

Effects of impoundment on nutrient availability and productivity in lakes

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Abstract

We investigate the hydraulic alteration and the effect on primary productivity of the Hugh Keenleyside Dam built at the outlet of the Arrow Lakes (British Columbia, Canada) in 1967. Three dam-induced hydraulic changes have been identified as relevant: (1) water level increase, (2) leveling of the seasonal outflow, and (3) subsurface release of water from the dam. The potential effect of these alterations on primary productivity were tested with a numerical model supported by field observations. Hydraulic modifications can reduce lake productivity by up to 40%, primarily as a result of altered flow path and allowing nutrients to pass through the reservoir without entering the productive zone near the surface. This productivity loss is comparable to the reduction caused by nutrient retention behind dams constructed upstream of the Arrow Lakes Reservoir. The combined productivity loss from both of these two mechanisms is significant and may well be responsible for the dramatic decline of kokanee (*Oncorhynchus nerka*) observed in the Arrow Lakes Reservoir in the 1990s.

Dams impose a variety of changes on downstream aquatic systems (McCully 1996). Dam management alters

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the naturally-occurring seasonal discharge and, in extreme cases, can even eliminate residual flow (Richter et al. 1997; Robinson and Uehlinger 2003). Physical properties such as river temperature (Hamblin and McAdam 2003; Meier et al. 2003), geochemical quantities such as carbon and nutrients (Friedl and Wüest 2002), and biological parameters such as fish (Zhong and Power 1996) even downstream vegetation (Friedman et al. 1998) can be influenced by impoundment. Enhanced particle settling behind dams leads to retention and subsequent removal of organic matter and nutrients (Conley et al. 2000; Vörösmarty et al. 2003). Because of changes in outflow temperature and suspended solids, dams can influence the plunging and intrusion (Macintyre et al. 2006) of downstream rivers into lakes or estuaries located below dams (Finger et al. 2006).

The transformation of lakes into managed reservoirs not only affects downstream aquatic systems but can also alter processes within the reservoir. A number of such mechanisms have been identified. Because of organic matter in newly flooded soils and vegetation, reservoir productivity typically increases during the first decade after dam construction (Ney 1996; Stockner et al. 2000). However

in the long run, reservoirs without major sources of pollution undergo oligotrophication as nutrient levels drop below preimpoundment values (Stockner et al. 2000). Increased water level fluctuation has been implicated in limiting the littoral ecosystem (Milbrink and Holmgren 1981), which can contribute significantly to pelagic production, particularly in small to medium-sized lakes (Wetzel 2001). The dam itself represents a barrier to anadromous fish and thereby blocks the marine-derived landward nutrient transport as they migrate upstream (Stockner and MacIsaac 1996; Cederholm et al. 1999). In addition, biogeochemical processes within reservoirs are affected by changes in the movement of water resulting from various hydraulic alterations, including changes in water level, changes in the inflow and outflow hydrographs, and changes in the depth(s) at which water is withdrawn from the reservoir.

There are often multiple dams in a catchment, and water quality may be affected by the presence of both upstream dams as well as the dam that created the reservoir. An example is the Arrow Lakes Reservoir, which was formed by Keenleyside Dam (1967) and was subsequently affected by the construction of upstream Mica (1976) and Revelstoke (1983) dams (Fig. 1). Attention was drawn to the Arrow Lakes Reservoir in the 1990s because of fast declining numbers of spawning kokanee (*Oncorhynchus nerka*), a landlocked sockeye salmon (Pieters et al. 1998, 2003). The dramatic decline of kokanee was most probably caused by lower food resources (zooplankton) as a result of fewer nutrients, primarily phosphorus (P). As kokanee are typically the first fish species to respond to a reduction in lake productivity (Ney 1996), future effects on other fish and wildlife were feared. In response to the decline in kokanee, intensive lake monitoring began in 1997.

We hypothesize that the two primary causes of reduced productivity in Arrow Lakes Reservoir are: (1) trapping of nutrients behind upstream dams and (2) changes in the hydraulics of the reservoir as a result of impoundment. Here we focus on the second and hypothesize that dam-induced hydraulic changes may have effects on primary productivity and lake-internal biomass. We want to understand how modifications of hydraulic processes can affect nutrient pathways and potentially other growth-influencing factors (such as light, temperature, and residence time). The operation of dams can vary considerably in response to multiple and complex demands on water resources. Understanding the effect of different flow regimes on productivity is necessary to avoid compromising aquatic systems.

The objective of this article is to assess the effect on productivity of converting a lake into a reservoir. We use field observations and a numerical model applied to a sequence of scenarios that represent the present-day Arrow Lakes Reservoir both with and without the Keenleyside Dam. We describe the study site, the numerical model, the model calibration, and the sequence of model scenarios that will be used to explore the effect of impoundment. The results for each of the model scenarios are presented and conclusions drawn. Finally the relevance of the results is discussed by comparing the effects of

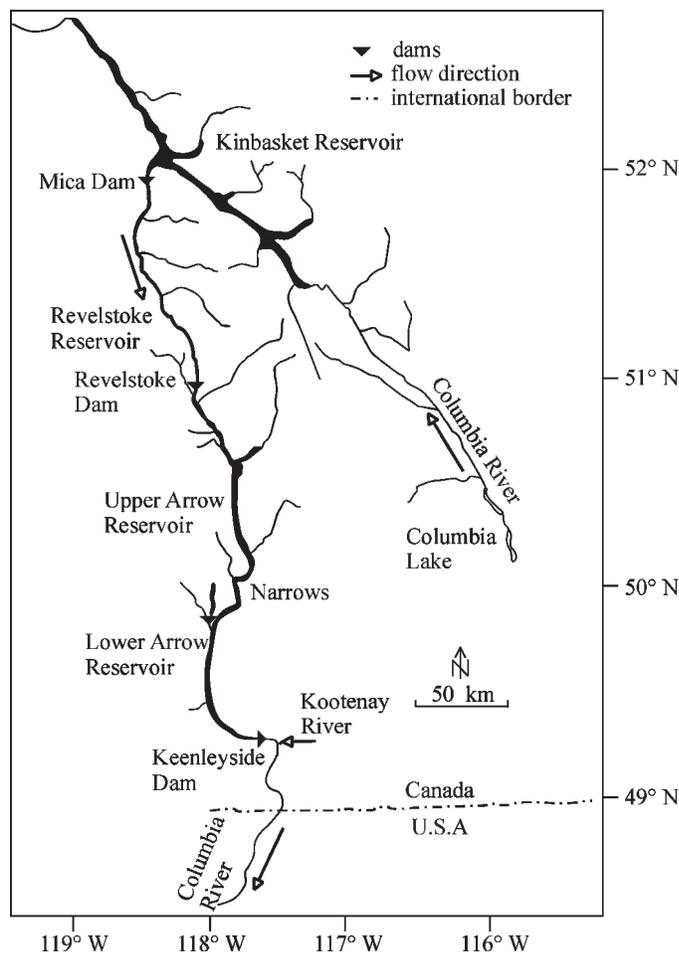


Fig. 1. Map of the Upper Columbia River basin. The Columbia River begins in Columbia Lake, flows through Kinbasket and Revelstoke Reservoirs and then through the study site: the Upper and Lower Arrow Lakes Reservoir. The Hugh Keenleyside Dam controls the outflow of Lower Arrow.

internal hydraulic changes on lake productivity with those of upstream dams.

Study site

Site description—The Arrow Lakes Reservoir is situated in southwest British Columbia, Canada, at 50°N and 118°W (Fig. 1; Table 1). Surrounded by the Selkirk and Monashee Mountains, it lies in a steep, narrow, and glacially-carved valley at 432 m asl. The reservoir is <3 km wide, yet >240 km in length. It consists of two deep basins, the Upper Arrow (maximum depth ~287 m) and the Lower Arrow (maximum depth ~194 m), which are connected by a shallow Narrows (minimum depth 14 m). In the following we use the term “Arrow” if the entire reservoir is addressed and “Upper Arrow (UA)” or “Lower Arrow (LA)” when we refer to the respective basin.

The Columbia River, entering at the north and leaving at the south (Fig. 1), accounts for ~69% of the inflow (Pieters

Table 1. Characteristics of the Arrow Lakes Reservoir.

Quantity	Symbol (units)	Upper Arrow	Lower Arrow
River inflow*	Q (m ³ s ⁻¹)	1,390	1,490
Basin volumes†	V (km ³)	28	11
Surface area†	A (km ²)	295	170
Maximum depth	(m)	287	194
Average depth	(m)	95	65
Average upwelling (w = Q A ⁻¹) at outflow level	w (m d ⁻¹)	0.4	0.8
Bulk residence time	(d)	230	90
Estimated in situ primary production‡	PP (g C m ⁻² yr ⁻¹)	19.5	22.5

* Average 1 April to 31 October 1997–1998.

† At mean water level.

‡ In 1998 before the fertilization program began in 1999 (Pieters et al. 1999).

et al. 1998). The bulk residence time is only ~230 days for UA and ~90 days for LA because of the high flow of the Columbia River (Table 1).

The Arrow Reservoir shows stratification typical of lakes at mid-latitude with a warm surface layer reaching ~20°C (Fig. 2a). Below the broad thermocline, the in situ temperature closely follows the temperature of maximum density (Fig. 2b) and the stability of the deep water is determined by a weak salinity gradient (Fig. 2b,c). This structure is representative of the deep water throughout the year. Although profiles of UA appear permanently stratified below 70 m, chloro–fluoro–carbon profiles (Pieters et al. 1999), reveal that the deep-water masses are not old. These observations indicate that deep-water renewal occurs mainly by plunging inflows, primarily of the Columbia River. LA shows a similar seasonal stratification as UA, although convective mixing in winter reaches deeper than in UA (Pieters et al. 1998, 1999, 2000).

With concentrations of soluble reactive phosphorus (SRP) near the detection limit of ~1 mg P m⁻³ (Pieters

et al. 2000), Arrow Reservoir is ultra-oligotrophic and P limited (Vollenweider and Kerekes 1980), with high oxygen concentrations throughout the water column during all seasons. Because of a decline in kokanee, a fertilization program—which is not investigated in this paper—was initiated in 1999 to compensate for decreasing lake productivity (Ashley et al. 1997; Pieters et al. 2003).

Major phytoplankton growth is observed in both basins from April/May to October (Pieters et al. 1998, 1999). In the following, we will refer to this period with the term “productive season.” Potential vertical extension of phytoplankton growth is quite large due to the clear water, with average light compensation depths of ~16 m for UA and ~19 m for LA (photosynthetically active radiation [PAR] measurements; Pieters et al. 1999).

Hydraulic changes due to Arrow impoundment—In the following analysis we focus on three hydraulic changes as the result of the Keenleyside Dam.

Submerged Narrows: Completion of the Hugh Keenleyside Dam in 1967 raised the water level by 12 m and transformed the riverine connection between UA and LA into a wider, lake-like Narrows (Pieters et al. 1998).

Seasonal flow management: Keenleyside Dam is operated to prevent downstream flooding; water stored in summer is released in winter for hydropower generation. As a result, Keenleyside Dam contributes to the leveling of the spring and summer flow of the Columbia River, and the outflow from Keenleyside Dam is relatively steady (Fig. 3).

Deep withdrawal from Lower Arrow: Finally, Keenleyside Dam affects the outflow depth(s) from LA. Since impoundment, the water from LA exits at two levels: while overflow sluices enables near-surface outflow, part of the outflow passes through tunnel ports ~20 m below the surface (Pieters et al. 1998).

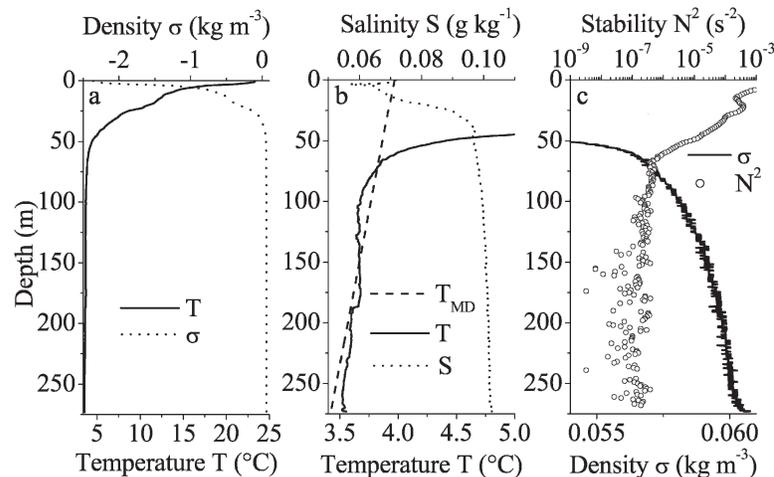


Fig. 2. Profiles from mid-basin (deepest location) in Upper Arrow on 14 August 1998 of (a) temperature, T, and density, ρ (shown as $\sigma = \rho - 1,000$ kg m⁻³), over the entire scale; (b) salinity over the entire scale and temperature in the hypolimnion; and (c) density and water-column stability in the hypolimnion. T_{MD} indicates the pressure-dependent temperature of maximum density. Data from Pieters et al. (1999).

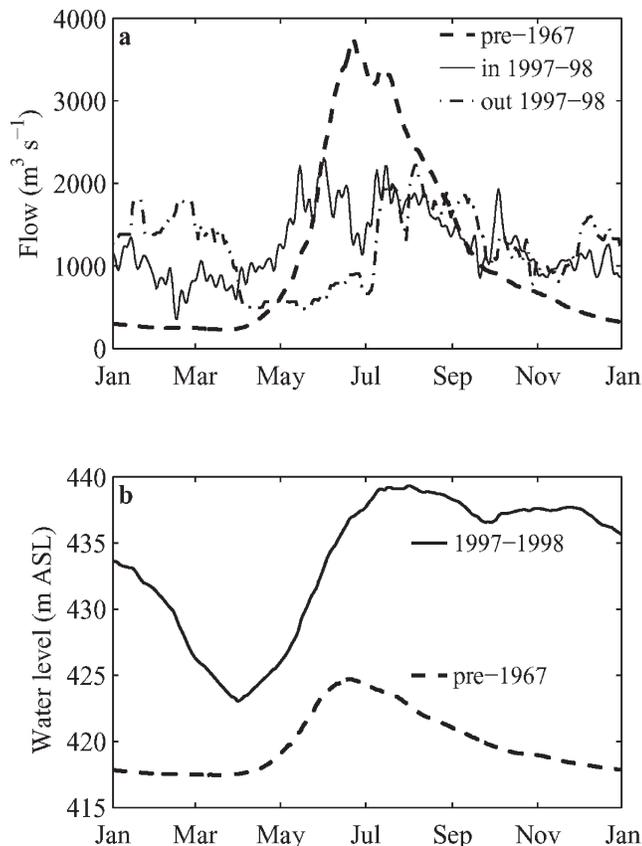


Fig. 3. (a) Total inflow to Arrow (Columbia River and local flow), and outflow from Arrow averaged for 1997 and 1998. The flow through the Narrows is similar to the outflow during the productive period. (b) Historic and present-day water level in Arrow. Data from Pieters et al. (1998, 1999).

Methods

Model approach—A vertical one-dimensional reaction–advection–diffusion model, implemented in the AQUASIM software package (Reichert 1994), was adapted for the Arrow. This biogeochemical model was developed by Omlin et al. (2001a, 2001b) for mesotrophic Lake Zürich and modified by Matzinger et al. (2007) and Finger et al. (pers. comm.) for the oligotrophic Lake Ohrid and Lake Brienz, respectively. As P is the limiting factor, and therefore of primary concern, nitrogen cycling is not included. Processes at the sediment–water interface are simplified by a fixed re-mineralization ratio of 60% of the settling organic material (Hupfer et al. 1995; Moosmann et al. 2006). Vertical mixing is implemented by eddy diffusivity. We use a constant, high diffusivity K ($\text{m}^2 \text{s}^{-1}$) in the surface layer and the turbulent kinetic energy budget approach (Wüest et al. 2000) for the stratified waterbody below. The epilimnion thickness is estimated from monthly temperature and salinity profiles (Fig. 2). The detailed model equations and parameters are given in Web Appendix 1 (http://www.aslo.org/lo/toc/vol_52/issue_6/2629a1.pdf).

Because Arrow consists of two distinct basins, UA and LA are simulated individually. The outflow from UA is used as the input to LA. The density of the inflow is calculated, and the inflow-water is inserted at the level of matching density in the water column. AQUASIM does not allow water level variations. In this application, we used discharge at the outlets (Narrows for UA and Keenleyside Dam for LA) to define the through-flow regime. This restriction is not critical, because upwelling in the two stratified hypolimnia and water exchange in the surface layers depend primarily on the outflows.

The model variables are temperature, three different forms of P, dissolved oxygen, total phytoplankton, total zooplankton, and dead organic matter. The following processes are simulated: primary production, growth of zooplankton, respiration, aerobic mineralization in the water column and at the sediment surface, death of phyto- and zooplankton, and P adsorption. Light availability is simulated as a function of a constant background extinction, phytoplankton density, and dead organic matter. The model period is February to October in order to cover the entire productive season.

Data required for initial and boundary conditions such as bathymetry, inflows, surface temperature, solar radiation, water quality (temperature, salinity, nutrients, dissolved oxygen), and plankton (phytoplankton, zooplankton, productivity) are based on the monitoring of Arrow and its tributaries in 1997 and 1998 before fertilization began in 1999. The available data and the methodology used are detailed in the reports by Pieters et al. (1998, 1999).

Model calibration—The model is calibrated with measured temperature profiles, phytoplankton, and zooplankton abundance. To maintain the temporal characteristics of the phytoplankton and zooplankton development, simulations are optimized for 1997. For LA only, the mean of 1997 and 1998 is used for phytoplankton as it lacks a clear seasonal maximum. We have adjusted mixing parameters, phytoplankton and zooplankton growth rates $k_{\text{gro,ALG},20}$ and $k_{\text{gro,ZOO},20}$, and SRP input $S_{\text{SRP,in}}$ for UA (Web Appendix 1). We outline our choice for $S_{\text{SRP,in}}$, $k_{\text{gro,ALG},20}$, and the settling velocity $v_{\text{sed,ALG}}$ in more detail as they are of particular importance.

We treated the SRP concentration of the inflow to UA, $S_{\text{SRP,in}}$ as a fit parameter, because most measured SRP concentrations are below the detection limit of $\sim 1 \text{ mg P m}^{-3}$ and its load contains correspondingly large errors (Pieters et al. 1998, 1999). The flow-averaged SRP concentration in the UA inflow was determined by parameter fitting to be $S_{\text{SRP,in}} \approx 0.85 \text{ mg P m}^{-3}$. This value is well within the expected range, namely below the detection limit of 1.0 mg P m^{-3} and in agreement with two profiles of high-resolution S_{SRP} measurements in UA (Pieters et al. 1999).

The phytoplankton growth rates were fitted separately for the two basins. The average effective growth rates (0.31 d^{-1} for UA and 0.32 d^{-1} for LA) are similar and low (Kalff 2002), as can be expected in a cool, nutrient-poor lake at high latitude.

Table 2. Model scenarios.

Scenario	Change relative to no Arrow impoundment	Narrows flow	Spring flow	Deep Lower Arrow outflow	Annual primary production (% of no Arrow impoundment)*		
					Upper Arrow	Lower Arrow	Total
1	No Arrow impoundment	riverine	high	0	100	100	100
2	Submerged Narrows	0–16 m	high	0	79	112	91
3	Seasonal flow management	riverine	low	0	96	86	93
4	Deep withdrawal from LA	riverine	high	50%	100	78	92
		riverine	high	100%	100	62	87
5	Arrow impoundment (scenarios 2, 3, 4b)	0–16 m	low	100%	76	54	68
6	Scenarios 2 and 3	0–16 m	low	0	76	98	84
7	Scenarios 2 and 4b	0–16 m	high	100%	79	52	70
8	Scenarios 3 and 4b	riverine	low	100%	96	61	84

* 100% of primary productivity are 24 g C m⁻² yr⁻¹ for UA, 21 g C m⁻² yr⁻¹ for LA and 23 g C m⁻² yr⁻¹ for total.

Settling velocities are particularly important, as they determine whether particles are washed out or remain in the system. We assumed that zooplankton are able to prevent flushing/sedimentation by active movement while alive. Thus, only zooplankton in the depth range of the outflow will be washed out of the reservoir. This is different for phytoplankton: using Stokes (1851), particles of diameter D_p (m) settle with velocity $\frac{\Delta\rho}{\rho} \frac{g}{18\nu} D_p^2$, where $\Delta\rho$ (kg m⁻³) is the density difference between particles and water, $g = 9.81$ m s⁻² is the gravitational acceleration, and ν (1 to 1.5×10^{-6} m² s⁻¹) is the kinematic viscosity of water. Two thirds of the phytoplankton biomass are smaller than 20 μ m (Pieters et al. 1998, 1999) and consequently settle with velocities $v_{\text{sed,ALG}}$ slower than the upwelling velocity in the Arrow of ~ 0.3 m d⁻¹ (see Results). Wetzel (2001) indicates values between 0 m d⁻¹ and 1 m d⁻¹ for some of the dominant algae species found in Arrow (Pieters et al. 1998, 1999). The second largest (by biomass) phytoplankton group present in Arrow is larger than 20 μ m; a sinking rate $v_{\text{sed,ALG}} = 0.5$ m d⁻¹ was used in the model. This value allows both sedimentation and flushing (upwelling velocities in Table 1). Dead organic matter undergoes two opposing effects: whereas cluster aggregation causes faster settling, scavenging and mineralization of the dead material reduces particle sizes and hence slows settling. Therefore we used the same sinking rate for dead organic matter as for living algae.

Model scenarios—In order to explore the hydraulic effects of impoundment on reservoir productivity we consider the three specific changes introduced above (see Site): (1) submerged Narrows; (2) seasonal flow management; and (3) deep withdrawal from LA. A model scenario is defined for each change, which enables testing of their individual and combined effect on productivity. In all of the model scenarios the same lake topography is used with present-day mean water level of 432.4 m asl. All scenarios assume the presence of the upstream dams, and we use the inflow temperature and light extinction levels observed in 1997 and 1998. As a result we are not comparing to the historic Arrow Lakes before impoundment, when upstream

Mica (1976) and Revelstoke (1983) dams were not in place (Fig. 1). In other words, the scenarios isolate the effects of the impoundment of Arrow Lake (1967) within the *present* river system along with the three specific changes. Here we briefly describe the motivation for the three changes and the resulting model scenarios (Table 2). For didactic reasons the present-day system without Keenleyside Dam (scenario 1) is used as a reference, although for model calibration, the starting point was the present-day system with Keenleyside Dam (scenario 5) described above.

Submerged Narrows (scenario 2): Before impoundment (scenario 1), the outflow from UA was limited to the surface bin of the model (0–2 m depth). In the present-day reservoir, the outflow from UA occurs from 0 to ~ 16 m depth during the productive season. The change is meant to reflect the increase in water level that transformed the riverine connection between UA and LA into a wider, lake-like Narrows (Pieters et al. 1998). With scenario 2 we test solely the effect of increased outflow depth from UA. Deeper outflow also occurs in scenarios 5, 6, and 7 (Table 2).

Seasonal flow management (scenario 3): In scenario 1, the flow through both UA and LA was set to the average 1997 and 1998 total inflow. It includes both the inflow from the Columbia River and the local flow to both basins. The effect of impoundment by the Keenleyside Dam can be observed in the difference between present-day inflow and outflow from Arrow (Fig. 3); storage results in reduced flow through the Narrows in spring and early summer. With scenario 3 we assess the effect of the seasonal leveling of the flow through the Arrow approximated using the Arrow outflow. Arrow outflow (average 1997 and 1998) is also used in scenarios 5, 6, and 8 (Table 2).

Deep withdrawal from Lower Arrow (scenario 4): Without Keenleyside Dam (scenario 1), the outflow from LA occurs from the surface bin of the model (0–2 m depth). However, since impoundment, water from LA can exit Keenleyside Dam at two levels: while overflow sluices allow near-surface outflow, part of the outflow passes through tunnel ports ~ 20 m below surface (Pieters et al. 1998). To

represent this deep withdrawal, 50% of the outflow is withdrawn at 20 m (± 5 m range) in scenario 4a; 100% of the outflow is withdrawn at 20 m in scenario 4b. The 20-m-deep outflow is also contained in scenarios 5, 7, and 8 (Table 2).

Combined scenarios (scenarios 5, 6, 7, 8): The goal of the scenario analysis is to understand the effect of the hydraulic changes that result from impoundment by stepping from the present-day system without Keenleyside Dam (scenario 1) to the present-day system with the dam (scenario 5). However, the individual changes may act in synergy or antagonistically. As a result, all of the possible combinations of the hydraulic changes were tested in scenarios 5 to 8 (Table 2).

Results and discussion

In this section we first compare the model results for the present-day impounded Arrow (scenario 5) to the field observations. The sensitivity of the model results to three key model parameters and the identifiability of the two most critical parameters are then described. Finally, the model results for the other scenarios are provided.

Present-day (scenario 5)—The calibrated model reproduces the temporal structure of the stratification reasonably well. Consistent with the observations, seasonal convective mixing—a result of winter cooling—reaches ~ 100 m deep in both basins. In summer, strong thermal stratification is similar to that observed. The vertical diffusivity approaches molecular levels of heat in the upper pycnocline, and toward the sediment the diffusivity increases as a result of bottom friction (Wüest and Lorke 2003).

The simulated light compensation depth was ~ 15 m for both basins, which is close to the measured depths of 16 m for UA and 19 m for LA (Pieters et al. 1998, 1999).

Plankton was reasonably well reproduced by the model in both basins (Fig. 4). In UA (Fig. 4a), the seasonal structure of the algal concentration is maintained. In LA (Fig. 4c), the simulation results show higher algal population at the onset of the season and lack a distinct seasonal signature as observed in the monitoring. The zooplankton density of both basins is in the correct range and shows a similar seasonal structure as that observed (Fig. 4b,d).

Interestingly, the simulated densities of algae and zooplankton in LA strongly depend on the inflow concentrations from UA. In a test run without plankton transfer from UA, the average seasonal concentrations of algae and zooplankton in LA decreased by 20% and 50%, respectively. As a result of this “start-up” transfer from UA, the algal densities, and especially zooplankton concentrations are higher in LA than in UA.

When primary production is maximal in summer, phytoplankton in UA are removed most efficiently by zooplankton (maximum ~ 0.1 d^{-1}), followed by flushing (~ 0.05 d^{-1}), respiration (~ 0.04 d^{-1}), and death (~ 0.02 d^{-1}). Nevertheless, zooplankton grazing does not reach the level of algal growth of ~ 0.3 d^{-1} . The reduction in algal biomass in mid-summer for UA, found both in the

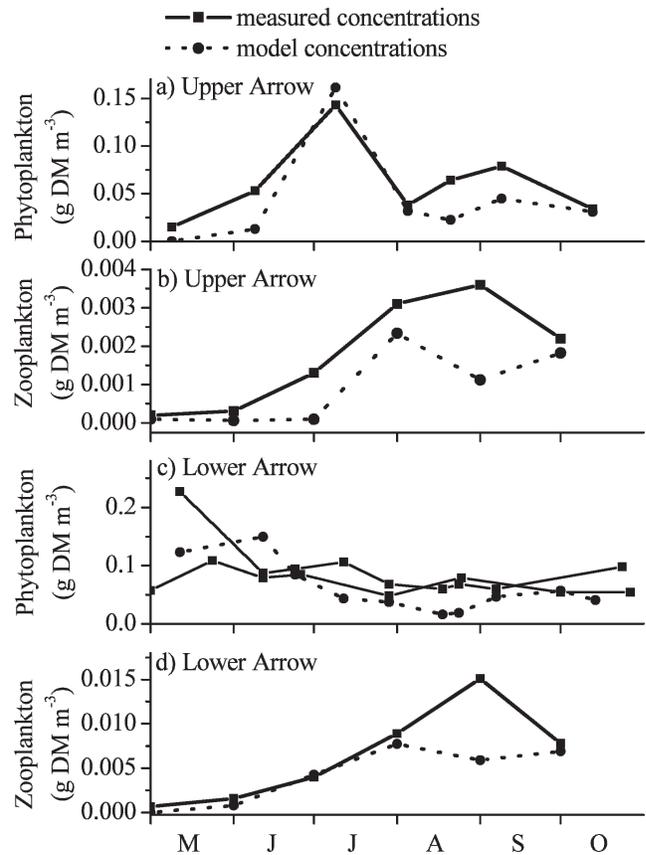


Fig. 4. Comparison between measured and simulated plankton for (a, b) Upper Arrow (1997) and (c, d) Lower Arrow. For Lower Arrow (c) phytoplankton data for both 1997 (peaking in May) and 1998 are shown (*see text*). Measured samples of (a, c) phytoplankton and (b, d) zooplankton are averaged over 20 m and 40 m, respectively (Pieters et al. 1998, 1999). Note the different scales for UA and LA.

model and the observations (Fig. 4a), must therefore occur for other reasons. In Fig. 5 the decrease in algae corresponds with the modeled depletion of S_{SRP} in the epilimnion. After phytoplankton abundance has reached a minimum, the trophogenic layer is “refilled” with S_{SRP} . The rapid decrease in phytoplankton in July (Fig. 5) is caused by algal washout from increased throughflow. The large outflow (Fig. 5) also replenishes S_{SRP} through upwelling, which consequently enables the phytoplankton population to recover. In LA, the phytoplankton population is controlled by zooplankton, which is much more abundant than in UA.

Model sensitivity (scenario 5)—We tested the sensitivity of the variables algal biomass, zooplankton biomass, in-lake SRP, and primary productivity in UA on three parameters: (1) sedimentation velocity $v_{sed,ALG}$, (2) SRP input concentration $S_{SRP,in}$, and (3) specific algal growth rate $k_{gro,ALG,20}$. The model was run with \sim double and \sim half of the values of $v_{sed,ALG}$, $S_{SRP,in}$, and $k_{gro,ALG,20}$. Figure 6 shows the effect of these changes on the primary production. Here we briefly discuss the sensitivity to, and

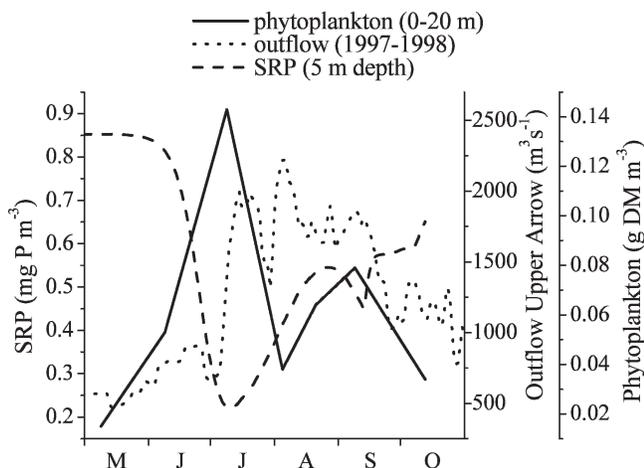


Fig. 5. Comparison of measured phytoplankton, simulated SRP concentrations, and reservoir outflow for Upper Arrow (average 1997/1998).

the identifiability (ability to discriminate between them) of these model parameters.

$v_{\text{sed,ALG}}$: The sedimentation velocity of 0.5 m d^{-1} was chosen based on literature values and enables both sedimentation and washout of algae and organic matter (recall that the settling rate for algae and organic matter were set equal). With a lower sedimentation velocity of 0.2 m d^{-1} , algae and organic matter are flushed out to a greater extent. However, when throughflow is low, algae can grow for longer before sinking below the trophogenic layer. A lower sinking rate leads to an earlier peak in primary productivity (Fig. 6a). The algal population decreases with the subsequent nutrient minimum (Figs. 5, 6a). The second production peak is more pronounced, as the upwelling of algae for low $v_{\text{sed,ALG}}$ is more effective. The increased sedimentation velocity of 1.5 m d^{-1} overcomes the upwelling for most of the year and therefore greatly reduces productivity. Only in July/August, when the flow increases (Fig. 5), can a small algal population build up again (Fig. 6a). These results indicate that the flushing of algae at high throughflow is less important, in comparison to the sinking rate, than expected.

$S_{\text{SRP,in}}$: The goal of varying the SRP of the inflow, $S_{\text{SRP,in}}$, was to test whether the model reacts as expected to these potentially large changes. The results for higher SRP input further underline the ultra-oligotrophy of Arrow. Moreover, the strong influence of nutrient supply on both seasonal structure and absolute level of productivity (Fig. 6b) show (1) the importance of fitting the nutrient input and (2) the strong sensitivity of the model to the nutrient level.

$k_{\text{gro,ALG,20}}$: It is important to note that $k_{\text{gro,ALG,20}}$ is a model parameter, which depends on water temperature, light availability and P concentrations (Web Appendix 1) and corresponds to an effective phytoplankton growth of $\sim 0.3 \text{ d}^{-1}$ for present-day Arrow. For a reduced specific

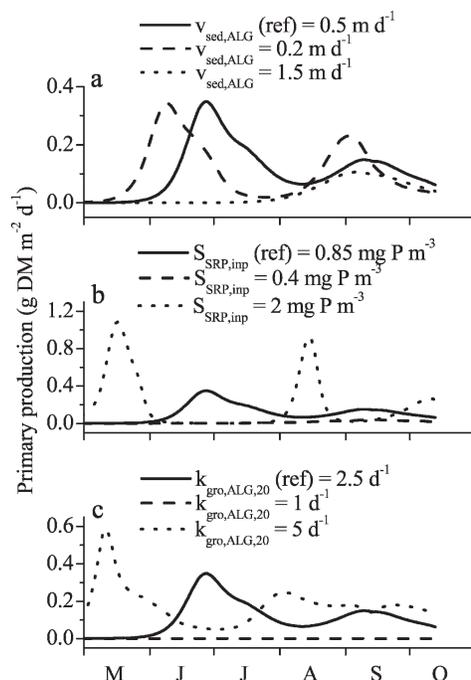


Fig. 6. Sensitivity of total primary production on (a) phytoplankton settling velocity $v_{\text{sed,ALG}}$, (b) SRP input concentration $S_{\text{SRP,in}}$, and (c) specific phytoplankton growth rate $k_{\text{gro,ALG,20}}$ in Upper Arrow. The solid line indicates the reference simulation with the calibrated model.

growth rate $k_{\text{gro,ALG,20}}$ —similar to the estimated value by Omlin et al. (2001a) for mesotrophic Lake Zürich—hardly any phytoplankton grows in the Arrow (Fig. 6c). A doubled $k_{\text{gro,ALG,20}}$ results in an increase in primary production in May, when light conditions are far from ideal (Fig. 6c). However, as the nutrient supply has not changed, algae consume nutrients at a higher rate and consequently collapse earlier. The faster growth enables efficient use of the nutrient supply, keeping the P level low with little fluctuation. This is evident in the primary production, which remains comparably high and closely follows the level of flow, and thus nutrient supply via upwelling, from July to October (Figs. 5, 6c).

Identifiability (scenario 5): Both the seasonal structure and the absolute level of productivity are strongly sensitive to $k_{\text{gro,ALG,20}}$ and $S_{\text{SRP,in}}$, indicating a potential problem uniquely identifying these two parameters. At the onset of the productive season, an increase in either parameter causes an earlier rise in productivity (Fig. 6b,c). After this first peak, the algal population collapses and does not recover until late August. The recovery is delayed because of increased flow and enhanced zooplankton biomass, a consequence of the earlier phytoplankton peak.

However there is a major difference between the model reactions to the two parameters $k_{\text{gro,ALG,20}}$ and $S_{\text{SRP,in}}$, which allows us to distinguish them. This difference concerns the upper limit of algal growth. With increased algal growth, the main limiting factor, apart from the high peak in spring, is the absolute amount of nutrients. A

second peak can only develop when nutrients are resupplied. In contrast, with a higher SRP input, nutrient limitation becomes a minor factor with the P level in the trophogenic layer staying relatively high throughout the year. Instead, zooplankton becomes the main factor reducing primary productivity. With higher $S_{\text{SRP},\text{in}}$, the algal crop peaks and “clear-water” periods alternate seasonally. Given this difference between the two parameters, we fit both simultaneously using measured phytoplankton and zooplankton abundance. Recall that the inflow SRP concentration was constrained by field measurement to be $\leq 1 \text{ mg P m}^{-3}$ and this eliminates the case of $S_{\text{SRP},\text{in}} = 2 \text{ mg P m}^{-3}$, which was shown here to illustrate zooplankton control (Fig. 6b).

Model scenarios—The effect of Arrow impoundment on productivity is assessed in the following by examining the three hydraulic changes of (1) submerged Narrows, (2) seasonal flow management and (3) deep withdrawal from LA, using the model scenarios defined above. Table 2 gives an overview of the scenarios, as well as their effects on primary productivity.

Submerged Narrows (scenario 2): Water level increase affects outflow from UA and inflow to LA. Before Arrow impoundment, the outflow of UA was from a thin surface layer of low density (Fig. 7a). Since impoundment, the river section connecting the two basins has been flooded and is, on average, 16 m deep during the productive season (Pieters et al. 1998, 1999, 2000). The outflow from UA is now composed of water from the surface to a depth of 16 m. As a result, the water flowing from UA into LA is now slightly denser. The corresponding increase in plunging depth in LA can be estimated by using conductivity-temperature-depth (CTD) profiles from both basins. For the productive season of 1999 (five profiles: May to September) the average intrusion depth in LA increased from $\sim 12 \text{ m}$ before Arrow impoundment to $\sim 28 \text{ m}$ today (Fig. 7b). In model scenario 2, a water level increase was taken into account through an increased depth range for UA outflow and deeper plunging in LA (Table 2). In addition, the overall water quality (plankton, organic matter, nutrients, etc.) of the inflow to LA changed.

Compared to model scenario 1 (the present-day Arrow system but without Keenleyside Dam) the simulated annual production of UA drops by 21% (Table 2) as a result of increased water level. The productivity decreases, although surface flushing is reduced and algae have more time to grow. In Fig. 8, this effect is shown by the earlier onset of primary production. However, the supply of P to the productive surface layer is reduced, because some water leaves UA without reaching the main euphotic zone. Comparing the density of the Columbia River with UA CTD profiles reveals that $\sim 50\%$ of the river inflow enters UA below the minimum depth of the Narrows during the productive season (April to October). Based on PAR measurements by Pieters et al. (1999, 2000) the light availability at 16 m depth is only $\sim 1\%$ of surface radiation. As a result, nutrients can short-circuit through the reservoir without reaching the top of the water column, where the

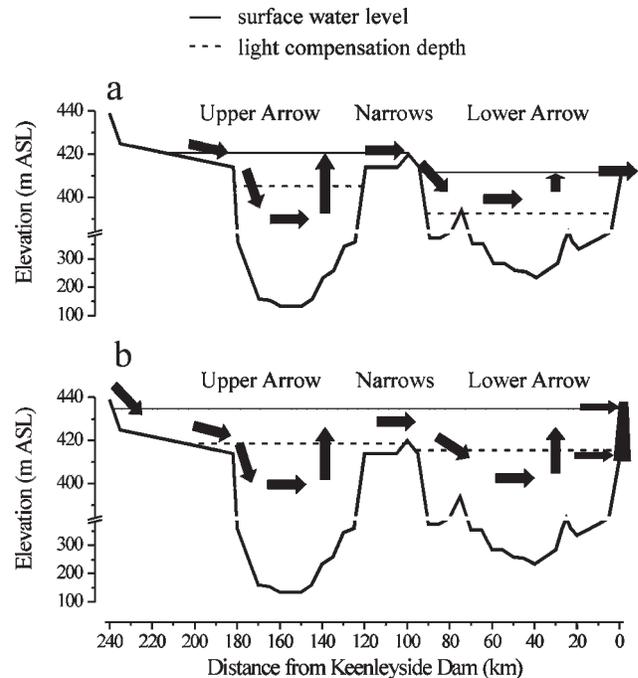


Fig. 7. Schematic of the flow through Arrow during the productive season. Horizontal arrows indicate flow path, vertical arrows indicate upwelling. (a) Without impoundment (but including the upstream dams), the inflows plunge (to $\sim 33 \text{ m}$ in UA; to $\sim 12 \text{ m}$ in LA) but move to the surface through upwelling and, as a result, inflows supply nutrients to the region above the light compensation depth ($\sim 16 \text{ m}$ in UA; $\sim 19 \text{ m}$ in LA). (b) With impoundment, inflows plunge to similar depths in both basins ($\sim 33 \text{ m}$ in UA; $\sim 28 \text{ m}$ in LA), but only a fraction of the inflow makes it to the photic zone, whereas the remainder leaves near or below the light compensation depth (outlet depth $0\text{--}16 \text{ m}$ in UA; $\sim 20 \text{ m}$ in LA). Note axis break in elevation to magnify the top 50 m of the water column.

conditions are optimal for primary production (Fig. 7). This reduced nutrient supply is responsible for lower primary production in summer (Fig. 8) and more than compensates for the advantage of reduced flushing.

Nutrients, bypassing the productive layer in the UA, become available in LA. Through upwelling, this additional SRP enters the productive layer, despite the deeper intrusion of the denser Narrows water into LA. As a result, productivity in the LA increases by $\sim 12\%$ as a result of higher water level in the Narrows (Table 2). Still, the overall productivity of the entire Arrow decreases by $\sim 9\%$ as a result of submerging the Narrows (scenario 2 in Table 2).

Seasonal flow management (scenario 3): The impact of Arrow impoundment on seasonal flow can be seen in the difference between the present-day inflow and present-day outflow (Fig. 3a). Because of water storage, the flow through the Narrows and through Keenleyside Dam is reduced during the early productive season (April to July) and slightly increased during August and September. The river inflow $Q(z)$ ($\text{m}^3 \text{ s}^{-1}$), which intrudes below depth z ,

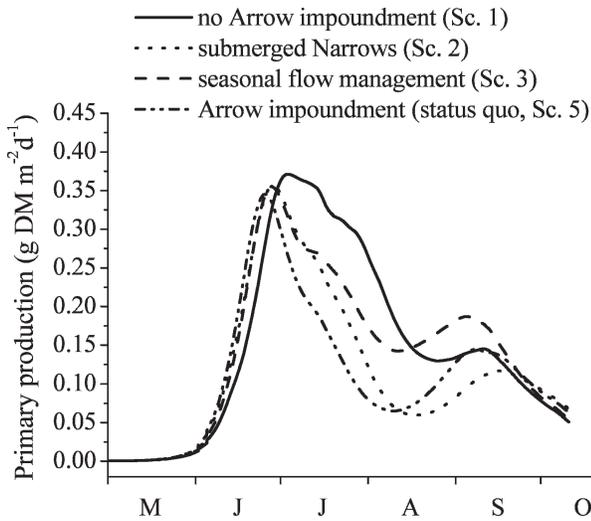


Fig. 8. Simulated primary production in Upper Arrow during the productive season for the different scenarios defined in Table 2.

has a direct influence on the upwelling velocity $w(z) = Q(z) \times A(z)^{-1}$, where $A(z)$ is the lake area (m^2) at z . As a result of Keenleyside Dam, upwelling is reduced in the first half of the productive period (April to July) from $\sim 0.50 \text{ m d}^{-1}$ without impoundment ($Q_{\text{in}} \approx 1,500 \text{ m}^3 \text{ s}^{-1}$) to $\sim 0.22 \text{ m d}^{-1}$ ($Q_{\text{out}} \approx 660 \text{ m}^3 \text{ s}^{-1}$) today (Fig. 3a). In contrast, upwelling is almost unchanged for the second half of the productive period with $w \approx 0.5 \text{ m d}^{-1}$ ($Q_{\text{in}} \approx 1,500 \text{ m}^3 \text{ s}^{-1}$, $Q_{\text{out}} \approx 1,570 \text{ m}^3 \text{ s}^{-1}$).

The reduction in flow through the Narrows from April to July increases the residence time in both UA and LA. On the one hand, this increase in residence time leads to a reduced nutrient supply to the productive surface layer due to less supply and more settling of organic particles. On the other hand, algae have more time to grow, leading to increased primary production in early June (Fig. 8). From mid-June until early August productivity drops because of reduced nutrient supply. From early August until early September, increased flow and reduced flushing result in late growth that partly compensates for the lost productivity earlier. Overall, UA productivity is slightly reduced compared to conditions without Keenleyside Dam (Table 2).

The dominant effect on productivity from “reduced nutrient supply” over “more time for algal growth” can be understood if we calculate which particle sizes are affected by flushing. Again following Stokes’ (1851) relation (see Model calibration), organic particles get washed out if their diameters are $>26 \mu\text{m}$ for $Q = 1,500 \text{ m}^3 \text{ s}^{-1}$ or $>17 \mu\text{m}$ for early summer with flow being stored by Keenleyside Dam. This includes the dominant (by biomass) phytoplankton species with diameters between $2 \mu\text{m}$ and $20 \mu\text{m}$ (Pieters et al. 1998, 1999). Consequently, almost all organic particles are flushed, which can negatively affect primary production. However, as flow rates remain high, algae get washed out both with and without Keenleyside Dam.

The reduction in productivity is greater in LA (minus $\sim 14\%$) than UA (minus $\sim 4\%$) for two reasons. First, before the Arrow impoundment, the spring pulse reached LA with a time lag and arrived in LA just at the start of the productive season. This implies that the timing of the nutrient input for LA was ideal without Keenleyside Dam. Second, the increased autumn flow in scenario 3 partly compensates lost productivity in UA, but less so in LA, as nutrients are low once the water arrives in LA.

Deep withdrawal from Lower Arrow (scenarios 4a and 4b): The deep withdrawal through tunnel ports of Keenleyside Dam at $\sim 20 \text{ m}$ depth affects only LA. Scenario 4 tests the effect of this change alone. Because the fraction of water leaving LA through the tunnel ports varies through the seasons, two scenarios of 50% (4a) and 100% (4b) deep withdrawal were tested (Table 2).

For surface (riverine) outflow from UA, the inflow to LA plunges during the productive season to $\sim 12 \text{ m}$, where light availability is $\sim 5\%$ of surface light. The outflow tunnel ports are just below the compensation depth of $\sim 19 \text{ m}$ (Pieters et al. 1999). Therefore, water that enters LA at 12 m depth is advected down from 12 m to 20 m , staying below optimal light conditions. Hence, we expect a nutrient bypass for scenario 4 similar to that observed in UA as a result of the deep Narrows (scenario 2).

The simulation results verify these expectations. For 50% of the water leaving LA through the tunnel ports, the primary productivity is reduced by $\sim 22\%$ (scenario 4a; Table 2), similar to the effect of increasing the depth of the Narrows on UA (scenario 2; Table 2), where a significant amount of P was still upwelling to the surface. However in scenario 4b, where none of the inflowing water reaches the surface (apart from turbulent mixing), the effect is much more pronounced with a productivity loss of almost 40% (Table 2).

Cumulative effects (scenarios 5, 6, 7, and 8): The model results indicate a decrease in annual production of $\sim 32\%$ in Arrow as a long-term result of the Keenleyside Dam (scenario 5; Table 2). Whereas the productivity of UA is more sensitive to the increase in the water level (increased depth of the Narrows), the productivity in LA is reduced more by deep withdrawal. In both scenarios, productivity is reduced because P bypasses the trophogenic layer. Moreover, both effects act in synergy: Although the productivity in LA is increased by deepening the Narrows (scenario 2), it is significantly decreased in combination with a deep outlet (scenario 7; Table 2). This results because water from the Narrows is denser during the productive period and plunges to $\sim 28 \text{ m}$, which is below the outlet ports, instead of plunging to only $\sim 12 \text{ m}$ without impoundment.

The mere 2% difference between scenario 7 and the current reservoir operation (scenario 5) indicates that seasonal flow management has only a minor effect (Table 2). In contrast, a comparison of scenario 6 (combination of scenarios 2 and 3) with scenario 5 shows that the deep water withdrawal is responsible for approximately half of the loss in productivity. Thus it may be worth releasing more water via overflow sluices at the

surface during the productive season to increase productivity in LA (compare scenarios 4a and 4b).

Relevance of results

Comparison of the different scenarios shows that productivity can be strongly altered when transforming lakes into reservoirs. The effect on productivity is caused by a reduction in availability of P for phytoplankton. Although the total nutrients entering the reservoir are not affected by the hydraulic changes, we show that the lake-internal nutrient supply is significantly modified. We find that by using a deep outlet, a relevant fraction of the nutrients can bypass the trophogenic layer and are thus not available for algal growth. Seasonal flow management also reduces productivity, but to a much smaller extent. The storage of spring and early-summer peak flow reduced the supply of nutrients during the critical growth period.

It is important to realize that the Arrow impoundment not only reduces primary productivity, but affects all levels of the food chain. According to the model calculations, algal abundance itself does not change significantly for different levels of primary production. However, reduced productivity transfers into reduced zooplankton, the consumer-side in the model; this is also seen in other, but similar, lakes (Finger et al. pers. comm.). As zooplankton are the main food for kokanee (Pieters et al. 1998, 2003), it is highly probable that kokanee populations declined as a result of lower zooplankton density, which, in turn, is a consequence of lower primary production. To test the model performance for increased primary productivity, it was run with the P input applied to UA during the fertilization program in 1999 (Pieters et al. 2003), with a much higher P availability than in the above scenarios. The productivity in the model changed by +61% and -7% for UA and LA, respectively, and closely resembled the measured changes in production of +53% for UA and -15% for LA (Pieters et al. 2003). At first sight, the predicted increase in zooplankton (+900%) seems far from the observed increase (+220%). However, the model does not account for higher consumers; in particular, mysids (observed: +280%) and kokanee (observed: +225%) are not included in the model. Because the model pooled all higher consumers as zooplankton, the reduction in phytoplankton in the model was too large (-51% vs. -3% observed). In summary, while the observed transfer of added productivity to the consumer level was well reproduced (Pieters et al. 2003), the nutrient increase—as a result of fertilization—is likely beyond the application of the model.

To evaluate the relevance of hydraulic changes on productivity, we compared results with the estimated effect of upstream dams, Mica and Revelstoke (Fig. 1). Three mechanisms are expected to be of importance: (1) changes in Columbia River temperature and sediment load affecting water density and plunge depth into UA (Fischer and Smith 1983), (2) an increase in water clarity because of upstream particle trapping, and (3) a decrease in P input because of upstream particle retention. In the following these three changes are briefly assessed.

(1) *Upstream river density*—Before upstream dams were built, the Columbia River water was $\sim 1^\circ\text{C}$ warmer in summer (McAdam 2001; Hamblin and McAdam 2003), but richer in suspended particles (Pieters et al. 2003) and thus denser than at present. Although, according to model runs, the river plunged much deeper in the UA without the upstream dams, the plunge depth had surprisingly little effect on productivity, as river intrusions are mostly below the trophogenic layer independent of the upstream dams.

(2) *Upstream water clarity*—There is little or no data on light availability in the Arrow Lakes before the upstream dams. However, the effect of inorganic particle retention on downstream lake productivity was assessed in detail for a similar glacial-fed lake in the Swiss Alps (Finger et al. 2006, 2007). They found an increase of $\sim 12\%$ in annual productivity, which is mainly due to enhanced productivity of up to $\sim 35\%$ during the summer season, as a result of upstream dams and the subsequent increase in water clarity (less particles). However, despite the significant difference in appearance of turbid and clear water, this effect is less than one may intuitively expect. Small particles, which are primarily responsible for light scattering and a turbid appearance, do not absorb much light. Although scattering lengthens the light path, the effect on productivity is limited (Jaun et al. 2007). Given the similarity of the two lake systems and the drainage areas of the Rocky Mountains and the Swiss Alps, we use the results by Finger et al. (2007) to help estimate the effect of upstream dams on Arrow productivity.

(3) *Upstream phosphorus trapping*—The conversion of the Upper Columbia River into a series of reservoirs effectively moves phytoplankton growth and the use of bio-available nutrients upstream of Arrow. A fraction of the algae growing upstream will settle and remain buried in the reservoir sediments. In addition, dissolved P can adsorb to inorganic particles (Müller et al. 2006) and settle without entering the food chain (Dittrich and Koschel 2002). For bio-available dissolved P, Pieters et al. (2003) estimated a fractional retention of 50% and 25% for Kinbasket and Revelstoke Reservoirs (Fig. 1), respectively, consistent with findings by Müller et al. (2007) for the above-mentioned case study described in Finger et al. (2007). To test the effect of P retention, the current total dissolved P concentrations were used to estimate the P input before the construction of upstream dams. A model simulation was run with an estimated historic input concentration of $0.85 \times (0.75 \times 0.5)^{-1} \approx 2.27 \text{ mg P m}^{-3}$. The model for UA shows that a 2.7-fold increase in P leads to an increase in primary productivity of 2.45 times under conditions without Arrow impoundment and 2.0 times under conditions with Arrow impoundment. The lower enhancement with Arrow impoundment further underlines the importance of the “nutrient bypass” as a result of the flooded Narrows and deep withdrawal. In contrast, LA productivity remains almost unchanged at the higher historic load of SRP in the Columbia River inflow, because nutrients are used in UA. For both basins combined, nutrient retention by upstream dams reduced productivity by $\sim 40\text{--}50\%$.

In summary, the net of all three effects of upstream dams—(1) change in river density, (2) increase in water clarity, and (3) retention of nutrients—can decrease productivity in Arrow by ~30%, although the large uncertainty in the two opposing effects (2) and (3) make a more detailed interpretation difficult. Nevertheless the estimates indicate that the effect of hydraulic changes from the Arrow impoundment is of the same order as the effect of the upstream dams.

We are aware that in long basins, relevant processes such as plunging inflows (Fischer and Smith 1983) or internal seiching (Okely and Imberger 2007) cause two-dimensional structures in the productive surface layer. Therefore the primary production values in Table 2 contain uncertainty related to those modeling deficits. However, we do not expect significant deviations because the one-dimensional modeling approach accounts for both the balance of nutrients and biomass as well as the key features of the investigated hydraulic changes.

In Arrow these hydraulic changes cause oligotrophication. For other systems with different trophic conditions and/or different hydraulic changes, the potential effects may be very different. For example, if Arrow were eutrophic, the residence time of the trophogenic layer or the deposition of organic matter could become the most relevant parameter. However this study clearly shows that hydraulic changes have a large effect on the biogeochemical cycling of natural lake systems. It is thus suggested that hydraulic changes to lakes be evaluated and assessed before dam construction.

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