Aquatic Sciences

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Aquatic habitat response to climate-driven hydrologic regimes and water operations in a montane reservoir in the Pacific Northwest, USA

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Abstract Freshwater systems are progressively becoming more stressed with increased human demands combined with expected trends in climate, which can threaten native biota and potentially destabilize the ecosystem. Numerical models allow water managers to evaluate the combined effects of climate and water management on the biogeochemical processes thereby identifying opportunities to optimize water management to protect ecosystem function, biodiversity and associated services. We used a 3D hydrodynamic model (ELCOM) coupled with an aquatic ecosystem dynamic model (CAEDYM) to compare two scenarios across three climatic and hydrologic conditions (extreme wet, extreme dry and average) for Deadwood Reservoir (USA). Additionally, we collected water temperature, water chemistry and biological data from the reservoir and inflowing tributaries to validate the model, as well as migration and growth data from Bull Trout (*Salvelinus confluentus*) the top predator of the food web. Modeled scenarios identified that reducing minimum outflows from 1.4 to 0.06 m^3 s^{-1} during the fall and winter months resulted in higher reservoir elevations and cooler water temperatures the following year, which extended reservoir rearing during the summer and fall seasons. The scenarios with reduced stream flow during the fall and winter seasons indicate benefits to the reservoir ecosystem, particularly during dry years, and could reduce the effects of climatic warming.

Keywords Reservoir · Aquatic ecosystem · ELCOM-CAEDYM · Bull Trout (*Salvelinus confluentus*) · Fish habitat · Water operations

Introduction

Many lakes and reservoirs in the temperate regions of North America are managed for competing interests such as: flood control, irrigation delivery, conservation of biodiversity, and recreational activities (i.e. boating, swimming and fishing). Competing interests require operating lakes and reservoirs with fluctuating water elevations that are associated with reduced habitat diversity, species richness, species abundances and increased invasive and/or non-native species (Zohary and Ostrovsky 2011). Additionally, climate change is altering patterns of regional hydrology and driving reservoirs and lakes toward new physical and chemical conditions directly impacting thermal structure and timing, oxygen dynamics, nutrient cycling and primary production (Williamson et al. 2009). Best management practices demand that dam operations be assessed to ameliorate ecological degradation and the impacts of climate change on reservoir ecosystems.

Current and future predicted climate conditions are leading to greater climatic extremes, with resultant impacts on freshwater resources (flooding, drought and other extreme

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weather events) (IPCC 2007; Milly et al. 2008). Human exploitation of water resources leads to increased annual and inter-annual fluctuations of water levels in lakes and reservoirs, which are also predicted to increase due to more frequent drier conditions and increased human demand (Zohary and Ostrovsky 2011; Jeppesen et al. 2015). Changes in lake or reservoir levels are predicted to have strong effects on the nutrient dynamics, nutrient concentrations, water quality and trophic structure. This climatic trend is predicted to increase water temperatures, increase eutrophication and cyanobacteria blooms, and alter food web structure (Jeppesen et al. 2015).

The effects of these altered lake and reservoir ecosystems become less clear when attempting to predict effects on the middle and upper trophic levels (zooplankton to fish) (Jeppesen et al. 2010). The littoral zone of lakes and reservoirs provides habitat complexity and food for many species of invertebrates and vertebrates (Zohary and Ostrovsky 2011). Fish are an important link between the littoral, benthic and pelagic zones through nutrient translocation and biotic interactions (Jeppesen et al. 2010). Bull Trout (*Salvelinus confluentus*), a native piscivorous charr, is heavily reliant on prey species and highly sensitive to environmental conditions, particularly water temperature (Dunham et al. 2003; Howell et al. 2010; DEQ 2010). Bull Trout are a migratory species that are often isolated in headwater habitats due to water development and/or habitat conditions (Rieman et al. 2007). Although dams may limit Bull Trout migrations to historically accessible riverine habitats, the reservoirs often provide rearing habitat and access to prey that are supported by the aquatic production in the reservoir that boost growth (Beauchamp and Van Tassell 2001). However, the effects of reservoir operations on the ecosystem interactions and impacts to sensitive species is not well understood, leaving water managers with little guidance particularly during drier cycles when environmental conditions and biota are most stressed.

Bull Trout, native to western North America, are currently listed as threatened under the Endangered Species Act in the US since 1998 and as a species of special concern in Canada since 1995 (Al-Chokhachy and Budy 2008). This species is sensitive to habitat alteration and degradation, such as increased fine sediment inputs, habitat fragmentation and increased water temperatures. Spawning and early rearing habitat is generally located in the uppermost tributary drainages where water temperatures are cooler. Young Bull Trout remain in the natal tributary habitat for 1–4 years, and subsequently migrate to larger reservoir or river habitats (Fraley and Shepard 1989; Rieman et al. 2007; Howell et al. 2010).

Our study examines the physical and biological effects of expected dam operations on reservoir conditions in Deadwood Reservoir, located in a montane basin in central Idaho, USA, and how a sensitive and threatened species, Bull Trout, responds to reservoir operations and conditions. Bull Trout were chosen as a focal species due to several characteristics: (1) high sensitivity to environmental conditions such as water quality and temperatures; (2) high reliance on the status and production from the lower trophic levels; and (3) extensive migrations and reservoir residence (Fraley and Shepard 1989; Beauchamp and Van Tassell 2001; Al-Chokhachy and Budy 2008; Howell et al. 2010). Additionally, the long life span of Bull Trout (up to 9 years) allows for the comparison of individual trout across a range of climatic conditions.

A coupled three-dimensional (3D) hydrodynamic and aquatic ecological model was used to describe physical, chemical and biological components of the Deadwood Reservoir and predict how reservoir conditions change with alternative reservoir operations over a range of climatic extremes. Reservoir conditions were measured and modeled under several operational scenarios. The objectives of this study were to: (1) describe how reservoir water temperature, dissolved oxygen (DO) and other ecosystem variables change in relation to dry, average and wet hydrologic years with two outflow scenarios; (2) identify how Bull Trout could respond to a range of climatic-driven conditions in the reservoir; and (3) identify how dam operations may compensate for expected future conditions.

Methods

Study area

Deadwood Reservoir, located in central Idaho's Payette River drainage, was created in 1931 by impoundment of the Deadwood River by Deadwood Dam. Prior to the construction of the dam, the watershed was accessible to anadromous (sea-run) species of salmon and steelhead (Wallace and Zaroban 2013). The 12.6 square kilometer (km^2) reservoir is located 38 km upstream of the Deadwood River's confluence with the South Fork of the Payette River (Fig. 1). The drainage upstream from the reservoir is about 287 km^2 of mountainous terrain. At the normal full-pool elevation of 1625.8 m, the reservoir contains 190 million cubic meters (m^3) and has a mean and maximum depth of 15.5 and 35 m, respectively. Annual water level fluctuations can be up to 15 m. Reservoir surface elevations peak about mid-June, and are at their minimum in September. The littoral zone in the reservoir (defined as <10 m depth which is equal to twice the median secchi disk transparency) moves as the reservoir surface elevation increases and decreases. At full pool, 3.9 km^2 or 31% of the surface area of the reservoir is littoral zone. At minimum pool, the littoral zone area increases to 7.4 km^2.

Fig. 1 Deadwood Reservoir (Idaho, USA): **a** location, **b** bathymetry including sampling stations and contours intervals are 5 m increments, and **c** hypsographic curve with the *shaded area* indicating the range of reservoir water level variation considered in this study
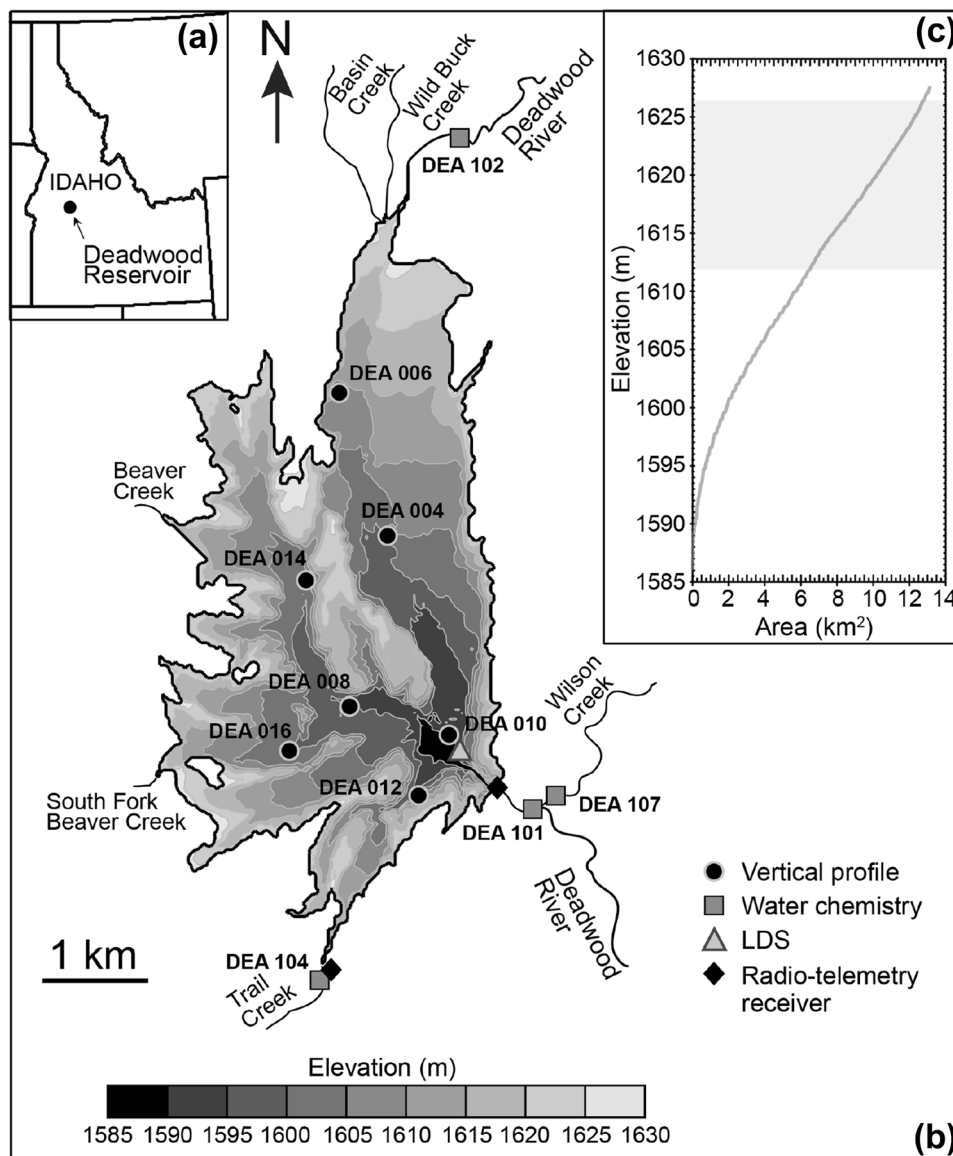
The majority of inflows to the reservoir occur during the spring when the winter snowpack melts. Inflows from tributaries enter the reservoir as inter-flow at about 5–10 m depth, due to density differences. Water is released for contractual irrigation during the summer (June through August) and water surface elevations decline during this time. Water is released from the dam primarily through two deep outlet gates with an invert elevation at 1586.4 m during the spring and summer months. In some years, water is also spilled over the crest of the dam from the reservoir surface for a short period of time between mid-June and early July. The post-irrigation season (September through June) historically released 0 m³ s⁻¹ from the dam. Since 1993, a minimum stream flow of 1.4 m³ s⁻¹ has been released at the dam, about equivalent to natural estimated fall and winter inflows into the reservoir during dry climatic conditions.

Pre-irrigation releases generally start in June and end in early July and are only conducted when inflows exceed storage capacity.

Besides irrigation and flood control, Deadwood Reservoir is managed for native and non-native fisheries and recreation. Fish species in the Deadwood Reservoir include Bull Trout (*Salvelinus fontinalis*), Kokanee Salmon (*Oncorhynchus nerka*), Rainbow Trout (*O. mykiss*), Mountain Whitefish (*Prosopium williamsoni*), Redside Shiner (*Richardsonius balteatus*), Dace (*Rhinichthys* spp.), and Sculpin (*Cottus* spp.). Westslope Cutthroat Trout (*O. clarki lewisi*) were stocked by Idaho Department of Fish and Game until 1998 and a reproducing population remains. Resident fall Chinook Salmon (*O. tshawytscha*) and Atlantic Salmon (*Salmo salar*) were also stocked in recent years, but were not captured during this study.

Reservoir and stream data

Reservoir and stream data presented in this study were collected from 2007 to 2009. Reservoir sampling (weekly, biweekly and monthly) consisted of full-depth water-column profiles (pressure, water temperature, DO, pH, conductivity, turbidity and fluorescence) and collection of water-quality samples at several depths analyzed for total concentrations of phosphorus and Kjeldahl nitrogen (organic plus ammonia nitrogen), dissolved concentrations of orthophosphate, nitrite plus nitrate, ammonia and silica, and chlorophyll *a* including identification and counting of phytoplankton. The reservoir sampling program was supplemented with real-time data collected with a Lake Diagnostic System (LDS) (Imberger 1994) deployed adjacent to station DEA010, the deepest station and the most consistently sampled reservoir station, and close to Deadwood Dam's deep release structures and spillway (Fig. 1). The LDS consisted of a fast response, high precision thermistor chain with 40 underwater temperature sensors equally spaced over the water column's full depth (about 35 m) and seven DO sensors. Five sensors were suspended within the upper 9 m of the water column in order to track biological productivity, while the two remaining sensors were installed at ~1.5 and ~14.0 m above the bottom to track DO depletion within the hypolimnion. The LDS was also equipped with a full meteorological station, allowing simultaneous measurements of wind speed and direction, short wave radiation, net total radiation, air temperature and relative humidity at 2 m above the water surface. The sampling interval was 60 s. The LDS meteorological station was moved onshore during the winter months to protect the frame structure from damage that would result from the winter ice cover on the lake. Sampling the two largest tributaries upstream from the reservoir (Deadwood River—DEA102 and Trail Creek—DEA104) and the reservoir's outflow immediately downstream of Deadwood Dam (DEA101) (Fig. 1) included collecting at continuous predetermined intervals water surface elevation, water temperature and water samples analyzed for the same parameters as reservoir water samples. Details of the limnological monitoring program conducted in Deadwood Reservoir are described in Reclamation (2016).

Numerical modeling and scenarios

Operational scenarios for comparison were identified a priori and focused on the post-irrigation stream flows where operations would not interfere with flood control or irrigation delivery. The period of hydrologic record spans 83 years from 1931 to 2014. General hydrologic conditions are described with the percent exceedance, which is the percentage of years in the period of record that hydrologic inputs exceed the condition described (Chow et al. 1988). For example, the wettest years on record have low exceedance values, whereas the driest years on record have high exceedance values. Water years representing wet (2.3% exceedance), dry (97.7% exceedance) and average (47.1% exceedance) climatic conditions were selected for model scenarios. The years modeled were from recent record (1997–2003) to capture current climatic conditions. Six scenarios were examined including three climatic conditions (wet, dry or average) with two rates of minimum post-irrigation season stream flows from the dam (0.06 and 1.4 m^3 s^{-1}). Outflows between 0.06 and 1.4 m^3 s^{-1} were not considered due to structural limitations at the dam and cavitation problems at the outlet.

The numerical simulations in this study were performed using the 3D hydrodynamic Estuary, Lake and Costal Ocean Model (ELCOM), described in detail in Hodges et al. (2000), coupled with the Computational Aquatic Ecosystem Dynamics Model (CAEDYM), detailed in Romero et al. (2004). ELCOM-CAEDYM has been successfully applied in numerous lakes and reservoirs and a review of the application of the coupled model system has recently been done by Trolle et al. (2012). The appropriate algorithms in ELCOM were activated to include atmospheric exchange, inflow dynamics, turbulent mixing dynamics, Coriolis forcing, and ice formation dynamics (Oveisy et al. 2012). CAEDYM was configured with the following state variables: dissolved oxygen (DO), nitrate (NO_3), ammonium (NH_4), dissolved organic nitrogen (DON), particulate organic nitrogen (PON), orthophosphate (PO_4), dissolved organic phosphorus (DOP), particulate organic phosphorus (POP), dissolved organic carbon (DOC), particulate organic carbon (POC), and four phytoplankton groups: cyanobacteria, dinoflagellates, diatoms, and cryptophytes. These represent the four main phytoplankton groups observed in Deadwood Reservoir during the sampling period, i.e., *Anabaena spiroides, Ceratium hirundinella, Fragilaria* spp., and *Cryptomonas* spp. Algal biomass was modeled as chlorophyll *a* (chl *a*), with a constant carbon to chl *a* ratio. Nutrient limitation considered dynamic nitrogen intracellular stores for dinoflagellates and cryptophytes, and constant nitrogen stores for cyanobacteria and diatoms. Phosphorus intracellular stores were considered constant for all groups. Light limitation did not include photoinhibition. Although grazing was not modeled explicitly, it was parameterized indirectly with the phytoplankton loss term. Active vertical migration was included for dinoflagellates and cryptophytes, estimated on the basis of the balance between irradiance and internal nitrogen stores. Cyanobacteria were set to be positively buoyant with a constant upwards velocity and diatoms were assigned a constant settling velocity based on their average size and

specific gravity. Nutrient and oxygen fluxes between the sediment and water were simulated using a simple static model based on empirical relationships between the sediment and water assuming constant sediment composition.

The simulations for the wet, dry and average climatic conditions were run for a period of 14 months starting on November 1. Bathymetric reservoir data were available from a survey completed in 2002. The domain of Deadwood Reservoir was discretized using a uniform 100×100 m horizontal grid and a uniform vertical grid with 1 m resolution. The time step was set to 120 s in order to satisfy the Couránt-Friederich-Levy (CFL) stability condition and the ratio of computational time to real time was around 900.

The simulations considered inflows from the six major tributaries to Deadwood Reservoir (Deadwood River and Trail, Wild Buck, Basin, Beaver, and South Fork Beaver Creeks), as well as outflows at the dam and spillway (when applicable). As discharge measurements were only available for Deadwood River and Trail Creek, the two primary tributaries of Deadwood Reservoir, a water balance was developed in order to determine flows from ungauged creeks. A storage curve was generated from the bathymetry data and used in conjunction with daily measured inflow and outflow values, water level fluctuations measured at the dam, and estimated evaporation rates to determine a residual inflow for each day. The residual flow was then split into five separate flows, according to measured rates during the period 2007–2009. Water temperature and water quality at the inflows were derived from the field monitoring program. Due to uncertainties in the water balance related to poorly known evaporation rates, groundwater flow and contribution from rainfall, the inflows were further adjusted based on the model results to match measured and simulated water levels at the dam.

The model was forced with a combination of measured and calculated data at the LDS (air temperature, relative humidity and wind speed) and meteorological stations present around the area of the reservoir (incoming short wave radiation). Cloud cover was calculated based on measured air temperature, relative humidity and short wave radiation and daily averaged values were used. All meteorological data were applied uniformly over the domain. The initial conditions of water temperature, DO and other water quality variables were compiled from the LDS, profiles and water samples collected in September/October 2007 and horizontally interpolated.

The period of October 3, 2007 through March 3, 2009 was used for model validation, and data collected during this period (meteorological, inflow scalar variables and initial conditions) were used during the model scenario runs; however, initial water levels and inflow and outflow rates reflected the scenario conditions being examined.

Fish data

Bull Trout were used as an indicator of reservoir conditions. Between 2006 and 2011, Bull Trout were captured upstream from Deadwood Reservoir using a variety of gear: fyke nets (trap nets), weir traps, horizontal gill nets, vertical gill nets, hook and line sampling, bag seines, electroshocking, and minnow traps. Fish were either anesthetized using Tricaine Methane Sulfanate (MS222) in 2006–2011 or by electronarcosis in 2011 (Hudson et al. 2011). All fishes captured were measured (total length for non-target species; total length, fork length, and weight for Bull Trout). Scales were collected from the area between posterior edge of dorsal fin and the lateral line. Scales were deposited on a small piece of paper and stored in a small envelope. All live specimens were returned to their approximate sampling location.

Bull Trout were implanted with radio telemetry transmitters (radio tags Lotek models MCFT2-3BM, MCFT2-3EM, MCFT2-3FM, SR-TP11-25, and SR-TP11-35), acoustic tags (Lotek model MM-M-8-SO), and/or archival temperature recording tags (archival tags Lotek Internal model 1410 or Lotek External model 1100). Expected life on the radio-tags was 186 days for smaller size tags (inserted in smaller trout) to 585 days for larger size tags (inserted in larger trout). Radio-tag signals are detectable when the tag is in depths less than 10 m, whereas acoustic tags are detectable at any water depth. During 2011, acoustic and archival tags were used to track Bull Trout in deeper water habitats and acquire measurements related to depth and temperature. Archival tags store data (depth and temperature) in an internal logger and require tag retrieval to download the data. Radio, acoustic, and internal archival tags were implanted with the modified shielded needle technique described by Ross and Kleiner (1982). Incisions were closed using sutures from 2006 to 2010, and stainless steel staples in 2011 (Swanberg et al. 1999). The external archival tags were attached with the method described by Howell et al. (2010).

Telemetry tracking occurred weekly by air or boat based on weather and available resources. When radio-tagged fish were located, the following data were recorded at that location: time, GPS location, pressure (water depth) and temperature at the fish's location (if the tags were equipped with those sensors). Tagged fish were also monitored using fixed telemetry stations (Fig. 1). Migration timing was estimated for radio-tagged Bull Trout leaving the reservoir and returning to the reservoir in 2006–2011. Migration timing estimates were based on when trout were last detected in the reservoir and first detected in the tributaries and vice-versa. The date was converted to the number of days after June 1 for statistical analysis. A Kruskal Wallis test was used to assess annual differences in migration timing (first

detection in river and last detection in river) (R Development Corps Team 2010).

Tags inserted in Bull Trout were determined to be tag loss or suspected mortality when one of the following conditions was met: (1) a tag was retrieved without the fish; (2) a tag recorded temperatures consistent with ambient air temperatures; and (3) a tag was not retrieved but did not move for an extended period of time (>14 days). Although these methods are used to infer mortality, an unknown number of expelled tags can be included in this count when a carcass is not found with the tag.

Bull Trout growth rates were back-calculated from annuli on the scale samples. In the laboratory, 3–4 scales were removed from the scale paper and placed on a standard 25×76 mm glass microscope slide approximately 1 mm thick. Three to four drops of water were added to the slide to re-hydrate scales for one minute. A 24×60 mm glass coverslip approximately 0.18 mm thick was then pressed onto the scales. Scales were magnified, photographed and displayed using PowerPoint (Microsoft Cooperation). Annuli were identified, marked and measured from the outermost edge of the annulus to the center of the focus with the scale oriented along the long axis. Estimates for growth and age were applied using the direct proportion back calculation method (Devries and Frie 1996). The estimated length at each checkpoint was rounded to the nearest one hundredth of a millimeter. The distance at last check was rounded to the nearest one thousandth. Differences among growth years were tested using an ANOVA. Growth years 2005–2009 that provided sample sizes greater than or equal to 30 individuals were used for the analysis. Years during data collection 2007–2011 were near average climatic conditions (40.0–56.5% exceedance) except for 2007 which was drier than average (78.8% exceedance).

Model based prediction of Bull Trout habitat

The model output of simulated water temperatures and DO values were used to compare the available habitat for Bull Trout in the reservoir for the operational scenarios and the validation year (2008). We also considered habitat utilized by Lake Trout (*Salvelinus namaycush*), a species functionally and biologically similar to Bull Trout (Coutant 1977; Sellers et al. 1998). We defined optimal and suitable habitat for Bull Trout within the water column with water temperature ≤15 °C (optimal) and ≤18 °C (suitable) with DO concentrations ≥6 mg L^{-1} and examined the amount of habitat over time that met this criteria. This and similar approaches have been useful in analyzing fish habitat under different climatic scenarios (e.g. Stefan et al. 1996; Fang et al. 2012), and would also indicate the general condition of fish habitat relevant to prey species important to Bull Trout.

Results

A detailed description of the model validation and output from ELCOM-CAEDYM is presented in Reclamation (2016). For the purposes of this paper, the data presentation will focus on measured and simulated water temperatures and DO concentrations during October 2007 through March 2009. These two variables are recognized as the most significant water quality parameters that influence fish habitat (Hondzo and Stefan 1996; Cline et al. 2013).

Model validation

A comparison between the measured and simulated vertical profiles of water temperature and DO at the deepest part of the reservoir (station DEA010) (Fig. 1) for the model validation period is shown in Fig. 2. The results reflect the water level changes due to spring inflows and summer withdrawals, with peak reservoir elevations typically occurring in mid-June, and low reservoir elevations in September. The reservoir thermal structure during spring and summer and the thermocline were well reproduced by ELCOM-CAEDYM, including the thermocline drawdown during the summertime irrigation releases. The mixed period through fall was captured reasonably well with a slight delay (Fig. 2a). The reverse stratification during the ice cover period is also captured well by the model, with colder water overlying warmer water approaching 4 °C near the lake bed. Unfortunately, we were unable to validate ice and snow thickness measurements in the reservoir due to logistical difficulties and safety concerns at the site. During the study period ice-cover spatial distribution was available from aerial photographs and used to provide validation of the ice cover extent only. In general, the spatial pattern of ice-formation was in qualitative agreement with the limited field observations (unpublished data).

The DO dynamics were also well reproduced by the model, including the timing of hypolimnetic anoxia (February 2008 under winter ice cover and October 2008) and re-aeration (October 2007 and May 2008) (Fig. 2b). The development of substantial hypoxia during the icing period resulted in released nutrients which in turn affected the reservoir's productivity during the following spring and summer months (Reclamation 2016). Nearly all comparisons of surface and bottom concentrations were within about 1 mg L^{-1}, though under-predicted results are visible in August and September 2008 and during the mixed periods in the fall 2007 and 2008. A super-saturated region at 7–10 m depth was remarkably persistent for a period of months associated with a deep measured chlorophyll fluorescence maxima (Reclamation 2016). These values were reproduced by the model, although not as pronouncedly as in the field data (Fig. 2b).
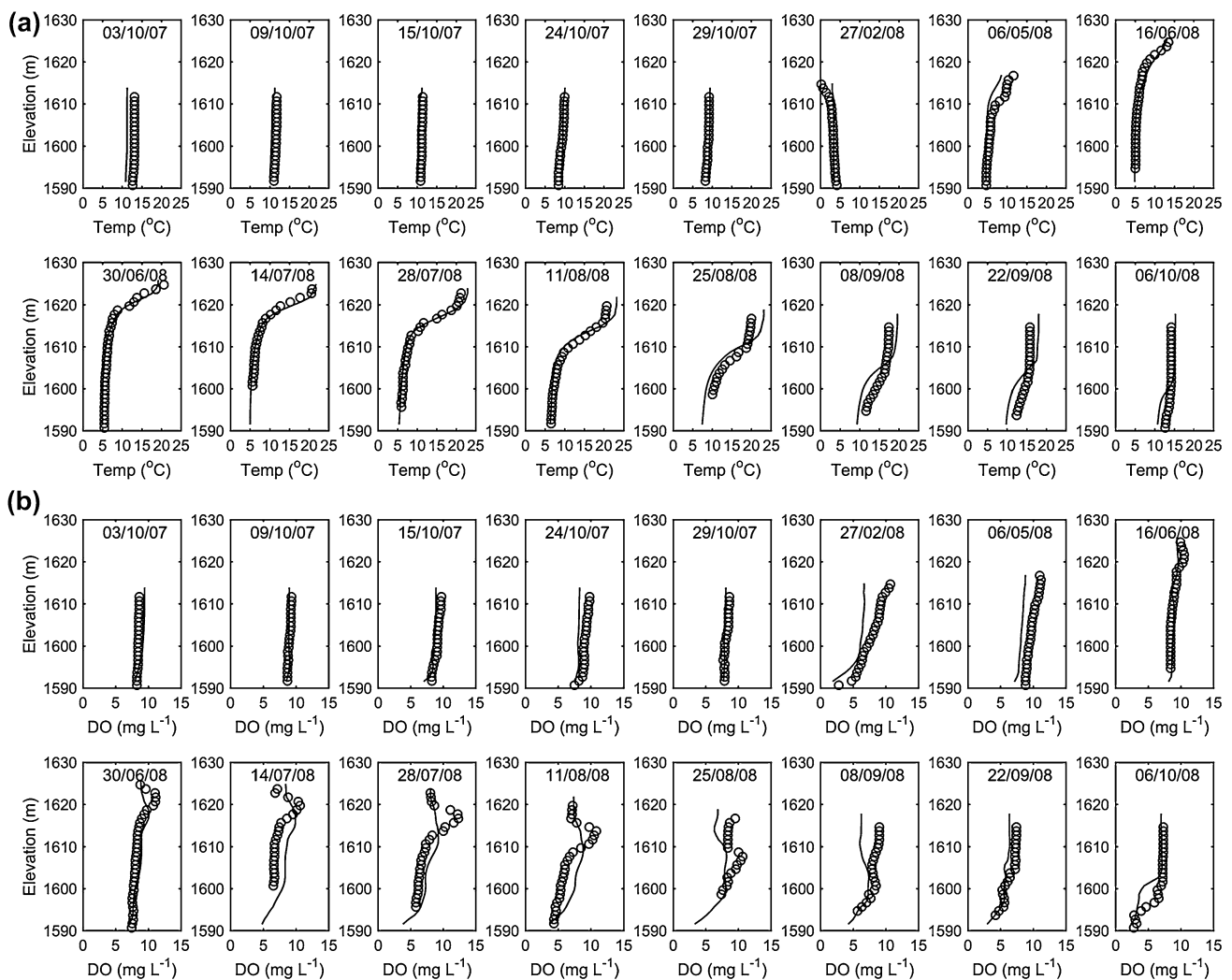
Fig. 2 Comparison of measured (*circles*) and simulated (*line*) water temperature (**a**) and dissolved oxygen profiles (**b**) at station DEA010 for the validation period. The days are indicated at the *top* of *each panel*

The root mean square error (RMSE) was applied to evaluate the model performance and calculated for water temperature and DO in Fig. 2. The RMSE of water temperature is 1.3 °C and for DO is 1.3 mg L^{-1}, providing confidence that ELCOM-CAEDYM simulations could be used to predict accurately water temperature and DO conditions from reverse winter stratification through autumn turnover (year-round simulation) under a range of reservoir operation and hydrologic scenarios.

Model simulation scenarios

The simulated scenarios allow direct comparisons of different climatic and hydrologic conditions and reservoir operations on the physical and biological variables in the reservoir. The model output for water temperature and DO at station DEA010 for the different scenarios

are shown in Fig. 3. The model output clearly shows the effects of water levels on water temperature at the time of the drawdown (Fig. 3a–f) and on the extent and timing of the low DO region at depth (Fig. 3g–l). When less water is released from the dam (Fig. 3b, d, f), this leads to higher storage levels, and bottom temperatures remain under 15 °C even during the summer. This effect is mostly visible for the dry year case (Fig. 3b), when 1.4 m^3 s^{-1} outflows led to bottom temperatures of ~20 °C during summer drawdown (Fig. 3a). The low DO region in the bottom waters is highlighted by contours drawn at concentrations of 3 and 6 mg L^{-1} (Fig. 3g–l), considered to be an important biological niche indicator for fish. The wet year scenario has higher water surface resulting in low DO in the hypolimnion (Fig. 3k, l) persisting until the middle of September—approximately 2–3 weeks longer than the dry or average scenarios. When reducing
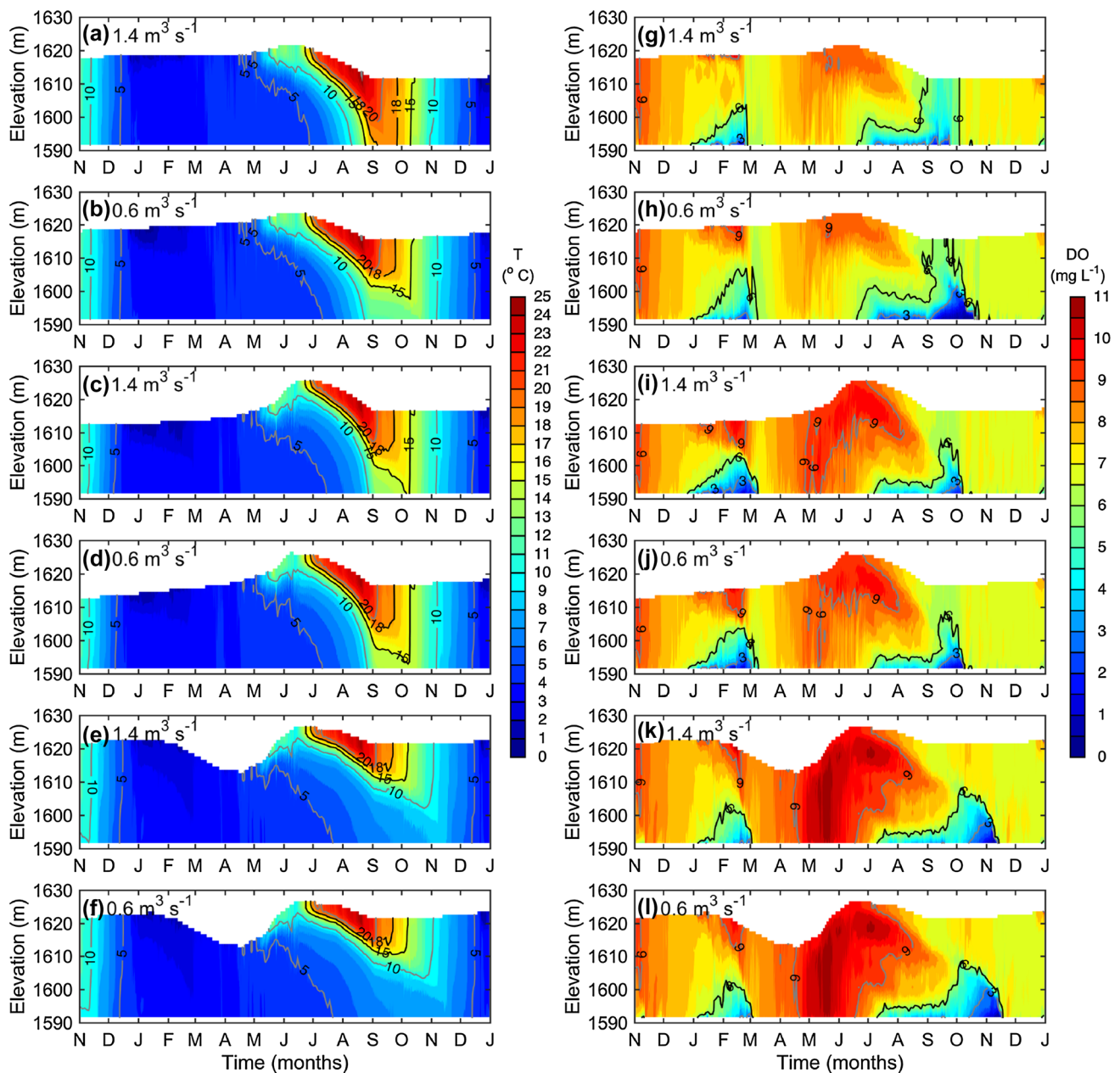
Fig. 3 Comparison of modeled water temperature (**a–f**) and dissolved oxygen (**g–l**) at station DEA010 under six scenarios: **a, b, g, h** dry climatic conditions and 1.4 and 0.06 m³ s⁻¹ outflows, **c, d, i, j** average climatic conditions and 1.4 and 0.06 m³ s⁻¹ outflows, and **e,** **f, k, l** wet climatic conditions and 1.4 and 0.06 m³ s⁻¹ outflows. The isotherms of 15 and 18 °C and DO isopleth of 6 mg L⁻¹ are indicated in *black* to illustrate the optimal and suitable Bull Trout habitats, respectively

the end of irrigation season outflow to 0.06 m³ s⁻¹, additional water remained in the reservoir which increased the period of low DO in comparison to the other operational scenarios (1.4 m³ s⁻¹). In summary, higher reservoir water levels that were a result of wetter climatic conditions and reduced outflows during the fall/winter months result in cooler bottom waters (Fig. 3b, d, e, f) providing cooler, deep water for fish; however, higher water levels also mean a greater oxygen drawdown, prolonging

the period of hypolimnetic hypoxia/anoxia at these deep locations (Fig. 3h, j, k, l).

Bull Trout migration and growth

Between 2006 and 2011, 51 Bull Trout captured in the reservoir and tributaries were tagged with radio tags and five acoustic tags. Of these tagged fish, seven Bull Trout were also tagged with archival tags during 2011. Bull Trout

radio-tagged upstream from the dam ranged from 209 to 585 mm total length (average 413 mm). Radio and acoustic tags indicate that Bull Trout upstream from Deadwood Dam utilized tributary and reservoir habitat and migrated between them seasonally. Tagged Bull Trout were dispersed throughout the reservoir during the winter and spring typically utilizing the outer portions of the reservoir (mid to shallow depths). Although this could be related to depth limitations in receiving radio-tag signals, the use of the acoustic tags during 2011 showed similar patterns of detection.

During 2006 through 2010, most Bull Trout tagged during this study migrated out of the reservoir during the summer (between June and August) and returned to the reservoir in the fall (between late September and late October). During the fall (September/October), Bull Trout spawn in

Fig. 4 Forebay elevation (m) in Deadwood Reservoir and first (*circles*) and last (*triangle*) detections of Bull Trout in tributaries, 2006–2011. Migration data were not collected during 2009

the tributary habitat. However, in 2011, radio-tagged Bull Trout were found throughout the reservoir and near the mouths of the tributaries during the months of July through November. This was unusual compared to previous years where the tagged Bull Trout migrated out of the reservoir in the months of August and September. Migration dates were variable year to year for all tagged Bull Trout (Fig. 4) and individual Bull Trout that were tracked multiple years (data not shown). The date of first detection in the river was significantly different across years (p < 0.01, Fig. 5). These data indicate that Bull Trout migrated into the tributary habitat 38 to more than 60 days earlier in 2007 than during the other years of the study. Reservoir elevation that corresponded with the average date of movement across years was 1623.7 m (SD 0.9 m). The date of last detection in the river was not significantly different (p = 0.91) across years during the study and varied by less than 10 days. Annual growth measured from scale growth identified no significant difference across years examined (2005–2009) indicating that growth is not affected during different reservoir levels and climatic conditions (p = 0.2) (Fig. 5).

Only three of the seven archival tags were retrieved to provide continuous data on depth and temperature for these tagged Bull Trout. Memory storage from these tags was depleted within a few months providing data only during the fall and winter period. Tags were primarily in shallow water (<2 m) with brief detections in deeper water (>5 m) typically for less than 30 min intervals. Temperature showed more variation than depth, but this variable also changes seasonally during these recording periods from warm summertime temperatures in August to cold wintertime temperatures in January and February (Table 1). Interestingly, these data indicate that Bull Trout are utilizing shallow habitats for extended time periods and only briefly
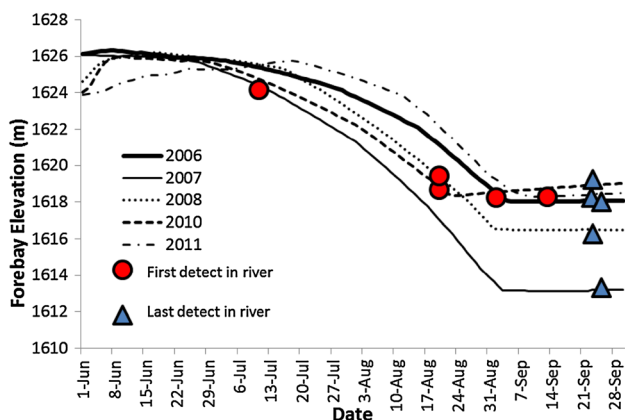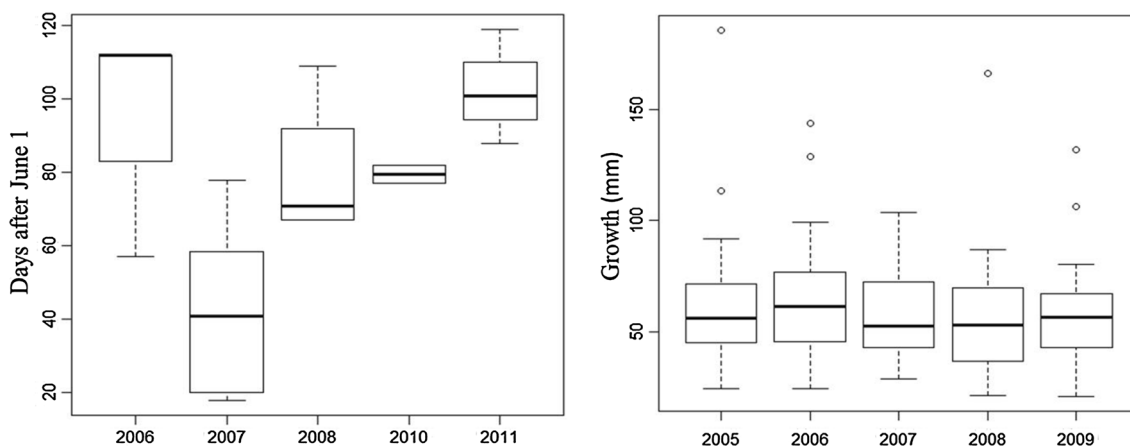
Fig. 5 Number of days after June 1 of first detection (upstream migration) in the upper Deadwood River tributaries by year (*left diagram*) and annual growth by year (mm total length) for Bull Trout collected upstream from Deadwood Dam (*right diagram*). Migration data were not collected during 2009

Table 1 Data summary from archival tags showing start and end date of logging, depth (m) and temperature (°C) (range, average and standard deviation)

Tag	Start	End	Depth (m)			Temp (°C)		
			Range	Avg	SD	Range	Avg	SD
148.420 code 23	8/23/2011	1/19/12	0–21.5	1.1	1.1	0–20.7	8.2	4.1
148.640 code 3	8/23/2011	10/27/2011	0–16.6	0.6	1.2	3.1–19.4	4.2	10.6
148.420 code 5	8/18/2011	2/8/2012	0–45	1.1	1.4	0–19.8	7.5	4.2

All tags recorded in 15 min intervals. Note that the period from mid-August to mid-September may be recording tributary habitat during spawning

utilizing the deeper habitats. The archival tags document individual Bull Trout mostly reared at temperatures ≤15 °C. Yet, the archive tags also indicate that individual Bull Trout were present for hours to days in high water temperatures ranging from 17 to 20.7 °C. Bull Trout spent most of the time at shallower water depths (<2 m) in the littoral zone.

During the 6 year study, 29 tags (51%) were lost from tag expulsion and mortality, ranging from 12.5% in 2011 to 66.7% in 2007. When considering all years in the study, % tag loss was not significantly related to the % exceedance values of the annual reservoir inflow (p=0.11, R^2=0.50); however, when 2010 was removed due to altered late season water operations, the correlation was significant (p=0.03, R^2=0.84). Collectively, the migration and growth data showed that Bull Trout remained in the reservoir for significantly more days during the summer and fall months when climatic conditions were average to wet. However, leaving the reservoir for upstream tributaries did not significantly alter annual growth. Bull Trout rearing in the reservoir during the summer and early fall months did not seek the cooler, deep water.

Model based prediction of Bull Trout habitat

The changes in the annual values within the two Bull Trout habitats (optimal and suitable) and between the seven simulations (validation period and six scenarios) ranged from 0.9 to 21.5% of the lake total volume with significant temporal redistribution (Fig. 6). The temporal pattern of habitat condition was similar for optimal and suitable habitat. Changes in the fish habitats can be seen early in the season (January through March) due to DO values less than 6 mg L^{-1} in the reservoir hypolimnion (~2–25% reduction). As the season progresses, the water surface elevation increases due to increased inflows from snow melt, the water column stratification develops as air temperature increases. During this time, percent available habitat for Bull Trout increases to a maximum in June. Available habitat declines when drawdown commences in June or July. During June, the lake volume habitats varied from 68% for the dry and high outflow scenario to 98% for the wet and average and low flow scenarios. The maximum values expanded by 1 week in the suitable habitat (Fig. 6b). From July to late September the increase in water temperature, reservoir drawdown (completed in September) and depletion of hypolimnetic dissolved oxygen result in a dramatic reduction of available suitable habitat (shaded area in Fig. 6b). For the optimal habitat, such reduction started 1 week earlier and expanded until early October (shaded area in Fig. 6a). The validation year and dry and average year scenarios with both outflow conditions resulted in a marked loss of habitat for Bull Trout (~3.0–8.7 and 3.1–9.2% of the lake total volume for the optimal and suitable habitats respectively). The duration of the period with no available suitable habitat extended from late August to the beginning of October for the dry year with the high outflow condition and lasted for about 1–2 weeks in mid-September for the other scenarios. The validation year did not depict zero suitable habitat (Fig. 6b). The period of no available optimal habitat extended from mid-August to early October for the dry year with the high outflow condition and lasted for about 2–4 weeks from early September to early October for the other scenarios and validation year. The wet scenarios showed about 4 days exposure to sudden optimal habitat change (~17% reduction) (Fig. 6a). After this period, both habitats increase during the loss of thermal stratification and the reaeration of the water column followed with minimal habitat changes.

The comparison of both predicted Bull Trout habitats across the simulated operational scenarios and validation year shows that both habitats experienced substantial changes over time during July and August (Fig. 6). In the dry and average hydrologic scenarios both habitats are lost during summer and early fall period (being shorter for the suitable habitat) when water temperatures and reservoir drawdown are greatest. The wetter climatic scenarios indicate a smaller effect of water operations on Bull Trout habitat. The prediction of suitable Bull Trout habitat (≤18 °C and 6 mg L^{-1} DO) coincided closely with the empirical Bull Trout migration data collected during the study where Bull Trout migrated in mid-July during dry years, mid-August during average years and remain in the reservoir during the entire summer during the wet hydrologic conditions. These data indicate that Bull Trout left the reservoir when the suitable habitat was reduced to 25–30% in relation to the total volume of the reservoir.

Fig. 6 Comparison of the lake volume habitats for Bull Trout normalized by the total lake volume (full pool surface elevation = 1627 m) in percent (%) based on simulated water temperature and dissolved oxygen values for the validation period and six scenarios. **a** Optimal habitat was defined as ≤15 °C and ≥6 mg L^{-1} DO. **b** Suitable habitat was defined as ≤18 °C and DO ≥ 6 mg L^{-1}. The annual total (January–December) and habitat reduction period (*shaded area*) of habitat values are indicated in parentheses as percent (%) of the lake volume. *Vertical dashed lines* in **b** indicates the observed migration days
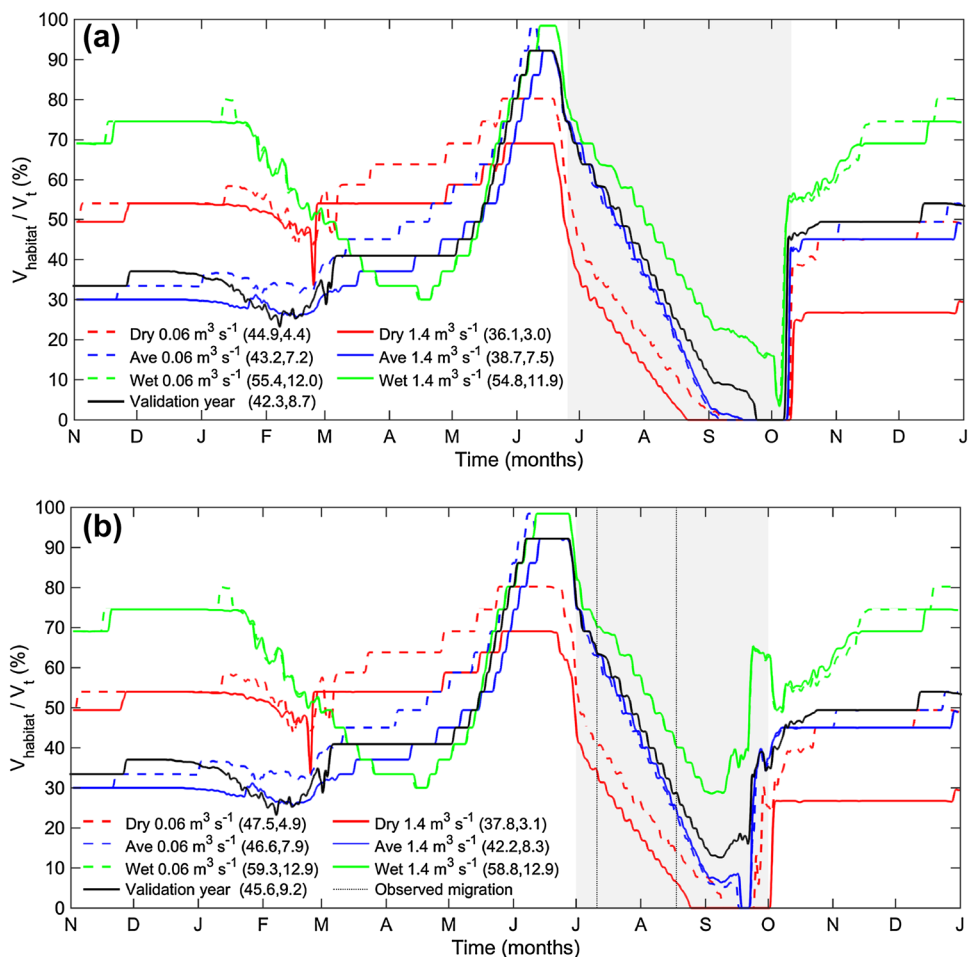
Discussion

The ELCOM-CAEDYM model revealed that lower reservoir outflows (0.06 m^3 s^{-1}) during the fall and winter seasons resulted in higher reservoir elevations and cooler water temperatures during the years with dry and average climatic conditions. Wet climatic conditions also resulted in colder water temperatures in the reservoir and higher reservoir elevations. However, the minimum stream flows during the fall and winter months exceed the current minimum stream flow of 1.4 m^3 s^{-1} during the wetter years. Therefore, water operations during wetter conditions are focusing on flood control and managing reservoir levels near full pool. Bull Trout utilized the reservoir habitat longer when reservoir surface elevations were higher and water temperatures cooler. Predictions of suitable Bull Trout habitat coincided with observed migration out of the reservoir at 25–30% of the total reservoir volume during the dry and average hydrologic conditions. During wet hydrologic conditions, the volume of predicted suitable Bull Trout habitat is greater than 30% and during 2011, a wetter than average year, Bull Trout remained in the reservoir all year.

The ELCOM-CAEDYM model identified the combined effects of expected climatic conditions and various water management options that coincided with predicted Bull Trout habitat. The model was more successful characterizing the spatial and temporal effects to physical, chemical and primary production variables, and less accurate predicting the effects to higher trophic levels (Reclamation 2016). Reduced DO concentrations in the hypolimnion occur naturally in lentic environments that exhibit seasonal thermal stratification. Although the low DO concentrations persisted for longer during the scenarios that had either wet climatic conditions or low reservoir outflow (0.06 m^3 s^{-1}), the cooler water temperatures and higher reservoir elevations provide more benefits to Bull Trout and the reservoir ecosystem.

Bull Trout migration and behavior generally followed water year conditions with the driest year, 2007, resulting in significantly earlier outmigration from the reservoir and higher rates of tag loss and suspected mortality. Bull Trout seasonally migrate into tributaries from the reservoir or lake either due to inhospitable environmental conditions in the reservoir or for spawning migration or both (Fraley

and Shepard 1989; Muhlfeld and Marotz 2005; Hogan and; Scarnecchia 2006; Watry and Scarnecchia 2008; Muhlfeld et al. 2011; Paragamian and Walters 2011). Similarly, Bull Trout remained in the reservoir longer, and some did not migrate into tributaries at all during 2011 when reservoir temperatures were cooler and surface elevations higher. Predicted suitable Bull Trout habitat across hydrologic scenarios showed agreement with Bull Trout migration behavior, where Bull Trout migrated earlier during dry years when the predicted habitat volume declines below ~30% of the total volume in the reservoir. In wet years, the volume of predicted suitable habitat remains above 30% and during the wetter year Bull Trout remained in the reservoir for the entire year. The defined optimal Bull Trout habitat is expected to coincide with optimal water temperatures for growth (Rieman and McIntyre 1995; Selong et al. 2001); however, the model indicates that optimal habitat becomes unavailable as early as mid-August during the dry year scenario with 1.4 m^3 s^{-1} outflow and between early September and early October for the other scenarios.

Bull Trout presence may not be a good indicator of habitat condition, because Bull Trout can survive in water temperatures that exceed the preferred temperature range. Although Bull Trout are thought to prefer temperatures 12–15 °C, Bull Trout have been shown to rear in water temperatures exceeding 20 °C for extended time periods without seeking cold/cool water refugia (Howell et al. 2010). Similarly, Lake Trout have been found to utilize a wide range of summertime water temperatures and are more strongly associated with dissolved oxygen concentrations ≥6 mg L^{-1} and prey distribution (Sellers et al. 1998). Temperature studies in the lab indicate that adult Bull Trout can withstand temperatures as high as 20 °C for up to 60 days (Selong et al. 2001). Yet, Selong et al. (2001) found that at lower water temperatures Bull Trout were evenly spaced in the water column and associated with the bottom, but at higher water temperatures (≥20 °C) Bull Trout swam near the surface and fed little.

Shifts in habitat and prey may indicate a stressed condition where Bull Trout do not have the energy reserves to pursue higher quality prey or are rearing in habitat where these prey are more available, such as the tributary inflows. The archival tags indicated that Bull Trout were typically utilizing the shallower reservoir habitat (≤2 m depth). Water temperatures in the epilimnion during the summer will regularly exceed 18 °C (as also described for Lake Billy Chinook in Beauchamp and Van Tassell 2001); however we would expect Bull Trout to vertically migrate to maintain optimal thermal conditions. However, the optimal habitat in Deadwood Reservoir is not available during the summer/fall months (exact timing dependent on water year conditions and water operations). In Deadwood Reservoir, maximum water temperatures typically reach 21 °C, but

Bull Trout appear to utilize the shallow near-shore areas of the reservoir. Additionally, Bull Trout in Deadwood Reservoir appeared to consume higher proportions of cottus and cyprinid fishes and little to no salmonids despite the availability of Rainbow Trout, other Bull Trout and Kokanee Salmon (Reclamation 2016). Summertime diets of Bull Trout in other systems typically include Rainbow and Bull Trout (Beauchamp and Van Tassell 2001; Guy et al. 2011). Annual estimates of trophic production in Deadwood Reservoir indicate that food base is not currently limiting population size (Reclamation 2016). Forage fish are abundant in the reservoir and Bull Trout growth rates are similar to other adfluvial populations (Reclamation 2016).

In terms of reservoir operations, the trophic analyses predict production of Bull Trout to be 15% higher for the 0.06 m^3 s^{-1} fall and winter stream flow scenarios than for the 1.4 m^3 s^{-1} scenario during dry years. While during average years, there was little effect of water operations on predicted production of Bull Trout (Reclamation 2016). Therefore, the lower fall and winter reservoir outflows benefit Bull Trout by boosting trophic production. High water temperatures in the reservoir and the river downstream from the dam are a concern for Bull Trout and other salmonids. Reservoir conditions create a boundary condition that directly determines the physical, chemical and biological composition of river habitat downstream from the dam. Analyses of the river downstream from the dam indicate additional benefits in the river at the 0.06 m^3 s^{-1} post-irrigation outflows compared to the 1.4 m^3 s^{-1} outflow. The greatest benefit downstream from the dam was water temperatures closer to natural, seasonal temperatures while the habitat can support greater biomass for fish and invertebrates (Reclamation 2016). The operational analyses in the river downstream from the dam similarly will not change during wetter climatic conditions due to outflows that greatly exceed 1.4 m^3 s^{-1} during the winter and spring months.

Generally, Bull Trout tag loss was within the range of other radio-telemetry studies (such as Al Chokhachy and Budy 2008). Percent tag loss was significantly correlated with the trend in climatic conditions excluding 2010 when the late summer water operations were altered due to construction projects at the dam. This relationship indicates that during dry years Bull Trout have higher pre or post-spawning mortality which could be due to a combination of factors such as increased environmental stress from higher water temperatures, reduced fish conditions from loss of habitat quality, disease or loss of prey, increased predation, or a combination of these factors. Carcass recovery is needed to determine the cause of mortality, and this is difficult in deeper water reservoir environments or when scavengers have access to mortalities. Yet, the 2010 data indicate that the tag loss can be reduced by altering late

summer water operations during dry years. During 2010, the outflow from the dam was reduced to <0.06 m³ s⁻¹ between August 24 and October 7 which increased the end of irrigation season reservoir surface elevation similar to 2011 when tag loss was the lowest (1618.4 and 1618.3 m in August 2010 and 2011, respectively). The August 2007 reservoir surface elevation was 5 m lower when tag loss was the highest during this study. The combined dry year effects of migration out of the reservoir due to loss of suitable habitat and the resulting mortality translates into a substantial demographic impact to the threatened Bull Trout population in the reservoir. If climate trends create longer and more frequent extreme climatic events, then we would expect to have longer cycles of drought that could cause a large decline in the Bull Trout population in the reservoir.

Conclusions

Balancing reservoir and downstream habitat requirements is challenging for water managers. Our analyses indicate that physical and chemical characteristics of the reservoir can alter Bull Trout habitat, migration and behavior. Reduced fall and winter dam releases will improve the available habitat for Bull Trout in the reservoir by extending the period with suitable habitat by about 20 days during the dry hydrologic conditions. Additionally, reduced outflow during the fall season will increase the water surface elevation for Bull Trout returning to the reservoir from the spawning migration which can reduce mortality during this time.

Compliance with ethical standards

Ethical approval All applicable federal guidelines for the care and use of Bull Trout in this study were followed in compliance with the Endangered Species Act permit.

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