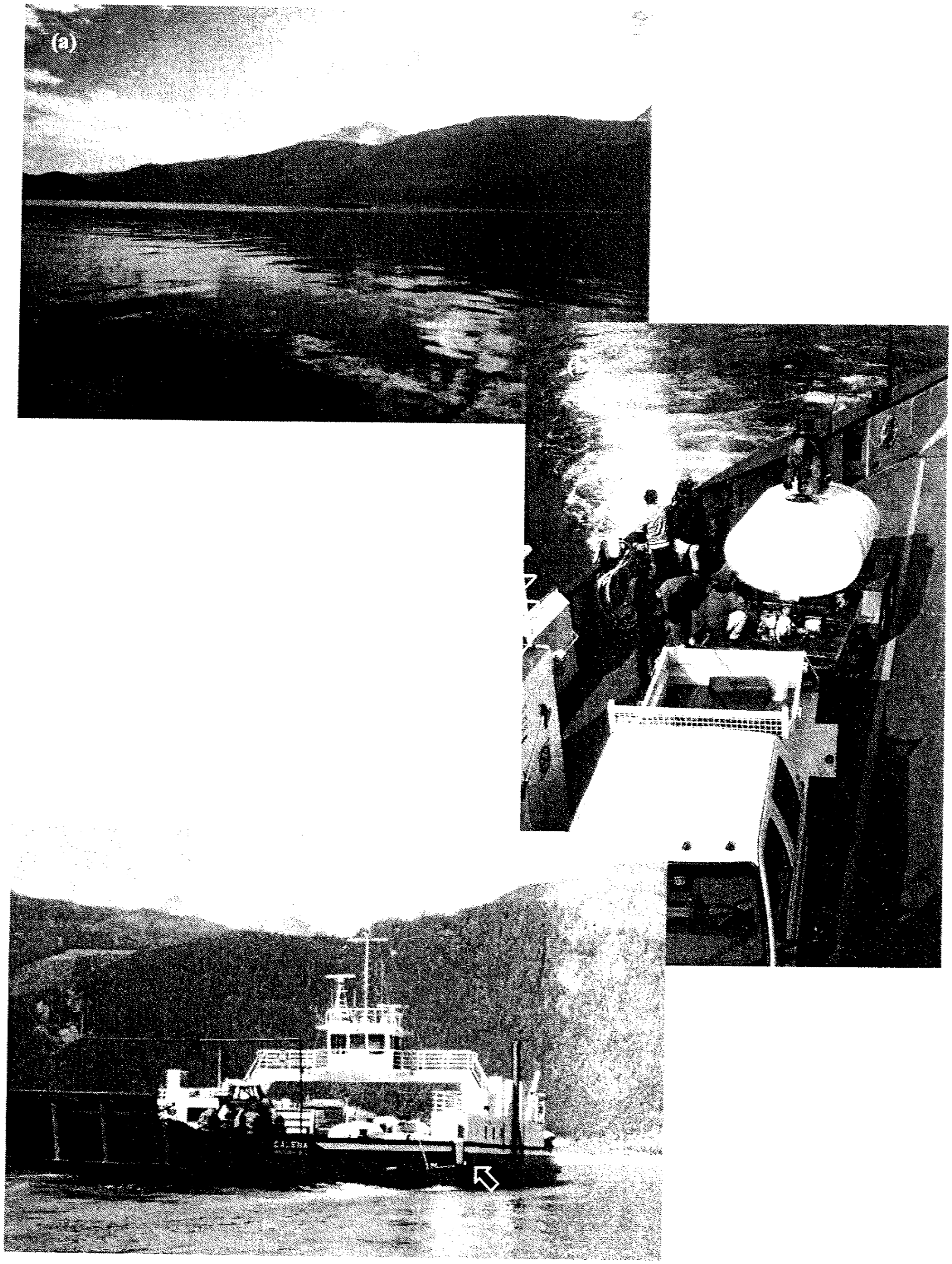

FIGURE 4. (a) The ferry *DEV* Galena crossing Upper Arrow. (b) Truck and fertilizer tank on the *DEV* Galena (c) dispensing from the diffuser (arrow) into the ferry propeller wash. [Photo credits: (a) C. Stevens, (b) Columbia Basin Fish and Wildlife Compensation Program, and (c) R. Pieters]

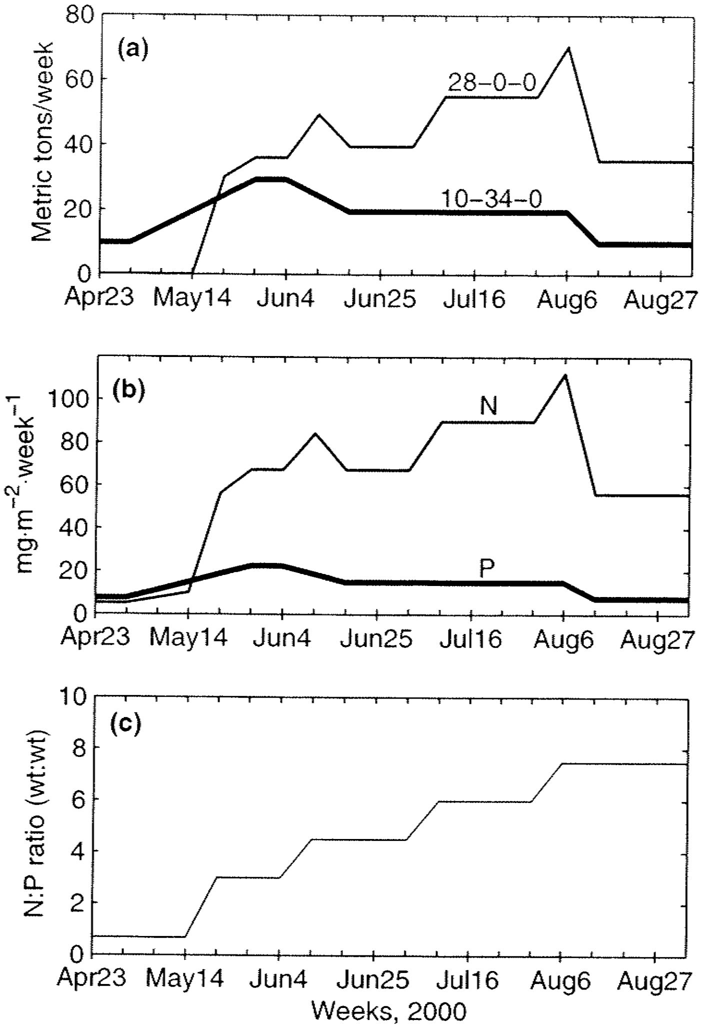

FIGURE 5. (a) Load of liquid ammonium polyphosphate (10–34–0) and urea-ammonium nitrate (28–0-0) fertilizer to the Upper Arrow Lakes Reservoir in 2000, (b) resulting load of phosphorus (P) and nitrogen (N) to the main-stem Upper Arrow (192 km^2), and (c) N:P ratio (wt:wt) for fertilizer applied.

green algae (cyanobacteria), which can fix nitrogen in low N:P ratio conditions (Smith 1983). As a result, increased levels of nitrogen are added through the summer.

Water Chemistry

Eight stations along the reservoir (AR 1–8; Figure 3) were sampled 10 months per year (January, March–November) beginning in May 1997. Two types of samples were taken. First, an integrated 0–30 m sample was taken with a 2.54 cm (ID) tube sampler. This depth range was chosen for consistency with prior work on Kootenay Lake. Integrated 0–30 m samples included water from both epilimnion and metalimnion. Second, a deep sample, approximately 5 m above bottom, was collected with a Niskin sampler. In June and August or September, a series of hypolimnetic depths were also sampled—50, 100, 150, 200, and 250 m, as depth allowed.

The main inflow (Columbia River at Revelstoke) and outflow (Columbia River below the Keenleyside Dam) were monitored monthly throughout the year. Eight local rivers and streams (Illecillewaet, Akolkolex, Incomappleux, Kuskanax, Mosquito, Caribou, Burton, and Inonoaklin) were sampled monthly from April to October, through the freshet and into the fall. For all, two additional samples were taken during freshet (May and June). An additional ten streams and rivers were sampled twice during freshet. All water samples were analyzed by the Environment Canada Laboratories, Pacific Environmental Science Centre, North Vancouver, British Columbia, Canada. Analysis included low-level orthophosphate (OP), total dissolved phosphorus (TDP), which excludes particulates by filtration through a 0.45-μm filter, total phosphorus (TP) determined from an unfiltered sample, ammonia (NH_3), nitrite and nitrate (predominately nitrate, NO_3^-), and chlorophyll *a* (for the 0–30 m samples). Samples for orthophosphate (a.k.a. soluble reactive phosphorus) were field filtered (0.45 μm mesh) and measured with the colorimetric molybdate method using ascorbic acid (Pieters et al. 1998–2000).

Nutrient Load

The flow into the Arrow Lakes Reservoir is composed of the main inflow of the Columbia River at the Revelstoke Dam with the balance being the local inflow from smaller rivers and streams along the length of the reservoir. The daily local flow to the Arrow Lakes Reservoir was computed from the Revelstoke inflow, Keenleyside outflow, water elevation, and a storage-elevation curve (K. Ketchum, B.C. Hydro, Burnaby, British Columbia, Canada). The local flow and stream nutrient data (from eight intensively monitored streams) were apportioned to four regions (Revelstoke Reach, Beaton Arm, Upper Arrow, and Lower Arrow with narrows; Figure 3). The local flow to these regions was 40%, 19%, 23%, and 18% of the total local flow, respectively. The local flow was apportioned to the four regions using the drainage area to each region multiplied by the estimated yield (precipitation per unit area per year) based on historic gauged stream data in each region. Nutrient data (TP, TDP) were interpolated to daily values, and using the daily main and local inflows, the daily nutrient load was estimated and this daily load was summed over the hydrologic year. The hydrologic year was defined to start on 21 November.

Determining the historic nutrient load directly requires nutrient data from before the completion of Mica Dam in 1973, but these data are sparse. Instead, the historic load was estimated by working back, using the impoundment retentions and mean 1997–2000 load from the Columbia River at Revelstoke. The data examined suggest a TP retention of 90% for both Kinbasket and Revelstoke Reservoirs and a TDP retention of 50% and 25% for Kinbasket and Revelstoke, respectively. These are comparable to the retentions determined from extensive data collected in 1994–1995 for the nearby Duncan Reservoir of 90% and 52% for TP and TDP, respectively (Perrin and Korman 1997).

Primary Productivity

Primary productivity was determined monthly at AR2 in Upper Arrow Reservoir and at AR7 in Lower Arrow Reservoir from May to September 1998, April to September 1999, and April to October 2000. The April–September rates, as available, were averaged for each year to allow for interannual comparison of production. Primary productivity was measured in situ at depths of 0, 1, 2, 5, 10, and 15 m. Water samples were transferred directly from an opaque Van Dorn bottle to 300-mL acid-clean BOD bottles, using a silicon filling tube. Samples were inoculated with 0.185 MBq (5 μCi) of $NaH^{14}CO_3$ New England Nuclear (NEC-086H) and incubated at the original sampling depths for 4 h, generally between 10:00 a.m. and 2:00 p.m.

The incubations were terminated by filtration onto a 0.2-μm polycarbonate filter using less than 100 mm Hg vacuum differential (Joint and Pomroy 1983) and placed in a scintillation vial. Each vial had 200 μL of 0.5 N HCl added and was left uncapped in the fumehood until the filters were dry (approximately 48 h). To each vial, 5 mL of Ecolite® scintillation cocktail was added and stored in the dark for more than 24 h before the samples were counted for 10 min in a Beckman liquid scintillation counter model #LS 6500 operated in an external standard mode to correct for quenching. Alkalinity was determined using the potentiometric method of APHA (1976) and converted to dissolved inorganic carbon for use in primary productivity calculations.

Primary productivity was determined from the amount of ^{14}C incorporated into particulate organic carbon retained on a filter (Steemann-Nielsen 1952) and was calculated according to Parsons et al. (1984). Solar radiation was collected from April to November using a Kipp and Zonen CM5 and a Rimco SP440 pyranometer in Upper and Lower Arrow, respectively, and was used to convert hourly to seasonally averaged, daily productivity rates.

Phytoplankton

A depth-integrated (0–20 m) sample from each of the eight monitoring stations (AR1–8; Figure 3) were obtained monthly from May to October in 1997 and monthly from April to October with two samples in June and August for 1998–2000. Samples for phytoplankton identification were fixed with acidic Lugol's iodine preservative (Parsons et al. 1984). The samples were stored in the dark until identification and enumeration were performed using inverted microscopy following Utermöhl (1958) procedures.

Zooplankton

Macrozooplankton (length >150 µm) were sampled monthly from May to October 1997 and April to October 1998–2000, using a flume-calibrated Clarke-Bumpus sampler (153-µm mesh), which was hauled obliquely at approximately 1 m/s from 40 to 0 m at each of six stations (AR1–3, 6–8) during the day. Tow duration was 3 min, with approximately 2,500 L of water filtered per tow. Samples were preserved in 70% ethanol. Zooplankton samples were analyzed for species density and biomass, as described in Pieters et al. (1998–2001) or Ashley et al. (1997, 1999a, 1999b).

Mysids

Mysids *M. relicta* were sampled monthly from May to December 1997, January to December 1998–2000. Sampling was done at night, around the time of the new moon, to decrease the chance that mysids would see and avoid the net. Three vertical hauls were done at each of six stations (AR1–3, 6–8), with the boat stationary, using a 1 m^2 square-mouthed net with a 1,000-µm primary mesh net, 210-µm terminal, and 100-µm bucket. The net was raised from the lake bottom with a hydraulic winch at 0.3 m/s. Samples were preserved in 95% ethanol and analyzed for density and biomass, as described in Pieters et al. (1998–2001) or Ashley et al. (1997, 1999a, 1999b).

Kokanee Salmon Escapements

Kokanee escapements to some Arrow Reservoir tributaries have been estimated periodically since 1966 and annually since 1988 (Sebastian et al. 2000). The kokanee salmon run generally occurs between late August and late September, with the peak of spawning usually occurring in the third week of September.

Adult kokanee returning to spawn in the Hill Creek and Bridge Creek spawning channels are enumerated annually using permanent fish fences (Andrusak 1999). Kokanee salmon at both channels are subsampled at the lower channel fence site for length, sex ratio, and fecundity. Fish downstream of the Hill Creek spawning channel were estimated by ground counts. Up to sixteen additional tributaries to Upper Arrow and ten to Lower Arrow had spawner returns estimated, to approximate a peak spawner count (Sebastian et al. 2000). Estimates were made from helicopter or on foot, due to canopy cover. Flight counts were periodically ground truthed by walking short sections of the larger streams. The index streams represent the vast majority of the total stream-spawning habitat available.

Results

Water Flow and Level

Besides trapping nutrients upstream, the dams have also had a large impact on both inflow and water level (Figure 6). The average annual inflow to the Arrow Lakes Reservoir is 1,080 m^3/s, of which 69% passes through the Revelstoke Dam. Before impoundment, the inflow at Revelstoke was a single peak dominated by snowmelt in spring to early summer and sustained by glacial melt in late summer to early fall. After impoundment, the main inflow is more uniform with two broad peaks, the first from the tail of the freshet after upstream reservoirs fill in summer and the second from release of water for power generation in winter (Figure 6b).

As a result of impoundment, the mean water level of the Arrow Lakes rose by 12.6 m, and mean water level variation doubled from 8 to 15.5 m with peak variations of 20 m (Figure 6c). Before impoundment, water levels remained near the low water level through the year with a brief peak in spring. In contrast, after impoundment, water levels remain near the high-water level with a drop in water level during late winter–early spring. Before impoundment, water covered a partially vegetated flood zone in the spring; now, winter release exposes a large and unvegetated drawdown zone in late winter to early spring (Figure 6d).

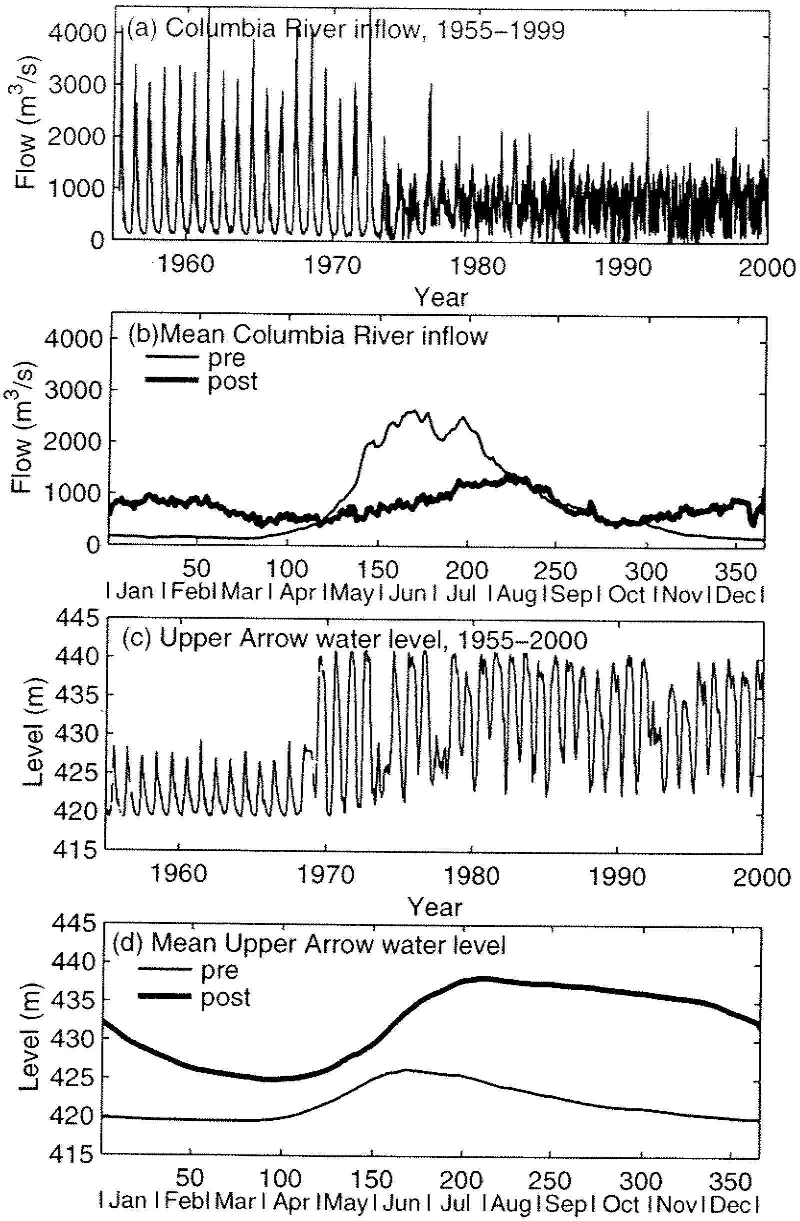

FIGURE 6. (a) Columbia River inflow from 1955 to 2000 showing the change in hydrograph on completion of the Mica Dam in 1973. (b) Mean pre- (light line, 1955–1964) and post-impoundment (heavy line, 1986–1994) inflow. (c) Water level of Upper Arrow at Nakusp from 1955 to 2000. Note the increase in water level variation on filling of the Keenleyside Dam in 1969. (d) Mean pre- (light line, 1930–1965) and post-impoundment (heavy line, 1970–1994) water level.

Weather and Hydrological Conditions

The global climate during the study period was dominated by ENSO (El Niño/Southern Oscillation) events, with an exceptionally strong El Niño in 1997–1998 followed by La Niña in 1998–1999. In 1997, flows were high (local flow 25% above average) in contrast to 1998, when flows were low (local flow 20% below average). Unlike the extremes of 1997 and 1998, in 1999 and 2000, the mean annual local flows were moderate, being 10% and 1% above average, respectively. In addition to low flow, spring and summer in 1998 were characterized by above average sunlight, air, and water temperatures (surface water temperatures were 23–26°C in the Upper Arrow in July 1998 in contrast to the usual 16–20°C).

Water Quality

Selected water quality parameters for the reservoir are summarized in Table 1 for the two prefertilization (1997, 1998) and two postfertilization (1999, 2000) years. Mean Secchi depths were less than 7 m, and mean chlorophyll *a* values were less than or equal to 2.2 μg/L, consistent with the oligotrophic character of the reservoir with no significant change after fertilization. Nitrogen levels were high with nitrate averaging 145 μg/L. Ammonia (NH_3), the form of nitrogen preferred by phytoplankton, was low and near the detection limit (5 μg/L), as would be expected. In contrast to nitrogen, phosphorus levels were low, and the N:P ratio ($NO_2 + NO_3 + NH_3$:TDP) was 60:1 (wt:wt), clearly indicating phosphorus limitation of organic production. Orthophosphate (OP) was at or near the detection limit. Note that all samples, including surface samples immediately downstream of the fertilization zone, were at or below the detection limit of OP (1 μg/L) during fertilization. Consequently, fertilization has not resulted in a detectable change in water quality with the measures used. As would be expected in an oligotrophic system, all of the added phosphorus is immediately utilized (Stockner and MacIsaac 1996).

As observed in the reservoir, annual average ammonia in all river and stream inputs was at or near detection level (5 μg/L). Mean nitrate over the study period ranged from 2 to 400 μg/L for the various rivers and streams. Again, as observed in the reservoir, rivers and streams had orthophosphate (OP) levels near the detection limit (1 μg/L). Values of total dissolved phosphorus (TDP) were low, with means over the study period ranging from 1 to 22 μg/L in the different streams, compared with a mean of 2.6 μg/L in the reservoir. As in the reservoir, TDP concentrations were highest in 1997. Total phosphorus (TP) in the streams was relatively high and variable as a result of a large particulate fraction, in contrast to the reservoir where TP was relatively low and uniform as a result of particle settling. The high nitrogen/low phosphorus loading is consistent with the phosphorus-limited nutrient ratios observed in the reservoir.

Nutrient Load

Traditionally, work on the trophic status of lakes (e.g., Vollenweider 1976) has been done using total phosphorus (TP) in order to include the phosphorus sequestered in cell biomass (Wetzel 1983). However, in the Arrow Lakes Reservoir, the large particulate load contributes to a large and variable TP load, most of which is likely of low biological availability (e.g., in the form of glacial flour, such as apatite) and most of which settles on entering the reservoir. The mean TP load is 1,100 mg/m^2 per year, whereas the historic load was estimated to be 4,000 mg/m^2 per year. While little can be said of the trophic status based on this TP load because of the large inorganic particulate component, a fraction of the historic TP load was biologically available and would have contributed to the productivity of the old Arrow lakes.

The load of total dissolved phosphorus (TDP) varied considerably between years, with changes in stream flow volume and concentration. TDP load was highest in 1997, lowest in

Table 1. Mean value for all (both integrated surface and deep) water samples from Arrow Lakes Reservoir for calendar years, 1997–2000. Included are the detection limit for the method of analysis and the average standard deviation for the annual means. Nutrient values are in μg/L of N or P, chlorophyll *a* is in μg/L, and Secchi depth is in m.

Year	Nitrogen		Phosphorus				
	NH_3	NO_2+NO_3	OP	TDP	TP	Chl *a*	Secchi
1997	5.7	143	1.2	3.2	4.8	2.2	7.1
1998	5.4	147	1.1	2.3	3.2	1.4	9.8
1999	5.8	146	1.0	2.4	4.1	1.4	8.7
2000	6.6	144	1.0	2.5	4.3	1.6	7.8
Detection limit	5.0	2	1.0	2.0	2.0	–	–
Average SD of annual means	±2.9	±23	±0.2	±0.9	±2.1	±1.3	±3.1

1998, and intermediate in 1999 and 2000 (Figure 7). The estimated historic mean load of TDP was 400 mg/m^2 per year, indicating that current TDP loads to Arrow are reduced to about two-thirds of historic values. The fertilizer increased the total loading in 1999 and 2000 by approximately 40%. Care must be taken in comparing TDP to fertilizer loadings, as the fertilizer consists of phosphorus in a highly biologically available form while the bioavailability of the natural TDP load is lower.

Primary Productivity

Primary productivity in Upper Arrow increased 1.5-fold, from 131 mg C·m^{-2} per day in the unfertilized year (1998) to 192 and 201 mg C·m^{-2} per day in the fertilized years, 1999 and 2000, respectively (Figure 8). In contrast to the increases measured in Upper Arrow, the primary production in Lower Arrow decreased from 131 mg C·m^{-2} per day in 1998 to 115 and 102 mg C·m^{-2} per day in 1999 and 2000, respectively. During the two years of fertilization, primary productivity measured in Upper Arrow was, on average, 1.8-fold greater than that measured in Lower Arrow, likely due in part to the effects of fertilization.

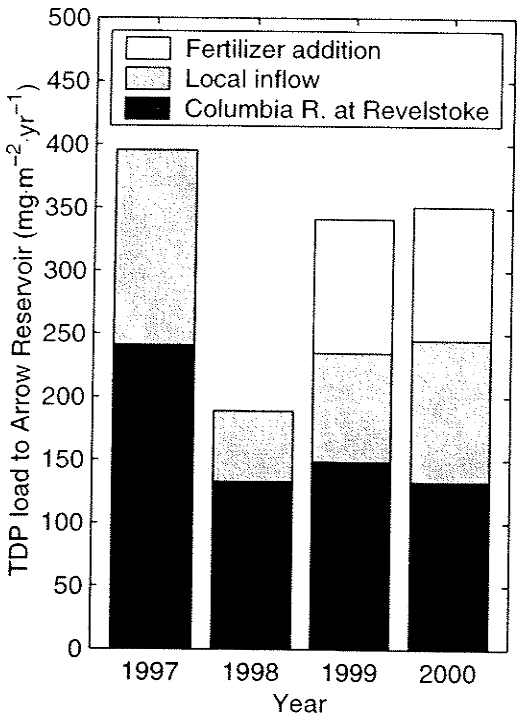

FIGURE 7. Estimated load of total dissolved phosphorus (TDP) to the entire Arrow Lakes Reservoir (498 km^2) from the Columbia River at Revelstoke, the local inflow and from fertilizer addition.

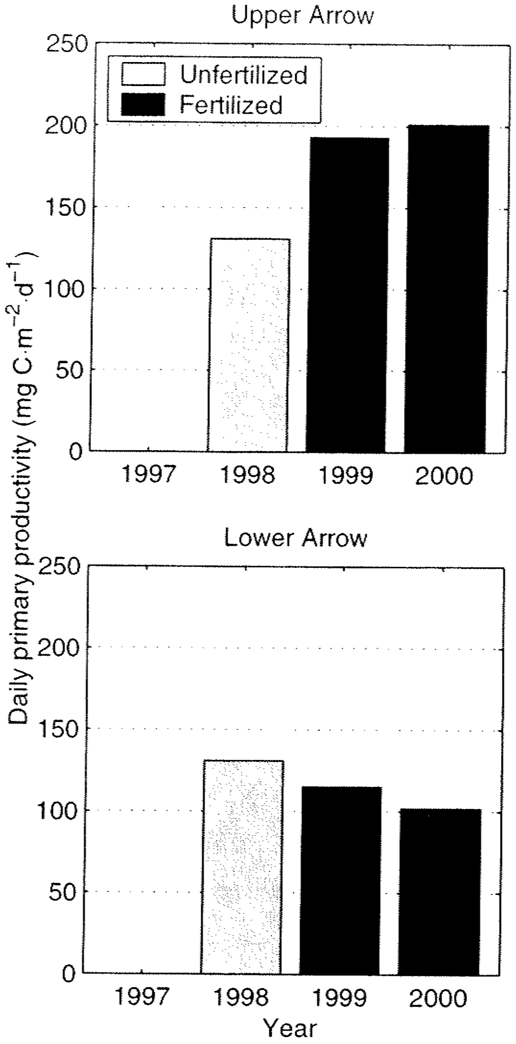

FIGURE 8. Seasonally-averaged daily primary productivity (mg C·m^{-2} per day) in the Upper and Lower Arrow Reservoir from 1998 to 2000. No data collected in 1997.

Phytoplankton

Phytoplankton enumeration in the postfertilization years 1999 and 2000 confirm the 1998 and 1997 observations of a community made up of small species typical of an oligotrophic lake and of a community with very low mean abundance and biomass lacking clear spring and fall blooms. These characteristics provide a clear signal of the oligotrophic status of Arrow Lakes Reservoir. The mean phytoplankton abundance for the Arrow Lakes Reservoir was 5,700, 4,000, 4,800, and 5,000 cells per milliliter in 1997–2000, respectively. The mean biovolume was 0.46, 0.31, 0.29, and 0.46 mm^3/L in 1997–2000, respectively. Note that the abundance and biovolume in the second treated year (2000) remain comparable to that of the first control year (1997).

While no unusual changes in species composition were observed, changes in relative community composition and seasonal succession were noted in the fertilized years. In 1999, abundance peaks were higher than in the previous two years, especially at Station AR1, where high densities of the picoplankter *Synechococcus* spp. were observed. In 2000, the increases in picoplankters were not as apparent; instead, increased densities of microflagellates were observed (two-fold increase in abundance in fall) together with very large populations of colonial diatoms in late summer to late autumn (>6-fold increase in abundance at AR1–3 in September and October 2000).

Zooplankton

During each successive year of the study period, the total zooplankton biomass increased in both Upper and Lower Arrow with the exception of Upper Arrow in 2000 (Figure 9). During all sampling years, Lower Arrow had higher zooplankton biomass than Upper Arrow. During fertilized years, zooplankton biomass increased more in Lower Arrow than Upper Arrow. The zooplankter *Daphnia* spp. is the preferred food of both kokanee and mysids (Thompson 1999), and biomass of *Daphnia* spp. as well as the proportion of total biomass that is composed of *Daphnia* spp. increased in each successive year, to 1999. In 2000, a change was noted; while the total zooplankton biomass in Lower Arrow continued to increase and the proportion of *Daphnia* spp. to total zooplankton biomass remained constant, in Upper Arrow, *Daphnia* spp. biomass declined. It is likely that, in 2000, *Daphnia* spp. biomass was extensively cropped by increased mysid and kokanee populations.

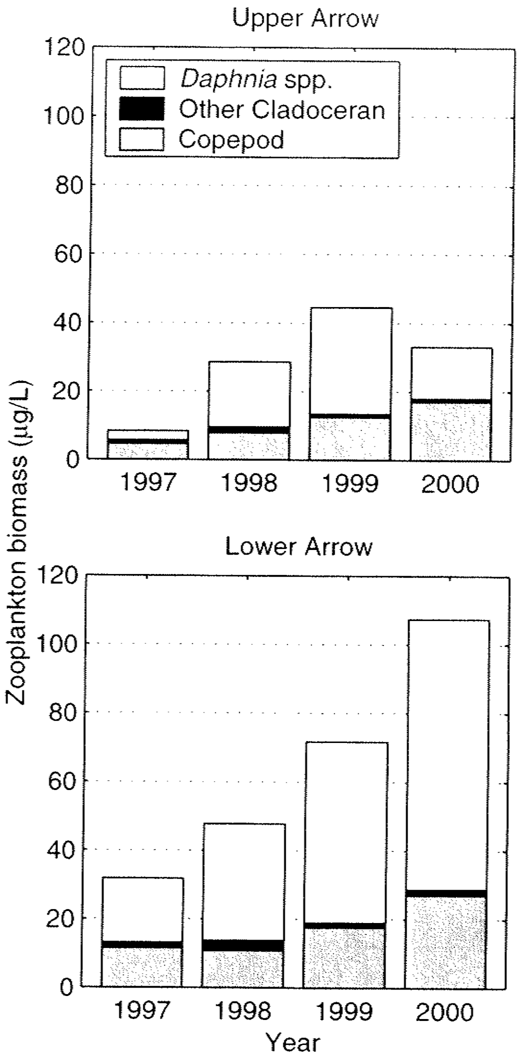

FIGURE 9. Zooplankton biomass (µg/L) in the Upper and Lower Arrow from 1997 to 2000. Values are total annual average biomass of samples collected from May to October 1997 and April to October 1998–2000.

Mysids

Mysis relicta population density increased progressively from 1997 to 2000 in both the Upper and Lower Arrow (Figure 10). In Upper Arrow, the annual average density increased six-fold from 32 individuals/m^2 in 1997 to 195 individuals/m^2 in 2000. Over the same period, density in Lower Arrow increased 3.5-fold from 63 individuals/m^2 to 223 individuals/m^2. The annual average mysid density was consistently higher in Lower Arrow

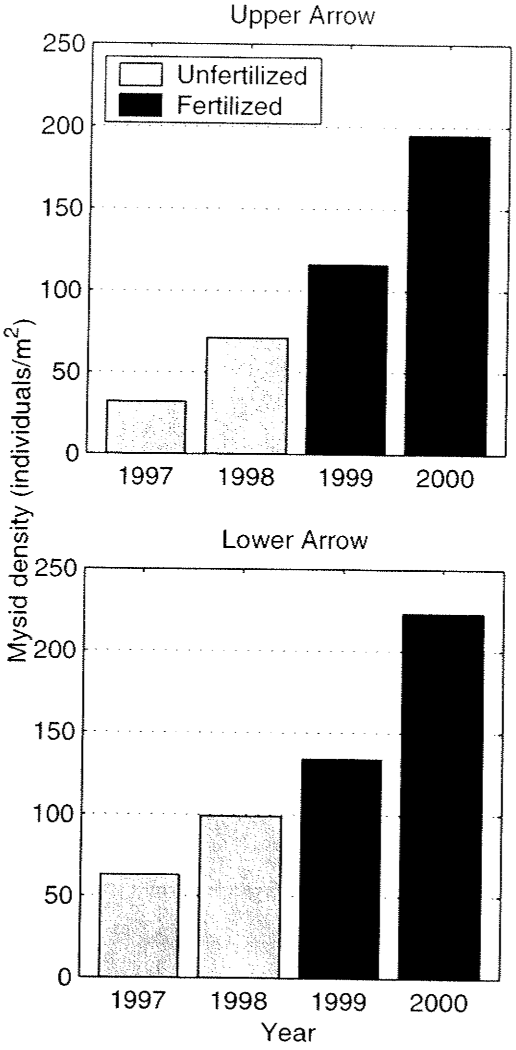

FIGURE 10. Mysid *Mysis relicta* density (individuals/m^2) in the Upper and Lower Arrow Lakes Reservoir from 1997 to 2000. Values are annual averages of deepwater samples collected from May to December 1997 and January to December 1998–2000.

than in Upper Arrow during all sampling years (based on data from deep stations from January to December, except for 1997 when sampling began in May). The mean mysid weight was approximately 4.5 mg/individual, similar in both basins and for all years.

Kokanee

Since the late 1980s, kokanee numbers had been steadily decreasing through their 4-year cycles (Figure 11). Even the modest increase in total numbers in 1998 represents a decline from its parent cycle in 1994. The recruit:spawner ratio for the Hill Creek and Bridge Creek spawning channels portrays the decline for 1992–1998, with values less than the replacement ratio of 1.0 (Figure 12).

Kokanee data suggest that a change occurred in the kokanee population after fertilization was initiated in 1999, with higher escapements, increased size at maturity, increased fecundity, and a recruit:spawner ratio of greater than one. Escapements for Upper Arrow index streams had trended downward through the 1990s to a record low of 47,000 in 1996. Upper Arrow escapements in 1999 and 2000 were 147,000 and 193,000, respectively (Figure 11). At the same time, the size of mature fish at the Hill Creek and Bridge Creek spawning channels, in 1999 and 2000, increased considerably compared with mean size in the 1990s (Figure 13). Mean sizes in 1999 and 2000 were the largest for the years on record for both channels. Fecundity recorded at the spawning channels also increased in 1999 and 2000. Compared with means that have usually been less than 300 eggs per female, the fecundity levels in 1999 and 2000 were among the largest on record (Hill Creek, 394 and 469 eggs/female in 1999 and 2000, respectively).

Arrow Reservoir kokanee return to spawn predominantly at age 4 (Sebastian et al. 2000). Based on otolith readings, the age of kokanee spawners at Hill Creek in 1999 was determined to be primarily 4 years. However, in 2000, a significant shift in age of Hill Creek spawners occurred, in which 52% of the spawners returned as age-3 fish. This shift is also reflected in the size-frequency data with two modes evident rather than one (Pieters et al. 2000, 2001). Because of the change in age at maturity in 2000, and to provide an estimate of the recruit:spawner ratio for 2000, it was assumed that all age-4 fish and 50% of age-3 fish contributed to the spawner numbers in 2000. In 1999 and again in 2000, the recruit:spawner ratios at Hill Creek and Bridge Creek were greater than one for the first time since 1992. While analysis of further data is ongoing, the substantial shift in the recruit:spawner ratio suggests a change in the kokanee population structure has occurred.

Discussion

Apart from a modest record of kokanee data, very little was known about the Arrow Lakes Reservoir

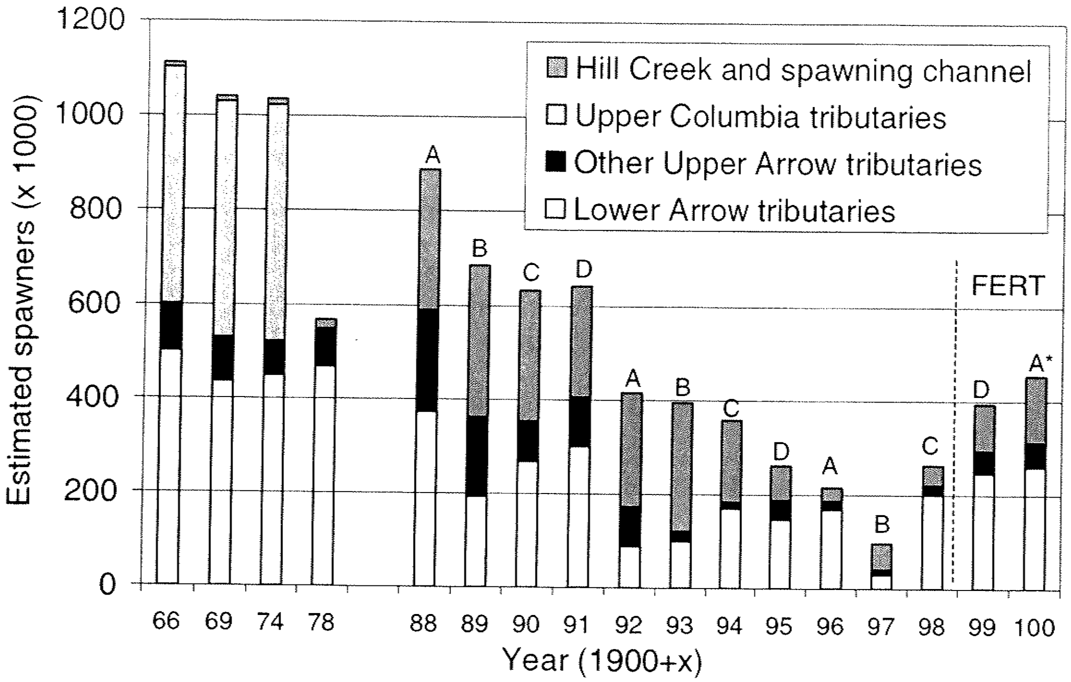

FIGURE 11. Kokanee spawner escapement for the Upper and Lower Arrow Reservoir, 1966–2000. As returning spawners are predominantly 4 years old, the year cycles are labeled A, B, C, or D for 1988–2000. In 2000 (*), returns include spawners of 3 years of age; see text. Number of spawners shown for the Lower Arrow in 1993 and 1994 are estimated. The Upper Columbia tributaries were above the Revelstoke Dam accessible before 1983. The Hill Creek spawning channel was completed in 1980 and was designed to replace the spawning habitat above the Revelstoke Dam.

prior to the present study. This lack of information is somewhat surprising in relation to its size and local importance, but not that unusual in comparison to the many other large lake/reservoir systems throughout the interior of British Columbia. Two years of baseline monitoring were completed in 1997 and 1998, and a 5-year fertilization experiment to replace limiting nutrients trapped upstream began in 1999, with preliminary results for 1999 and 2000 reported here. To many, the term 'fertilization' connotes high levels of nutrient additions, as in a fishpond where water quality is sacrificed for productivity. In contrast, the goal of the nutrient additions to the Arrow Lakes Reservoir has not been enhancement, but the maintenance of natural kokanee populations to avoid either their extinction or population decline to a level no longer genetically viable. Unlike the dangers associated with most exotic species introductions, experience with the relatively light addition of nutrients to coastal lakes indicates that the effects of fertilization are reversible (Stockner and MacIsaac 1996).

In Arrow Lakes Reservoir, observations from all trophic levels in both the pre- and post-treatment years are consistent with a system experiencing low levels of productivity. This is supported by the reservoir water chemistry and nutrient loading data, which shows a very high N:P ratio and phosphorus limitation. The phosphorus load from river and stream inflows has varied significantly between years, but the trapping of nutrients behind upstream dams has reduced TP to approximately one-quarter and TDP to approximately two-thirds of historic levels, based on an estimate of historic pre-impoundment nutrient loads.

In 1999 and 2000, the system was treated with a seasonally adjusted load of phosphorus and nitrogen at a high N:P ratio to prevent blooms of nitrogen-fixing blue-green algae. During fertilized years, levels of orthophosphate in the lake remained at or below detection limits, even at the station just below the fertilization zone. No obvious changes in TP, TDP, or other water quality parameters were apparent during fertilization.

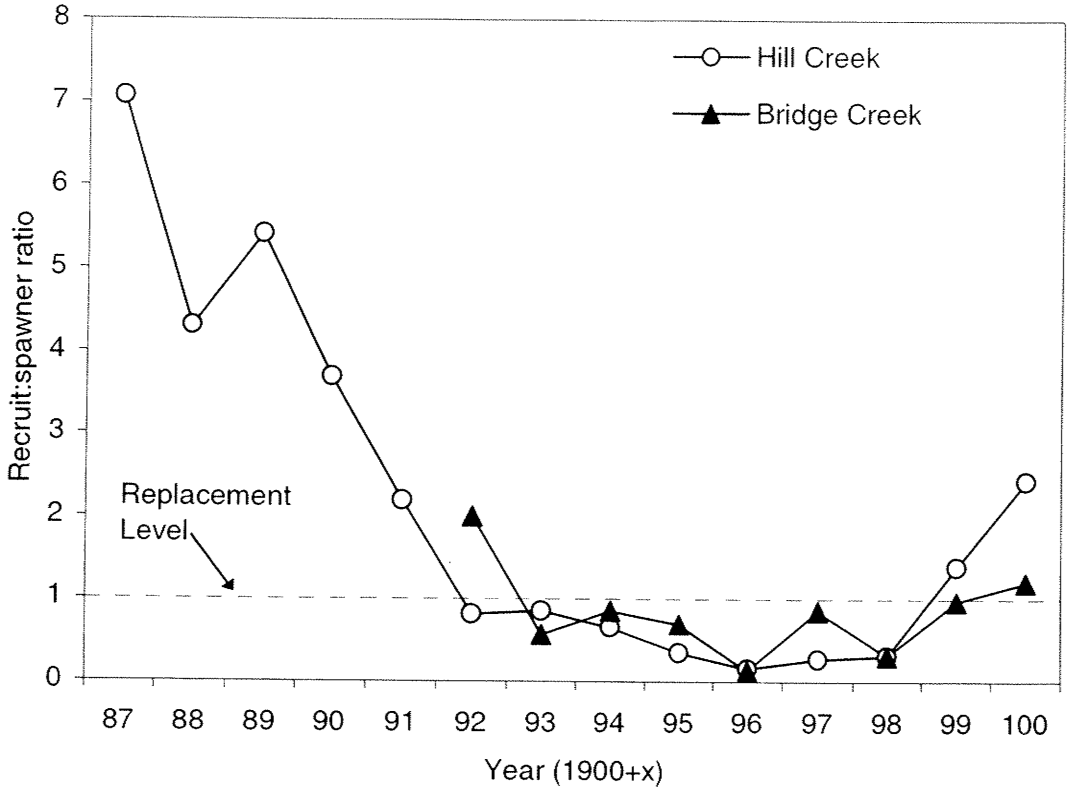

FIGURE 12. The kokanee recruit:spawner ratio, 1987–2000, for Hill Creek and Bridge Creek. The recruit:spawner ratio of, for example, 1997 is the number of spawners that returned in 1997 divided by the number of spawners that returned in 1993. This assumes that all spawners were aged 4. For computation of the 2000 ratio, see text. Replacement occurs when the ratio is above one.

Unlike abundance and biomass at a given trophic level, primary productivity provides a direct measure of the rate of production and is an important key to monitoring the effect of nutrient additions (Stockner and MacIsaac 1996). Primary productivity in Upper Arrow showed an increase in the fertilized years of 1.5-fold over that in 1998. In contrast, Lower Arrow productivity was reduced in 1999 and 2000 compared to that in 1998. If Lower Arrow were considered a control, then the change in the Upper Arrow primary productivity is likely due to the nutrient additions. Note, however, that primary productivity was not measured in 1997 and that the single untreated year, 1998, was characterized by warm surface waters, low flow, and a low load of natural nutrients.

While no unusual changes in phytoplankton species composition were observed, changes in the relative community composition and seasonal succession were noted in the fertilized years, changes that suggest the system was shifting from ultra-oligotrophic to oligotrophic conditions. In 1999, increased abundance peaks and high densities of the picoplankter *Synechococcus* spp. were observed, especially at the northernmost station (AR1). Though this minute picoplankter did not contribute substantially to phytoplankton biomass, it is a vital base for the microbial food webs that dominate the plankton communities and is a strong indicator of the oligotrophic condition of the reservoir. Blooms of *Synechococcus* spp. have been observed in almost all whole-lake fertilization experiments conducted in both coastal and interior regions of British Columbia (Stockner 1987; Stockner and MacIsaac 1996). In 2000, the increases in picoplankters were not as conspicuous; instead, increased densities of microflagellates were observed along with very large, late summer to late autumn populations of diatoms. A response in diatoms of this size has not been observed be-

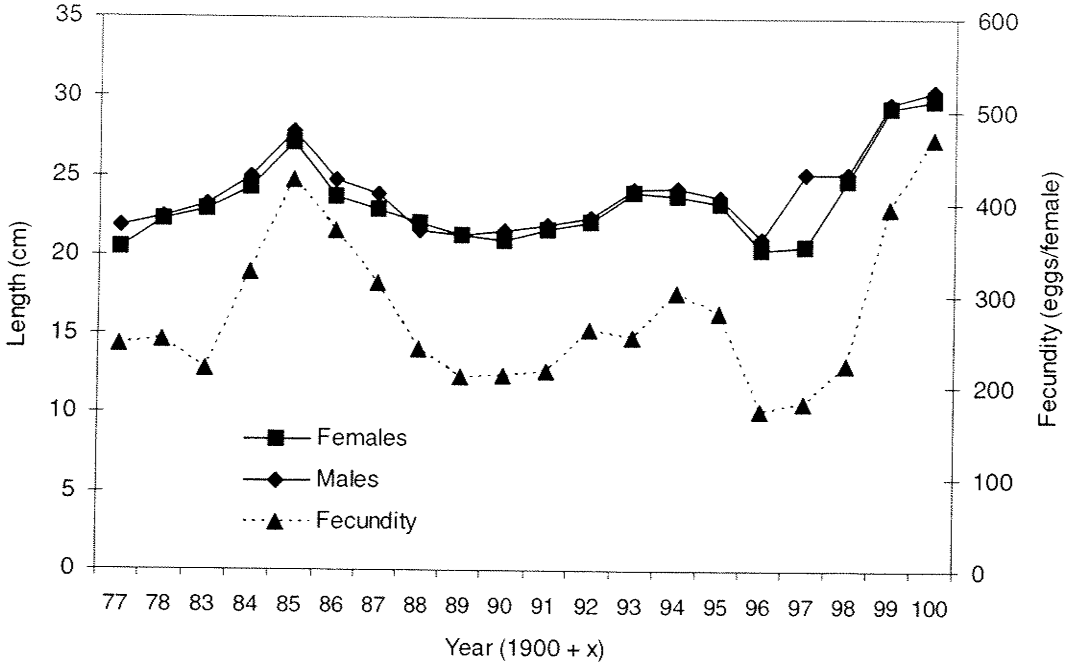

FIGURE 13. Mean length (cm) and fecundity (eggs/female) of Hill Creek kokanee spawners, 1977–2000.

fore in fertilized coastal or interior subalpine lakes (Stockner and MacIsaac 1996; Stockner and Shortreed 1994). The presence of more diatoms in the pelagic zone of Arrow Reservoir should be viewed as a positive sign, indicating that the system is likely increasing its trophic efficiency and forage production through shorter food chains (Stockner and Porter 1988).

Beside increases in primary productivity and changes in the seasonal succession of phytoplankton, increases have also been observed both in total zooplankton biomass, particularly that of *Daphnia* spp., and in mysid density. Early modeling work on Kootenay Lake indicated that mysids may out-compete kokanee for preferred food sources such as *Daphnia* spp. (Walters et al. 1991). While mysid populations appear relatively stable in Kootenay Lake (Ashley et al. 1997, 1999b) this potential problem in Arrow Reservoir will continue to be monitored.

As kokanee numbers in the Arrow Reservoir declined through the 1990s, their size and fecundity showed little change with no density-dependent response, strongly suggesting a productivity problem. During fertilization in 1999 and 2000, the large size at maturity of kokanee further suggested that a density dependent growth response has yet to occur. A decrease in size would be expected once the lake's carrying capacity has been reached, and this will likely occur in Arrow, similar to the response of kokanee salmon in the North Arm of Kootenay Lake (Andrusak 2000).

The 5-year experimental fertilization of Arrow Reservoir (1999–2003) is well underway and full evaluation is pending completion. Results collected during 1999 and 2000 suggest that Arrow Reservoir is responding favorably to nutrient additions with more efficient carbon (energy) flows within the pelagic community. The documented increase in kokanee size, numbers, and the improvement in the recruit:spawner ratio from values below to above replacement levels are particularly encouraging.

Acknowledgments

Funding was provided by the Columbia Basin Fish and Wildlife Compensation Program (CBFWCP), with additional funding from the Columbia Power Corporation, the B.C. Ministry of Fisheries, the B.C. Ministry of Water, Land and Air Protection (MWLAP), the National Sciences and Engineering Research Council of Canada, and the University of British Columbia (UBC).

This work was initiated by Jay Hammond (Fisheries Section Head, Nelson, MWLAP) and Ken Ashley (B.C. Ministry of Fisheries). The authors acknowledge that none of this project would have been possible without the tireless work of Mark Young, Don Miller, Adam Croxall, and Gary Monroe (Kootenay Wildlife Service); Grant Thorpe, Diana Koller, Bob Millar, Les Fleck, John Bell and Melvin Wong (MWLAP); Karen Bray, Harold Manson, Steve Arndt (CBFWCP). We also acknowledge the help of Gary Birch, Don Druce, Kelvin Ketchum, Dan Nixon, Ric Olmsted, Brian Gadbois, Dean de Biesen, Chris Madland (B.C. Hydro); the town of Nakusp; and Sabine and Ulf Burmeister (Kokanee Bay Resort). We are grateful for laboratory equipment made available by Paul Harrison (UBC) and for field equipment made available by Douw Steyn and Tim Oke (UBC). We thank the many UBC student volunteers who have helped with the productivity sampling, and thanks to M. Derham, C. Sewell, A. Eskooch, and L. Zaremba for their help in data processing. We also gratefully acknowledge discussions with Dale Sebastian and George Scholten. We thank the reviewers for their helpful suggestions.

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