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Reservoir-derived subsidies provide a potential management opportunity for novel river ecosystems

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A B S T R A C T

Aquatic ecosystems world-wide are being irreversibly altered, suggesting that new and innovative management strategies are necessary to improve ecosystem function and sustainability. In river ecosystems degraded by dams environmental flows and selective withdrawal (SWD) infrastructure have been used to improve habitat for native species. Yet, few studies have quantified nutrient and food web export subsidies from upstream reservoirs, despite their potential to subsidize downstream riverine food webs. We sampled nutrient, phytoplankton, and zooplankton concentrations in outflows from the Shasta-Keswick reservoir complex in Northern California over a 12-month period to understand how SWD operation and internal reservoir conditions interact to influence subsidies to the Sacramento River. We found that nutrients, phytoplankton, and zooplankton were continuously exported from Shasta Reservoir to the Sacramento River and that gate operations at Shasta Dam were important in controlling exports. Further, our results indicate that gate operations and water-export depth strongly correlated with zooplankton community exports, whereas internal reservoir conditions (mixing and residence time) controlled concentrations of exported zooplankton biomass and chlorophyll *a*. These results demonstrate that reservoirs can be an important source of nutrient and food web subsidies and that selective withdrawal infrastructure may provide a valuable management tool to control ecosystem-level productivity downstream of dams.

1. Introduction

As a result of sustained anthropogenic disturbances including habitat homogenization, climate change, and invasive species colonization, resource managers have entered an era of irreversibly altered ecosystems (Ellis and Ramankutty, 2008; Hobbs et al., 2009; Masson-Delmotte et al., 2018; Bergstrom et al., 2021). In response, management concepts and frameworks that integrate both historical and contemporary states, as well as truly novel ecosystems, have been proposed (Rosenzweig, 2003; Hoegh-Guldberg et al., 2008; Hobbs et al., 2009; Bowman et al., 2017). Although consensus has been difficult to achieve, these concepts suggest that resource managers must not only consider the current state of an ecosystem, but innovative ways to manage novel habitats in an ever-changing future. Within ecosystems where habitat has been heavily modified (e.g., dammed rivers), changes in infrastructure operations

may benefit native species. For instance, dam releases, qualified as environmental flows, have been used to benefit native organisms and reinstate ecosystem processes, while meeting societal needs such as electrical power generation and water exports (Kiernan et al., 2012; Chen and Olden, 2017; Poff and Olden, 2017; Sabo et al., 2017).

Dams significantly alter ecosystem processes in numerous ways including eliminating off-channel habitat inundation, promoting channelization and benthic homogenization, increasing the spread of invasive species, impeding movement of native species, truncating sediment transport, shifting temperature, nutrient and hydrologic residence time regimes, and reducing downstream productivity (Ward and Stanford, 1995; Yoshiyama et al., 1998; Friedl and Wüest, 2002; Kondolf et al., 2014; Steel et al., 2018; Dudgeon, 2019; Aspin et al., 2020, Hu et al., 2020). Considering the ubiquity and permanence of large dams in the United States, as well as the growth of large dam construction globally,

understanding how operations can be used to ameliorate such adverse effects and benefit degraded river ecosystems is of fundamental interest. For example, in hydrologically-altered ecosystems, reinstating functional flows that mimic important components of the natural flow regime has been shown to improve survival of native species and reduce the presence of non-native fishes (Kiernan et al., 2012; Yarnell et al., 2020; Stein et al., 2021). Similarly, cold water releases have been used to protect migrating and rearing salmonids downstream of dams and may be an important strategy for protecting native coldwater species under future climate projections (Yates et al., 2008; Benjankar et al., 2018; Zarri et al., 2019). While discharge, temperature and other physical conditions have been the focus of many dam operation studies (see Olden and Naiman, 2010; Kondolf et al., 2014; Yarnell et al., 2020), there is a relative paucity of empirical data quantifying nutrient and food web subsidies exported from reservoirs to downstream ecosystems.

Dams alter downstream productivity by capturing and retaining nutrients or by processing and exporting excess nutrients; both have the potential to alter downstream ecological processes and biological productivity (Ellis and Jones, 2013; Maavara et al., 2015; Aspin et al., 2020, Hu et al., 2020). Sabo et al. (2017) hypothesized that reservoir exports, such as dissolved nutrients (e.g., NO_3^- and PO_4^{3-}), may enhance downstream productivity when releases are timed to periods of upstream nutrient mobilization. Similarly, Chen, Shi, *et al.* (2020) found that reservoirs export elevated levels of nutrients associated with redox conditions in hypoxic sediments and within the hypolimnion. Reservoirs also have the potential to export food web subsidies, such as phytoplankton and zooplankton, that may positively affect downstream consumers or provide additional nutrients to primary producers (Lieberman et al., 2001; Warnken and Santschi, 2004; Chang et al., 2008; Powers et al., 2014). Quantifying reservoir exports and understanding their potential to subsidize downstream river ecosystems is particularly critical for native coldwater fishes in severely altered ecosystems, where productivity may be managed to improve rearing habitat and offset changes in water temperature associated with climate change (Lusardi et al., 2020).

To control reservoir and water release temperatures selective withdrawal devices (SWDs) have been installed at dams throughout the United States (Cassidy, 1989). In addition to temperature, management of SWDs can influence discharge as well as water quality in downstream ecosystems by drawing water from variable elevations (e.g., epilimnion versus hypolimnion) within a reservoir (Christenson et al., 1996; Andrea et al., 2014; Azadi et al., 2021; Stein et al., 2021). SWD installation has been shown to alter nutrient and carbon export from reservoirs to downstream tailwaters (Lieberman et al., 2001). Further, because these devices extract water from different depths within the reservoir, they have the potential to export varying types and quantities of reservoir-derived subsidies due to vertical heterogeneity in reservoir biogeochemical processes and resources (Lieberman and Horn, 1998; Lieberman et al., 2001; Bartholow et al., 2001). Despite this apparent management utility and flexibility, few have examined the potential to export nutrients and food web resources to downstream lotic environments.

Here we examine nutrient, basal carbon, and zooplankton exports from a selective water withdrawal system in northern California. Specifically, our research objectives were to (i) quantify exported nutrients, basal carbon sources, and zooplankton abundance and community composition, (ii) determine which reservoir conditions and dam operations regulate the quantity and quality of nutrient and food web subsidies, and (iii) relate this information to potential management options to improve downstream aquatic ecosystem productivity. Ultimately, this knowledge may be used to optimize exports and identify research areas critical to improving subsidy management from the built environment.

2. Methods

2.1. Study site

The Sacramento River system is the largest watershed in California, covering approximately 68,634 km^2, with an average flow of 793 m^3 s^{-1} near the city of Sacramento. It is one of the most regulated rivers in the world, with large dams impounding the main river and almost all its major tributaries (Shelton, 1995). Mainstem flows in the upper watershed are regulated by Shasta Dam and its afterbay, Keswick Afterbay (Fig. 1). Shasta Dam is a concrete structure measuring 183.5 m in height and spans 1054.6 m in length (USBR, U. S. B. of R, 2022a). The reservoir stores 5.6×10^9 m^3 of water at full pool and drains an area of 17,262 km^2, making it California's largest reservoir. Outflows from Shasta Dam flow directly into Keswick Afterbay. Keswick Dam is a concrete structure measuring 47.8 m in height and spanning 318.8 m in length, which forms the Keswick Afterbay, capable of storing 2.9×10^7 m^3 at full pool (USBR, U. S. B. of R, 2022b). Shasta Dam was completed in 1945, while Keswick Dam was completed in 1950. Both dams are part of the Central Valley Project (CVP), which stores and delivers water from the state's northern and eastern mountain watersheds to farms and cities along the Central Valley and Southern California (Hanak et al., 2011).

The Sacramento River historically sustained high abundances of native fishes, including steelhead (*Oncorhynchus mykiss*) and four distinct runs of Chinook salmon (*Oncorhynchus tsawytscha*) (Moyle et al., 2017). The construction of Shasta and Keswick dams precipitated a strong decline in native fishes by modifying the natural hydrograph, greatly reducing the extent and frequency of off-channel inundation, and altering flow cues used by native species (e.g., del Rosario et al., 2013). Furthermore, the dams created a physical barrier that extirpated migratory salmonid species from upstream habitats and historical spawning grounds at cold, spring-fed systems (e.g., McCloud River) (USBR, U. S. B. of R, 2015). As such, several salmon runs are restricted to marginal spawning locations downstream of Keswick Dam, relying on flow and temperature releases from Shasta Dam (Yoshiyama et al., 1998). This is especially true for federally endangered winter-run Chinook salmon that rely on temperature control management from Shasta Dam to maintain appropriate egg incubation temperatures below Keswick Dam. To maintain water exports and power generation objectives while providing coldwater storage and discharge for federally endangered spawning winter-run Chinook salmon, Shasta Dam was retrofitted with a SWD, also referred to as a Temperature Control Device (TCD), in 1997 (Lieberman and Horn, 1998). The SWD consists of top, middle, and bottom release gates as well as low elevation side release gate (Supplemental Figure 1). The SWD releases surface water during November–April to conserve cold hypolimnetic water, enabling managers to release deep, cold water during the hot summer and early fall months (e. g., May–October) to provide suitable temperatures for spawning winter-run Chinook salmon (Supplemental Figure 1). Our study began in March 2018 and concluded February 2019, straddling a below normal and above average run-off water years for the Sacramento River system (DWR, 2019).

2.2. Nutrients and basal carbon

We collected monthly water grab samples from below Keswick Afterbay (0.05 rkm) from March 12th, 2018 to February 20th, 2019. Each sample was taken ~15 cm below the water surface and stored on ice in the field and then at 4 °C in the laboratory, prior to analysis. We sampled suspended chlorophyll *a* by filtering 1 L of river water through a pre-combusted glass-fiber filter (GF/F). Filters were placed on ice in the field and then stored at −20 °C in the laboratory until analysis. Water samples were analyzed for a suite of parameters including, total nitrogen (TN), $NO_2^- + NO_3^-$ [NO3–N], ammonium (NH_4^+), total phosphorus (TP), soluble reactive PO_4^{3-} [SRP] and DOC. Dissolved constituents were analyzed after filtering through a 0.2 μm polycarbonate membrane
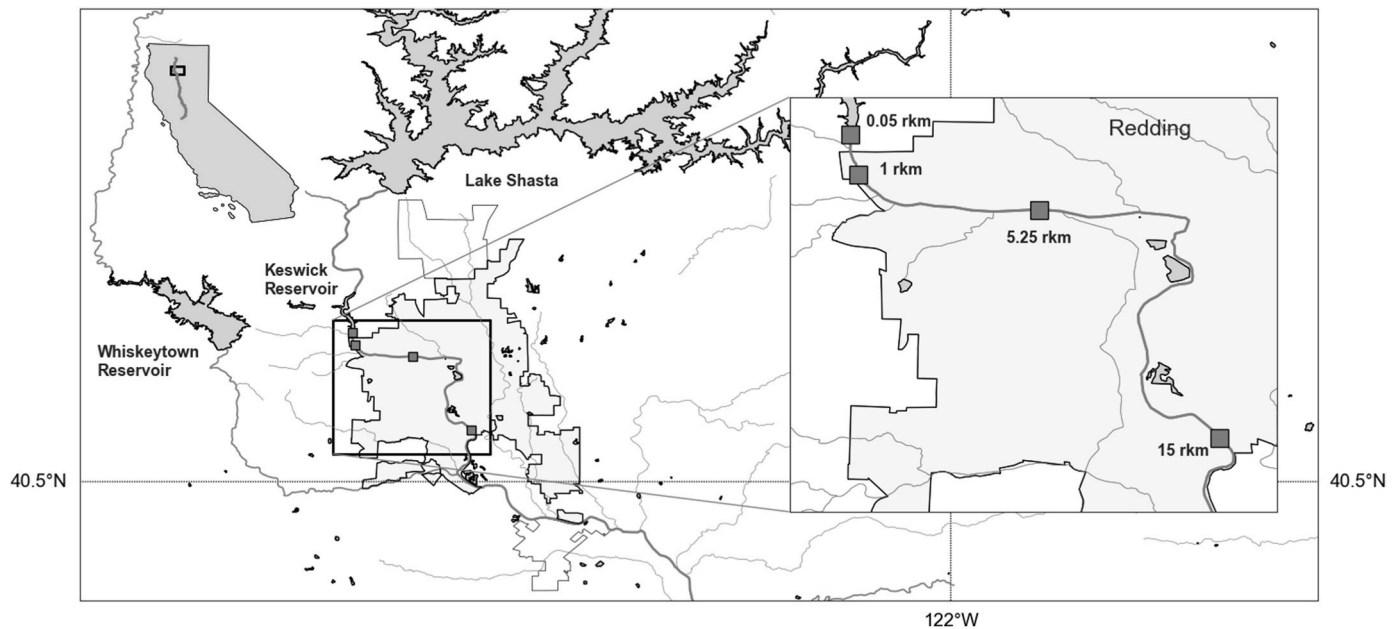
Fig. 1. Sampling site locations below Keswick Afterbay (rkm = river kilometer downstream from Keswick dam).

filter. Chlorophyll *a* concentrations were measured using APHA standard techniques (LOD ~0.1 μg L^{-1}; Clesceri et al., 1998). SRP was measured using the ammonium molybdate spectrophotometric method (LOD ~0.005 mg L^{-1}) and NO$_3$–N using vanadium chloride spectrophotometric method (LOD = 0.01 mg L^{-1}). DOC concentration was determined by persulfate digestion on a Dohrmann UV-enhanced persulfate TOC analyzer (Phoenix 8000, Teledyne Tekmar, Mason, Ohio; LOD ~ 0.1 mg L^{-1}). Laboratory quality assurance and quality control included implementation of Surface Water Ambient Monitoring Program (SWAMP) compatible standard laboratory procedures including replicates, spikes, reference materials, setting of control limits, criteria for rejection, and data validation methods (Puckett, 2002).

2.3. Zooplankton

Zooplankton samples were collected monthly between March 12th, 2018 and February 20th, 2019 from below Keswick Afterbay at 0.05, 1, 5.25, and 15 rkm downstream. Samples were collected between 11:00 and 13:00 by towing a 30 cm, 150 μm mesh zooplankton net via boat for 1 min ~15 cm below the water surface. All samples were placed in Whirlpak™ bags (Nasco, USA) and preserved in 95% ethyl alcohol. In the laboratory, samples were rinsed through a 150-μm mesh screen, emptied into a beaker, and sub-sampled with a 1–2 mL large bore pipette. Zooplankton species were counted until greater than 200 individuals were enumerated. All invertebrates were identified to the lowest taxonomic level possible using Thorp and Covich (2009) and Hanak et al. (2011). However, because of the difficulties in identifying copepodids and nauplii, family level assignment of Copepods was used, except for Acanthocyclops sp. and Psuedodiaptomus sp., which were common in our samples. Terrestrial invertebrates and macroinvertebrates were rare and were not included in final counts. Rotifers were excluded from all analyses due to the use of 150-μm mesh that does not accurately sample smaller rotifers.

To standardize zooplankton abundance estimates, we quantified the water volume sampled using a General Oceanics flow meter (Miami, FL, USA). Zooplankton biomass was estimated using dry weight and carbon contents from the literature (Jørgensen et al., 1979; Jeffres et al., 2020), as well as unpublished values from the Kimmerer Lab Group, San Francisco State University. For the purpose of estimating biomass, we assumed that copepodids belonged to the most common calanoid and

cyclopoid species (Psuedodiaptomus sp. and Acanthocyclops sp., respectively) in our samples due to the difficulty of identifying copepodids. Species that could only be identified to family were excluded from biomass analysis; however, these species were not numerically dominant and were typically rare in our samples. Total biomass exported over the 12-month sampling period was estimated by multiplying average daily outflow from Shasta Dam by monthly zooplankton biomass estimates.

2.4. Reservoir stratification and mixing potential

Reservoir stratification and mixing dynamics were explored as a factor potentially influencing export concentrations from Shasta Reservoir. The stability of the reservoir water column and the potential for turbulent mixing was quantified using the square root of the inverse of the Richardson number (denoted as Δ) (Monismith and MacIntyre, 2009). The transformation allows for higher parameter values to represent greater potential for mixing (e.g., fully mixed conditions; weak stratification and stronger winds), while smaller values indicate a stable or stratified water column (e.g., strong summer stratification),

$$\Delta = \sqrt{\frac{1}{Ri}} = \sqrt{\frac{\rho\, C_D u^2}{g \partial \rho / \partial z}} = \sqrt{\frac{\rho\, u_*^2}{g \partial \rho / \partial z}} = \sqrt{\frac{u_*^2}{N^2}}$$

where ρ is the water density (a function of temperature), g is gravitational acceleration (9.81 m s^{-2}), $u_*^2 = C_D u^2$ is the shear velocity in the water, u is the wind velocity measured at 10 m above the water surface, C_D is the drag coefficient computed following Amorocho and DeVries (1980), and N^2 is the Brunt-Väisälä or buoyancy frequency. A higher Brunt-Väisälä frequency indicates stronger stability and stratification, while a lower frequency indicates weaker stability and greater potential for vertical mixing. Moving averages of 5–20 days were considered to capture the required length of mixing events that brings enough nutrients to trigger primary and secondary productivity within the reservoir.

During stratified conditions (i.e., $\Delta \ll 1$), Brunt-Väisälä frequency values, computed for discretized water layers of 0.5 ft width, were used to determine the location of the epilimnion and metalimnion within the water column. Epilimnion depth was defined by identifying the depth at which the highest buoyancy frequency was computed (i.e., greatest temperature-density gradient), while the metalimnion was defined as

the layer between the epilimnion and the depth at which the buoyancy frequency decreased to <0.0005.

Shasta reservoir temperature profiles were provided by the U.S. Bureau of Reclamation, measured weekly throughout stratified conditions (from May to November 2018), biweekly at the onset of stratification (March–April 2018 and 2019), and monthly during fully mixed conditions (December 2018 to February 2019); to depths over 91.5 m using a sonde with a 1 s recording frequency. Daily estimates of temperature profiles were obtained by linear interpolation between available dates (Fig. 2). Wind speeds at 10 m above the water surface were retrieved from the European Center for Medium-Range Weather Forecasts (ECMWF) ERA-5 hourly reanalysis dataset at surface level on a 30

× 30 km grid for the period of interest (Hersbach et al., 2020).

2.5. Data analysis

Spearman's correlation was used to assess relationships between nutrient, phytoplankton, and zooplankton exports and hydrologic/operational conditions in Shasta Reservoir and Keswick Afterbay. Keswick Afterbay conditions included outflow and 1-day average hydraulic retention time (HRT = storage/outflow) (Table 1). Shasta Reservoir hydrologic conditions included water surface elevation at the dam, outflow, 10-day average HRT, 5-day average modified Richardson number, proportional gate operation (proportion of upper, middle, and
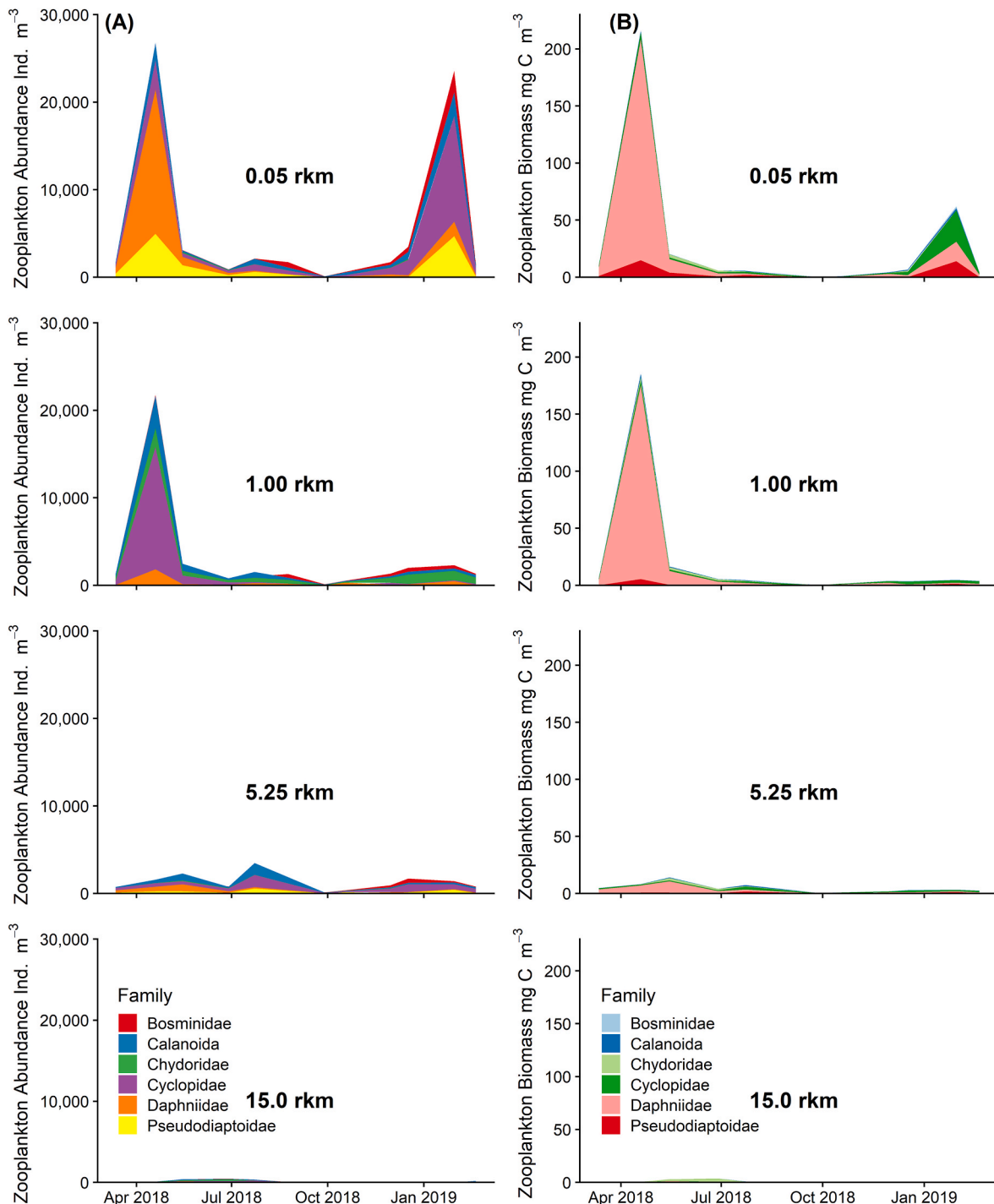

Fig. 2. Stacked plot of zooplankton (A) abundance and (B) biomass by date and distance downstream from Keswick Dam. rkm = river kilometer.

Table 1

Shasta Reservoir and Keswick Afterbay operations and conditions for dates sampled during the March 2018 through February 2019 study period.

	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb
Shasta Dam Daily Average Outflow ($m^3\ s^{-1}$)	84	88	231	281	329	214	189	175	74	77	68	53
Shasta Reservoir 10-day average HRT (days)	566	713	222	151	121	101	102	102	359	330	751	1037
Proportion of top gates in operation	0.62	1.00	0.71	0.4	0.24	0	0	0	0	0	0	0.62
Proportion of middle gates in operation	0.38	0	0.29	0.6	0.63	0.2	0	0	0	0	1	0.38
Proportion of bottom gates in operation	0	0	0	0	0.13	0.8	0.67	0.5	0	1	0	0
Proportion of side gates in operation	0	0	0	0	0	0	0.33	0.5	1	0	0	0
Mean Extraction Depth (m)	11.1	15.9	27.2	22.0	34.0	52.6	62.4	64.0	58.8	44.0	18.6	18.8
5-day average Mixing Coefficient	0.23	0.16	0.13	0.08	0.04	0.05	0.11	0.18	0.13	0.23	0.48	0.44
Keswick Afterbay Daily Average Outflow ($m^3\ s^{-1}$)	89	90	244	343	372	258	214	217	113	115	89	95
Keswick Afterbay 10 average HRT (days)	3.49	3.55	1.23	0.98	0.85	1.16	1.44	1.41	2.56	2.70	3.52	3.10

lower gates in operation during sampling; USBR 2022), and mean release depth. Mean release depth was based on the gates used and relative depth of release from the water surface elevation at Shasta Dam.

We used nMDS of Bray-Curtis dissimilarity to visualize similarities in community composition for monthly zooplankton samples collected at the outlet of Keswick Afterbay. We fitted reservoir data based on significant pairwise Mantel tests and species abundance data to the ordination. This information was used to demonstrate significant relationships between community variation, species abundance, and reservoir conditions. We used pairwise Mantel tests for correlations between zooplankton community similarity exported and Keswick Afterbay conditions/operations, Shasta Reservoir conditions/operations, and water quality measurements. For the pairwise Mantel tests we calculated Bray-Curtis dissimilarity among zooplankton samples and Euclidean distance for reservoir and afterbay operations/conditions. Reservoir and afterbay data were mean centered for better comparison between factors. For each test, significance was assessed at α = 0.10 by a permutation with 10,000 iterations.

All community analyses were conducted in R 3.6.2 (R Core Team, 2019) using *vegan* and (Oksanen et al., 2013). For data sorting and transformation we used the packages *dplyr*, *reshape2*, and *tidyr* (Wickham, 2007; Wickham et al., 2023; Wickham 2021). Visualizations were created using packages *ggplot2*, *ggforce*, and *cowplot* (Wickham, 2011; Wickham and Wickham, 2016; Pedersen, 2019; Wilke et al., 2019).

3. Results

3.1. Zooplankton abundance, biomass and community composition exported

Zooplankton were continuously exported from Shasta Reservoir and through Keswick Afterbay during the sampling year, with spikes in abundance during April 2018 and late January 2019 (Fig. 2). Exported zooplankton included cladocerans (Daphniids, Bosminids, and Chydorids), as well as copepods such as Pseudodiaptoids and Cyclopoids. During the high abundance peak in April 2018, the community largely consisted of Daphniids and Psuedodiaptoids, whereas the late January peak community was primarily composed of Cyclopoid (*Acanthocyclops* sp.) and Psuedodiaptoid copepods. Higher biomass was associated with greater abundances of Daphniids and Psuedodiaptoids, likely due to their larger sizes (Fig. 2). Zooplankton biomass and abundance strongly decreased downstream, with extremely low abundances at 15 rkm. Notably, there was evidence of local production at 5.25 rkm during the late summer. This production coincides with summertime flash board installation for water diversions in that reach that may have created lentic-like conditions conducive to local production or retention of zooplankton.

3.2. Upstream controls

During the sampling period, several stratification stages occurred at
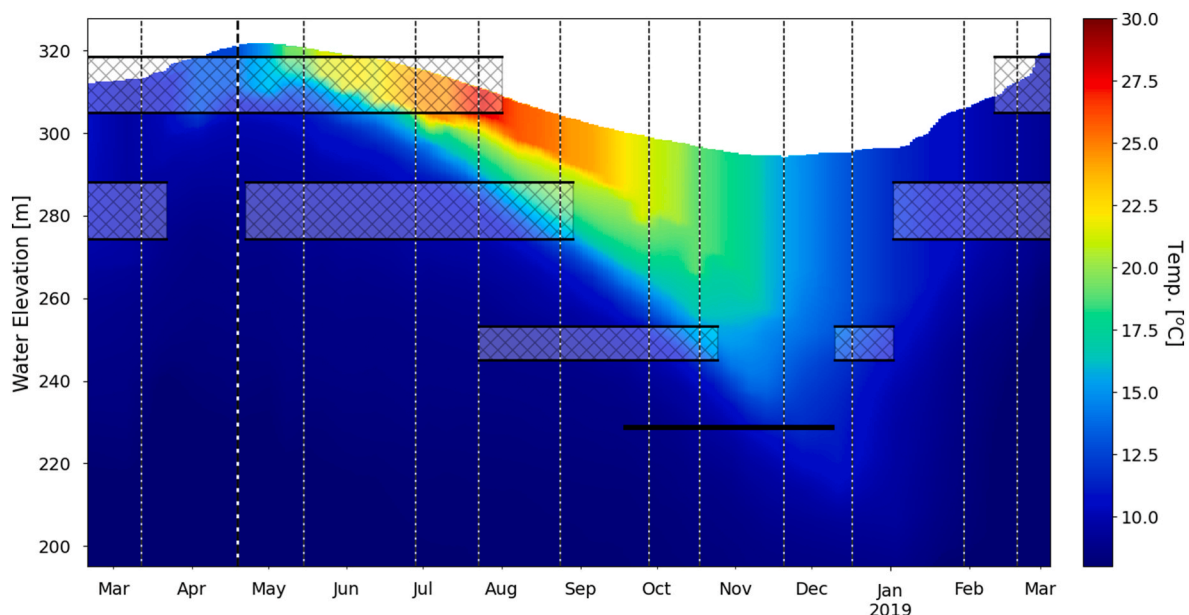
Fig. 3. Temperature profile and water surface elevation (above sea level) at Shasta Dam during the study period. Dashed vertical lines indicate sampling dates. Shaded areas represent Selective Withdrawal Device gate operations; elevation 311 m = top gates, 281 m = middle gates, 249 m = bottom or pressure gates, and 219 m = side gates (USBR 2022).

Shasta Lake (Fig. 3). A fully mixed water column was observed until April 2018 when stratification started developing (ΔT < 5 °C along the water column), reaching stratified conditions by June (ΔT > 15 °C between epilimnetic and hypolimnetic waters), with a ~8 m deep epilimnion and an ~8.5 m thick metalimnion. Stratification continued strengthening during summer reaching surface temperatures >30 °C in August (ΔT > 20 °C), with an epilimnion still around 8.5 m deep, but a much thicker metalimnion (~18 m). September presents the beginning of stratification weakening, with progressively cooler surface temperatures deepening the epilimnion (15 m in mid-Sept to 30 m in mid-Oct) and enhancing mixing with the upper metalimnion, that decreased its thickness progressively. This process continued until similar fully mixed conditions occurred by the end of 2018.

Spearman's correlation between upstream conditions and nutrient, basal carbon, and zooplankton export (Table 2) highlighted the role of reservoir and afterbay conditions/operations on subsidies from Shasta Reservoir. Total phosphorus (TP) export at 0.05 rkm was negatively and significantly associated with water surface elevation at Shasta Dam as well as the proportion of top gates used; bottom side gates and mean release depth were positively and significantly associated with total phosphorus export. Similarly, there were significant negative associations between SRP and 10-day average HRT in Shasta Reservoir, surface water elevation at the dam, and middle gate operations, while bottom (i. e., pressure) gate proportion and Keswick outflow were positively, but not significantly associated with SRP concentrations. The strongest predictor of both TP and SRP export was mean release depth from the water surface, with deeper extractions (generally hypolimnetic or deep metalimnetic waters; Fig. 3) being positively and significantly correlated with phosphorus concentrations. Total nitrogen had no significant association with upstream reservoir and afterbay conditions, however, there was a strong negative association between water elevation at Shasta Dam and total nitrogen measured below Keswick Afterbay. Nitrate concentrations were negatively associated with water elevation at Shasta Dam as well as SWD top gate operation, while pressure gate operations (extraction depths greater than 70 m) were positively associated with nitrate export (hypolimnetic water releases; Fig. 3). Ammonium export was positively and significantly associated with Keswick outflows.

DOC was positively associated with Keswick outflows, yet negatively associated with HRT at Keswick Afterbay. Chlorophyll *a* exported was negatively associated with outflows from Shasta and Keswick, but positively associated with HRT in both locations. Similarly, chlorophyll *a* was positively associated with Shasta Reservoir mixing potential, indicating the possible role of mixing on phytoplankton production. Zooplankton abundance was not significantly associated with reservoir and afterbay conditions/operations; however, zooplankton biomass was significantly associated with both Shasta and Keswick hydraulic conditions. Biomass was negatively associated with outflows from both dams. Further, biomass was positively associated with 10-day average HRT and modified Richardson number following a similar trend as chlorophyll *a* concentration. The association of chlorophyll *a* and zooplankton export with modified Richardson number is suggestive of the role of stratification and mixing on food web exports, where nutrient availability in warmer euphotic waters can lead to bloom conditions that may facilitate greater export of these resources.

Correlation between species abundance and nMDS values demonstrated that *Daphnia* sp., Pseudodiaptomid calanoids, *Acanthocyclops* sp., *Bosmina* sp. and Calanoid and Cyclopoid copepod abundances were significant (α = 0.10) drivers of community differences between months sampled (Fig. 4). Pairwise Mantel tests showed that community composition was not significantly correlated with hydraulic conditions within Keswick Afterbay (Pairwise Mantel, r = −0.025, p = 0.55) or water quality conditions at the Keswick Afterbay outlet (Pairwise Mantel, r = −0.04, p = 0.52; Table 3). However, zooplankton community composition was significantly correlated with Shasta Reservoir hydraulic conditions and dam operations (Pairwise Mantel, r = 0.22, p = 0.056). Greater proportional releases from top gates and Shasta Reservoir elevation were positively associated with communities with high abundances and biomass of *Daphnia pulex* and Pseudodiaptomid calanoids, while lower gate operations were associated with communities with high abundances of *Bosmina* sp. and *Acanthocyclops* sp. (Fig. 4). Pairwise Mantel tests and fitted vectors indicate that gate operations, reservoir elevation, and release depth were strong determinants of zooplankton community export.

4. Discussion

This study demonstrates that large dam infrastructure can export and

Table 2

Spearman's rank correlation between exports below Keswick Dam (0.05 rkm) and hydraulic/operation conditions in Keswick Afterbay and Shasta Reservoir. Bold P < 0.10, *P < 0.01.

	Keswick Outflow	Keswick HRT	Shasta Outflow	Shasta HRT	Shasta Elevation	Top gate Proportion	Middle gate Proportion	Pressure gate Proportion	Side gate Proportion	Richardson Number	Mean Release Depth
Nutrients											
Total Phosphorus (mg L^{-1})	0.04	−0.06	−0.06	−0.23	**−0.64**	**−0.69**	−0.37	0.31	**0.64**	−0.09	**0.60**
SRP (mg L^{-1})	0.38	−0.38	0.21	**−0.50**	**−0.50***	−0.38	**−0.52**	0.48	0.57	−0.33	**0.73***
Total Nitrogen (mg L^{-1})	0.25	−0.03	−0.01	−0.29	−0.43	−0.24	−0.34	0.25	0.34	−0.29	0.37
NO$_3$–N (mg L^{-1})	−0.02	−0.02	−0.41	−0.15	**−0.71***	**−0.55**	−0.34	0.47	0.26	0.15	0.50
NH$_4$–N (mg L^{-1})	**0.52**	−0.41	0.34	−0.26	0.10	0.14	−0.08	0.35	0.33	−0.28	0.18
Basal Carbon											
DOC (mg L^{-1})	**0.52**	**−0.55**	0.20	−0.27	−0.24	−0.11	−0.12	−0.07	0.47	−0.43	0.48
Chlorophyll-a (µg L^{-1})	**−0.79**	**0.84**	**−0.68**	**0.71**	0.01	0.25	−0.17	−0.21	−0.20	**0.73**	**−0.52**
Zooplankton											
Abundance (ind. m^{-3})	−0.32	0.39	−0.20	0.48	0.27	0.23	0.11	−0.20	−0.46	0.20	−0.45
Biomass (µg m^{-3})	**−0.78**	**0.70**	**−0.82***	**0.72**	−0.13	0.15	−0.09	**−0.59**	0.30	**0.78***	−0.27

HRT: Hydraulic Residence Time; SRP: Soluble Reactive Phosphorus; DOC: Dissolved Organic Carbon.
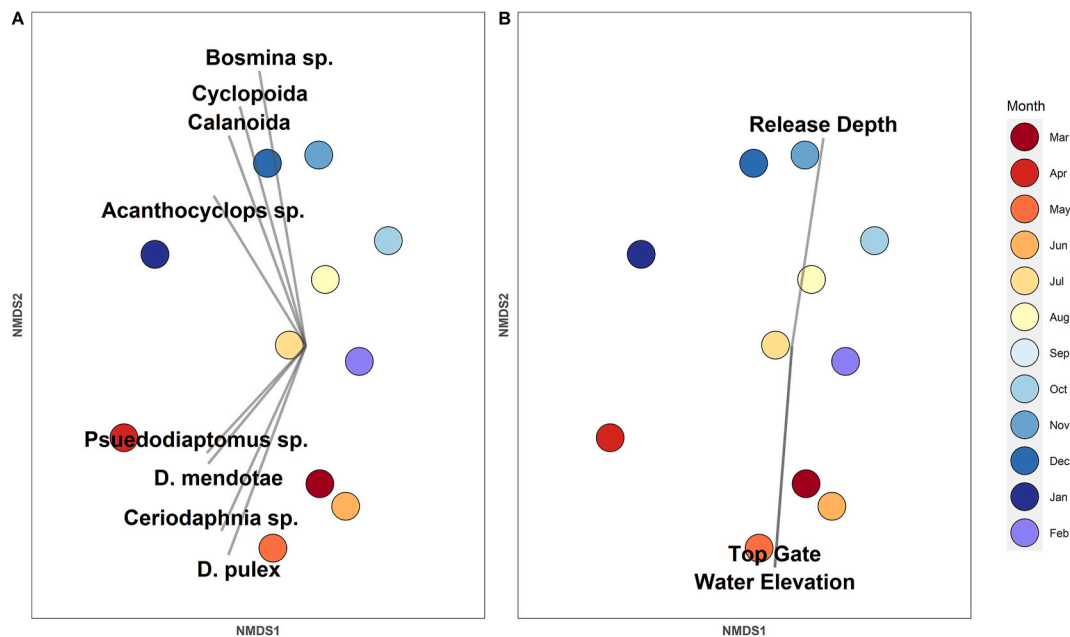
Fig. 4. nMDS plots of monthly zooplankton Bray-Curtis dissimilarity, (A) fitted vectors of zooplankton species abundance and (B) Shasta Reservoir dam operations and water elevation. Length of vectors is proportional to the strength of the association, while direction indicates correlation degree between community similarity. Only vectors significant at $\alpha = 0.10$ are shown, stress $= 0.03$.

Table 3
Nutrient concentrations sampled below Keswick Dam at 0.05 rkm.

Date	TN (mg L^{-1})	NO$_3$–N (mg L^{-1})	NH$_4$–N (mg L^{-1})	TP (mg L^{-1})	SRP (mg L^{-1})	DOC (mg L^{-1})	Chlorophyll-a (µg L^{-1})
3/12/2018	0.16	0.09	<0.01	0.017	0.014	1.0	0.2
4/19/2018	0.14	0.06	<0.01	0.021	0.014	1.1	0.1
5/15/2018	0.16	0.09	0.02	0.021	0.020	1.2	0.4
6/28/2018	0.18	0.09	0.02	0.023	<0.005	1.4	0.3
7/23/2018	0.16	0.08	<0.01	0.027	0.021	1.3	0.3
8/24/2018	0.23	0.15	0.01	0.020	0.020	1.2	0.3
9/28/2018	0.36	0.12	0.01	0.047	0.015	1.2	0.4
10/18/2018	0.15	0.11	<0.01	0.035	0.035	1.3	0.5
11/30/2018	0.19	0.12	<0.01	0.067	0.025	1.7	0.7
12/17/2018	0.17	0.13	0.03	0.038	0.020	1.1	1.1
1/30/2019	0.13	0.09	<0.01	0.036	0.010	0.9	1.5
2/20/2019	0.26	0.13	0.02	0.014	0.011	1.3	1.2

TN = total nitrogen, TP = total phosphorus, SRP = soluble reactive phosphorus, DOC = dissolved organic carbon.

potentially control nutrient and food web subsidies to downstream ecosystems. The operation of the SWD, releasing at various depths, significantly affected downstream nutrient concentrations and community composition of zooplankton exported, while basal carbon and zooplankton biomass were strongly associated with internal reservoir conditions (e.g., mixing and residence time). These results indicate that reservoirs with selective withdrawal systems may be an important source of nutrient and food web subsidies to downstream habitats, potentially bolstering lotic ecosystem productivity. Hence, the optimization of these resources may be important for future conservation efforts, providing flexibility in managing novel and critical habitats for native and listed species in areas where large reservoirs are permanent fixtures across the landscape. Most studies to date have only considered the effects of dam releases on biophysical conditions in downstream habitats, yet our study clearly indicates that releases also export nutrient and food web resources that may enhance ecosystem productivity. The work presented here warrants further study to understand potential tradeoffs between reservoir storage, discharge release and depth, and food web subsidies to downstream habitats.

4.1. Exports and controls

P and N export in our study were controlled by the SWD and reservoir water elevation at Shasta Dam. As such, SWD operation has the potential to regulate downstream nutrient dynamics and, potentially, ecosystem primary productivity. Both P and N exports were negatively associated with shallower releases (e.g. epilimnetic waters during stratified periods) and positively associated with deeper release depths and gate operations (i.e., hypolimnetic waters). While dams capture and store nutrients within reservoirs (Maavara et al., 2015), reservoir bottom releases have the potential to export nutrients due to changes in chemical and biological conditions (Chen, Shi, et al. 2020). For example, SRP is known to accumulate and be released from sediments within the hypolimnion of lakes and reservoirs due to reduced P demand, changes in pH, microbial extracellular enzymes, and lower redox potential within sediments (Søndergaard et al., 2003; Hupfer and Lewandowski, 2008; Chen, Rucker et al. 2020).

Similarly, ammonium, due to reduced biological demand and redox potential, was expected to have a strong correlation with release depth but was only weakly correlated in our study (Beutel, 2006; Chen, Shi, et al. 2020). Low ammonium concentrations may have resulted from rapid oxidation of ammonium to nitrite and nitrate or uptake by

suspended and benthic primary producers during transport from Shasta Dam through the Keswick Afterbay. This hypothesis is supported by the positive relationship between Keswick Dam discharge and ammonium concentration that may have reduced the transit time for ammonium oxidation to occur; however, we found little association between nitrate export and hydraulic conditions within the Keswick Afterbay. Additionally, phytoplankton and zooplankton exported may represent another source of nutrients associated with transport related mortality and subsequent remineralization, thus leading to additional releases of P and N (Tasnim et al., 2021). Understanding the effect of phytoplankton and zooplankton remineralization on downstream nutrient availability may be an important component of future nutrient export studies.

In addition to nutrients, we found that food web subsidies were continuously exported throughout the year from the Shasta-Keswick complex, as observed previously and in other regulated river reaches (e.g., Hiji and Parana Rivers; Chang et al., 2008; Doi, 2009; Lieberman et al., 2001; Portinho et al., 2016). We detected two relatively large pulses of zooplankton abundance and biomass during the study indicating that these subsidies were variable through time. Although both pulses were similar in abundance (24,587 ind. m^{-3} and 18,405 ind. m^{-3}), they differed substantially in their community composition and estimated biomass exported. High abundances in April 2018 were primarily composed of large high-biomass Daphniid and Psuedodiaptomid zooplankton. Conversely, the January 2019 zooplankton pulse largely consisted of smaller cyclopoid copepods. Differences between spikes illustrate the importance of seasonal cycles in zooplankton communities on reservoir exports.

Phytoplankton and zooplankton biomass export was strongly linked to stratification and internal mixing dynamics in Shasta Reservoir. The association between stratification, mixing and food web exports was likely due to the creation of bloom conditions triggered by the movement of nutrients from lower, colder hypoxic waters to the warmer euphotic layer, where they could be utilized by phytoplankton (Tasnim et al., 2021). However, chlorophyll *a* exhibited a significant positive relationship with release depth and top gate operations. It is likely that these exports occurred from deeper depths within the epilimnion during periods of top gate operation, coinciding with chlorophyll *a* maxima at 5–13 m below the reservoir surface (Bartholow et al., 2001) (Fig. 2). Although zooplankton productivity typically occurs in the epilimnion, we did not observe a significant relationship between release depth and zooplankton export. Interactions between stratification, mixing, seasonal zooplankton dynamics, zooplankton vertical movement, and gate operations may have obscured this association. For instance, to optimize releases for water exports and power generation while maintaining cold water storage and discharge for winter-run Chinook salmon, water is often pulled from multiple depths using the SWD (Bartholow et al., 2001). Release depth is likely important for phytoplankton and zooplankton export, as these resources typically are found within the epilimnion and metalimnion of reservoirs and cannot be exported without operation of upper water column gates as demonstrated by Lieberman et al. (2001). Furthermore, Bartholow et al. (2001) reported that gate operations can affect mixing dynamics and productivity within Shasta reservoir, where hypolimnetic withdrawals can weaken summer stratification and enhance early fall peak productivity.

Shasta Reservoir and Keswick Afterbay HRT was positively related to both zooplankton biomass and chlorophyll *a*. Shasta Reservoir residence times ranged from 102 to 1037 days, with low HRT between August and October, which may have limited phytoplankton production (Soballe and Kimmel, 1987). However, the relationship between HRT and zooplankton biomass exported from Shasta Reservoir may be due to seasonal population cycles and mixing dynamics that correspond with high residence times and does not reflect the effect of residence time on productivity. Phytoplankton and zooplankton biomass were positively correlated with Keswick Afterbay HRT. It is unlikely, however, that zooplankton production in the afterbay itself was appreciable given its short (<4 days) HRT (Sluss et al., 2008). It is possible, however, that

increased residence time in Keswick Afterbay may have reduced zooplankton mortality. Previous studies have found that phytoplankton and zooplankton abundance are enhanced in habitats exhibiting longer residence times due to reduced abiotic stress associated with turbulence (Brook and Woodward, 1956; Cowell, 1967; Sluss et al., 2008).

Although selective withdrawal device operations were not strongly correlated to zooplankton biomass exports, both gate operations and release depth were associated with the zooplankton community exported. Communities associated with deeper releases were characterized by small cladocerans such as *Bosmina* sp., while communities with higher abundances of large species such as *Psuedodiaptomus* sp., *Daphnia pulex,* and *D. mendotea* were associated with releases from the top gates and during periods of high reservoir water elevations. Observed differences in community export and strong associations with different gate operations may be due to vertical stratification of zooplankton communities as observed in other systems (Burns and Mitchell, 1980; Lieberman et al., 2001; Helland et al., 2007; Doulka and Kehayias, 2011; Khalifa et al., 2015). However, the strong association between reservoir elevation and zooplankton community export may indicate hydrologic or seasonal differences in export potential that occur with gate operations. For instance, zooplankton vertical distribution has been reported to be sensitive to thermal stratification (Thackeray et al., 2006; Helland et al., 2007; Doulka and Kehayias, 2011), thermocline depth (Cantin et al., 2011) and internal waves (Rinke et al., 2007); all of which are affected by gate operations (Bartholow et al., 2001).

4.2. Implications for management

Previous studies have examined the potential of SWDs to regulate release temperatures, discharge (e.g., functional flows), and water quality (Christenson et al., 1996; Lieberman et al., 2001; Bremigan and Stein, 2008; Andrea et al., 2014; Azadi et al., 2021). Nonetheless, the potential to export nutrients and food subsidies has rarely been studied, yet the implications are numerous and may expand the reconciliation ecology portfolios of environmental managers. The control of nutrient exports from reservoirs is fundamental to managing fisheries and productivity in novel downstream ecosystems. Sabo et al. (2017) hypothesized that dam operations were key to nutrient exports in the Mekong River, when outflows could be timed to receding flood inundation that mobilized nutrients from sediments. Modelling of such dynamics suggested that optimizing the timing of releases would increase downstream fishery production (Sabo et al., 2017). Previous studies of the SWD at Shasta Reservoir found that releases from the epilimnion and metalimnion from late fall to early spring enhanced nutrient concentrations in the hypolimnion compared to pre-SWD conditions (Lieberman and Horn, 1998). Such nutrient accumulation has the potential to be transported downstream to boost ecosystem productivity if release depths are managed accordingly. For instance, nitrate values sampled during August (over 0.15 mg L^{-1}), just after release depths exceeded 54 m (hypolimnetic waters during strong stratification conditions; Fig. 2), were equal to values observed in nutrient rich, highly productive spring-fed rivers, and much greater than local oligotrophic run-off streams (Lusardi et al., 2016).

Phytoplankton and zooplankton exports also have the potential to subsidize primary, secondary, and tertiary production and bolster overall ecosystem productivity, benefitting higher-level consumers, such as benthic macroinvertebrates or juvenile salmonids. Zooplankton exports, in particular, have been attributed to increased macroinvertebrate abundance and utilization by fishes at downstream locations (Chang et al., 2008; Doi, 2009). During our 12-month study, an estimated 95 metric tons of zooplankton carbon was exported to the Sacramento River below Keswick Dam, with the bulk of this export occurring during April 2018 and January 2019. Longitudinally, all zooplankton subsidies, regardless of magnitude, were substantially depleted within the first 5 km downstream of Keswick Dam, which is consistent with studies where resource subsidies from upstream lakes

and reservoirs are utilized within similar distances downstream (Chang et al., 2008; Ellis and Jones, 2013; Portinho et al., 2016). Although not quantified in this study, the first 5 km of the Sacramento River below Keswick Dam are considered a productive and economically important fishery, with high primary, secondary, and tertiary production, highlighting the potential importance of these subsidies within this reach (Moyle et al., 2017). Understanding ecosystem level utilization of these subsidies and the importance of subsidy spikes will be critical to future management and warrant additional mechanistic investigations, such as stable isotope tracers and nutrient modeling.

Further, direct benefits to macroinvertebrates or fish may depend on the type of zooplankton exported, with species such as large bodied cladocerans (e.g., *Daphnia pulex* and *D. mendotea*) being preferentially utilized over smaller species (Adams et al., 2015; Katz et al., 2017). Significant correlations between Shasta Reservoir operations and zooplankton community composition suggest that gate depth selection and seasonal timing may be an important tool to control zooplankton subsidy quality and, perhaps, quantity. This might be particularly important during productivity peaks within Shasta Reservoir in early spring and early fall (Lieberman and Horn, 1998; Bartholow et al., 2001) to subsidize downstream habitats. This was best exemplified during April, with zooplankton densities greater than 20,000 individuals m^{-3} during shallow releases (3–15 m), compared to low densities exported during early fall, consistent with hypolimnetic releases (>45 m).

The influence of SWD operation on nutrient and food web export presents a potentially important management opportunity. The Sacramento River below Keswick Dam supports four runs of Chinook salmon and numerous other native fishes (e.g., green sturgeon), many of which are listed under state and federal Endangered Species Acts (Moyle et al., 2017; Grantham et al., 2017). Today, SWD management focuses exclusively on maintaining adequate water temperature for listed coldwater species (e.g., winter-run Chinook) and discharge for downstream water users (Zarri et al., 2019). However, under a rapidly changing climate, more frequent and severe droughts are projected (Mann and Gleick, 2015). This suggests that SWD systems may play a uniquely important role in attempts to optimize reservoir operations for water supply and ecosystem benefits under future climate conditions. Our study demonstrates that there are significant exports of food web resources under current SWD management and understanding the potential for optimizing temperature and exports while meeting societal needs will be an important area of research in this system.

Several studies have recently discussed the importance of high prey availability to foraging success and growth of native fish, particularly under warm water conditions (Lusardi et al., 2016, 2020; Armstrong et al., 2021). Bioenergetic theory and recent empirical evidence suggest that foraging fish may be able to compensate for incremental shifts in water temperature when prey availability is enhanced (Lusardi et al., 2020), thereby potentially helping to offset energetic constraints associated with increasing water temperature. As such, controlling nutrient and food web export subsidies may be an important management tool under a warming climate or during periods of extended drought. This may be especially true for novel ecosystems downstream of dams, in which ecosystem processes and dynamics strongly rely on the operation of water control infrastructure (Hobbs et al., 2009). Management flexibility associated with SWD operations in these ecosystems may ultimately promote coldwater storage during periods of high prey abundance export, while at the same time optimizing temperatures for downstream native fishes that presently experience thermal regimes much colder than historically (Astles et al., 2003; Zarri and Palkovacs, 2019; Zarri et al., 2019).

5. Conclusion

Reservoir subsidies are not typical of most fluvial systems yet may provide important resources to native species or promote ecosystem processes in highly altered novel river ecosystems. While the primary management objectives of the SWD are to maintain water exports, hydroelectric power generation, and coldwater for spawning winter-run Chinook salmon, we found that Shasta Dam operations and internal reservoir conditions controlled nutrient and food resource exports. Thus, operation of the SWD to regulate food web resources represents a potentially important tool for future management scenarios. Provided that most habitats downstream of dams are highly altered, understanding how dam operations affect export subsidies may be an important factor in managing these habitats for native species, particularly under a rapidly changing climate.

Author contribution statement

Nicholas J. Corline: Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. Francisco Bellido-Leiva: Conceptualization, Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. Adriana Alarcon: Conceptualization, Investigation, Validation, Writing – review & editing. Randy Dahlgren: Conceptualization, Resources, Writing – review & editing. Erwin E. Van Nieuwenhuyse: Conceptualization, Writing – review & editing. Michael Beakes: Conceptualization, Writing – review & editing. Robert A. Lusardi: Supervision, Project administration, Funding acquisition, Conceptualization, Methodology, Writing – original draft, Writing – review & editing.

Open research statement

Data are provided as private-for-peer review at the Dryad online repository.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2023.118852.

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