



A hierarchical modelling framework for assessing physical and biochemical characteristics of a regulated river



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ABSTRACT

Regulated rivers below dams have traditionally been managed using a minimum instream flow to provide adequate aquatic habitat. However, dam management, in conjunction with changes in climate and land use, challenges downstream ecosystem functions that cannot be properly addressed by a simple minimum flow requirement. Depending upon the river system, additional parameters such as water temperature and nutrient loading provide more critical ecological value for organisms than ensuring a constant minimum release. A new modelling methodology, utilizing a cascading hierarchical approach, is proposed and tested on a 614 km² headwater basin in central Idaho, USA. Application of the methodology illustrates that below large dams the river discharge becomes independent of the seasonal hydrology and specifying the discharge alone is insufficient for evaluating ecosystem response. Upstream reservoirs interrupt the watershed continuum and internally modify the thermal, chemical, and biological properties of water prior to release into a downstream river. These water properties depend on the annual hydrologic regime, characteristics of the reservoir and the offtake strategies, offtake structure depth, dam discharge, and the water column thermal stratification. This study describes the use of climatically driven hydrologic forcing and variable dam operations in a coupled reservoir-river system to optimize river ecosystem health by linking physical processes with in situ observations and incorporating multi-trophic species requirements. Such an approach can support real-time decision making on existing reservoir-river systems and provide a virtual means of evaluating ecosystem impacts prior to disturbance from new dam construction or implementation of restoration activities in a watershed.

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1. Introduction

In recent years, three major sources of change have impacted ecological communities in river systems. First, large reservoirs (10^7 – 10^9 m³ cf [Graf, 2005](#)) interrupt the natural pattern of flow and longitudinal connectivity, disrupting fish migration, temperature and nutrient regimes, as well as timing and magnitude of peak

and low flows. In brief, reservoirs act to create new boundary conditions for downstream rivers ([Ward and Stanford, 1982](#); [Nilsson et al., 2005](#); [Magilligan and Nislow, 2005](#); [Graf, 2006](#); [Vinson, 2001](#); [Konrad et al., 2011](#); [Powers et al., 2014](#); [Yin et al., 2015](#)). Second, land use changes alter both the precipitation ([Andrich and Imberger, 2013](#)) and the resultant runoff characteristics ([Molina et al., 2012](#); [Zhou et al., 2016](#); [Deng et al., 2016](#)). Third, global warming has been observed to impact both the geographic distribution of precipitation and its variability ([Hamlet and Lettenmaier, 2007](#); [Luce and Holden, 2009](#); [Merz et al., 2011](#)). Combined, these “external” changes increase the ecological challenges faced by water

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resource managers concerned with optimizing reservoir and river systems for multiple beneficial uses (Nilsson et al., 2005; Poff et al., 2010; Naiman and Dudgeon, 2011; Gillespie et al., 2015).

Reservoir operations and downstream flow modifications have been considered detrimental to many native ecosystems (Ward and Stanford, 1982; Poff and Zimmerman, 2010) and minimum instream flow regulations were imposed on dam operations to counter these negative effects (Bovee et al., 1998; Magilligan and Nislow, 2005). Instream flows were traditionally determined by historic channel cross sections and discharge conditions, often based on very short observation periods. These regulations were implemented irrespective of land clearing, global warming, reservoir offtake level, or ecological system cues. Alternatively, 'environmental flows' aim to achieve the best attainable ecological conditions for individual river systems by utilizing reservoir operational flexibility (Bunn and Arthington, 2002; Brierley and Fryirs, 2009; Acreman and Ferguson, 2010; Poff and Zimmerman, 2010). Environmental flows go beyond minimum instream flow conditions by accounting for parameters such as discharge variability, water temperature, nutrient concentrations, and substrate stability, which are equally important for riverine ecosystems and must be collectively tailored to the needs of the particular river basin under consideration (Power et al., 1996; Wootton et al., 1996).

Therefore, a new holistic approach is required for reservoir-river systems where all the above changes in river properties, brought about by land use changes and global warming, are viewed as inputs to the reservoir-river ecology. Ecological systems can then be evaluated with respect to the primary reservoir function, such as hydropower or bulk water supply, but also the water properties discharged to the downstream river for aquatic and riparian productivity (Yin and Yang, 2011; Yin et al., 2015). The reservoir thermal structure determines the internal physical, chemical, and biological processes that dictate the properties of the outflowing water and determine the boundary conditions for the downstream river(s) (Ward, 1974; Vinson, 2001; Marti et al., 2016). Furthermore, the thermal, chemical, and biological processes in the reservoir-river system are strongly influenced by the annual hydrologic regime (wet vs. dry), complicating prediction of downstream ecosystem response (Konrad et al., 2011). Given the primary function of the reservoir and composition of the downstream ecosystem, effective river management depends on understanding the internal reservoir dynamics, flexibility of dam operations, and potential geomorphic and biochemical interactions.

It is important to stress that for a reservoir-river system, where the reservoir discharge is determined by contractual demand for electricity production, bulk water, or irrigation delivery new hydraulic regimes are imposed on the downstream river that are independent of hydrologic factors. Once the river discharge regime and water temperature become disconnected from the natural catchment hydrology, the sustainability of the original aquatic ecology is drawn into question (Vinson, 2001). In light of these challenges, this work investigates how a systems approach to reservoir-river modelling can identify the potential ecological impacts of changing the downstream river discharge boundary conditions by optimizing the physical and biogeochemical properties of the discharge water, providing water managers with a real-time, adaptive, coupled reservoir-catchment-river modelling system to improve downstream ecological conditions (Lett et al., 2008; D'Agostini et al., 2015; Marti and Imberger, 2015; Garcia-Garcia et al., 2016).

The modelling framework forming the foundation of such a rational approach is still in its infancy, so benchmark studies combining physical and biological responses are necessary to calibrate regional or classification-type ecological models (Arthington et al., 2006). Predictive hydro-ecological models are the future to optimizing beneficial uses in multi-objective water resources with

associated complex aquatic ecosystems. To optimize management decisions on existing reservoir-river systems, predictive modelling must be combined with real-time observations to assimilate current environmental conditions and update the predictive power of the model (Krause et al., 2015).

This study presents a set of cascading hierarchical models for the Deadwood River basin (central Idaho, USA), a complex system of high elevation rivers and creeks divided by a mid-watershed reservoir, to identify combined impacts of climate driven hydrologic regimes and water operations on the productivity of multiple trophic levels in the basin. Many modelling and restoration activities address ecological systems separately, such as individual reservoirs or intermediate river reaches; however, cascaded simulations offer insight from a systems approach on how reservoirs react to different hydrologic forcing and dam operations, in turn, altering downstream conditions of temperature, nutrients, and productivity (Bernhardt et al., 2005; Deus et al., 2013; Wen et al., 2016; Cunha-Santino et al., 2017; Weigel et al., 2017). The current work expands the scope of the investigation beyond singular species of interest or a specific type of ecosystem to show how aquatic ecosystems are spatially linked and driven by the annual hydrologic conditions in the basin. To investigate this, the thermal and biochemical properties of a reservoir were investigated via a coupled three-dimensional (3D) hydrodynamic and ecological model to provide downstream boundary conditions under dry, average, and wet hydrologic forcing to a one-dimensional (1D) hydrodynamic river model, a nutrient mass balance model, and a macroinvertebrate regression model. These physical and biochemical conditions were collectively evaluated with respect to the five major native fish species found in the river system to assess hydrologic effects of potential climate change and operational control of a reservoir on higher trophic native aquatic species.

2. Study site

The Deadwood River basin (614 km^2) is a north-south oriented intrusive valley located in central Idaho, USA (Fig. 1). The upper basin consists of multiple headwater streams; the upper Deadwood River and Trail Creek are the two largest streams that drain into Deadwood Reservoir near the center of the watershed. The lower Deadwood River begins at the reservoir dam and runs 38 km to the confluence with the South Fork Payette River. The lower river flows through a semi-confined canyon with limited, discontinuous floodplains along its extent (Tranmer et al., 2015). The river channel is approximately 30 m wide and has an average channel gradient of 1.2%, although local channel slope fluctuates between 1 and 8% due to geologic constraints. Channel substrate is dominated by cobbles interspersed with large boulders and sand transport can be significant during irrigation releases and storm events.

Deadwood Reservoir, draining an area of 287 km^2 , is a large reservoir ($12,600 \text{ m}^3$) with two primary hypolimnetic offtake gates and a volume of 190 million m^3 at full-pool elevation (1,625.8 m). Deadwood Dam (50 m tall) is operated for flood control and irrigation storage that activates the dam spillway once full-pool elevation is achieved. Directly below the dam, a deep stilling basin provides unique river habitat that is conditioned by the upstream reservoir properties and maintains a resident fish population.

Contractual water releases during the summer irrigation season provide steady flows of $27 \text{ m}^3 \text{ s}^{-1}$ to the river from June through September that is greater than the approximately $6 \text{ m}^3 \text{ s}^{-1}$ that occurred during the unregulated period. Post-irrigation season, dam design restricts outflows to high ($1.4 \text{ m}^3 \text{ s}^{-1}$) or low ($0.06 \text{ m}^3 \text{ s}^{-1}$) values as a means of managing downstream river conditions. At the beginning and end of the irrigation season, the

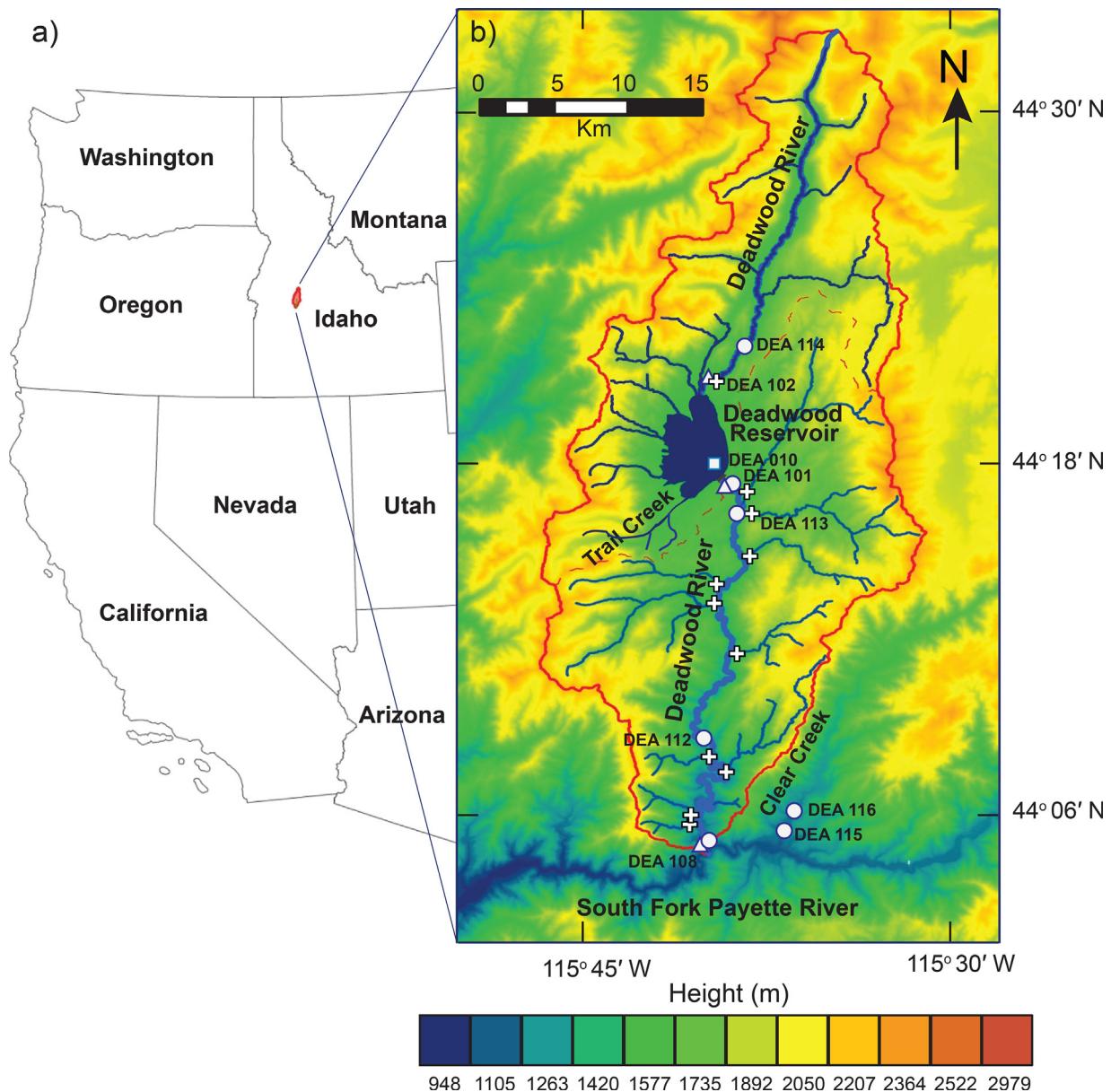


Fig. 1. a) Location and b) digital elevation map of the Deadwood River Basin with relevant sampling stations. Dashed line delineates Deadwood Reservoir drainage area. Triangles indicate the nutrient and chlorophyll *a* river sampling stations. Square indicates the reservoir profile and in-situ monitoring station. Circles indicate the periphyton and benthic macroinvertebrates site locations. Crosses indicate the major tributaries considered in the 1D river model and mass balance model.

primary offtake gates can incrementally ramp stream discharge up or down to modify the flow conditions in the river.

3. Materials and methods

To assess the potential ecological impacts of climate driven hydrologic regimes on the reservoir and downstream river environments, a series of operational scenarios were evaluated that represent the spectrum of hydrologic conditions, including expected climate change. These scenarios encompassed three hydrologic years representing dry, average, and wet conditions in the basin, that correspond to 40%, 100%, and 150% of historic mean reservoir inflow. Hydrographs for each representative hydrologic year (dry, average, wet) were compared with the corresponding unregulated (natural, no dam) flow regime. The unregulated flow regime of the river was calculated from measured tributary inputs upstream of the reservoir and collectively used as an upstream boundary condition to the 1D river hydrodynamic model. Addi-

tionally, ecological effects of post-irrigation dam releases were evaluated using the high ($1.4 \text{ m}^3 \text{ s}^{-1}$) and low ($0.06 \text{ m}^3 \text{ s}^{-1}$) options with a fast ramping rate (two-day change in flow) and a slow ramping rate (ten-day change in flow).

3.1. Hierarchical conceptual model

The study was designed according to a cascaded numerical model approach together with field data in order to assess how impacts translate through the reservoir-river ecosystem (Fig. 2).

A coupled 3D hydrodynamic-ecological model (Estuary, Lake and Coastal Ocean Model – Computational Aquatic Ecosystem Dynamics Model; AEM3D) (Romero et al., 2004; Silva et al., 2014) was implemented for the Deadwood Reservoir to simulate reservoir hydrodynamic and ecological response to the three hydrologic (dry, average, wet) inflow conditions including the post-irrigation releases and ramping rates (Weigel et al., 2017). AEM3D has been employed in numerous lakes and reservoirs and a review of the

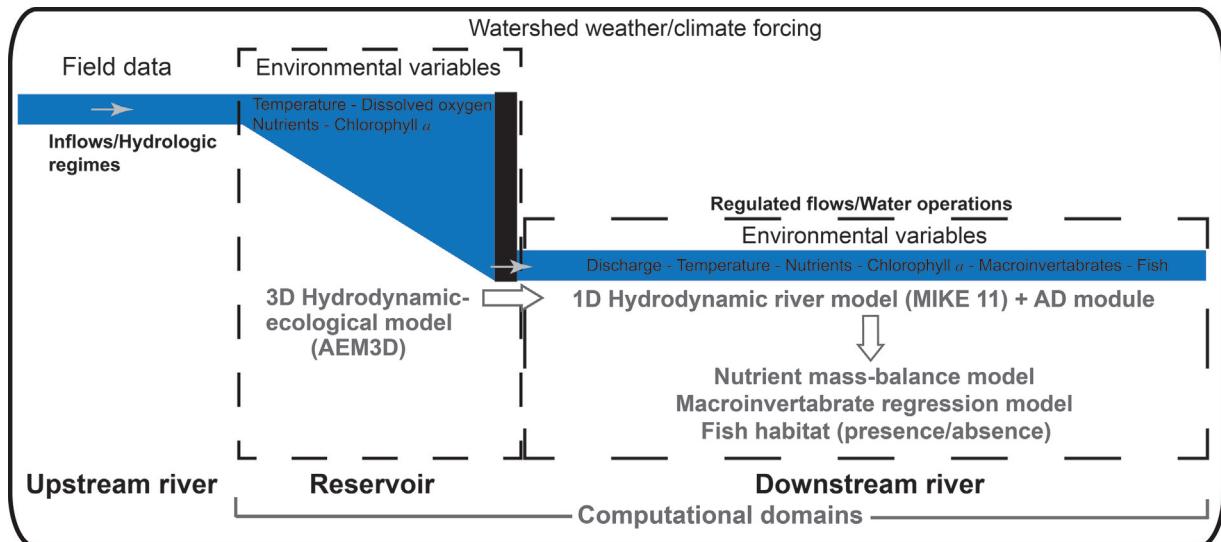


Fig. 2. Conceptual model summarizing the cascading hierarchical modelling framework on the Deadwood River, Idaho, USA used in this study.

coupled model system has recently been performed by Trolle et al. (2012). Outputs from the reservoir model were used as upstream boundary conditions for a 1D hydrodynamic and temperature model (MIKE 11 + Advection-Dispersion (AD) module developed by the Danish Hydraulic Institute) of the lower Deadwood River below the reservoir (Marzadri et al., 2014; Tranmer et al., 2015). The MIKE 11 model was selected due to success in nearby study locations (Parkinson, 2003; Loinaz et al., 2013). The effects of dam operations on downstream nutrient uptake were evaluated by means of a mass-balance model that used the hydraulic outputs from the MIKE 11 model and measured nutrient concentrations below the dam. A macroinvertebrate regression model, developed for similar stream conditions in Colorado, USA (McCutchan and Lewis, 2002), was adapted for the lower Deadwood River. Modeled values of water depth, flow velocity, and water temperature were examined in the river for the three hydrologic conditions including the post-irrigation releases and ramping rates to determine how well native fish preferences/tolerances are met and compared with field fish surveys for species presence/absence.

3.2. Deadwood reservoir model

The physical and biogeochemical simulations in this study were conducted using AEM3D, which couples ELCOM and CAEDYM routines to simulate the hydrodynamics, nutrient cycles, and food web dynamics in three dimensions (Hodges et al., 2000; Silva et al., 2014). ELCOM is a 3D hydrodynamic model based on the numerical solution of the unsteady Reynolds-averaged Navier-Stokes equations using both the Boussinesq and hydrostatic approximations. The model uses a semi-implicit method for free surface evolution, a third order Euler-Lagrangian scheme for convective terms, an ULTIMATE-QUICKEST scheme for the advection of scalars, and a numerical diffusion filter that is appropriate for stratified lakes (Laval et al., 2003). ELCOM does not require calibration because it is physically based and its parameters can be specified from literature values. CAEDYM consists of a series of process-based partial differential equations that dynamically simulate concentrations of biogeochemical variables accounting for primary and secondary production, nutrient cycling, oxygen dynamics, and sediment-water interactions. CAEDYM requires specification of several parameters used to simulate the biogeochemical processes but they are also constrained within ranges found in literature. ELCOM and CAEDYM have been described elsewhere in

detail (Hodges et al., 2000; Laval et al., 2003; Romero et al., 2004; Silva et al., 2014).

The physical model domain of Deadwood Reservoir was discretized with a uniform horizontal grid of 100 m by 100 m, and a vertical resolution of 1 m. The model used a time step of 120 s. Extensive field data (meteorological, inflow scalar variables, and initial conditions) were collected during the period October 2007 through March 2009, so this period was chosen for model validation. The ELCOM model activated the appropriate algorithms to include atmospheric exchange, inflow dynamics, turbulent mixing dynamics, Coriolis forcing, and ice formation dynamics (Oveisy et al., 2012). CAEDYM was configured to simulate nitrogen and phosphorus in both particulate and dissolved organic forms and dissolved inorganic forms to include particulate organic nitrogen (PON), dissolved organic nitrogen (DON), ammonium (NH_4), nitrate (NO_3), particulate organic phosphorus (POP), dissolved organic phosphorus (DOP), orthophosphate (PO_4), dissolved oxygen (DO), particulate organic carbon (POC), dissolved organic carbon (DOC), as well as the four dominant phytoplankton groups observed in the reservoir during the field data collection period: dinoflagellates, cyanobacteria, cryptophytes, and diatoms simulated as chlorophyll *a*, with a constant carbon to chlorophyll *a* ratio. ELCOM parameters relevant to the hydrodynamic processes were not adjusted and minimal adjustment of CAEDYM parameters was performed using literature values or direct estimates within default literature ranges (Table 1).

A detailed description of the configuration of AEM3D used here and its validation against water level, water temperature, dissolved oxygen, and chlorophyll *a* for 2007–2009 is presented in detail in USBR (2016) and Weigel et al. (2017). Model performance over the validation period was assessed using the root mean square error (RMSE), as defined by:

$$\text{RMSE} = \sqrt{\frac{1}{n} \sum_{i=1}^n (M_i - S_i)^2} \quad (1)$$

where M_i is the measured variable, S_i is the simulated variable, and n is the number of values. For water temperature, dissolved oxygen concentration, and chlorophyll *a* concentration profiles in the reservoir near the dam wall (DEA 010, Fig. 1), RMSE were 1.3 °C, 1.3 mg L⁻¹, and 2.0 µg L⁻¹ respectively. These provide confidence that AEM3D simulations could be used to predict the physical and biochemical variables under a range of climate driven hydrologic

Table 1

List of selected parameters used for AEM3D simulations presented in this study.

Parameter description	Units	Values and references
Thermodynamics		
Mean albedo for short-wave radiation	–	0.08 ^a
Mean albedo for long-wave radiation	–	0.03 ^a
Background extinction coefficient of pure water	m^{-1}	0.25 ^a
Extinction coefficient for near infrared radiation	m^{-1}	1.0 ^a
Extinction coefficient for ultraviolet A wavelength	m^{-1}	1.0 ^a
Extinction coefficient for ultraviolet B wavelength	m^{-1}	2.5 ^a
Bulk transfer coefficient for heat at air-water interface	–	0.0013 ^b
Bulk transfer coefficient for momentum at air-water interface	–	0.0013 ^b
Turbulent mixing		
Mixing coefficients for: Wind stirring	–	1.33 ^c
Bottom generation of turbulent kinetic energy (TKE)	–	2.2 ^d
Shear generation of TKE	–	0.15 ^c
Energy generated from convective overturn	–	0.2 ^c
Dissipation of excess energy	–	1.15 ^c
Bottom drag coefficient	–	0.002
Dissolved oxygen (DO)		
Temperature multiplier of sediment fluxes	–	1.05 ^e
DO half-saturation constant for nutrient sediment fluxes	mg DO L^{-1}	0.5 ^f
Static DO consumption rate by sediments	$\text{g DO m}^{-2} \text{ day}^{-1}$	1.2 ^g
Phosphorus (P), Filterable Reactive Phosphorus (FRP), Particulate Organic Phosphorus (POP), Dissolved Organic Phosphorus (DOP)		
Ratio of P to Chlorophyll <i>a</i>	$\text{mg P [mg Chl } a\text{]}^{-1}$	0.3 ^h
Max transfer of POP labile to DOP labile	day^{-1}	0.05 ^e
Max mineralization of DOP labile to FRP	day^{-1}	0.01 ^e
Release rate of FRP from sediments	$\text{g P m}^2 \text{ day}^{-1}$	0.0001 ^e
Nitrogen (N), Nitrate (NO_3), Ammonium (NH_4), Particulate Organic Nitrogen (PON), Dissolved Organic Nitrogen (DON)		
Ratio of N to Chlorophyll <i>a</i>	$\text{mg N [mg Chl } a\text{]}^{-1}$	9.0 ^h
Max transfer of PON labile to DON labile	day^{-1}	0.01 ^e
Max mineralization of DON labile to NH_4	day^{-1}	0.003 ^e
Nitrification stoichiometry ratio of DO to N	mg DO [mg N]^{-1}	3.43 ^h
Release rate of NH_4 from sediments	$\text{g N m}^{-2} \text{ day}^{-1}$	0.019 ^e
Nitrification rate	day^{-1}	0.05 ^e
DO half-saturation constant for nitrification	mg DO L^{-1}	2.0 ⁱ
Denitrification rate	day^{-1}	0.01 ⁱ
DO half-saturation constant for denitrification	mg DO L^{-1}	0.5 ⁱ
Dinoflagellates, cyanobacteria, cryptophytes, diatoms		
Photosynthetic stoichiometry ratio of DO to Carbon (C)	mg DO [mg C]^{-1}	2.67 ^h
Ratio of C to Chlorophyll <i>a</i>	$\text{mg C [mg Chl } a\text{]}^{-1}$	40 ^j
Fraction of algal DO lost to photosynthetic respiration	–	0.014 ⁱ
Maximum growth rates of algae	day^{-1}	0.25 ^k , 0.75 ⁱ , 0.5, 1.7 ^f
Algal respiration, mortality, and excretion	day^{-1}	0.05 ^k , 0.074 ⁱ , 0.08, 0.11 ^f
P half-saturation constant for algal uptake	mg PL^{-1}	0.0024 ^k , 0.0052 ⁱ , 0.005, 0.006 ^f
N half-saturation constant for algal uptake	mg NL^{-1}	0.11 ^k , 0.045 ⁱ , 0.05, 0.075 ^f
Light half-saturation constant for algal limitation	$\mu\text{E m}^{-2} \text{ s}^{-1}$	110 ^k , 62.5 ⁱ , 60, 60 ^f
Standard temperature for algal growth	°C	20 ^k , 20 ⁱ , 20, 25 ^f
Optimum temperature for algal growth	°C	33 ^k , 33 ⁱ , 33, 28 ^f
Maximum temperature for algal growth	°C	39 ^k , 39 ⁱ , 39, 35 ^f
Temperature multiplier for growth rates of algae	–	1.07 ^k , 1.09 ⁱ , 1.08, 1.06 ^f
Temperature multiplier for respiration rates of algae	–	1.08 ^k , 1.04 ⁱ , 1.07, 1.07 ^f
Algal settling velocities	m day^{-1}	8.64 ^g , 0.015 ^g , -0.02 ^g , -0.2 ^g
Critical shear stress for algal resuspension	N m^{-2}	0.001 ⁱ
Resuspension rate of algae	$\text{g Chl a m}^{-2} \text{ s}^{-1}$	0.000008 ⁱ
Half-saturation constant of available phytoplankton mass on sediments for algal resuspension	g Chl a m^{-2}	0.00001 ⁱ

Sources: ^a Woodward et al. (2017); ^b Imberger and Patterson (1990); ^c Spigel et al. (1986); ^d Sherman et al. (1978); ^e Chung et al. (2014); ^f Vilhena et al. (2010); ^g Estimated; ^h Stoichiometry relation; ⁱ Romero et al. (2004); ^j Griffin et al. (2001); ^k Bruce et al. (2006).

regimes and water operations and as upstream boundary conditions to the 1D river model (Tiedemann, 2013).

For the three hydrologic years with two post-irrigation dam releases ($0.06 \text{ m}^3 \text{ s}^{-1}$ and $1.4 \text{ m}^3 \text{ s}^{-1}$) and fast and slow ramping rates, the 12 simulations were driven with the same data used for the validation period; however, initial water levels and inflow and outflow rates reflected the hydrologic year, post-irrigation releases, and ramping up/down rates being examined. These simulations were run for a period of 14 months starting on November 1 and the results of these scenarios are described in detail in USBR (2016). The parameter values listed in Table 1 were the same for the twelve simulations.

3.3. Lower deadwood river model

MIKE 11 is a 1D hydrodynamic model that solves the unsteady Saint-Venant shallow water equations with a semi-explicit finite difference scheme. For this study the hydrodynamic model was used in conjunction with the AD module. The lower Deadwood River model extends 38 km from Deadwood Reservoir to the confluence with the South Fork Payette River (Fig. 1) and was supported by high resolution 30-m spacing of cross-sections, which were extracted from the bathymetry generated by an Experimental Airborne Advanced Research Lidar survey (McKean et al., 2009; McKean et al., 2014). Time series of measured outflows and water temperature from the reservoir and field-derived stage-discharge

rating curves were used as upstream and downstream boundary conditions. Lateral tributary discharges and water temperatures were obtained from measurements at each main tributary (see Fig. 1). Meteorological data (air temperature, relative humidity, and sunlight hours per day) were used from a nearby weather station, Bearskin Creek. Calibration and validation of the 1D model for the lower Deadwood River were performed for year 2009 using a time step of 4 s, and are reported in previous publications for both hydraulic and stream temperature modelling (Marzadri et al., 2014; Tranmer et al., 2015). The calibration of flow resistance utilized a value of Manning's n roughness coefficient, which it was set equal to $0.06 \text{ m}^{1/3} \text{ s}^{-1}$ for the entire model domain. The canyon-like nature of the lower river required shifting the sunlight timing and amount in order to accurately represent the river temperatures (Tiedemann, 2013). The comparison between measured and predicted water surface elevations at low flows near the two ends of the study site resulted in RMSE of 20 cm. RMSE of $1.48 \text{ m}^3 \text{ s}^{-1}$ and $R^2 = 0.98$ between measured and predicted flood wave discharges near the confluence with the South Fork Payette River were reported. The comparison between measured and predicted hourly stream water temperatures resulted in RMSEs of $0.9\text{--}1.9^\circ\text{C}$, with error increasing with distance downstream from the dam (USBR, 2016).

The model was run for three hydrologic inflow conditions with two post-irrigation dam releases ($0.06 \text{ m}^3 \text{ s}^{-1}$ and $1.4 \text{ m}^3 \text{ s}^{-1}$) and fast and slow ramping rates. Meteorological data and tributary temperature data used for the calibration period were utilized. For each of the hydrologic years, times series of measured outflows and simulated water temperatures at the dam outlet using AEM3D and a field-derived, stage-discharge rating curve were used as upstream and downstream boundary conditions. Lateral tributary discharges were adjusted to account for the hydrologic conditions (Tiedemann, 2013). These simulations were repeated for a theoretical unregulated lower Deadwood River, where discharge and temperature time series used as AEM3D inflow inputs to the reservoir were used as direct inputs to the 1D river model to circumvent the reservoir influence.

3.4. Nutrient, chlorophyll a, and dissolved oxygen sampling

Data used to characterize nutrient uptake and primary production in the lower Deadwood River were collected during the period from 2008 through 2011. Total phosphorus (TP), total nitrogen (TN), dissolved inorganic nitrogen (DIN), dissolved orthophosphate (DOP), and discharge data were obtained at three water quality sampling stations (Fig. 1) located in one of the reservoir primary tributaries (upper Deadwood River, DEA 102), directly downstream of the dam (DEA 101), and immediately upstream of the confluence at the lower end of the river (DEA 108). The data were collected during 2008 with biweekly sampling commencing in the first week of June and ending the first week in October. Chlorophyll a data were obtained for the same monitoring stations between 2008 and 2011. During 2008 biweekly sampling commenced the first week in June and concluded the first week in October. Samples were collected about monthly during 2009, beginning in late June and ending in late September. Sampling began again in early July in 2010 and concluded in early November. Finally in 2011, monthly sampling started in July and concluded in October.

Periphyton data were collected monthly from June through October 2010 and July through October 2011 at ten sites (Fig. 1) including four located in the regulated lower Deadwood River (DEA 101, DEA 113, DEA 112 and DEA 108) and six in unregulated reference rivers (two sites each on the upper Deadwood River – DEA 102 and DEA 114, upper South Fork Payette River – not shown, and Clear Creek – DEA 115 and DEA 116; see Fig. 1). On each sampling date, three transects were selected randomly within an established 100

m-long sample site. At each transect, depending on the amount of periphyton present, three or four cobble-sized rocks were collected and periphyton was scraped within a 58.1 cm^2 quadrat. All samples for a site were pooled and analyzed within 48 h for chlorophyll a, and ash-free dry mass (AFDM).

Full-depth water column profiles of pressure, water temperature, and dissolved oxygen were collected at a reservoir station near Deadwood Dam's deep offtake structures and spillway (DEA 010, depth $\sim 35 \text{ m}$, Fig. 1). Synoptic data were collected through the ice in February 2008 and then biweekly profiling started the first week in June and concluded the first week in October. Data from the profiles were supplemented with data from one continuous in situ station, adjacent to the profiling station (DEA 010, Fig. 1), measuring water temperature and dissolved oxygen at different depths.

Nutrient uptake in the river was calculated by means of a mass-balance model for the dissolved constituents DIN and DOP. By way of example, the average uptake of DIN by primary production in the lower Deadwood River was evaluated, by assuming all tributaries behaved similarly, as follows:

$$C_{\text{River}} = \frac{Q_{\text{Res}} C_{\text{Res}} + Q_{\text{Tribs}} C_{\text{Trib}}}{Q_{\text{Res}} + Q_{\text{Trib}}} \quad (2)$$

where C_{River} is the concentration of DIN in the river (mg L^{-1}), C_{Res} is the concentration of DIN input from the reservoir (mg L^{-1}), Q_{Res} is the volumetric discharge from the reservoir ($\text{m}^3 \text{ s}^{-1}$), C_{Trib} is the background concentration of DIN in the monitored tributaries (mg L^{-1}), Q_{Trib} is the volumetric discharge from the surrounding tributaries ($\text{m}^3 \text{ s}^{-1}$) shown in Fig. 1 (Chanson, 2004). The mass balance model accounts for reservoir and tributary contributions as well as tributary dilution, with differences between measured and predicted DIN concentrations at the confluence with the South Fork Payette River providing the minimum biological uptake rate.

3.5. Macroinvertebrate production model

Simulated water temperatures in the lower Deadwood River for each hydrologic year using the 1D river model were used in a temperature-dependent macroinvertebrate growth model to estimate secondary productivity within the river. The growth model was developed according to the methods of McCutchan and Lewis (2002) using macroinvertebrate data collected from June through October 2010, and July through October 2011 at the same 10 sites as the nutrient sampling (Fig. 1). Physical habitat was similar among all sample sites. For each site, macroinvertebrate production for each taxonomic group was estimated over the intervals between sampling dates. The instantaneous exponential form of the increment-summation method was used to estimate production of taxa that could be identified to species and followed over time as distinct cohorts, whereas the instantaneous growth method was used to estimate production of taxa that could not be identified to species or could not be followed over time as distinct cohorts (Gillespie and Benke, 1979). The growth rates of non-cohort taxa were estimated with a multiple regression equation developed from growth rates of all species in this study that could be followed as cohorts:

$$\ln g = -(4.86 \pm 0.23) + (0.155 \pm 0.019) T - (0.53 \pm 0.36) \quad (3)$$

$$\ln W; R^2 = 0.35$$

where g is the instantaneous growth rate (g day^{-1}), T is the average water temperature ($^\circ\text{C}$) over the time interval and W is the mean individual mass (g) at the start of an interval; and the macroinvertebrate production was estimated as follows:

$$P = gxBxt \quad (4)$$

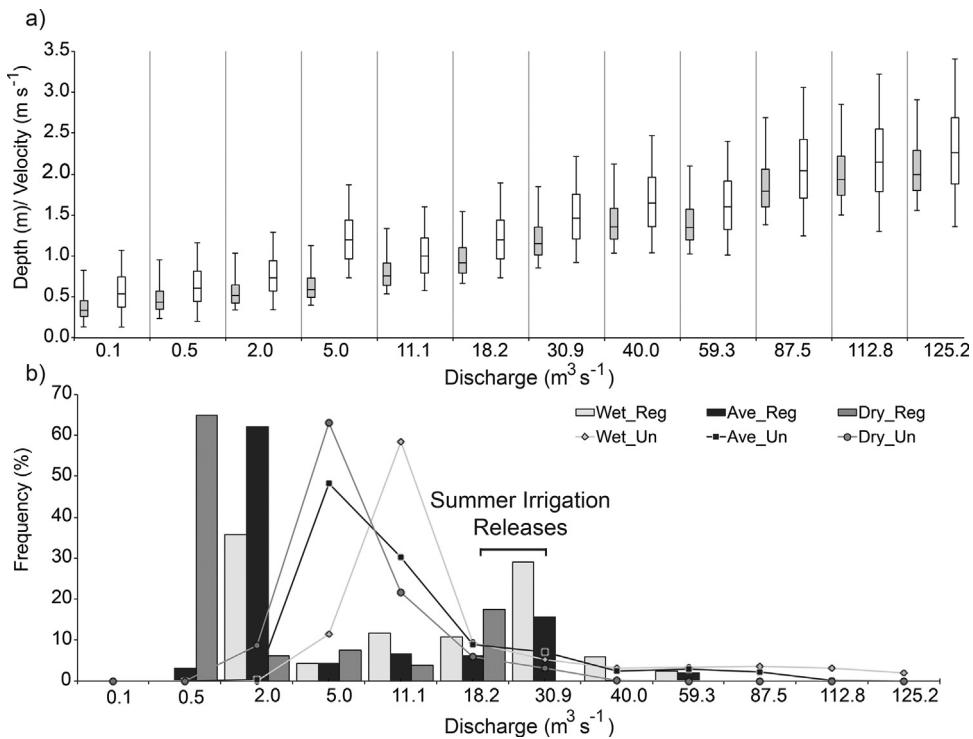


Fig. 3. a) Simulated 1D water depth (white) and flow velocity (grey) distributions for the lower Deadwood River (see Fig. 1). Box plots depict 25th, 50th, and 75th quartiles with the whiskers showing the lower 5th and upper 95th percentiles. b) Frequency histogram of unregulated (lines) and regulated (bars) discharges for dry, average and wet years respectively.

where P is the macroinvertebrate production ($\text{g m}^{-2} \text{ day}^{-1}$), g is the growth rate (g day^{-1}) calculated for each taxon using Eq. (3), B is the mean biomass for the taxon over the interval that was collected in the field (g), t is the number of days in the interval between sampling dates (day).

It should be pointed out that the sampling in the lower Deadwood River occurred at four sites in low-gradient riffles near the dam and river mouth, with no sampling performed in the middle reaches due to inaccessible terrain (Fig. 1). Physical substrate and morphology (distribution of pools, riffles, etc.) may differ in intermediate reaches thereby limiting the accuracy of results; however, overall trends in productivity should remain similar.

Macroinvertebrate production was calculated for dry, average, and wet years under scenarios of unregulated, high, and low dam releases at the four lower Deadwood River sites. For each scenario, the mean modeled hourly water temperature using the river model (T) for each interval between sampling dates was used with measured mean individual mass (W) in Eq. (3) to estimate growth rates for both cohort and non-cohort taxa. Interval production for each taxon was estimated using Eq. (4). Total macroinvertebrate community production for each sampling interval equaled the sum of production for all taxa; using these estimates total annual production ($\text{g m}^{-2} \text{ yr}^{-1}$) was calculated. Results were averaged across all four sampling sites (DEA 101, DEA 113, DEA 112 and DEA 108, see Fig. 1) to provide a representative estimate of macroinvertebrate production within the river.

3.6. Fish sampling

Field surveys for fish presence/absence in the upper Deadwood River and tributaries above the reservoir and lower Deadwood River and tributaries below the reservoir, extended over a six-year period from 2006 to 2011. Surveying methods included a combination of weir traps, electroshocking, gill netting, hook and line, bag seines, and minnow traps. Native fish species considered

in this study were Longnose Dace (*Rhinichthys cataractae*), Short-head Sculpin (*Cottus confusus*), Mountain Whitefish (*Prosopium williamsoni*), Rainbow/Redband Trout (*Oncorhynchus mykiss gairdneri*), and Bull Trout (*Salvelinus confluentus*). Data on captured fish included location, measured fork and total length, and weight-at-closure (Tranmer et al., 2015) and given the reduction in peak flows, river morphology has stabilized over time allowing the river hydraulics to become predictable from year to year. Minor deviations occur from these predictable conditions during the winter months owing to ice formation and during wet years once the spillway is activated or tributaries experience local rain-on-snow events. In-stream values of water depth and velocity, as a function of dam operation, are largely independent of season or hydrologic inputs and show a high degree of overlap as discharge increases. The bimodal distribution of regulated flows (Fig. 3b) characterizes the irrigation season releases ($27 \text{ m}^3 \text{ s}^{-1}$) and the post irrigation releases ($1.4 \text{ m}^3 \text{ s}^{-1}$).

4.2. Deadwood reservoir thermal response

The reservoir water level changes by up to 15 m during the year due to spring inflows and summer withdrawals, with peak reservoir elevations typically occurring in mid-June, and low reservoir elevations in September (Fig. 4). An exception is during wet years, when low water can occur any time in the winter or spring as large dam releases must manage reservoir storage capacity for estimated spring run-off. Thermal stratification commences by early May and is well-established by early July. Over the months from July to early September the surface temperature is relatively constant with the rate of deepening being almost constant at about 2 m per month. Thermal stratification begins to weaken in mid-September, when the deepening of the thermocline is observed to accelerate owing to convective cooling and by mid-November the water column is isothermal.

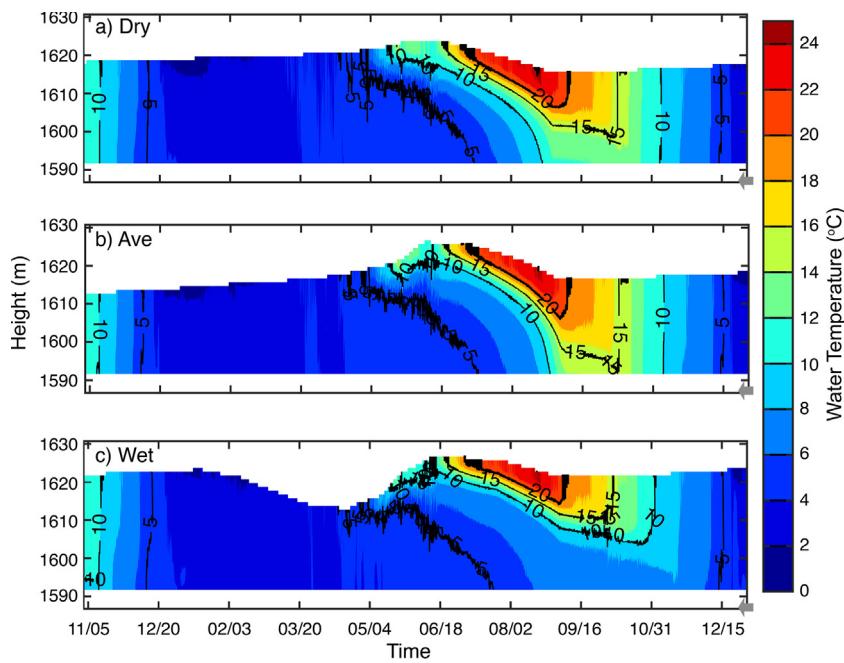


Fig. 4. Simulated thermal structure in the Deadwood reservoir near the dam wall (DEA 010) for a) dry (upper) b) average (middle), and c) wet (lower) years with low post-irrigation dam release and fast ramping rate. Arrows at bottom right of each graph indicate dam offtake elevation (1586.4 m).

Dam operations evacuate the cooler water from the reservoir during the summer irrigation months, with the thermocline progressively drawn down owing to deep hypolimnetic offtake gates. The effects of water levels on water temperature at the time of drawdown can be seen clearly (Fig. 4). During the period from January to July, the bottom temperature is around 4 °C independent of the rate of inflow; however, from August to January the large inflow associated with the wet year causes the water column to deepen, sufficiently delaying the complete water column overturn from October to December. Wet hydrologic years result in cooler bottom waters less than 10 °C throughout the summer, whereas dry years maintain bottom temperatures below 15 °C during the same period. Average year bottom temperatures reach ~15 °C in mid-September. The simulated water temperatures at the offtake gates are then directly exported to the downstream river model as upstream boundary conditions.

4.3. Lower deadwood river thermal response

The thermal response and hydrologic regime of the lower Deadwood River, computed with the 1D river model (Fig. 5), are presented (0.9 km – DEA 101 and 37.9 km downstream of the dam, near the confluence with the South Fork Payette River – DEA 108) to compare the unregulated and regulated scenarios for each hydrologic year with two post-irrigation dam releases (low 0.06 m³ s⁻¹ and high 1.4 m³ s⁻¹) under the fast ramping rate. Thermal properties in the river change between the dam and confluence due to tributary inputs, short and long wave radiation, ambient air temperature, conduction, convection, and diffusion; consequently the site below the dam resembles the reservoir and the near-confluence site resembles unregulated conditions under non-irrigation dam releases. During winter, high dam releases export ~4 °C water to the river that is warmer than the unregulated scenario (0 °C), affecting minimum temperatures and ice cover for substantial distances downstream (~20 km). The low-discharge option provides less warm water from the reservoir and allows tributary inputs to provide natural temperature conditions in the river. The low-

release option allows ice cover to persist throughout the winter while still providing overwintering pools (>1 m depth) and fish passage (>0.15 m depth) in the river (Auble et al., 2009; Tranmer et al., 2017). The thermal regime of the unregulated scenario steadily increases during the spring until it reaches warm summer temperatures of 12–14 °C; however, spring releases from the reservoir maintain consistently cool temperatures (4–6 °C) in the river. Wet hydrologic years prove inflexible for temperature management as lower irrigation demand and larger reservoir volume suppress temperatures throughout the spring, summer, and fall (Figs. 4c and 5e,f). Winter flows during wet years are affected by large precipitation events that require dam releases to evacuate 4 °C water, clearing all winter surface ice.

In contrast, dry years can export reservoir water in excess of 18 °C providing instream water temperatures greater than the unregulated condition during irrigation releases. Tributary inputs reduce water temperatures similar to the unregulated condition before it reaches the downstream confluence (Fig. 5a, b). Dry years provide more operational flexibility to the reservoir as alterations to the thermal regime during the post-irrigation season can be modulated by adjusting the rate of offtake gate closure on the dam (fast versus slow ramping). Downstream thermal effects can be substantial during dry and average hydrologic years, owing to the drawdown of the warm reservoir pool late in the season. The 1–2 °C difference can persist up to 50 days later in the season, by simply ramping down the flow slowly over ten versus two days (Fig. 5g).

4.4. Dissolved oxygen and nutrient response

River water temperature can be predicted by monitoring the environmental parameters in the basin and adjusting dam operations accordingly; however, primary and secondary productivity depend upon stream temperature and additional parameters determined by the upstream reservoir conditions, such as thermal structure, dissolved oxygen concentrations, nutrient cycling, and biological activity. Average water transit time from the dam to the confluence fluctuates between approximately 5 h during irriga-

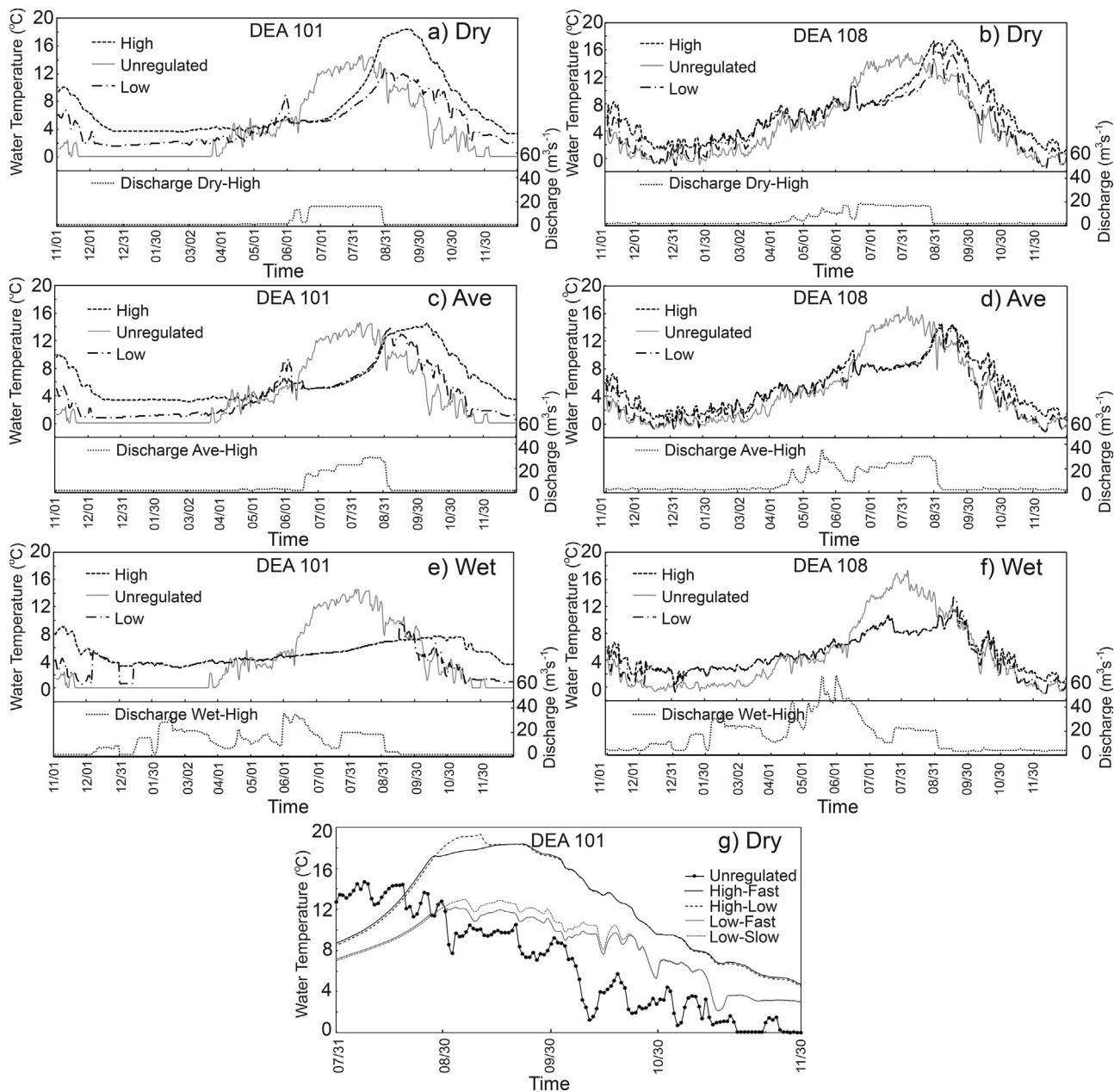


Fig. 5. Simulated daily mean temperature in the river 0.9 km below dam (DEA 101 on left) and 37.9 km below dam (DEA 108 on right) for a) and b) dry, c) and d) average, and e) and f) wet hydrologic years. Discharges shown in the lower panel. g) Close up of river temperature during a dry year for DEA 101, illustrating thermal effects of post-irrigation ramping rates.

tion releases and 15 h throughout the rest of the year. The limited time that constituents remain in the river create a “frozen flow” condition, where the response time of organisms in the river is greater than the advective time scale of the water (Imberger, 1977; Imberger et al., 1983). The river system, therefore, is fundamentally dependent upon the conditions in the reservoir that are exported downstream. The annual hydrologic forcing in the basin will determine reservoir volume, thermal structure of the water column, and timing of physical mixing events, which all affect downstream water quality parameters (USBR, 2016).

The simulated DO structure throughout the water column (Fig. 6) in the reservoir near the dam wall (DEA 010, Fig. 1) acts as a surrogate for nutrient concentrations in each hydrologic year. Winter ice cover on the lake reduces atmospheric gas exchange and biological decomposition depletes the DO concentration in the lower water column, creating a zone of anoxia in the hypolimnion

in January–February. Anoxic conditions remineralize nutrients in the sediments, increasing the concentrations of nitrogen and phosphorus exported to the river throughout the winter and early spring (USBR, 2016). Spring turnover in the reservoir mixes the bottom nutrients in the water column, thereby reducing concentrations that are exported to the river. After mixing, primary productivity (phytoplankton) reduces epilimnetic nutrients through uptake and causes super saturation of DO at 7–10 m depth during the summer season (Fig. 6). Phytoplankton senescence begins in mid-summer, depleting DO in the hypolimnion and increasing nutrient concentrations. Dam operations in the post-irrigation season determine how temperature, nutrients, and organic carbon are exported to and affect productivity in the downstream river.

Water level exerts a strong control on the extent and timing of the low DO region at depth and consequent nutrient export to the river (Figs. 6 and 7). During dry years, lower reservoir volume allows

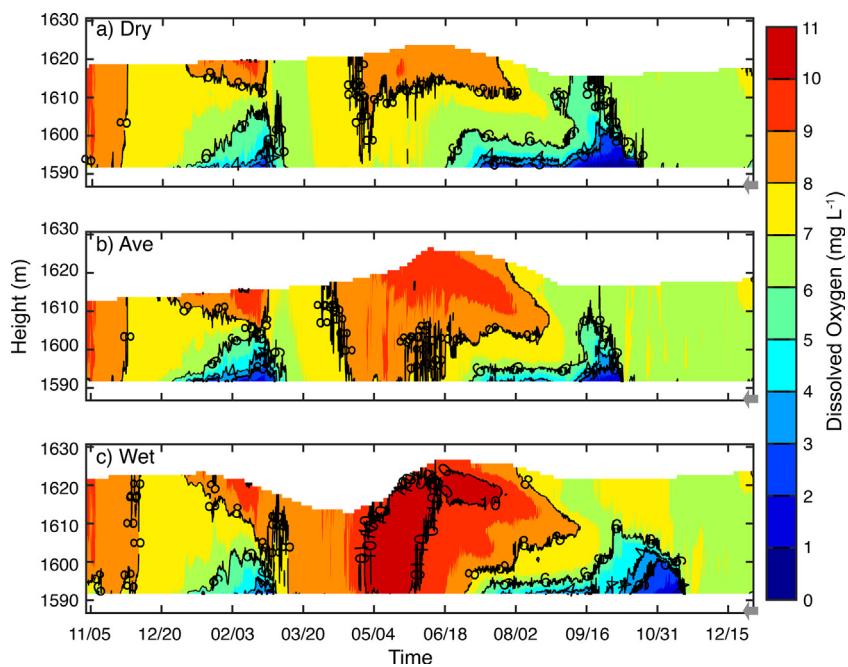


Fig. 6. Simulated dissolved oxygen in the Deadwood reservoir near the dam wall (DEA 010) for a) dry, b) average, and c) wet years with low post-irrigation dam release and fast ramping rate. Arrows at bottom right indicate dam offtake elevation (1586.4 m).

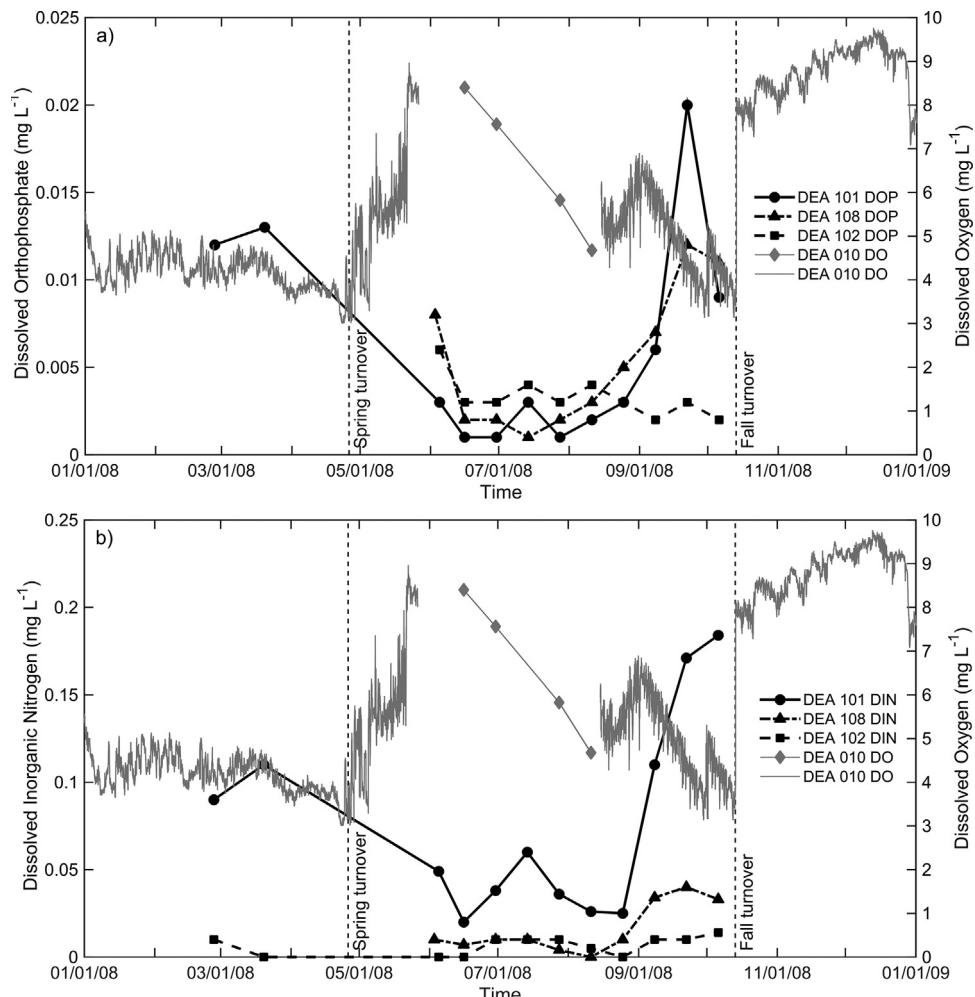


Fig. 7. Annual measured river time-series of a) dissolved orthophosphate and b) dissolved inorganic nitrogen in relation to dissolved oxygen concentration of reservoir hypolimnion. DEA 101 located 0.9 km below dam, DEA 108 located 37.9 km below dam, DEA 102 located 1.2 km above the reservoir (baseline conditions in the basin), DEA 010 reservoir station near the dam wall. Values of zero identify those below levels of laboratory detection.

the warm pool to be drawn down farther, induces earlier physical mixing in the fall, increases DO concentrations in the hypolimnion, and decreases nutrient recycling in the bottom sediments (Fig. 6). This equates to reduced availability of nutrients in the river during the fall, winter, and spring seasons. In wet years the converse is true, with greater volume, enhanced thermal stratification and later fall mixing, longer periods of anoxia in the bed sediments (~2–3 weeks longer than the other two hydrologic years), extended remineralization of nutrients from the bottom, and higher export of nutrients to the river.

The measured DOP and DIN concentrations in the upper Deadwood River above the reservoir (DEA 102) and in the lower Deadwood River (DEA 101 and DEA 108) in relation to the measured DO concentration in the reservoir hypolimnion (DEA 010) are shown in Fig. 7. These trends illustrate the availability of nutrients in the river during 2008 (an average hydrologic year) and their direct dependence on upstream reservoir conditions modeled in Fig. 6. Dissolved orthophosphate concentrations upstream of the reservoir show background values for the basin that are similar to those in the downstream river during the summer irrigation season (Fig. 7a). Later in the summer, as DO decreases and nutrient remineralization occurs in the reservoir, DOP concentrations in the river increase above background values until the fall turnover event occurs in the reservoir. A similar trend is evident in DIN concentrations, with the reservoir exporting higher than background values throughout the year (Fig. 7b). Both DOP and DIN tend to have higher concentrations at the site below the dam, especially in the autumn following reservoir drawdown.

Total nitrogen and TP concentrations (not shown) present similar trends to dissolved nutrients, but fluctuate by an order of magnitude depending upon season and respective dam operations. Values of TN and TP range between $0.04\text{--}0.44\text{ mg L}^{-1}$ and $0.01\text{--}0.107\text{ mg L}^{-1}$ over the course of the year. Seasonal changes occur in the river depending upon dam operations, with summer irrigation flows maintaining average background concentrations for forested watersheds ($\text{TN} = 0.159\text{ mg L}^{-1}$, $\text{TP} = 0.015\text{ mg L}^{-1}$) and post-irrigation flows producing much higher average concentrations ($\text{TN} = 0.263\text{ mg L}^{-1}$, $\text{TP} = 0.059\text{ mg L}^{-1}$) (Allan, 1995; Smith et al., 2003). These reservoir derived nutrients become available for primary production in the river and lead to enhanced algal productivity below the dam that diminishes in the downstream direction.

Using Eq. (2) the minimum nitrogenous consumption rate over the length of the lower Deadwood River can be quantified using a first order reaction rate. Loss rates account for uptake during primary production and energy production for organisms in the sediments during denitrification. For an average year, consumption rates for DIN fluctuate seasonally between 2.3×10^{-5} and $5.6 \times 10^{-5}\text{ m}^{-1}$ (1.71 and 6.82 day^{-1}), which are comparable to those reported for small and large streams in temperate alluvial systems (Sjodin et al., 1997; Mulholland et al., 2008). Conversely, DOP rates show both consumption and production ranging from 3.0×10^{-5} to $-5.8 \times 10^{-5}\text{ m}^{-1}$ (3.5 and -7.0 day^{-1}), with negative values illustrating an increase in DOP from tributary inputs. Wet years are fundamentally different than average and dry years with greater reservoir nutrient export, DIN and DOP, from the dam that peaks in July/August. Dissolved nutrient consumption rates show similar temporal trends over the course of the growth season, reaching a maximum in late July owing to increased biological activity and algal growth, particularly periphyton, then dropping off substantially by late October as low light conditions and colder ambient temperatures occur.

4.5. Primary production

Primary production is a function of hydrologic year, water temperature, nutrient availability, and dam operation. Low nitrogenous

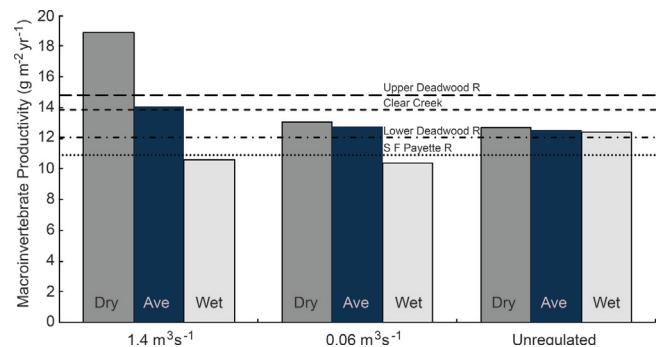


Fig. 10. Simulated average annual macroinvertebrate productivity ($\text{g m}^{-2} \text{yr}^{-1}$) in the Deadwood River per hydrologic condition, based on post-irrigation discharge releases. Dashed lines are measured productivity at nearby control sites.

uptake rates indicate the lower river is not a highly productive system. Chlorophyll *a* concentrations on the streambed (periphyton) and in the water column (phytoplankton) (Figs. 8 and 9) decrease in the downstream direction to background levels, which accounts for the spatial trend in nutrient uptake over the course of the river. Ash-free dry mass measures the total amount of all organic material (including autotrophs, heterotrophs and detritus). The site immediately below the reservoir (DEA101) had the highest AFDM followed by the next site downstream (DEA108, Fig. 8).

Measured algal biomass in the river illustrates the level of primary production in the fluvial system is elevated below the dam compared to the control site above the reservoir and farther downstream (Fig. 9) owing primarily to warm water temperature and higher nutrient concentrations at certain times of year (Morley et al., 2008; USBR, 2016). Additionally, the algal community composition changes in the downstream direction as phytoplankton settles out and the river becomes a periphyton dominated ecosystem (USBR, 2016).

4.6. Macroinvertebrate production

The predictable hydraulic conditions (water depth and flow velocity) as well as elevated nutrients and primary productivity below the reservoir provide a sufficient base for macroinvertebrate production, which depends primarily on instream temperatures. Macroinvertebrate species composition and diversity is reduced directly below the dam, but returns within 1–2 km downstream (USBR, 2016). Macroinvertebrate production varies depending upon the combination of hydrologic year and dam operation (Fig. 10), but is within the range of nearby unregulated control sites (background levels in the surrounding Payette River basin). Under variable hydrologic conditions the reservoir will alter the thermal and chemical properties of the water that is exported to the downstream river affecting regulated flows during the dry and wet years. In all scenarios, wet years are detrimental to macroinvertebrate production (14–16%) due to cold, hypolimnetic water being released (Fig. 4). For dry and average hydrologic years, secondary production will depend upon dam operation in the post-irrigation season. Average years show gains in productivity of 2–12% and dry years show substantial increases in productivity 3–49% above the unregulated natural condition (Fig. 10).

4.7. Fish habitat preferences

Habitat preferences were examined to see how native fish species (Table 2) that rely on access to resources at variable trophic levels would respond to ecosystem changes and compared with field surveys of species presence/absence. Comparison of physical habitat preferences (Table 2) to simulated river conditions for

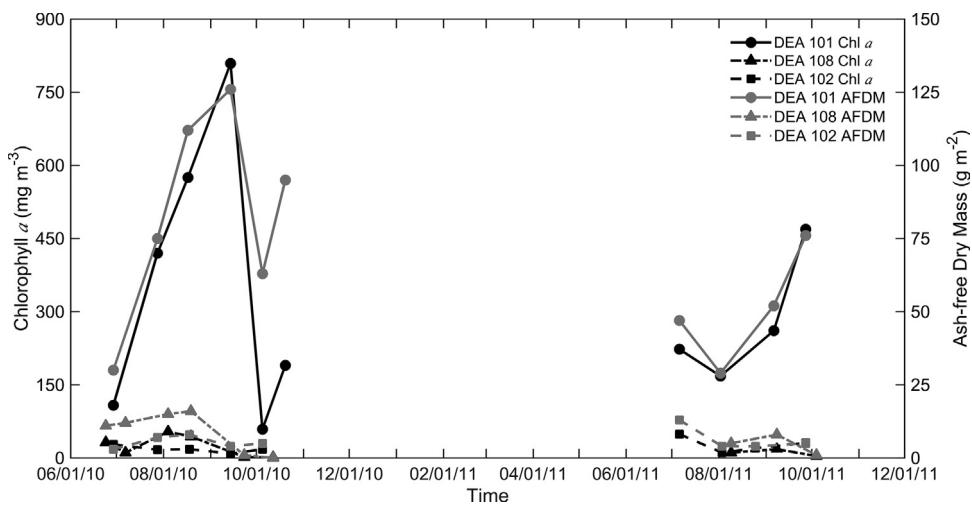


Fig. 8. Measured periphyton on the streambed as chlorophyll *a* concentration (mg m^{-2}) – black lines and ash-free dry mass (AFDM) (g m^{-2}) – grey lines. DEA 101 located at 0.9 km below dam, DEA 108 located at 37.9 km below dam, and DEA 102 located at 1.2 km above the reservoir (baseline conditions in the basin).

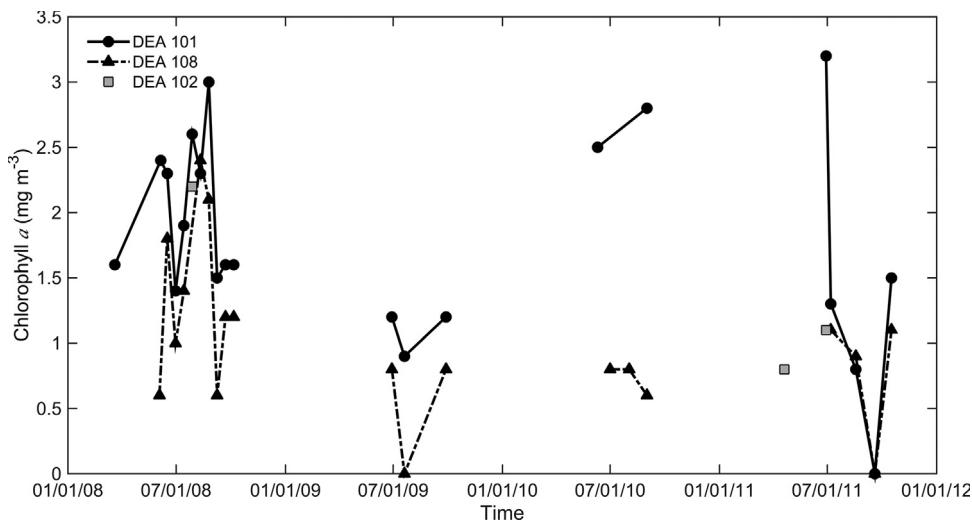


Fig. 9. Measured phytoplankton in water column as chlorophyll *a* concentration (mg m^{-3}). DEA 101 located at 0.9 km below dam, DEA 108 located at 37.9 km below dam, and DEA 102 located at 1.2 km above the reservoir (baseline conditions in the basin).

Table 2

Habitat preferences for adult and juvenile fish species that use the Deadwood River for rearing and passage. MW – Mountain Whitefish, LD – Longnose Dace, SS – Shorthead Sculpin, BT – Bull Trout, RT – Rainbow/Redband Trout, A – Adult, J – Juvenile.

Species	Source	Velocity (m s^{-1})			Depth (m)			Temperature ($^{\circ}\text{C}$)		
		Min	Max	Opt	Min	Max	Opt	Min	Max	Opt
MW – A	1	0	1.37	0.40–0.61	0.15	–	>0.76	0	23.9	15.5
MW – A	2	0	1.52	0.67	0.30	–	>0.88	–	–	–
MW – A	3	0	1.52	0.76	0.21	–	>0.91	–	–	–
MW – J	1	0	1.22	0.43	0.15	–	0.30–0.91	0	23.9	15.5
MW – J	2	0	1.22	0.61	0.15	–	0.91	–	–	–
MW – J	3	0	1.22	0.61	0.15	–	–	–	–	–
LD – A	4	0	1	0.45–0.65	0	1.2	0.3–0.8	10	22.7	14–18
SS – A	5, 6	0	0.2	<0.20	0.1	0.9	<0.9	0	20	7.5–16
BT – A	3, 7	0	1.04	0.61	0.26	–	>0.31	20.9	13.2	
BT – A	2, 8	0.06	0.91	0.61	0.15	–	>0.31	0	11	
BT – J	9	0	0.80	–	0.16	0.94	–	13.9	7.8–13.9	
RT – A	1	0	0.88	0.40	0	1.2	>0.5	0	28.9	13.9–17.8
RT – A	3	0	1.01	0.64	0.15	–	0.91	–	–	
RT – A	2	0	1.37	0.46	0.15	–	1.07	–	–	
RT – J	1	0.03	1.22	0.21–0.46	0.15	–	0.2–0.3	0	28.9	13.9–17.8
RT – J	2	0.09	0.52	0.52	0.12	–	0.61	–	–	

¹Bovee (1978), ²PaciCorp. (2004), ³WDFW (2008), ⁴Edwards et al. (1983), ⁵Hughes and Peden (1984), ⁶Hendricks (1997), ⁷Bonneau and Scarneccchia (1998), ⁸Selong et al. (2001), ⁹Baxter and McPhail (1996).

the five major species of fish in the drainage (Figs. 3 and 5) agree throughout most of the year. Some stream conditions fell outside the tolerable range, but largely did not impact fish presence during sampling. Simulated flow velocities during the irrigation season (Fig. 3a) exceed maximal values for Shorthead Sculpin, juvenile Bull Trout, and Redband Trout. Sculpin and Redband Trout are the most numerous species captured in the river and although Bull Trout were not captured in the main river, they were documented via telemetry in the river for rearing and migration (USBR, 2016). Additionally, minimum water temperature fell below the lowest reported for Longnose Dace, but Dace accounted for 30% of the total number of fish captured ($n = 2651$), illustrating their common occurrence in the Deadwood system. Results indicate that physical river habitat is suitable and is utilized for these species, regardless of conditions exceeding their documented pReferences

5. Discussion

The ecosystem downstream of Deadwood Reservoir is typical of regulated rivers in headwater catchments, experiencing reduced variability in peak and low flows, limited seasonal temperature fluctuations, and modified nutrient concentrations (Ward, 1974; Power et al., 1996; Poff et al., 1997; Graf, 2006; Chai et al., 2009; Powers et al., 2014). Depending upon the annual hydrologic forcing, a surrogate for climatic extremes, the upstream reservoir will condition the physical and biogeochemical parameters of the water released to the downstream river over the course of the year. Therefore, ecological productivity depends on a combination of the annual hydrologic conditions in the watershed and the operations strategy of the dam. Because of this, previous prescribed instream flow requirements that focused solely on hydraulics (PHABSIM approach, cf. Wen et al., 2016) and did not incorporate biophysical linkages within the native ecosystem proved to be detrimental. For example, the high post-irrigation discharge option in the lower Deadwood River provides greater depths, velocities, and wetted useable area that are similar to the unregulated conditions of the basin (USBR, 2016). However, with the reservoir present, the high-release option during winter exports 4°C water from the dam, destabilizing the ice cover for up to 20 km downstream and allowing super-cooling ($<0^{\circ}\text{C}$) of the water during frigid air temperatures. Exposed water surface, when ambient air temperatures reach -25°C in the Deadwood basin, facilitates formation of subsurface anchor and frazil ice that is detrimental to resident invertebrate and fish species (Maciolek and Needham, 1952; Martin et al., 2001; Brown et al., 2011). Therefore, river hydraulic variables (i.e. flow velocity, water depth) alone are insufficient for evaluating full ecosystem function. Other parameters such as water temperature, DO, and nutrients must be monitored and jointly managed to maximize species diversity and production (Wootton et al., 1996; Vinson, 2001; Konrad et al., 2011).

Water temperatures outside of natural conditions, because of reservoir operations, were hypothesized to explain the lack of trophic production and salmonid populations in the lower Deadwood River (USFWS, 2005), but model results do not support that finding. Through internal processing, the reservoir exported dissolved nutrients to the downstream river that were greater than those available under unregulated conditions, promoting increased algal production. This is in contrast to recent findings in lowland and agricultural basins where reservoirs reduce nutrient export to downstream river systems (Harrison et al., 2009; Ounissi and Bouchareb, 2013; Powers et al., 2014), indicating that forested headwater reservoirs may provide benefits for downstream ecosystems under certain conditions. Increased DOP and DIN concentrations facilitated algal growth and metabolic consumption to denitrifying organisms, which would otherwise be

nutrient limited in this headwater system. Consequently, primary productivity was not limiting as a food base for higher trophic levels below the dam. Measured chlorophyll *a* and ash-free dry mass of algae were both elevated above nearby control reaches upstream and downstream from the reservoir establishing a sufficient caloric base for macroinvertebrate and fish populations (USBR, 2016). This suggests that the increase in dissolved nutrients, especially during wet years, may have compensated for lower stream water temperature during the summer irrigation flows.

For macroinvertebrates, low productivity has been associated with thermal dam effects and Vinson (2001) speculates that populations may not be able to recover if thermal restoration is not done within a few years after dam closure; yet little difference is apparent in macroinvertebrate production, composition, or species richness between the regulated Deadwood River and surrounding unregulated control sites (USBR, 2016). In addition, predicted mean annual macroinvertebrate production in the lower Deadwood River was greater than that reported for the unregulated St. Vrain Creek ($7.5 \pm 3.3 \text{ g m}^{-2} \text{ yr}^{-1}$), a forested montane stream in Colorado (McCutchan and Lewis, 2002), but depended on the hydrologic conditions and dam operations. Generally, wet hydrologic years reduced macroinvertebrate productivity regardless of dam operations, which may in turn increase primary production in the river, as grazing pressure is reduced and nutrient export from the reservoir increased. Alternatively, dry years increased macroinvertebrate production 6–7% in the river under the high-release option by providing a longer duration of warm productive water. With such operational flexibility, high- and mid-elevation reservoirs can buffer rivers during dry years from extreme low water events or cool ambient fall temperatures, which may become increasingly important given increased climatic variability.

Modelling results show that the operational flexibility for ramping down the flow after irrigation provides an additional means of adjusting rivers for potential ecosystem improvement. Traditionally, ramping rates have been investigated to primarily avoid fish stranding, yet the thermal impacts can be substantial. Ramping down the flow in the lower Deadwood River can be performed incrementally, to extend warm instream temperatures into the late fall or quickly, to return the river to natural temperatures. During dry years the slow-ramping option (ten-day flow reduction), which requires only eight more days to complete, can affect the downstream thermal regime for up to 50 days owing to the drawdown of the warm metalimnion of the upstream reservoir. Thermal manipulation in the river can provide warmer temperatures later in the season to extend the growth period for species of interest; however, this may have unintended impacts such as lethal conditions for invertebrates that hatch during freezing ambient temperatures (Nebeker, 1971). Therefore, ramping rates should be investigated to address concerns of fish stranding, dewatering locations of invertebrate oviposition, and the impact of late season thermal cues (Bradford, 1997; Vinson, 2001; Halleraker et al., 2003; Irvine et al., 2009).

Simulated flow velocities, water depths, temperatures, nutrients, and food availability all indicate that there is sufficient habitat to support a sustainable population of multi-trophic fish species in the lower Deadwood River. Dam operations for Deadwood Reservoir alter the distributions of water depth and flow velocity in the lower river that are independent of the basin hydrology and are predictable at any time of the year. The altered water depth and flow velocity are within the tolerance of most native fish species in the river system, except Shorthead Sculpin, juvenile Redband Trout, and Bull Trout. Sculpin are common above and below the reservoir, so suitable microhabitats are available near the water-sediment interface that are not captured in the simulated velocity results (Lamouroux et al., 1995; Anderson et al., 2006). Examples of microhabitats for sculpin and juvenile trout are the coarse sub-

strate along riffles, channel margins, and the lee of larger substrate such as boulders and large woody debris that experience boundary layer effects and greatly reduced velocities. Therefore, these habitat attributes would be present in any riverine system with complex geomorphic features and would provide habitat for these species even though the 1D hydrodynamic model indicates values outside of the preferred range. Redband Trout are the most abundant of the sampled fish species in the river; however, Rainbow/Redband Trout are annually stocked in the Deadwood Reservoir (IDFG, 2016) and can pass through the dam into the downstream river, potentially increasing the numbers of this species. Bull Trout have a low resident population in the lower Deadwood River, with all captured fish residing in a large pool below the dam originating from upstream populations (DeHaan and Ardren, 2008; USBR, 2016). For upper trophic fish species like Bull Trout, the Deadwood River is on the edge of their geographic distribution based on stream width, elevation, gradient, etc. and robust populations exist only in the surrounding tributaries (Rieman and McIntyre, 1995; Rieman et al., 2007). For species that rely on these habitats for rearing and migration, the success of the environmental flows approach may be limited as drainages affected by discontinuity and fragmentation may not be able to recover robust ecosystem functions (Rieman and McIntyre, 1993; Dunham et al., 1997; Konrad et al., 2011; Yarnell et al., 2015). Without a hierarchical model framework to link hydrologic forcing and water operations in the basin to resultant downstream multi-trophic ecological responses, providing detailed guidance to water resource and ecosystem managers would not be possible.

While most investigations will not have the available resources to employ a coupled 3D hydrodynamic-ecological reservoir model to investigate impacts on the downstream river ecology, results illustrate the value of simple reservoir monitoring to inform downstream river modelling (Ounissi and Bouchareb, 2013; Powers et al., 2014). Given the strong control of DO on nutrient export from the reservoir, measuring reservoir profiles of temperature and DO can provide insight into the internal structure of the water column and the drivers of biochemical export. Then, in lieu of a full hydrodynamic model, relating nutrient export to the temperature and DO values, especially in the hypolimnion, can provide crucial information for managing downstream ecosystems.

Further modelling of the Deadwood River basin could be incorporated into the hierarchical framework to improve understanding and decision making by accounting for aspects of disturbance, discontinuity, and habitat incorporation. A 2-dimensional (2D) hydraulic model would provide coupled spatial data for water depth and flow velocity that could identify zones of improved life stage habitat. However, the method of Lamouroux et al. (1995) could be used in conjunction with the results of the 1D model to provide statistical distributions of flow velocities if necessary. A 2D model would additionally increase the spatial understanding of tributary mixing and thermal distribution throughout the river domain. Future steps to linking ecosystem performance to physical processes would include development of a bioenergetics model for species of interest over the extent of their life stages, providing an opportunity to evaluate reduced fish populations owing to discontinuity and fragmentation, loss of anadromous passage, and juvenile production. Restoration initiatives could assess ecosystem productivity through increased floodplain connectivity, introduction of fish ladder structures, and thermal remediation via the introduction of multilevel dam outlets or intermittent spillway operation.

Previous investigations have employed either complex hydrodynamic reservoir/river models (Parkinson, 2003; Lindim et al., 2011; Deus et al., 2013; Marti et al., 2016) or a cascading study approach (Wen et al., 2016; Cunha-Santino et al., 2017) to determine singular water quality and/or biological response parameters; however, this study examines how the annual hydrologic regime

controls the reservoir structure and in turn conditions the many physiochemical parameters that impact the downstream river ecosystem. In addition, it illustrates that small changes to dam operations can have substantive cascading ecosystem effects at various trophic levels. The direct transferability of these model configurations and results is limited given the unique climatic and geomorphic setting; yet, the methodology of hierarchical models can be leveraged for use in coupled reservoir-river systems worldwide. This is important as climate change, clean energy production, and increasing demand for water resources will require new dam construction to support global communities. Prior to construction, a system of cascading models can be implemented that simulates the ecological effects of reservoir management and further habitat disturbance, allowing for evaluation of virtual dam designs and operations that reduce ecosystem impacts or improve ecosystem performance.

6. Conclusions

Results from Deadwood Reservoir and River models illustrate that solely monitoring hydraulic properties is insufficient for quantifying the impacts of reservoir operations on riverine ecosystems and a holistic systems approach is required. Reservoirs create a break in the river continuum causing a reset of environmental constituents, in which the degree of resetting depends upon the annual hydrologic conditions, reservoir operations, size, and its location in the watershed. In the Deadwood basin, the hydraulics, temperature, nutrients, and biological productivity under the regulated flow regime are comparable or superior to the unregulated cases for dry and average years. Wet hydrologic years are detrimental to the downstream ecosystem for all cases. Under such constraints in the Deadwood River system, flow releases should focus on promoting productivity and preserving natural temperature cues for organisms rather than minimum instream flows, provided that flow properties, including refugia and connectivity, are within natural seasonal ranges.

Understanding the impacts of hydrologic forcing and reservoir operations on downstream riverine ecosystem and habitat quality requires a set of integrated hierarchical models to link the physical processes with the appropriate biological responses. Reservoir properties are controlled by climatic forcing and thus an adaptive management strategy for reservoir operations would prove more effective than fixed minimum instream flows in protecting riverine ecosystem functions and fulfilling reservoir objectives. This will increase management responsibilities, but will provide decision-making capacity driven by data and modelling based information that is agreeable to basin stakeholders.

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