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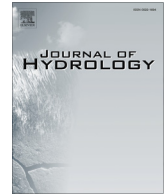
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The upside-down river: Reservoirs, algal blooms, and tributaries affect temporal and spatial patterns in nitrogen and phosphorus in the Klamath River, USA

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S U M M A R Y

The Klamath River, located in Oregon/California of the Northwestern U.S., is highly impounded and also experiences large seasonal algal blooms and impaired water quality. We investigated nitrogen (N) and phosphorus (P) constituents for one year (2010–2011) across 193 km of the Klamath River at sites above and below reservoirs and major tributaries to determine the influence of these features on longitudinal and temporal trends in concentrations, loads, and N:P ratios. In general, the headwater lake (Upper Klamath Lake) and reservoirs appeared to be the dominant influence on water quality and nutrient dynamics in the upper river, whereas tributaries appeared to exert stronger influence in the lower river. Overall, high nutrients and poor water quality at upstream sites were ameliorated downstream, however the downstream reductions in N were much greater relative to P. Seasonality appeared to play a major role in the overall appearance and magnitude of longitudinal trends. The greatest upstream–downstream differences occurred during periods of time following large algal blooms in the upper portion of the river. Overall, the amount and composition of N appeared to be strongly driven by algal blooms and biogeochemical conditions such as low oxygen, high pH and warm temperatures in the upper portion of the river, whereas P was more strongly driven by seasonal hydrology. The spatiotemporal influence of reservoirs and tributaries on nutrient flux and nutrient ratios may have significant implications for aquatic communities and ecosystem health. Nutrient objectives should be considered when designing restoration, management, and monitoring objectives for projects involving habitat suitability for anadromous fish and potential dam removal.

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1. Introduction

Actively moving, or lotic, waters exhibit longitudinal gradients that influence aquatic ecosystem structure and function, and therefore also affect nutrient fate and transport (Vannote et al., 1980; Newbold et al., 1983). River impoundments alter longitudinal gradients by causing upstream–downstream shifts in physical, chemical, and biological processes (Ward and Stanford, 1983). Impoundments often create reservoirs that disrupt lotic connectivity and alter in-stream biogeochemical cycling (Friedl and Wüest, 2002; Humborg et al., 1997), organic matter dynamics (Miller, 2012), and downstream transport of sediments and nutrients (Kelly, 2001; Houser et al., 2009). Timing of the processing and export of materials may also be disrupted, leading to seasonal changes in downstream productivity (Ahearn et al., 2005). For example, lentic bodies are composed of still waters and are frequently viewed as annual net sinks for phosphorus and nitrogen (Harrison et al., 2009), but are also important sub-annually by influencing the export of nutrients to downstream reaches (Wurtsbaugh et al., 2005; Kendall et al., 2001). The magnitude of these effects shifts with position in the watershed and river network (Jones, 2010; Swanson et al., 1988), as well as with relative proximity to other lentic bodies (Epstein et al., 2012; Kelly, 2001). Lentic waters also affect processing within adjacent lotic reaches; comparisons between river reaches above and below lentic bodies have shown significant differences in water quality and nutrient processing (Goodman et al., 2010). Ultimately, the variety of alterations due to impoundments may have cascading effects, with consequences for water quality and aquatic communities.

In the western U.S.A., many rivers draining to the Pacific Ocean, such as the Klamath River, serve as critical habitat for anadromous

fish. The Klamath River emanates from Upper Klamath Lake (UKL; surface area ~250 km^2) in south-central Oregon and flows 402 km southwest to the Pacific Ocean (Fig. 1). Although UKL is a naturally occurring lake, for the past century the water level has been regulated by a dam as part of the Klamath Reclamation Project. In the ~94 km below UKL, the Klamath River is further regulated by five dams for the management of flow, storage, and hydropower. These dams create a series of reservoir and river reaches within the river's upper longitudinal gradient. Below the lowest dam (Iron Gate) the river flows 306 km uninhibited to the Pacific Ocean. In contrast to many large river systems in the western U.S., the Klamath River begins as a low gradient system within a wide basin and transitions downstream to a higher gradient system within a narrower basin (elevation profile: Appendix B). In contrast with more pristine headwaters, the upper portions of the Klamath River include higher temperatures, higher concentrations of pelagic algae, high nutrients, and reduced water quality. Previous acknowledgment of these trends (e.g. Asarian and Kann, 2006; FERC, 2007; PacifiCorp, 2005), in addition to distinctions between watershed characteristics of the upper versus lower river basins (Mount, 1995), has led to a conceptual framework of the Klamath River as structurally and functionally "upside-down" in comparison to many other river systems (PacifiCorp, 2006).

Historically, the Klamath River supported large runs of anadromous fish, including Chinook salmon (*Oncorhynchus tshawytscha*), Coho salmon (*O. kisutch*), and steelhead trout (*O. mykiss*). Today, the decline of the Klamath River fisheries is attributed to multiple factors, including dams, water diversions, land-use change, disease, loss of genetic diversity, fishing, forest harvest, mining, eutrophication, and climate fluctuations (Brown et al., 1994). The Klamath

River is largely in equilibrium with meteorological conditions, and as a result warm temperatures are typical throughout the river from late spring through early fall (Bartholow and Henricksen, 2006; PacifiCorp, 2008). Warm warmer temperatures are seen as a major obstacle for fish recovery, particularly in regards to the possibility of dam removal, which has the potential to shift thermal regimes throughout the river (Bartholow et al., 2005).

In addition to warm seasonal temperatures, the upper portion of the Klamath River experiences large seasonal (summer and fall) algal blooms dominated by the N-fixing cyanobacteria *Aphanizomenon flos-aquae* (Eilers et al., 2004; Jacoby and Kann, 2007). Blooms contribute to multiple water quality impairments, including organic matter and nutrient enrichment, low dissolved oxygen, and high pH (ODEC, 2010). While nutrients (i.e. N and P), are important indicators of trophic status, resource availability, and water quality, they are rarely considered priority objectives in managing and restoring rivers for anadromous fish. In the Klamath River, high ammonia concentrations are considered a major stressor to endangered suckers (Bortleson and Fretwell, 1993; Martin and Saiki, 1999). Therefore, full assessment of fish habitat and resources in rivers like the Klamath requires understanding of not only temperature and flow regimes, but also spatial and seasonal nutrient dynamics, including the role of nutrients in algal blooms and the effects of algal bloom and nutrient propagation to downstream reaches.

In this study, N and P within the Klamath River were tracked for one year across a longitudinal gradient of lentic and lotic reaches to investigate how river impounds, flow regulation, and algal blooms altered N and P dynamics across spatial and temporal scales. Results of this study may be utilized to better understand
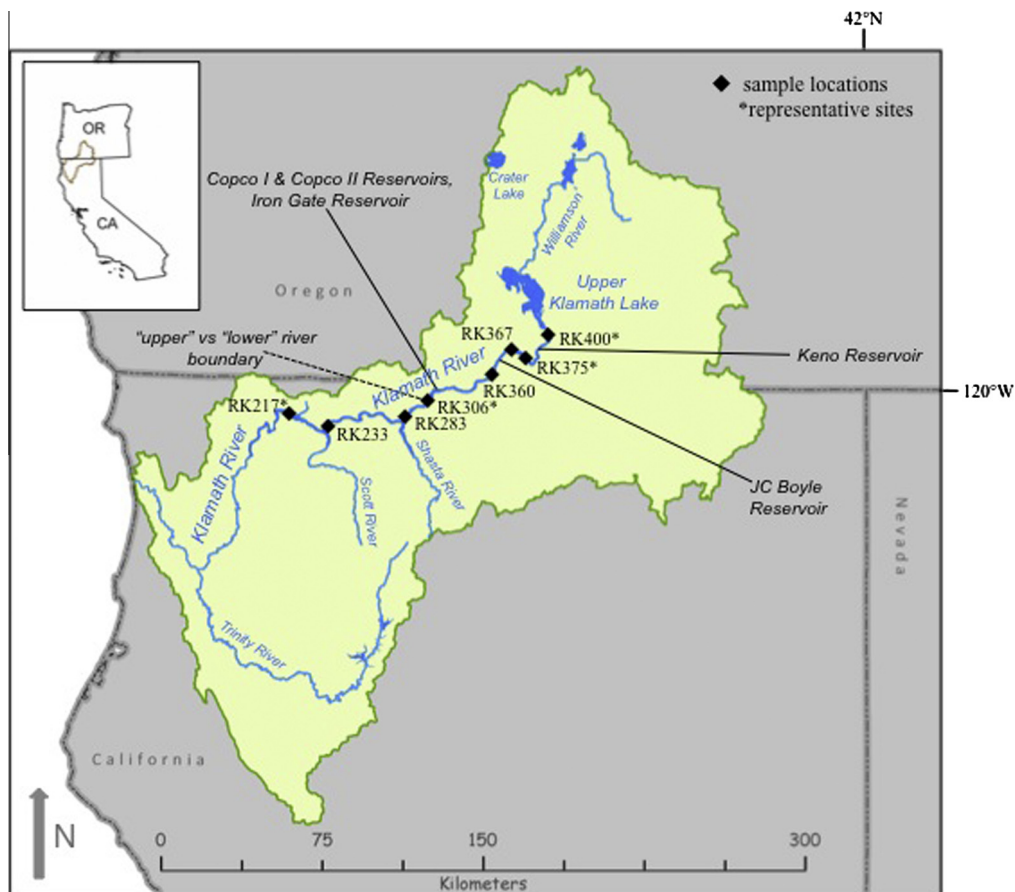

Fig. 1. Map of the Klamath River basin with sampling locations.

water quality and aquatic communities in the Klamath River, and in other rivers with similar attributes, as well as aid the development of comprehensive restoration, monitoring, and management plans surrounding dam removal.

2. Methods

2.1. Study area: The Klamath River

The Klamath River watershed is divided into an upper (20,875 km^2) and lower basin (19,757 km^2) (Fig. 1) having distinct geology, hydrology, and geomorphology. The upper basin ("upper river" $\sim$94 km) is predominantly low relief (Appendix B) and is semiarid; average annual precipitation ranges from 330 to 1650 mm yr^{-1} (Western Regional Climate Center (WRCC), available at http://www.wrcc.dri.edu/summary/Climsmor.html) and the majority of hydrologic inputs are derived from groundwater and snowmelt runoff (Gannett et al., 2007). Klamath Falls, located in the upper basin, is the largest urban area in the watershed (2011 population: 66,300) but overall population in the region is rural, and the majority of land use (>50%) is agriculture and rangeland (NRC, 2008). During our study (May 2010–June 2011), flows from Upper Klamath Lake (UKL) into the Klamath River ranged from 10 m^3 s^{-1} during winter baseflow to 110 m^3 s^{-1} during spring snowmelt (USGS station 11507500). In the upper basin, there are six dams on the mainstem river that divide the uppermost 97 km into a series of reservoir and river reaches. These dams are operated for a variety of purposes including storage of water for agricultural, municipal use, wildlife refuges, and hydropower generation.

The lower Klamath basin ("lower river" $\sim$306 km) is designated here as the watershed area downstream of the lowest dam, Iron Gate Dam, just upstream of river kilometer 306 (RK306; Fig. 1). The Klamath River basin differs from many watersheds in that the greatest relief and topographic complexity occurs in the lower basin (Mount, 1995), which is mountainous and primarily forest (>50%). As the river flows west towards the Pacific Ocean, the lower basin climate becomes increasingly temperate and wet, and average annual precipitation can exceed 2350 mm yr^{-1} (WRCC). Flows entering the lower basin are controlled by operations at Iron Gate Dam. Downstream, flows increase and exhibit greater seasonal flow variability due to accretion from tributaries and storm events. During our study, releases from Iron Gate Dam ranged from 23 to 161 m^3 s^{-1} (USGS station 11516530; RK306), with accretion downstream contributing to flows of 80–2692 m^3 s^{-1} at the river mouth near Klamath, CA (USGS station 11530500; RK6).

2.2. Sample collection and processing

Water samples were collected monthly from May 2010 to June 2011 at eight sites along the Klamath River (Fig. 1) spanning 183 km from UKL (RK400) to Seiad Valley, CA (RK217). Sites were selected to capture conditions throughout the study area, including above and below reservoirs and major tributaries. Hydropower peaking operations upstream of RK360 caused diel fluctuations in flow and nutrient concentrations. Protocols for the timing of sampling in this reach to maximize the likelihood of representative sampling have been previously described in Asarian et al. (2009). While data from all eight sites on the main stem were analyzed, for descriptive purposes the major changes in downstream conditions can be accurately described using four "representative sites": the uppermost site located below the outlet of UKL (RK400), below Keno Reservoir (RK375), below Iron Gate Reservoir (RK306), and the furthest downstream site at Seiad Valley (RK217). Samples were also collected from the two largest tributaries within the

study reach, the Shasta River (SHR; confluence at RK283.5) and Scott River (SCR; confluence at RK233.5). Tributary samples were collected $\sim$0.5 km upstream from confluence with the Klamath River.

There are five reservoirs along the upper Klamath River (Table 1). The three lowest reservoirs (Copco I, Copco II, and Iron Gate Reservoirs; total storage $\sim$13 * 10^7 m^3) are located in series with no intermediate river reaches. Due to the continuity of water and limited access between these three reservoirs, sampling in this reach was only conducted below Iron Gate Reservoir. Overall storage in Copco II is small with a short residence time, and while we recognize that the two larger reservoirs, Copco I and Iron Gate, are discrete bodies with unique characteristics, herein, these two reservoirs will not be assessed individually.

At five of the nine sites (RK400, RK375, RK360, RK306, RK217), and the two tributary sampling locations (SHR, SCR), river discharge was obtained from USGS gauges. Where gauges were unavailable (RK367, RK283, RK233), flows were estimated using the one-dimensional form (i.e., laterally and depth averaged) of the hydrodynamic model, RMA-2 (King, 2001). Details on the inputs, run specifications, and evaluation of the performance of the RMA-2 hydrodynamic model are given in Appendix C. Flow boundary conditions were established with data from USGS gauges, as well as reservoir storage data provided by PacifiCorp. RMA-2 has been previously calibrated and applied on the Klamath River (Deas and Orlob, 1999; PacifiCorp, 2005; Basdekas and Deas, 2007; ODEQ, 2010), and further calibration for this study was not required. Error statistics were determined by comparing modeled flows at boundary conditions with observed flows from USGS gauge stations where available.

Grab samples were collected from the upper 50 cm of the water column near the midpoint of a well-mixed channel (river depth range 100–400 cm). A YSI 556 (Yellow Springs, OH, USA) was used for field measurements of temperature, dissolved oxygen, pH, and electrical conductivity. Samples were stored in the dark at 4 °C, and analyzed within 72 h of collection. Aliquots of water were filtered through a pre-rinsed 0.4 μm polycarbonate membrane filter (Millipore) for spectroscopic quantification of NO$_3^-$-N (LOD = 0.01 mg L^{-1}), NH$_4^+$-N (LOD $\sim$ 0.01 mg L^{-1}), and soluble reactive P (SRP; LOD $\sim$ 0.005 mg L^{-1}). Determination of NO$_3^-$-N was made using the vanadium chloride method (Doane and Horwath, 2003), NH$_4^+$-N using the Berthelot reaction with a salicylate analog of indophenol blue (Forster, 1995), and SRP using the ammonium molybdate method (Clesceri et al., 1998). Nonfiltered samples were used to determine total N (TN) and total P (TP) following oxidation with 1% persulfate using the methods described above for NO$_3^-$ and SRP, respectively. Estimates of total organic N (TON) were obtained by subtracting DIN (NO$_3^-$ + NH$_4^+$) from TN. Estimates of non-SRP (organic and particulate P) were obtained by subtracting SRP from TP. Pelagic algal standing biomass was determined using chlorophyll pigments (ChlP), as chlorophyll *a* (chl-*a*) + phaeophytin *a* (pha-*a*), by filtering 0.5–1 L of well-mixed water sample using a glass fiber filter (GF/F). Filters were freeze-dried and extracted with 90% ethanol prior to quantification by fluorometry (Clesceri et al., 1998).

2.3. Nutrient load calculations

Nutrient loads for each site were estimated using LoadRunner (Booth et al., 2007), which automates runs of the USGS load estimator program LOADEST (Runkel et al., 2004). Our monthly sampling regime satisfied the minimum number of sampling points required by LOADEST and was adequate for model development. LOADEST uses a time series of paired constituent and discharge data to determine a best-fit calibration regression equation from one of nine model structures using Akaike's information

Table 1
Descriptive characteristics of the five Klamath Reservoirs, excluding Upper Klamath Lake. Adapted from PacifiCorp (2008).

	Reservoir				
	Keno	JC Boyle	Copco I	Copco II	Iron Gate
Length (km)	36.21	5.79	7.40	0.48	9.98
Max surface area (km^2)	10.02	1.70	4.05	0.16	3.82
Max depth (m)	5.94	12.71	35.20	8.53	49.56
Total storage capacity (m^3)	$2.28 * 10^7$	$4.31 * 10^6$	$5.78 * 10^7$	$9.00 * 10^4$	$7.25 * 10^7$
Residence time (days) at 20 m^3 s^{-1}	13	2.5	32	0.5	42
Residence time (days) at 43 m^3 s^{-1}	6	1.2	15	0.03	20
Residence time (days) at 85 m^3 s^{-1}	3	0.6	8	0.01	10

criterion. Discharge and time were centered to avoid multicollinearity, and the calibration equation was fit using the adjusted maximum likelihood estimator. Each calibration regression equation was applied to continuous daily discharge to obtain flux estimates for daily constituent loads.

2.4. Determination of seasonal time periods

For purposes of comparisons and discussion, our study was subdivided into four time periods representing distinct hydrologic and water quality conditions: "bloom", the onset and initial peak of the algal bloom (May–July); "post-bloom", following the initial bloom peak and throughout the subsequent bloom decline in early fall (August–October); "winter low", low flows during late fall and early winter (November–January); and "winter/spring high", high flows during late winter storms and spring runoff (February–April). Data from the different subperiods differed in sample size and lacked homogenous variance, and therefore was analyzed using the Kruskal–Wallis ANOVA test on ranks (Kruskal and Wallis, 1952), which identified selected subperiods statistically different ($p < 0.001$) for temperature, flow, DO, pH, and ChlP.

3. Results

3.1. Hydrology

Annual precipitation in the upper river during our study period was 36.5 cm, or 125% of average (average annual precipitation for 1998–2009, ~29 cm). During late winter and early spring (February–June 2011), large winter storm events and snowmelt runoff generated flows of 12–124 m^3 s^{-1} across sites in the upper river, and 37–346 m^3 s^{-1} across sites in the lower river (Fig. 2). In contrast, during drier months (May 2010–January 2011), flows ranged from 9 to 54 m^3 s^{-1} in the upper river, and 23 to 222 m^3 s^{-1} in the lower river.

Tributary discharge from the Shasta (SHR) and Scott (SCR) Rivers contributed 1–28% (range 0.31–32.83 m^3 s^{-1}, med = 4.8 m^3 s^{-1}) and 1–360% (range 1.08–125.42 m^3 s^{-1}, med = 17.7 m^3 s^{-1}), respectively, of discharge relative to the volume of the Klamath River upstream from the tributary confluence. SHR hydrology is dominated by spring-flow resulting in lower variability and maximum discharge (mean = 5 m^3 s^{-1} ± std 4 m^3 s^{-1}) than SCR hydrology (mean = 22 m^3 s^{-1} ± std 19 m^3 s^{-1}), which is dominated by snow-melt and precipitation events. The remaining tributaries within the study reach are all relatively small and are estimated to deliver 5–10% of the total flow below Iron Gate Reservoir (RK306) to the river mouth (Turwar, RK5) (Asarian et al., 2010).

3.2. Water quality

Summary statistics for temperature, dissolved oxygen, pH, and conductivity are given in Appendix D. Sites in the uppermost portion of the river experienced an initial onset of algal blooms

in late spring (May 2010). The bloom peaked at the uppermost sites from mid- to late-summer (July–August), and endured through early fall (end of September) (Fig. 4). Although median ChlP concentrations were similar from RK400 (median ChlP = 17.0 µg L^{-1}; range 2.8–237.4 µg L^{-1}) to RK375 (median ChlP = 20.6 µg L^{-1}; range 3.1–162.3 µg L^{-1}), maximum concentrations at RK400 were sometimes three to twenty times greater than at RK375. Downstream of RK375, ChlP decreased substantially to RK217 (median ChlP = 3.9 µg L^{-1}; range 1.2–19.9 µg L^{-1}).

3.3. Concentrations of N and P in the Klamath River

Concentrations of N and P exhibited spatiotemporal trends, and concentrations tended to decrease and be less variable downstream. N exhibited stronger longitudinal trends and greater variability relative to P, and seasonality appeared to be a major influence in the overall appearance and magnitude of these trends.

3.3.1. Longitudinal and seasonal patterns in N concentrations

N concentrations exhibited strong longitudinal trends, and the majority of N constituents decreased downstream (Fig. 3; Table 2). On average, 65% (stdev ± 23%) of total nitrogen (TN) was comprised of organic N (TON). Both TN and TON concentrations were the highest at upstream sites and generally decreased downstream. Maximum TN concentrations were observed at RK375, while maximum TON concentrations were observed at RK400. Minimum values for both TN and TON were observed at RK217.

In contrast to TN and TON, concentrations of dissolved inorganic N (DIN = NO_3^- + NH_4^+) exhibited site-specific differences, particularly in the upper river, but also weaker upstream-to-downstream trends throughout the entire river. The lowest concentrations of NO_3^- occurred at the most upstream sites (RK400, RK375) but increased dramatically at RK367 and continued to increase to maximum values at RK360. At RK306 and subsequent downstream sites, NO_3^- concentrations began to decrease from maximum values, but still remained higher than the most upstream sites. NH_4^+ concentrations exhibited slightly more consistent longitudinal trends than NO_3^-; NH_4^+ increased substantially from RK400 to RK375, and then progressively decreased from RK367 downstream to RK217.

For the majority of N constituents, while longitudinal trends remained consistent throughout the year, seasonal shifts occurred in the magnitude and range of concentrations (Table 3). TN concentrations were the highest and most variable during the winter low period, and the lowest and least variable during the winter/spring high period. Seasonal patterns in TON were similar, except that maximum TON concentrations and variability occurred in the post-bloom period. Both NO_3^- and NH_4^+ showed minimum concentrations during the bloom period and maximums during the winter low period. The winter/spring high period was marked by low concentrations of NH_4^+ throughout the river, while NO_3^- remained high.
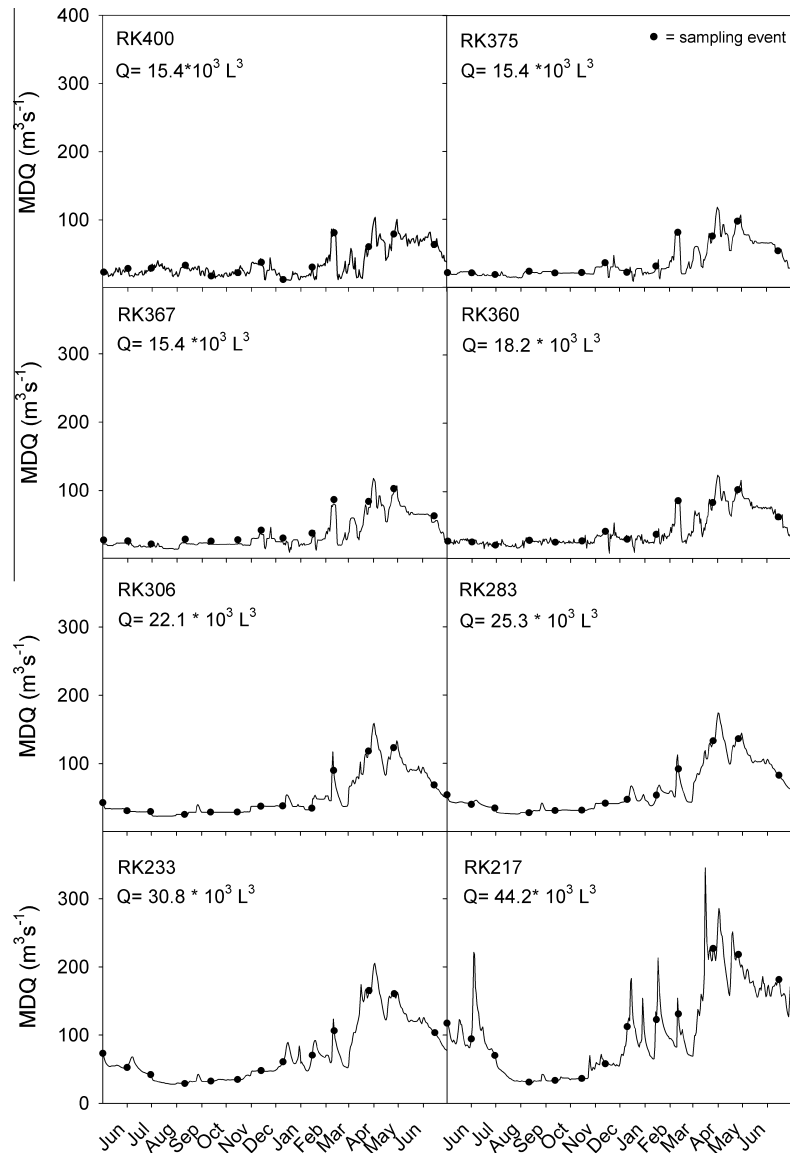
Fig. 2. Klamath River hydrographs for each sample location (RK400–RK217). *y*-Axis "MDQ" represents the mean daily discharge. Timing of sampling events are indicated by filled circles, and *Q* represents the total amount of flow at each sampling location over the duration of study.

3.3.2. Longitudinal and seasonal patterns in P concentrations

Longitudinal trends in P concentrations were not as strong as observed for N (Fig. 4; Table 2). TP concentrations were low at RK400 and increased downstream to maximum values at RK367, but then decreased to RK217. SRP concentrations at the uppermost sites exhibited some patterns similar to TP, for example, SRP also initially increased from RK400 to RK367. However, although SRP increased below RK306 on several occasions, there were no consistent downstream trends observed from RK360 to RK217. Non-SRP concentrations also increased from RK400 to RK375, and were generally higher in the upper river than in the lower river.

Seasonality was important for P dynamics (Table 3). During the bloom period, TP concentrations were lower but variability was the greatest. During the post-bloom period, TP concentrations increased to maximum values, and then decreased during the winter low and winter/spring high periods. Seasonal dynamics of SRP concentrations were similar to TP. Non-SRP exhibited high variability across all seasons, and was higher in the post-bloom and winter/spring high periods relative to the bloom and winter low periods.

3.3.3. TN:TP ratios

Throughout the river, TN:TP was most often near or below the Redfield ratio (~16.1 by molar). TN:TP values in the upper river exceeded the Redfield ratio more frequently and exhibited higher seasonal variability than sites in the lower river, where TN:TP values were generally close to or below Redfield, and showed lower seasonal variability. While downstream increases in TP maintained lower TN:TP at downstream sites, seasonal increases in TN within the upper river during post-bloom and winter low periods contributed to higher TN:TP throughout the entire river during these subperiods.

3.4. N and P loading in the Klamath River

Loads for N and P were determined on an annual, seasonal, and daily basis. Four representative sites were used to elucidate seasonal changes in loads between sites above and below Keno Reservoir (RK400 and RK375), below the lowest reservoir (Iron Gate Reservoir; RK306), and at the most downstream site (RK217).
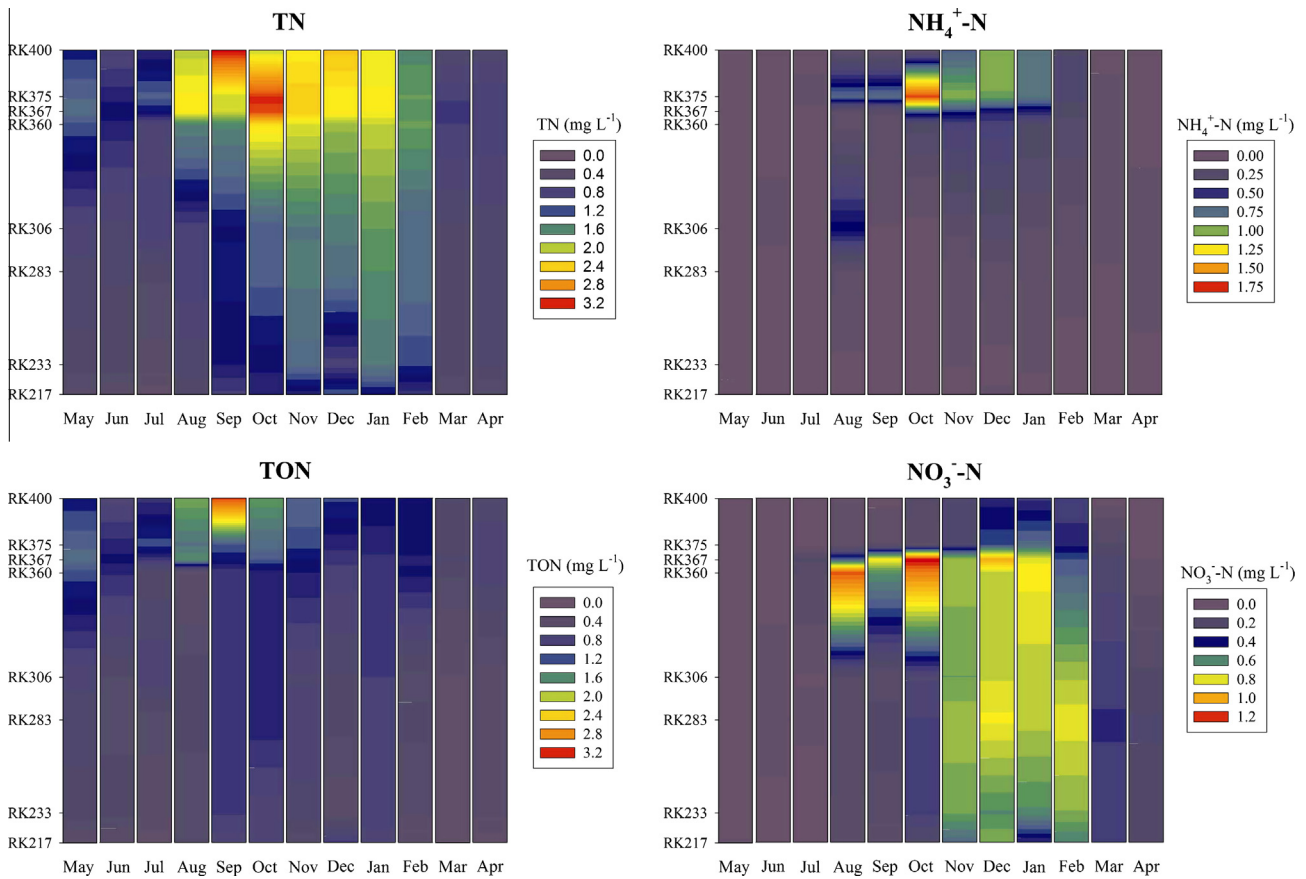
Fig. 3. Thermal plots of N concentrations in the Klamath River from May 2010–June 2011. Locations of sample sites are shown on the y-axis.

Table 2
Summary of nutrient concentrations for all sampling locations. Mean ± standard deviation (min–max) from data collected May 2010–June 2011.

Site[a]	TN (mg L^{-1})	TON (mg L^{-1})	NO$_3^-$-N (mg L^{-1})	NH$_4^+$-N (mg L^{-1})	TP (mg L^{-1})	Non-SRP (mg L^{-1})	SRP (µg L^{-1})	Chl-a + Ph-a (µg L^{-1})
RK400	1.26 ± 0.84	1.00 ± 0.46	0.08 ± 0.17	0.19 ± 0.33	0.10 ± 0.03	0.09 ± 0.03	9 ± 4	52.1 ± 19.7
	(0.69–2.79)	(0.67–2.08)	(<0.01–0.59)	(0.02–0.99)	(0.07–0.15)	(0.05–0.14)	(6–17)	(2.8–237.0)
RK375	1.29 ± 0.77	0.83 ± 0.26	0.13 ± 0.18	0.34 ± 0.51	0.15 ± 0.01	0.12 ± 0.02	30 ± 25	28.2 ± 11.5
	(0.56–2.88)	(0.56–1.32)	(<0.01–0.47)	(<0.01–1.40)	(0.12–0.16)	(0.08–0.13)	(7–79)	(3.1–162.3)
RK367	1.30 ± 0.75	0.73 ± 0.30	0.40 ± 0.43	0.18 ± 0.23	0.16 ± 0.04	0.12 ± 0.03	40 ± 34	22.5 ± 8.3
	(0.56–2.85)	(0.40–1.16)	(<0.01–1.12)	(0.01–0.70)	(0.10–0.22)	(0.06–0.16)	(10–110)	(3.8–118.5)
RK360	1.11 ± 0.55	0.58 ± 0.18	0.43 ± 0.40	0.13 ± 0.13	0.14 ± 0.02	0.10 ± 0.02	42 ± 32	16.1 ± 6.3
	(0.47–2.21)	(0.38–0.93)	(<0.01–1.05)	(0.01–0.38)	(0.11–0.17)	(0.05–0.11)	(12–119)	(2.6–87.6)
RK335	0.95 ± 0.46	0.60 ± 0.16	0.38 ± 0.49	0.04 ± 0.03	0.13 ± 0.03	0.08 ± 0.03	47 ± 42	13.6 ± 5.3
	(0.32–1.83)	(0.37–0.95)	(<0.01–1.59)	(<0.01–0.10)	(0.08–0.18)	(0.03–0.13)	(17–130)	(2.9–72.1)
RK306	0.91 ± 0.42	0.52 ± 0.18	0.31 ± 0.31	0.08 ± 0.05	0.12 ± 0.06	0.09 ± 0.07	53 ± 48	12.8 ± 5.0
	(0.45–1.69)	(0.35–0.95)	(0.05–1.02)	(0.01–0.18)	(0.08–0.28)	(<0.01–0.26)	(22–211)	(1.1–51.5)
RK283	0.82 ± 0.40	0.43 ± 0.20	0.40 ± 0.30	0.05 ± 0.04	0.12 ± 0.04	0.05 ± 0.03	65 ± 33	15.1 ± 6.8
	(0.45–1.69)	(0.25–0.97)	(0.02–0.88)	(0.02–0.13)	(0.08–0.19)	(<0.01–0.09)	(28–118)	(1.2–79.9)
RK233	0.71 ± 0.37	0.41 ± 0.14	0.27 ± 0.22	0.03 ± 0.01	0.12 ± 0.03	0.07 ± 0.01	53 ± 22	8.5 ± 2.7
	(0.37–1.24)	(0.37–0.68)	(<0.01–0.67)	(0.01–0.05)	(0.08–0.16)	(0.04–0.08)	(32–93)	(1.6–33.5)
RK217	0.54 ± 0.32	0.28 ± 0.17	0.24 ± 0.21	0.02 ± 0.01	0.09 ± 0.04	0.05 ± 0.02	37 ± 27	6.8 ± 1.8
	(0.24–1.07)	(0.15–0.63)	(<0.01–0.66)	(0.01–0.04)	(0.04–0.16)	(0.02–0.10)	(18–96)	(1.2–19.9)
TSH	0.50 ± 0.24	0.34 ± 0.22	0.13 ± 0.12	0.02 ± 0.01	0.16 ± 0.09	0.03 ± 0.06	0.12 ± 0.06	4.9 ± 4.2
	(0.12–1.02)	(0.08–0.77)	(<0.01–0.34)	(<0.01–0.04)	(0.02–0.28)	(<0.01–0.10)	(0.02–0.28)	(1.3–15.9)
TSC	0.37 ± 0.12	0.21 ± 0.16	0.13 ± 0.11	0.01 ± 0.01	0.05 ± 0.06	0.03 ± 0.04	0.02 ± 0.04	3.4 ± 2.7
	(0.20–0.56)	(<0.01–0.51)	(<0.01–0.35)	(<0.01–0.03)	(<0.01–0.19)	(<0.01–0.15)	(<0.01–0.15)	(0.4–9.4)

[a] All sites $n = 13$, values are flow-weighed mean concentration ± standard deviation (min–max).

3.4.1. Annual and seasonal longitudinal patterns in N loads

Annual TN and DIN loads for each sample location are given in Appendix E. For the annual duration of our study, TN load (TN$_L$) was fairly similar across all sites (Fig. 5, inset). Annual DIN load (DIN$_L$ = NO$_{3L}^-$ + NH$_{4L}^+$) increased from RK400 to RK217, but did not necessarily increase between all sites. The proportion of TN$_L$, comprised of DIN$_L$ increased overall from RK400 (DIN$_L$:TN$_L$ = 0.22) to RK217 (DIN$_L$:TN$_L$ = 0.48). In contrast, annual TON load (TON$_L$) tended to be higher upstream and decrease downstream. The proportion of TN$_L$ comprised of TON$_L$ was the highest at RK400 (TON$_L$:TN$_L$ = 0.83), and fairly consistent across all other sites (TON$_L$:TN$_L$ range = 0.57–0.69).

Table 3
Summary of nutrient concentrations for seasonal periods.

Period[a]	Seasonal concentrations (mg L^{-1})[b]							Chl-a + Ph-a (µg L^{-1})
	TN	TON	NO$_3^-$-N	NH$_4^+$-N	TP	Non-SRP	SRP	
Bloom	0.81 ± 0.31	0.74 ± 0.31	0.04 ± 0.03	0.03 ± 0.02	0.12 ± 0.04	0.07 ± 0.4	0.06 ± 0.03	36.9 ± 47.0
	0.19–1.34	0.08–0.71	0.01–0.08	<0.01–0.06	0.05–0.18	0.02–0.12	<0.01–0.10	2.9–162.3
Post-bloom	1.48 ± 0.64	0.86 ± 0.45	0.43 ± 0.37	0.23 ± 0.33	0.17 ± 0.02	0.08 ± 0.03	0.09 ± 0.03	30.8 ± 49.2
	0.73–2.30	0.48–1.84	0.08–0.94	0.02–1.04	0.14–0.20	0.03–0.13	0.01–0.12	2.9–237.0
Winter low	1.80 ± 1.04	0.78 ± 0.21	0.69 ± 0.22	0.35 ± 0.35	0.12 ± 0.02	0.06 ± 0.03	0.06 ± 0.02	4.1 ± 2.8
	0.52–2.41	0.45–1.16	0.39–1.01	0.04–0.96	0.09–0.16	0.03–0.10	0.02–0.10	1.1–8.7
Winter/spring high	0.78 ± 0.15	0.47 ± 0.18	0.24 ± 0.12	0.07 ± 0.03	0.11 ± 0.03	0.09 ± 0.03	0.03 ± 0.01	12.0 ± 9.3
	0.48–0.93	0.21–0.73	0.03–0.44	0.03–0.11	0.07–0.15	0.04–0.13	<0.01–0.05	1.2–28.7

[a] Seasonal periods designated as: "bloom" (May–July), "post-bloom" (August–October), "winter low" (November–January), "winter/spring high" (February–April).
[b] Nutrient values for each seasonal period are flow-weighted mean concentration ± standard deviation, min–max, $n = 24$.
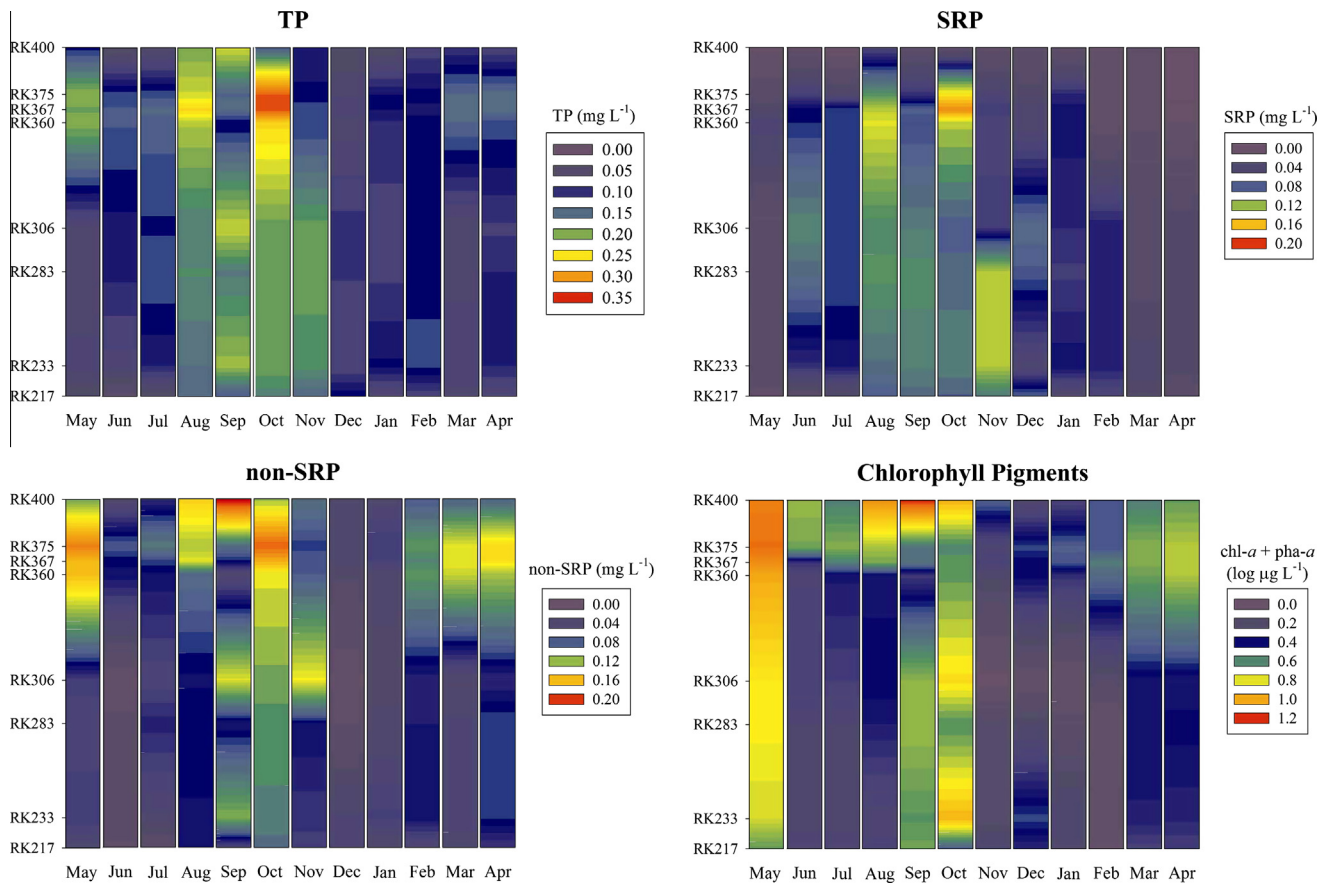

Fig. 4. Thermal plots of P concentrations and chlorophyll pigments in the Klamath River from May 2010–June 2011. Locations of sample sites are shown on the y-axis.

In contrast to similar annual TN$_L$ across all sites, on a seasonal basis, TN mean daily loads (TN$_{MDL}$) exhibited very different longitudinal patterns (Fig. 5). During the bloom period, all sites showed relatively similar TN$_{MDL}$. However, during the post-bloom period, TN$_{MDL}$ was the highest at the most upstream sites and decreased substantially downstream. During the winter low and winter/spring high periods, this pattern reversed and TN$_{MDL}$ were the lowest upstream and increased downstream.

Overall, seasonal downstream trends could be effectively summarized using comparisons between the four representative sites (Fig. 6). Relationships between representative sites shifted seasonally; patterns in TN$_{MDL}$ were the most similar throughout the year at RK400 and RK375 but exhibited larger seasonal shifts between downstream sites. In contrast, patterns in DIN$_{MDL}$ showed distinct seasonality across all representative sites. In particular, there were dramatic seasonal differences between RK400 and RK375,

although relationships between downstream sites also shifted seasonally. In comparison with DIN$_{MDL}$, TON$_{MDL}$ had lower spatial and seasonal variability. TON$_{MDL}$ was generally higher at RK400 relative to other representative sites, particularly during the post-bloom period, but no other consistent longitudinal trends were observed.

3.4.2. Annual and seasonal longitudinal patterns in P loads

Annual TP total load (TP$_L$) increased from RK400 to RK217 (Fig. 7, inset; annual loads for all P constituents are given in Appendix E). Similarly, SRP$_L$ increased from RK400 to RK217. In contrast, although overall non-SRP$_L$ increased between RK400 and RK217, the downstream trend between sites was not consistent.

Similar to annual patterns in TP$_L$, seasonal values of TP$_{MDL}$ also increased downstream. Especially large downstream increases in TP$_{MDL}$ occurred between RK400 and RK375, and between RK283
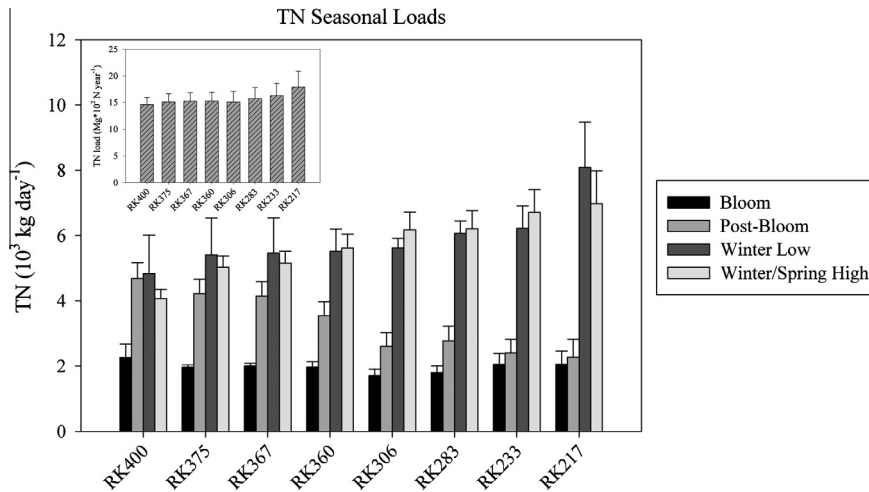
Fig. 5. TN seasonal loads at study sites on the Klamath River. Seasonal periods are designated as: bloom (May–July), post-bloom (August–October), winter low (November–January), and winter/spring high (February–April). Inset shows annual TN load at each site for May 2010–June 2011.
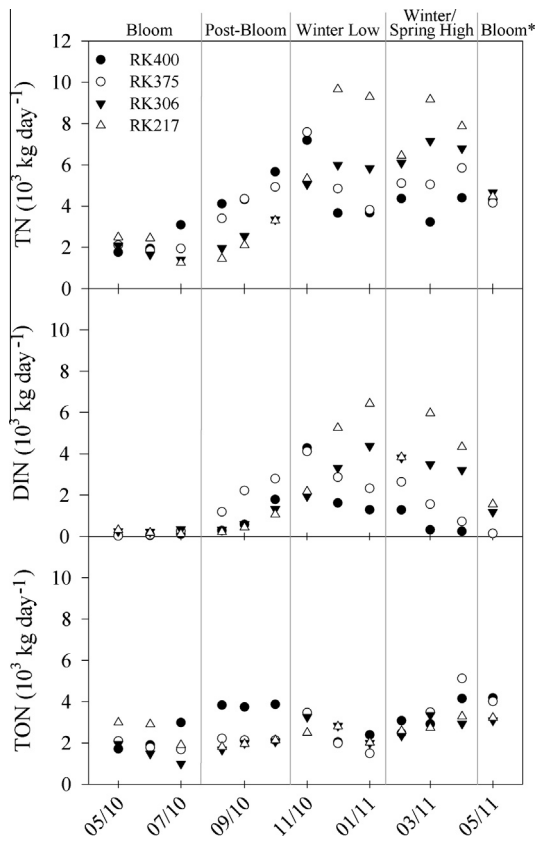

Fig. 6. TN average daily load at four selected representative sites. Seasonal periods are designated as: bloom (May–July), post-bloom (August–October), winter low (November–January), and winter/spring high (February–April). Note that the second "bloom" period (represented by [*]) experienced above average flows and consists only of May samples.

and RK233 during the winter low and winter/spring high periods. The notable exception to the trend of downstream increases in TP_{MDL} was a decrease in TP_{MDL} between RK360 and RK306 during the bloom and winter/spring high periods (Fig. 7).

Selected representative sites were useful for describing downstream trends in seasonal and spatial patterns of P loads (Fig. 8). As previously discussed, TP_{MDL} tended to increase in the downstream direction, although some seasonal differences in this trend

were observed. Most often, the largest downstream differences occurred between RK400 and RK375. SRP_{MDL} showed similar downstream trends as TP_{MDL}, although seasonal relationships between sites varied. All representative sites had relatively similar non-SRP_{MDL} throughout the majority of the year, although notable exceptions occurred during the winter/spring high period when non-SRP_{MDL} increased at all sites and became more variable throughout the river.

3.5. Annual nutrient contributions from major tributaries

Relatively large differences in the hydrology and water quality were observed between the Shasta River (SHR) and the Scott River (SCR). Seasonal details of tributary loads were beyond the scope of this project, only annual values of tributary loads are presented herein. Flows are generally high in winter, low in summer, and overwhelmed by flows and processes occurring upstream in the mainstem Klamath River. SHR contributed relatively consistent loads throughout the year in comparison to SCR, which was more seasonally-driven. Although SHR contributed lower total discharge, it had high P concentrations and notable loads of TP (TP_L = 42 Mg; range TP_{MDL} = 12–312 kg day^{-1}) and SRP (SRP_L = 23 Mg; range SRP_{MDL} = 5–175 kg day^{-1}) relative to loads in the Klamath River (SHR TP_{MDL}: RK288 TP_{MDL} = 0.17, range 0.04–0.37; SHR SRP_{MDL}: RK288 SRP_{MDL} = 0.19, range 0.02–0.39). In comparison, SHR contributions of TN (TN_L = 82 Mg; range TN_{MDL} = 53–840 kg day^{-1}) and DIN (DIN_{TL} = 36 Mg; range DIN_{MDL} = 1–406 kg day^{-1}) were less relative to TN loads in the Klamath River (SHR TN_{MDL}: RK288 TN_{MDL} = 0.04, range 0.02–0.11; SHR DIN_{MDL}: RK288 DIN_{MDL} = 0.03, range <0.01–0.07).

In comparison to SHR, the majority of loading from SCR occurred during periods of higher discharge (i.e., January–May 2011). SCR contributed slightly more TP_L (TP_L = 67 Mg; range TP_{MDL} = 10–630 kg day^{-1}) than SHR, but overall contributed a similar proportion relative to TP_L in the mainstem upstream from the SCR confluence (SCR TP_{MDL}: RK233 TP_{MDL} = 0.16, range 0.02–0.34). Overall SRP_L from SCR (SRP_L = 25 Mg; range SRP_{MDL} = 1–175 kg day^{-1}) was similar to that from SHR, but the proportion of SRP_L contributed from SCR to the mainstem was lower (SCR SRP_{MDL}: RK233 SRP_{MDL} = 0.04, range <0.01–0.10). In contrast, TN_L from SCR (TN_L = 338 Mg; range TN_{MDL} = 64–1789 kg day^{-1}) and DIN_L (DIN_L = 61 Mg; range DIN_{MDL} = 9–501 kg day^{-1}) were higher than SHR and contributed more to TN loads in the mainstem (SCR TN_{MDL}: RK233 TN_{MD} = 0.17, range 0.03–0.47; SCR DIN_{MDL}: RK233 DIN_{MDL} = 0.20, range 0.02–0.37).
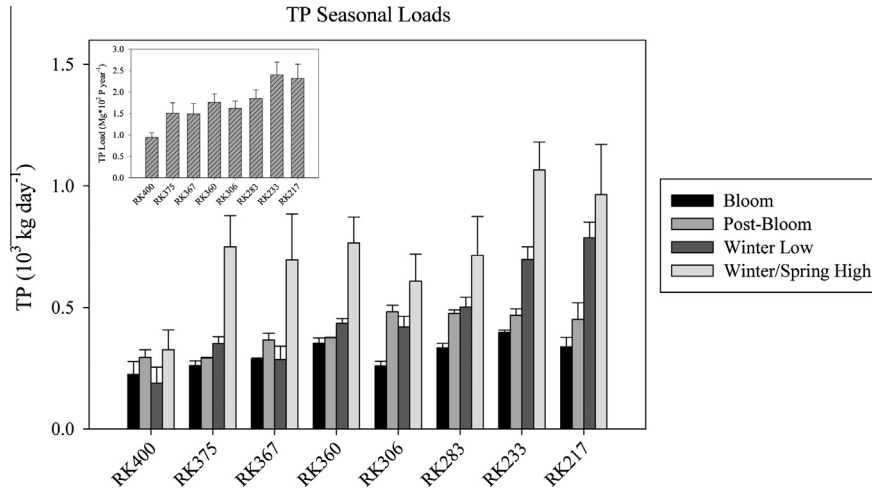
Fig. 7. TP seasonal loads at study sites on the Klamath River. Seasonal periods are designated as: bloom (May–July), post-bloom (August–October), winter low (November–January), and winter/spring high (February–April). Inset shows annual TP load at each site for May 2010–June 2011.
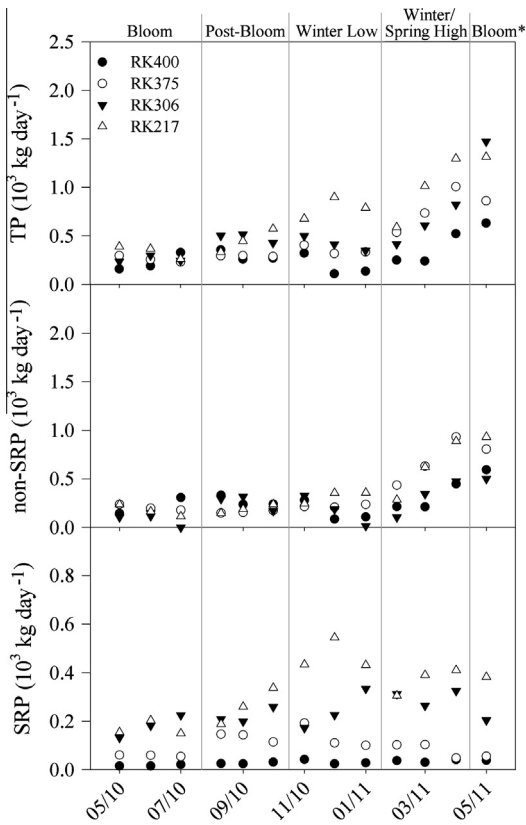

Fig. 8. TP average daily load at four selected representative sites. Seasonal periods are designated as: bloom (May–July), post-bloom (August–October), winter low (November–January), and winter/spring high (February–April). Note that the second "bloom" period (represented by *) experienced above average flows and consists only of May samples.

4. Discussion

4.1. Upstream to downstream trends in water quality

In corroboration with previous descriptions of the Klamath River as an "upside down" river system, we found that poor water quality conditions and high nutrient concentrations at upstream sites were ameliorated downstream. This appears to result from a combination of factors including the influence of reservoirs on both the production and retention of materials, as well as downstream accretion of flows and dilution from tributaries and springs with lower nutrient concentrations. In the Klamath River, reservoirs (including UKL) appeared to be the dominant influence over water quality and nutrient dynamics in the upper river, whereas tributaries appeared to exert stronger influence in the lower river.

Reservoirs have been described as sinks of nutrients and organic matter (Garnier et al., 1999; Harrison et al., 2009; Knoll et al., 2013). However, it is possible for a reservoir to temporally shift from being a sink to a source (Jones, 2010; Kraus et al., 2011; Cole et al., 2007) and seasonal changes in the composition of outflows influence downstream processing (Kling et al., 2000; Goodman et al., 2010). While UKL has previously been described as a source of nutrients (Kuwabara et al., 2012), additional reservoirs within the Klamath River appear to have varying effects on downstream trends in N versus P. Identifying stoichiometric relationships between N and P is critical for understanding ecological processes, therefore N and P should be addressed both individually and together, and in the context of other water quality characteristics.

4.2. Reservoir influence on nutrient concentrations

Total nutrient loading is a function of both discharge and concentration. As river discharge increases, nutrient concentrations can be diluted but loads can remain high. In the Klamath River, comparison of patterns in N and P loads with N and P flow-weighted concentrations elucidated that while discharge increased substantially downstream, concentrations of certain constituents also decreased independent from dilution effects. Trends shifted depending on the constituent in question; concentrations of N decreased more strongly downstream than concentrations of P. It should be noted that due to longer residence times, lag effects, and internal hydrodynamics, caution must be taken when making direct comparisons between the same sampling events at locations directly above and below large reservoirs. We discuss conditions as they present across all sites at a given period of time, with the understanding that these conditions are the result of a variety of processes occurring within the river and integrated over time.

The decreasing trend in N concentrations, representative of the "upside-down" nature of the Klamath River, was largely influenced

by Upper Klamath Lake (UKL) and Keno Reservoir (Fig. 1). During our study, the highest N concentrations were consistently observed below these lentic bodies. UKL has high background concentrations and bed load of P as a result of natural factors and surrounding land-use change (e.g. loss of wetlands, increased agriculture, etc.) (Snyder and Morace, 1997; Abrams and Jarrell, 1995). A high proportion of the P in surface sediments of UKL is considered bioavailable (Simon and Ingle, 2011), and consistent positive benthic fluxes of SRP from UKL sediments have been observed from April through August (Kuwabara et al., 2007, 2012). High P-availability is considered the controlling factor in the development of large cyanobacteria blooms in UKL (NRC, 2004). These blooms contribute appreciable amounts of organic matter and nutrients to the system and exacerbate eutrophication and poor water quality in the headwaters of the Klamath River (ODEQ, 2010; Mrazik, 2007). Due to the large volume and long hydrologic residence time of UKL (HRT $\sim$ 250 days), water entering the Klamath River is representative of conditions within UKL.

Outflow from UKL enters Keno Reservoir, a long, sinuous, reservoir with a relatively homogenous depth (mean $\sim$ 3 m). Concentrations of TN below Keno (RK375) were comparable to or greater than those above (RK400), especially during the post-bloom period and early in the winter low period. Although hydrologic residence times in Keno (HRT $\sim$ 3–13 days) are markedly shorter than those in UKL, they are sufficient to maintain algal blooms. Due to low water velocities, a large amount of the organic matter that enters or is produced within Keno settles out of the water column and decomposes, causing decreased dissolved oxygen and increased SRP and NH_4^+ (Deas and Vaughn, 2011; Sullivan et al., 2009).

The increasingly lotic nature of the river between Keno and Iron Gate Reservoirs (including RK375–RK360) results in shorter residence times, well-mixed channels, and greater bed surface area relative to river volume, all factors conducive to higher rates of benthic processing (e.g. nitrification). Dissolved oxygen levels increased in this portion of the river, the dominant form of DIN shifted from NH_4^+ to NO_3^-, and TN concentrations decreased, potentially due to uptake and immobilization of N by river biota and/or denitrification. Although the river enters JC Boyle Reservoir directly below RK367, this reservoir is small and essentially a flow-through system resulting in no obvious changes in nutrient concentrations.

In contrast, below Iron Gate Reservoir (RK306), N concentrations decreased and water quality improved throughout most of the year, with the greatest downstream differences observed during the post-bloom period. However, there were several notable exceptions to this trend. On one occasion (October 2010), increased NH_4^+ was observed below Iron Gate, possibly from mineralization of TON emanating from upstream reservoirs at the end of the post-bloom period. In addition, occasional increases in NO_3^- were observed during the winter low and winter/spring high periods below both Keno and Iron Gate Reservoirs, and may reflect discordance between the accumulation of nutrients and flushing from the reservoir (Ahearn et al., 2005). Higher winter concentrations of NO_3^- may reflect longer residence times and the accumulation of TON, followed by mineralization and nitrification prior to export. During winter periods of low biological activity, these conditions could be conducive to the increased export of NO_3^-. The lag in export is not likely a result of seasonal reservoir turnover, which could mix nutrients accumulated in the hypolimnion over the previous season (Deemer et al., 2011), since sudden turnover events are uncommon in reservoirs on the Klamath River.

As previously described, the Klamath River was relatively high in P (mean TP > 0.10 mg L^{-1}). Because P was not limiting, biological uptake was less likely to reduce downstream values of P than mechanisms of retention such as settling and sorption. Downstream increases in P can be attributed to watershed inputs as well

as internal release of P from reservoir sediments, which may contribute the majority of P inputs to reservoirs during summer months (Welch and Jacoby, 2001; Sosiak and Trew, 1996). These processes are more likely in lentic water bodies of lower gradient and lower kinetic energy, which were more prevalent in the upper river. Relative to reservoir reaches in the upper river, the lower river had greater capacity to transport P via sediments and organic matter due to larger flow velocities and steeper gradient. While reservoirs appeared to increase P concentrations within the river, reservoir P export was largely dependent on seasonal changes that influence reservoir productivity, P processing, and hydrology.

Despite seasonal differences in P concentrations, the temporal influence of reservoirs on P was not as strong or as consistent as observed for N. TP concentrations below UKL were variable, but concentrations below Keno Reservoir were frequently the highest in the river, particularly during the bloom and post-bloom periods when algal productivity was high and hypoxic or anoxic conditions were widespread.

Reservoirs appeared to influence shifts in the dominance of SRP versus non-SRP, with non-SRP consistently being higher at locations below reservoir outlets and SRP being higher downstream of lotic reaches. Algal production in reservoirs contributes to high amounts of organic P, and mortality results in the rapid microbial breakdown of the labile organic matter and the settling of the more recalcitrant fraction. The majority of recalcitrant organic P is found in particulate form, either in microbial biomass (Boström et al., 1988) or adsorbed to inorganic or detrital organic material in sediments (Rijkeboer et al., 1991). While SRP often has a rapid turnover time, adsorption processes and biotic pools can create stabilized forms of P that may persist for long periods of time within reservoir sediments, particularly in systems with abundant available P (Olsson and Jansson, 1984; Wetzel, 1999). During low oxygen conditions, sediment release of P is comprised of SRP and soluble forms of organic P (Boström et al., 1988). Due to the abundance of SRP during the growing season, P was available in excess and thus export of SRP from reservoirs was more consistent, while non-SRP was more likely to be trapped and retained within reservoirs.

4.3. Tributary and spring influence on nutrient concentrations

Reservoirs appear to play a dominant role in nutrient and water quality dynamics in the upper river. While this area also has multiple inputs from small springs and tributaries, most are considered negligible. However, there is one notable cold-water spring source ($\sim$6.4 m^3 s^{-1}) located between JC Boyle Reservoir and RK360. During our study, this spring contributed to $\sim$17% of Klamath River flows and contributed to dilution, however the spring also contributes relatively consistent nutrients ($\sim$0.029 mg L^{-1} NH_4-N, $\sim$0.25 mg L^{-1} NO_3-N, $\sim$0.066 mg L^{-1} PO_4-P) (NCRWQCB, 2010).

In contrast to the upper river, tributaries and spring inputs in the lower river were more significant in both number and volume and played a larger role in nutrient dynamics. As previously described, the tributaries of the Shasta and Scott Rivers are influenced largely by different watershed factors and therefore exhibited varying patterns in hydrology, nutrients, and water quality (i.e. SHR was more consistent in its delivery of water and nutrients across the hydrograph, whereas SCR was more ephemeral). In general, tributary TN concentrations were lower than in the Klamath River, and therefore tributaries primarily contributed to the dilution of TN. However, SCR did contain sufficient amounts of NO_3^- during periods of high discharge and as a result, NO_3^- concentrations within the Klamath River below SCR were similar or elevated relative to values above the SCR confluence.

Flow accretion from tributaries in the lower river was less effective at diluting P than N. This was largely due to contributions

from SHR, a spring-fed system naturally high in P, which increased mainstem P concentrations that were frequently than diluted below SCR. This suggests that the influence of tributaries can be stronger drivers of fluctuation and patterns in water quality than processes occurring within the main stem river and therefore should be considered when designing water quality targets and monitoring plans.

4.4. Seasonal effect of reservoirs and tributaries on nutrient loads

Depending on reservoir characteristics (i.e. size, residence time, location within the watershed, surrounding land use, etc.) the insertion of reservoirs into a riverine landscape may shift patterns in downstream loads (Bouwman et al., 2013; Jones, 2010). During our study, annual N loads were relatively similar across upper river sites, and increased slightly with distance downstream. However, on a sub-annual seasonal basis, upstream to downstream dynamics were very different. Despite downstream flow accretion throughout the year, N loads were relatively similar and/or decreased downstream during the bloom and post-bloom periods, but this pattern was reversed during the winter low and winter/spring high periods. This shift indicated that during the bloom and post-bloom periods the upper river was contributing equal or greater amounts of TN, likely as a result of additional TN via N-fixing algal blooms, most significantly in UKL, as well as contributions from agricultural and wetland runoff. During the bloom and post-bloom periods, TN loads decreased below Keno and Iron Gate Reservoirs, indicating retention or loss of TN via processes such as algal sedimentation or denitrification. The potential role of these processes within Keno and Iron Gate reservoirs was further supported by an overall decrease in TON, as well as observed decreases in the NO_3^- fraction of total DIN loads below Iron Gate Reservoir. In the lower river, TN inputs from tributaries were low and the lack of precipitation contributed little runoff from the watershed and therefore limited terrestrial TN inputs.

During the winter low and winter/spring high periods, the pattern in TN loads reversed and loads increased downstream. Higher contributions of TN from the upper river during the winter low period may result from initial flushing from UKL, Keno Reservoir, and the surrounding landscape. The lower river also had higher TN loads during these periods, although Iron Gate Reservoir did not seem to contribute significant amounts of TN until discharge increased in the winter/spring high period. The most dramatic seasonal differences in loads were observed in the lower river. Lower variability in the upper river reflected both the dampening effect of reservoirs and arid climate (i.e., less overland flow), whereas higher variability in the lower river reflected tributary accretion of flows and materials downstream of Iron Gate Dam.

In comparison to TN loads, patterns in TP loads appeared to be less influenced by algal blooms in the upper river (i.e. changes in upstream concentration) and more by seasonal changes in discharge. Higher TP loads were observed during greater discharge and where the river was increasingly lotic in nature. Transport of both particulate and dissolved P appears dependent upon conditions that contribute to the availability and release of P within reservoirs and the sediment carrying capacity of flows.

Many studies have shown that rivers can act as sinks of P during low flows, and sources of P during high flows (Haggard et al., 2001; Henson et al., 2009; Kronvang et al., 1999). High flows have been shown to agitate sediments and stimulate the release of P (Johnson et al., 1976) as well as provide increased load capacity (Keup, 1968). Higher precipitation can also increase the delivery of materials from the surrounding watershed, including erosion of P-rich sediments and delivery of P through saturated soils.

In our study, the greatest increase in TP loads below Keno Reservoir occurred during the winter/spring high flow period,

whereas during the same period TP loads decreased below Iron Gate Reservoir. In comparison to Iron Gate Reservoir, Keno Reservoir is shallower, has a shorter residence time (see Table 1), does not seasonally stratify, and has hydrologic connectivity with marginal wetlands and surrounding agricultural lands. These characteristics increase the propensity of higher flows to contribute more organic matter, sediment, and nutrients from the surrounding landscape as well as encourage the resuspension and transport of these materials from the bed. In contrast, Iron Gate Reservoir has a higher propensity to trap and retain larger sediments and particulate organic matter and export a greater proportion of colloidal and dissolved materials. Internal hydrodynamics, thermal stratification, and management operations within Iron Gate may also influence downstream export of nutrients; for example, export is more likely to occur during periods when internal reservoir dynamics result in mixing and export of nutrient rich, hypolimnetic reservoir waters. However, convective cooling in Iron Gate usually occurs slowly over months, and therefore sudden turnover events are uncommon (Deas, 2003). As a result, mixing processes are likely to result in the slow release of nutrients and organic matter over time, as opposed to large pulses associated with rapid turnover events. Export from Iron Gate may also occur during periods of strong reservoir thermal stratification, when the flow path of incoming water can "short-circuit" the reservoir and reduce mixing as warmer, high-nutrient flows are shunted through the reservoir without significant internal mixing (Fischer et al., 1979). Although this may increase productivity within a specific portion of the limnion, it also leads to decreased residence times and reduced rates of settling and processing.

4.5. Nutrient ratios and ecological stoichiometry

The stoichiometric relationship between TN:TP has ecological implications at a variety of levels, from individual species physiology and behavior, to community trophic dynamics, to whole ecosystem biogeochemistry (Sterner and Elser, 2002). TN:TP within the Klamath River vary dramatically both spatially and temporally, but were generally low and representative of eutrophic or hypereutrophic status. Low TN:TP reflects the sources of nutrients, and may indicate increasing urban, pasture, agricultural, and sewage runoff, as well as higher denitrification (Downing and McCauley, 1992). However, the naturally high P composition of soils in the upper Klamath River watershed suggests persistent stoichiometric conditions that favor seasonal dominance by N-fixing algal species, which then shift seasonal stoichiometric relationships. For example, the upper river exhibited it's highest TN:TP values during post-bloom and winter low periods, reflecting the high contribution and export of algal-derived N during these times. Due to coupling between nutrient dynamics and time scales of population change, community structure in downstream reservoirs and river reaches may shift on a seasonal basis in response to changing nutrient ratios. Understanding these responses has implications for the management of aquatic communities. For example, stoichiometric imbalances may favor species that are good competitors versus those with higher growth-rate life histories (Sterner and Elser, 2002), such as the macroalga *Cladophora*, which has been identified as preferential habitat for vectors of fish disease on the Klamath River (Stocking and Bartholomew, 2007).

5. Conclusion

Along the longitudinal gradient of the Klamath River, nutrient dynamics were influenced differently in lotic and lentic environments with seasonality playing a large role in the retention, production, and form of nutrients. Due to the importance of nutrient controls on ecological processes and productivity, an

understanding of nutrient sources, sinks, and stoichiometry should be included in monitoring programs aimed at understanding ecosystem processes, habitat suitability, and restoration of aquatic communities. This is particularly important in systems such as the Klamath River, where dam removal and anadromous fish restoration are being considered but basic water quality variables, such as temperature, may have limited capacity for improvement and so addressing nutrients may be a more viable restoration goal. Dam removal can alter the downstream fate and transport of nutrients and water quality, and can shift the role of a river reach as a nutrient source or sink (Stanley and Doyle, 2003; Ahearn et al., 2005; Doyle et al., 2005). While specific recommendations regarding dam removal are beyond the scope of this paper, the nutrient dynamics described herein should be carefully considered when weighing options for dam removal and fish restoration on the Klamath River. The "upside-down" nature of the Klamath River provides an example of a system that may benefit from inclusion and utilization of nutrient dynamics into a restoration framework, particularly in regards to the seasonal timing of reservoir and tributary influences on nutrient export and water quality.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.jhydrol.2014.06.025.

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