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Time Scales of Change in Chemical and Biological Parameters after Engineered Levee Breaches Adjacent to Upper Klamath and Agency Lakes, Oregon

Open-File Report 2012-1057

U.S. Department of the Interior
U.S. Geological Survey

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Contents

Figures

Tables

Conversion Factors

Multiply	By	To obtain
cubic foot per sec (ft^3 s^{-1})	35.31	cubic meter per sec (m^3 s^{-1})
foot (ft)	0.3048	meter (m)
liter (L)	1,000	milliliter (mL)
inch (in)	2.54	centimeter (cm)
millimole (mmol)	1,000	micromole (μmol)
micromolar (μM)	molecular weight	microgram per liter (μg L^{-1})
microgram per liter (μg L^{-1}) or part per billion (ppb)	0.001	milligram per liter (mg L^{-1}) or part per million (ppm)
micron (μm)	1,000,000	meter (m)
mile (mi)	1.609	kilometer (km)

Temperature in degrees Celsius (°C) can be converted to degrees Fahrenheit (°F) as follows: °F=(1.8×°C)+32.

Abbreviations and Acronyms

Abbreviations and Acronyms	Meaning
ALR	Agency Lake Ranch Storage Wetland
DO	dissolved oxygen
DOC	dissolved organic
J	diffusive benthic flux in milligrams per square meter per day
kg d^{-1}	kilograms per day
μg cm^{-2}	micrograms per square centimeter
m^3 d^{-1}	cubic meters per day
MDN	Mid-lake North sampling site
mg L^{-1}	milligrams per liter
mg m^{-2} d^{-1}	milligrams per square meter per day
MRM	Modoc Rim site
mS cm^{-1}	milli-Siemens per centimeter
ORP	oxidation-reduction potential
%	percent
SD	standard deviation
SRP	dissolved (soluble) reactive phosphate
TNC	sampling site in reconnected wetland managed by The Nature Conservancy
USEPA	U.S. Environmental Protection Agency
USGS	U.S. Geological Survey
WET	Sampling site within the Upper Klamath Lake National Wildlife Refuge
WMR	Sampling site near the mouth of the Williamson River
WSC	Water Science Center, USGS

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Executive Summary

Eight sampling trips were coordinated after engineered levee breaches hydrologically reconnected both Upper Klamath Lake and Agency Lake, Oregon, to adjacent wetlands. The reconnection, by a series of explosive blasts, was coordinated by The Nature Conservancy to reclaim wetlands that had for approximately seven decades been leveed for crop production. Sets of nonmetallic porewater profilers (U.S. Patent 8,051,727 B1; November 8, 2011; http://www.uspto.gov/web/patents/patog/week45/OG/html/1372-2/US08051727-20111108.html) were deployed during these trips in November 2007, June 2008, May 2009, July 2009, May 2010, August 2010, June 2011, and July 2011 (table 1). Deployments temporally spanned the annual cyanophyte bloom of *Aphanizomenon flos–aquae* and spatially involved three lake and four wetland sites. Spatial and temporal variation in solute benthic flux was determined by the field team, using the profilers, over an approximately 4-year period beginning 3 days after the levee breaches. The highest flux to the water column of dissolved organic carbon (DOC) was detected in the newly flooded wetland, contrasting negative or insignificant DOC fluxes at adjacent lake sites. Over the multiyear study, DOC benthic fluxes dissipated in the reconnected wetlands, converging to values similar to those for established wetlands and to the adjacent lake (table 2). In contrast to DOC, benthic sources of soluble reactive phosphorus, ammonium, dissolved iron and manganese from within the reconnected wetlands were consistently elevated (that is, significant in magnitude relative to riverine and established-wetland sources) indicating a multi-year time scale for certain chemical changes after the levee breaches (table 2). Colonization of the reconnected wetlands by aquatic benthic invertebrates during the study trended toward the assemblages in established wetlands, providing further evidence of a multi-year transition of this area to permanent aquatic habitat (table 3).

Both the lake and wetland benthic environments substantively contribute to macro- and micronutrients in the water column. Wetland areas undergoing restoration, and those being used for water storage, function very differently relatively to the established wetland within the Upper Klamath Lake National Wildlife Refuge, adjacent Upper Klamath Lake. Developing long-term management strategies for water quality in the Upper Klamath Basin requires recognition of the multi-year time scales associated with restoring wetlands that provide natural, seasonal ecosystem function and services.

Potential Management Implications

Long-term goals of maintaining or restoring endangered fisheries resources in Upper Klamath Lake and the downstream Klamath River Basin are dependent on the transport of essential nutrients and toxicants through benthic and pelagic food webs. The base of those food webs, from which trophic transfer begins, is dependent on sediment and water quality. In order to meet water-quality objectives for the lake (for example, to reduce the impact of nutrient cycling on endangered fish populations in the lake), an understanding of the processes governing nutrient transport and distribution is required to explain temporal and spatial trends in benthic and pelagic community composition. The structure and abundance of these communities are, in turn, linked to nutrient accumulation within the lake and wetlands as well as solute loads from upstream. Upper Klamath Lake is considered hypereutrophic; that is, the lake is characterized by excessive nutrient concentrations such as nitrogen and phosphorus that result in elevated primary productivity and associated sediment-oxygen demands. Predominance of the nitrogen-fixing cyanophyte *A. flos–aquae* in Upper Klamath Lake suggests limitation by a solute other than nitrogen. Because wetland areas became hydrologically connected to both Upper Klamath and Agency Lakes after levees were breached in October 30, 2007, this report focuses on the benthic nutrient sources from these wetlands undergoing restoration after decades of agricultural use. This study provides and evaluates measurements of benthic sources of dissolved macro- and micronutrients that may be significant relative to potentially regulated allochthonous (external) sources. In addition to phosphorus, we examine the consistency of significant ammonia and dissolved micronutrient fluxes from the sediments in these wetland areas, as was previously reported for the lake. Nonmetallic porewater profilers (U.S. Patent 8,051,727 B1), designed and fabricated for previous studies of Upper Klamath Lake (Kuwabara and others, 2009), were successfully deployed at four contrasting sites in adjacent wetland environments, including two within the reconnected wetlands. The rate at which benthic fluxes from these reconnected wetlands shift toward those levels observed in adjacent aquatic ecosystems (the established wetlands or lake habitats) should also be of interest to resource managers. Information provided herein is intended to help identify reasonable expectations when evaluating load-allocation or habitat-restoration strategies, and to understand appropriate response times for those restoration efforts. In addition, initial examination of the Agency Lake Ranch water-storage area provides insight into potential nutrient sources to the adjacent lake. Benthic-flux measurements in the wetland areas contribute to ongoing efforts to locate and quantify major nutrient sources for subsequent assessments of restoration activities in the lake and basin in general.

Background

In hypereutrophic Upper Klamath Lake, Oregon (table 1), organic carbon generated by massive cyanophyte blooms that is not transported out of the lake ultimately settles to the bed of the lake or, to some extent, wetland habitats and imposes a benthic demand for oxygen. Such a demand poses an environmental stress for endangered fish populations (Wood and others, 2006). Although phosphorus (P) may typically serve as the limiting nutrient for those nitrogen-fixing cyanophytes, the author's previous lake studies indicated that internal loading of dissolved micronutrients (for example, iron) should also be further examined. Therefore, we present water-column and benthic-flux information for both macro- and micronutrients that may be critical to source management for the basin (U.S. Fish and Wildlife Service, Hatfield Restoration Program; http://www.fws.gov/klamathfallsfwo/ero/er.html). With increasing recognition of the ecosystem services provided by wetlands, this study serves as a rare opportunity to quantify the temporal and spatial scales associated with wetland reclamation and restoration projects after levee breaches (whether engineered or due to unanticipated weather or flooding).

During the past century, massive phytoplankton blooms dominated by *A. flos–aquae* have occurred each summer in Upper Klamath Lake (UKL). After buoyant *A. flos–aquae* layers (scum) are concentrated by wind over the lake surface and cells senesce, biomass settles, and water-column dissolved oxygen is depleted at the lakebed. Such hypoxia may affect the recruitment and survival of lake fauna, including endangered populations of the shortnose sucker (*Chasmistes brevirostris*) and Lost River sucker (*Deltistes luxatus*). Indeed, the sustainability of sucker populations is linked to the water quality in the lake and to the nutrient sources that regulate the intensity of *A. flos-aquae* blooms and the succession of algal assemblages before and after those blooms. Of particular significance is the appearance of the non-nitrogen-fixing, hepatotoxin-producing cyanobacterium *Microcystis aeruginosa* (Kann, 2006). Though not abundant relative to *A. flos-aquae*, *M. aeruginosa* has been consistently detected in both Agency and Upper Klamath Lakes. Sources and distributions of microcystin in Upper Klamath Lake are currently being investigated by other collaborating U.S. Geological Survey (USGS) projects within the Ecosystems Mission Area and the Oregon Water Science Center.

To restore ecosystem services to a historic wetland area adjacent to Upper Klamath Lake, Oregon, a series of ~2,000 blasts, using >90,000 kg of explosives once again flood the area on October 30, 2007 (fig. 1). This hydrologically reconnected wetland, with an area of 11 km^2, had been used for crop production for approximately seven decades. Across Agency Strait from the reconnected wetland, an established wetland exists within the Upper Klamath Lake National Wildlife Refuge. The established wetland, with an area of 56 km^2, has been protected as a wildlife refuge since 1928 and is administered by the U.S. Fish and Wildlife Service and the Bureau of Reclamation. To the north of the established wetland, a regulated wetland within Agency Lake Ranch (40-km^2 area, table 1) has served as a water-storage area since 2002 to maintain water elevations in the adjacent lakes during the summers. Flow into and out of the water-storage wetland is temporally variable over multiple time scales (daily to yearly). For example, in 2008, water flowed into the storage wetland from January 2 to April 7, and then was pumped out to Agency Lake between April 8 and April 21. However, additional late precipitation that year allowed further flow into the storage wetland between May 2 and May 14 for a total of 1.1x10^7 m^3 that calendar year. Discharge from the storage wetland restarted on June 2 and did not end until July 21, 2008. By contrast, in 2011, the storage wetland had not been used (that is, was not flooded) the prior year due to inadequate precipitation, but flow into the storage-wetland occurred over a single interval, starting on January 20 and ending on May 16, 2011, for a similar total of 1.1x10^7 m^3 that year. Pumping from the storage wetland into Agency Lake commenced on May 19 and ceased on June 28, 2011. In summary, the timing of flow into and out of the water-storage wetland in 2008 and 2011 varied greatly. The authors hypothesized that this variability would affect benthic solute flux and the composition of benthic invertebrate assemblages within the storage wetland.

Problematic algal blooms are fueled by external and internal loads of particle-reactive solutes (for example, ligands like phosphorus as orthophosphate or metals like iron). As these solutes repartition and change in chemical speciation, benthic sources of these nutrients may play a major role in phytoplankton dynamics and succession (Kuwabara and others, 2009). Following the decades-old statement by Miller and Tash (1967) that “It is imperative to know the extent to which nutrients in the sediments can interchange with the overlying water,” we provide benthic-flux determinations for macro- and micronutrients in Upper Klamath Lake and adjacent wetland environments following the engineered levee breaches by The Nature Conservancy on October 30, 2007.

Objectives

In support of science-based restoration/management strategies for Upper Klamath Lake and downstream ecosystems, this report presents the results of a study that provides measurements of the benthic fluxes of dissolved macronutrients and trace elements between the bed material and overlying water column at three lake and four wetland sites following planned levee breaches that hydrologically reconnected Upper Klamath and Agency Lakes to adjacent wetlands. Taxonomic composition of benthic invertebrate assemblages, benthic-chlorophyll and water-column solute concentrations were also analyzed to help interpret solute-flux results. The present study tests two hypotheses. First, because some of the macronutrients (for example, SRP and ammonia) and many of the trace elements (for example, cadmium, copper, iron, manganese, nickel, and zinc) are chemically reactive and adsorb to biotic and abiotic surfaces, the authors hypothesize that benthic nutrient sources could be significant relative to previously quantified fluvial sources within these predominantly shallow water habitats (<3 m in depth). Although many trace elements (for example, copper, iron, manganese and zinc) serve as essential micronutrients, they are sometimes required at such low concentrations that even sub-micromolar concentrations can be excessive and produce a toxic response (for example, algicidal response of copper and zinc in uncomplexed form). Given the paucity of trace-metal information for this or any other part of the Klamath River Basin, we provide preliminary information on trace-element benthic flux for Upper Klamath Lake and the adjacent wetlands with the intent of contributing scientific information for future resource-management decision making. Secondly, we hypothesize based on the physical, chemical, and biological parameters measured in this study that the reconnected wetlands, water-storage wetland, established wetland within the Upper Klamath Lake National Wildlife Refuge, and adjacent lake function differently. Because flows into and out of the water-storage wetland are dependent on the timing and volumes of precipitation and runoff that vary over multiple time scales, we also provide preliminary chemical and biological characterization for this water source to the adjacent lakes.

Results and Discussion

Ancillary Parameters

Ancillary parameters (for example, temperature, specific conductivity, pH) at the profiler deployment sites are provided to establish the basic physical and chemical context necessary to interpret benthic-flux results. Except for the mid-lake north (MDN) site (~4 m depth), the sites where profilers were deployed were shallow (<3 m depth), with minimal haloclines or thermoclines. Specific conductivity values varied over a narrow range (0.04 to 0.12 mS cm^{-1}), with an expected trend of lowest values during the pre-bloom and early-bloom deployments as snow melt diluted lake waters (June 2008 and May 2009) and elevated values during the post-bloom samplings as lake waters evaporated and water elevations decreased (November 2007 and July 2009). Consistent temperature ranges reflected seasonal air-temperature patterns affecting the shallow water column at the three lake and four wetland sites (table 1; 6.0 to 7.6^{o}C in November 2007 and 23.0 to 25.1^{o}C in July 2009). Observed seasonal ranges are consistent with previous and ongoing monitoring of Upper Klamath Lake by Wood and others (2006). For pH, with the exception of the Upper Klamath Lake National Wildlife Refuge (WET; pH range 4.9 to 7.3 over the 4 deployment days), pH was typically above 7 and as high as 9.5. Profiles were routinely taken within the 3 hours after sunrise (just before profiler retrieval), and therefore even higher pH values may be expected (for example, >9.5 pH values reported by Wood and others (2006)) as solar energy increases later in the day and phytoplankton accelerate their removal of dissolved inorganic carbon from the water column. As pH increases, the chemical speciation and partitioning of biologically reactive solutes are significantly affected. For example, as pH rises above 9.3, the negative logarithm of the acid dissociation constant for the ammonium ion (NH_4^+), uncharged and toxic ammonia (NH_3) (Arillo and others, 1981; Randall and Tsui, 2002) becomes more thermodynamically stable relative to the ammonium ion. Consistent with these observations for ammonium speciation, Falter and Cech (1991) reported a maximum pH tolerance of 9.55 ± 0.43 for shortnose suckers. Secondly, as pH elevates, adsorbed anions (for example, orthophosphate) repartition from particulate to the more biologically available, dissolved phase (Sigg and Stumm, 1981; Goldberg, 1985; Fisher and Wood, 2001). Furthermore, in an oxic (aerobic) environment biologically reactive trace elements (for example, iron and manganese and copper) become less soluble (and hence less bioavailable to primary producers) because precipitates and adsorbed forms become more stable (Hogfeldt, 1982; Kuwabara and others, 1986) thereby decreasing uncomplexed (that is, more bioavailable) metal species.

Benthic Flux of Macronutrients

Upon retrieving the porewater profilers from restored-wetland sites TNC1 and TNC2 within the reconnected wetlands in 2007 following the levee breaches, a concentration gradient for dissolved organic carbon (DOC) was visible in profiler samples (table 2) with clear overlying waters transitioning to black-tea colored samples at a 10-cm depth. Porewater samples were similarly tea colored in the storage wetland (ALR) along with the water column (fig. 2), suggesting new input of organic carbon. Benthic fluxes, calculated using Fick's Law, for DOC were greatest at the newly restored sites (as high as 712+498 mg m^{-2} d^{-1} at the newly restored wetland site TNC1, table 2). A positive flux denotes transport from the benthos to the overlying water column. This initial elevated DOC flux in the restored wetland is consistent with measurements by Aldous and others (2005) of elevated organic carbon in the soils of the reconnected wetlands (prior to the levee breaches) as compared to soils from undisturbed wetlands (for example, within the Upper Klamath Lake National Wildlife Refuge). This soil organic carbon could serve as a source for release to the overlying waters of the reconnected wetland. Over the past three years, those positive DOC fluxes have consistently decreased over each sampling event to negligible levels as concentration gradients near the sediment-water interface in the reconnected wetlands have dissipated, converging to values representative of the established wetlands in the Upper Klamath Lake National Wildlife Refuge and in the lake (table 2). Consistent with that observation, the tea-colored porewater samples faded near the sediment-water interface and became confined to the deeper porewater depths (that is, 5.5 and 10 cm). It should, however, be noted that DOC fluxes in the reconnected wetland in July 2011, our final set of profiler deployments, exhibited an increase relative to the previous year (i.e., 16.0+9.4 and 47.7+15.3 mg m^{-2} d^{-1} at sites TNC1 and TNC2, respectively). In contrast to initial DOC fluxes in the restored wetland sites, both lake sites and the established wetland site in the Upper Klamath Lake National Wildlife Refuge exhibited concentration gradients that were orders of magnitude smaller (table 2). In fact, both lake sites displayed an insignificant DOC flux immediately following the levee breaches (-2.3+ 2.9 and -4.2 + 4.6 mg m^{-2} d^{-1} for sites MRM and WMR, respectively). On the basis of this contrast, one might hypothesize that the observed wetland DOC source to the adjacent lake after the levee breaches may serve to inhibit primary production by constraining nutrient bioavailability or by producing toxic photolytic byproducts (Jackson and Hecky, 1980; Jones and others, 1993; Kim and Wetzel, 1993; Klug, 2002; Haggard, 2008; Lindenberg and Wood, 2009). However, a lake-wide response to DOC input from the reconnected wetlands was not observed (Kannarr and others, 2010; Wong and others, 2010). The DOC concentration at site WMR, closest to the mouth of the Williamson River, increased from 4.3 mg L-1 on October 30, just prior to the breaching of the levees, to 6.4 mg L-1 on November 6, 2007, and efflux from the reconnected wetland may have contributed to this increase. However, that increase at WMR site was within the temporal variability of DOC data for that year (Kannarr and others, 2010). The concentration at WMR 7 days later on November 13, 2007, was 4.0 mg L^{-1}, so any contribution from the newly connected Delta was short-lived. At all other sites, no elevated DOC concentrations in the lake water column were determined during weekly water-quality monitoring in 2007 immediately following the levee breach on October 30 (Kannarr and others, 2010), and at most sites the concentration decreased between the sampling date immediately prior to and immediately following the levee breach. In addition, no elevated DOC concentrations were detected in the lake water column during porewater profiler sampling in 2008 or any other sampling period following the levee breaches (table 2), not even at lake sampling sites nearest the northern boundary, where overlying waters from the reconnected wetlands drain into the lake and become entrained in the clockwise lake currents (sites WMR and MRM). Second, no discernible decreases in chlorophyll *a* concentrations in the Upper Klamath Lake water column were observed in the year after the levy breaches. April and May chlorophyll *a* concentrations measured during routine monitoring were lower in 2008 than in 2007, but this is as expected given that spring temperatures were lower in 2008 as well (Kann, 2010). The surface area of the reconnected wetlands (11 km^2) is less than 10% of the area of Upper Klamath Lake (approximately 200 km^2) with similar depths of 2 to 3 m at sites TNC1 and TNC2. Wetland sources of DOC may, therefore, have been effectively diluted by the lake and absorbed by the lake benthos. The net DOC effect of the wetland restoration appears to have been spatially constrained to the reclaimed area, and temporally constrained to our 3-year period of observation. A motivation for the 2011 spring sampling was to acquire comparative flux data from the storage wetland ALR. Because of insufficient precipitation in 2010 water years, ALR was not used to regulate lake water levels. DOC fluxes in ALR indicate a site with notable small-scale (within-site) variability relative to the other sampling sites. The coefficients of variation (CVs) for ALR were 20.4 and 1.4, whereas CVs for all other sites were 0.9+1.0 (n=44). However, DOC benthic fluxes at ALR were two orders of magnitude lower than maximum values observed in the reconnected wetland after the levee breaches. One might expect that diffusive DOC fluxes would be suppressed in ALR relative to other sites because water-column DOC was highest at ALR (fig. 2; table 5).

Benthic flux of ammonia, particularly at elevated pH in the overlying water column, has toxicological implications for endangered fish populations in both lake and wetland environments. Concentrations within or above the mortality threshold for Lost River suckers (0.37 to 0.69 mg-N L^{-1}; Meyer and Hansen (2002)) were determined in surface water-column samples three times in this study (table 2). Although no fish mortality was observed or reported, such incidents would compel fish populations to migrate to other less toxic areas of the lake. In addition, Arillo and others (1981) observed sublethal dissolved-ammonia effects in both brain and liver in rainbow trout at much lower concentrations (0.02 mg-N L^{-1} in un-ionized form). In this study, 15 of 22 surface-water samples from both the lake and wetlands exceeded that un-ionized dissolved-ammonia concentration of pH.8.6 (table 2). Furthermore, consistently positive benthic fluxes of dissolved ammonia indicate elevated solute concentrations in bottom waters above the sediment-water interface, where the endangered suckers feed. Martin and Saiki (1999) determined in their fish-cage studies of the Lost River sucker (Deltistes luxatus) that elevated concentrations of un-ionized ammonia may be contributing to the precipitous decline of sucker populations in Upper Klamath Lake, although depletion of dissolved oxygen in the water column (a factor that covaries with ammonia) exerted an even stronger influence on sucker mortality. As reported in previous lake studies (Kuwabara and others, 2009), ammonium fluxes to the water column were consistently positive except for two measurements at the restored wetland sites (TNC1 and TNC2) immediately following the levee breaches in November 2007 (-0.39+0.28 and -0.96+0.30 mg m^{-2} d^{-1}, respectively; table 2). Minimum and maximum ammonium fluxes in the wetlands bracket those observed for the lake sites, with the highest ammonia fluxes observed in the established wetland site, WET (306+38 mg m^{-2} d^{-1}). Consistent with previous ammonium-flux estimates for the lake (Kuwabara and others, 2009), dissolved ammonium during this study displayed positive benthic fluxes of 5 to 35 mg m^{-2} d^{-1} (approximately 1,000 to 6,900 kg d^{-1} when areally averaged). In contrast, dissolved ammonia was consistently <0.05 mg-N/L in tributary samples, so even at the highest discharge to the lake measured during the present study in May 2009, riverine input for dissolved ammonia would be <128 kg d^{-1} considerably lower than the benthic fluxes determined in the present study. Following the November 2007 sampling, ammonium fluxes at TNC1 and TNC2 subsequently shifted to positive fluxes, out of the benthos, with one exception at TNC1 in May 2011 (-0.28+0.44 mg m^{-2} d^{-1}). The predominance of positive ammonia fluxes within the reconnected wetland in this study is consistent with all other lake and wetland sites. The highest value (125+62 mg m^{-2} d^{-1}; table 2) was measured in the established wetland after the *A. flos-aquae* bloom in August 2011. Kuwabara and others (2012) observed a positive correlation (r=0.92, n=17) between dissolved-ammonia benthic flux and water-column dissolved ammonia within wetland sites, suggesting a benthic source that affects water-column concentrations, particularly in late summer after the *A. flos-aquae* bloom. That correlation was primarily affected by elevated values of both constituents that were typical for post-bloom conditions in the established wetland. As with DOC fluxes, the potential importance of within-site variability for ammonia fluxes in ALR was also measured with CVs of 0.6 and 1.7, compared to CVs for other sampling sites (0.4+0.3, n=44). Although consistently positive, the magnitude of ammonia benthic fluxes in ALR (1.5+1.8 mg m^{-2} d^{-1}, n=2) were unremarkable relative to the maximum value mentioned above. Yet water-column dissolved ammonia in ALR was the highest among all sites for both sampling dates. For those managing lake elevations, it may therefore be prudent to monitor dissolved ammonia in ALR prior to water release because of the toxicological implications of ammonia.

As with DOC porewater gradients, concentration gradients for dissolved nitrate initially decreased with depth after the levee breaches like adjacent Upper Klamath Lake (that is, consumed by the sediment bed to generate a negative benthic flux). During subsequent sampling trips, nitrate concentrations decreased to consistently non-detectable (<30 µg/L) concentrations above and below the sediment-water interface, like the established wetlands in the wildlife refuge (table 5). Negative nitrate fluxes have been previously reported for Upper Klamath Lake (Kuwabara and others, 2009) and typically represent a benthic microbial demand for dissimilatory nitrate reduction. Nitrate fluxes were also low in ALR (that is, non-detectable and 0.02+0.04 mg m^{-2} d^{-1} in June 2008 and May 2011, respectively).

As previously reported for Upper Klamath Lake (Kuwabara and others, 2009), benthic flux of soluble (0.2-µm filtered) reactive phosphorus (that is, a biologically available form of dissolved phosphorus, SRP) was consistently positive (table 2), with the exception of the established wetland refuge (WET) in May 2009. Unlike DOC fluxes, SRP benthic flux did not decrease at either of the reconnected wetland sites TNC1 or TNC2. The SRP benthic flux ranged from a negligible value (-0.19±0.91 mg m^{-2} d^{-1}; table 2) within the established wetland refuge to 74±48 mg m^{-2} d^{-1} at the newly restored wetland site TNC1, which is somewhat removed (>100 m away) from the levee breach. Both extreme SRP-flux values were measured in samples collected in May 2009 before the annual *A. flos-aquae* bloom. The magnitude of such SRP fluxes is not anomalous for wetland environments. Using flux chambers, Duff and others (2009) measured SRP fluxes from the Wood River wetland of 72±36 mg m^{-2} d^{-1} before the summer bloom in 2005, decreasing to insignificant levels (19±60 mg m^{-2} d^{-1}) by August after the bloom. When areally averaged (11 km^{2} for the newly reconnected wetlands; Wong and others (2011)), the SRP flux to the overlying water column is approximately 87,000 kilograms (kg) over the 3-month *A. flos-aquae* bloom season, exceeding the magnitude of riverine inputs to the whole system (28,000±17,000 kg for the season, table 4). In laboratory studies, Aldous and others (2007) observed a total P release of 1 to 9 g m^{-2} from restored-wetland soils, mostly during the first 48 hours of soil-core incubation. They observed no significant total-P release beyond the initial 62 days of core incubation. If one averages those fluxes over the 62-day initial period (an underestimate relative to the fluxes observed during the first 48 hours of incubation), those observed total-P fluxes would be approximately 16 to 145 mg m^{-2} d^{-1} of total P (or 210 to 1,887 kg d^{-1} of total P over the 11 km^{2} area of the reconnected wetlands). Different conclusions about the rates and trends of these benthic sources have been reached by others working in the reconnected wetland using different spatial and temporal scales. Laboratory incubations and studies of horizontal water-column concentration gradients (Aldous and others, 2005; Wong and others, 2011) have reported attenuation in horizontal water-column gradients and greater dissolved P efflux from the restoration-wetland sediments than those from undisturbed ones, like the wildlife refuge (our WET site). For example, using water-column concentrations before and up to three weeks after the wetland flooding, Wong and others (2011) calculated benthic flux of total P (primarily as SRP) of 10 mg m^{-2} d^{-1}, less than that predicted by laboratory experiments (Aldous and others, 2007), but within the range reported herein. They also hypothesized that the benthic source of dissolved phosphorus would be short-term; that is, constrained to the initial months after the wetlands were flooded.

Our direct measurements of the porewater concentration profiles that drive diffusive flux indicate a longer-term source that did not exhibit significant signs of dissipation over our 3-year sampling period. The discrepancy between results previously reported from the water-column and laboratory approaches, and those reported herein may be explained by three conceptual differences. As multiple years elapse after wetland flooding, both water and sediments exchange between the wetlands and adjacent lakes, such that the wetlands serve as both sources of remobilized SRP and a sink for adsorbed phosphorus species accumulated in lake sediments. That is, while the substrate existing in the wetlands at the time of the flood may begin to lose some of its original P, the bottom sediment of these hydrologically reconnected wetlands may also accumulate P from freshly settled lake sediment and algae, facilitating and sustaining internal recycling. Although a sedimentation rate has not been quantified for the reconnected wetlands, a surficial layer (~5 – 10 cm in depth) of unconsolidated sediment overlies remnant grain stalks from prior agricultural use. Secondly, the approach of calculating vertical flux across the sediment-water interface from temporal differences in water-column concentrations may be constrained by assumptions of negligible, or at least constant, horizontal transport between the newly reconnected wetlands and the lakes both north and south. This is because the water column concentration at any particular site and time of a constituent that enters the water column from the benthos depends on 1) the length of the pathway that the sampled parcel of water has taken over the substrate and 2) the speed of the currents, which together control the amount of time that the parcel of water has spent overlying the benthos. Simulations of numerical tracers with a hydrodynamic model have shown that the rate at which water moves through the reconnected wetlands depend on the speed and direction of the wind, the lake elevation, and the flow in the Williamson River (Wood, 2012). Because the wind, in particular, is highly variable over short time scales, it is to be expected that even a fairly consistent benthic flux will result in water column concentrations that are highly variable over time scales as short as a day (Wood, 2012). Third, as aquatic benthic invertebrate assemblages recolonize the reconnected wetlands (table 3), diffusive solute fluxes will be enhanced (Devine and Vanni, 2002; Kuwabara and others, 2009). These results in no way diminish the importance and potential benefits of wetland restoration for habitat and water-quality management. They do, however, offer a different time scale for transitions toward those restoration goals based on concentration gradients that drive benthic flux. Elevated SRP benthic flux at TNC1 relative to all other lake and wetland sites (including TNC2 near the breached levee) in 2009 suggest that the reconnected wetlands, at least chemically, remain in a transition period after the levee breaches on October 30, 2007. Benthic fluxes of SRP in ALR (0.57 ± 0.18 and 1.14 ± 0.79 mg m^{-2} d^{-1} for June 2008 and May 2011, respectively) were well below maximum values mentioned above for other wetland sites (for example, 74 ± 48 mg m^{-2} d^{-1} at site TNC1 in May 2009). However, during the pre-bloom sampling in June 2011, the highest water-column SRP was observed at ALR (0.70 ± 0.27 µg L^{-1}) relative to the other six sites sampled on that trip. This suggests that further examination of dissolved phosphorus inputs from ALR may be warranted to aid in the timing of water releases from ALR.

Among macronutrients, SRP (primarily as dissolved orthophosphate) is an extremely particle-reactive solute as pH becomes elevated, meaning that it can form surface complexes on a variety of mineral and biotic surfaces (Sigg and Stumm, 1981; Goldberg, 1985; Kuwabara and others, 1986; Ruttenberg, 1992). As particulate P settles in the lake, it accumulates in the bottom sediments. Various biogeochemical processes related to changes in acid-base and redox (oxidation-reduction) chemistry near the sediment-water interface can recycle this P and generate a benthic flux of bioavailable P that may far exceed external sources (Kuwabara and others, 2003). Because the dominant phytoplankton taxon, *A. flos-aquae*, is a nitrogen-fixing cyanophyte, it may be reasonable to assume that a nutrient other than nitrogen (for example, phosphorus, iron or manganese) may serve as the limiting nutrient (Istvánovics, 2008). The implications of dissolved micronutrient results (that is, coordinated benthic flux, water-column, and tributary-inlet data; table 2; table 4) suggest that they also should be carefully considered as potential regulators of primary productivity.

Dissolved (0.2-µm filtered) Nutrients in the Water Column

Soluble reactive phosphorus (SRP) was lower than detection limits (<0.03 mg-P L^{-1}) at all lake and wetland sites in November 2007 following the planned levee breaches (table 5). Wong and others (2011) reported SRP values between 0.05 and 0.53 mg-P L^{-1} in the wetlands and 0.02 to 0.07 mg-P L^{-1} in Upper Klamath and Agency Lakes three weeks after the levee breaches. In June 2008, during the bloom 7 months after the levee breaches, SRP was again below detection limits in the lake and consistently <0.1 mg-P L^{-1} at all three wetland sites. Consistent with previous studies within the Upper Klamath Basin (Kuwabara and others, 2007; Kuwabara and others, 2009), SRP concentrations from 2009 sampling trips indicate higher concentrations at the end of the annual *A. flos-aquae* bloom (July 2009) relative to before (May 2009) for all six lake and wetland sites. That is, SRP was not depleted but rather increased over the bloom period. This observation suggests the possibility of other limiting factor or factors. It is, however, worth noting that benthic interactions affecting water-column solute concentrations are subject to short-term (subseasonal) variability in shallow lakes like Upper Klamath Lake, contrasting seasonal nutrient trends typical of mono- or dimictic lakes (that is, vertically stratified lake water columns that vertically mix during one or two periods of the year, respectively; Wetzel, 2001).

Wetland samples from the newly restored wetland areas (sites TNC1 and TNC2) in July 2009 yielded the highest SRP concentrations (0.21 and 0.20 mg-P L^{-1}, respectively) providing additional evidence that the newly reconnected wetlands remain in a period of chemical transition. In an independent study by the Bureau of Reclamation (unpublished data, Klamath Falls, OR), orthophosphate (a major component of SRP) in the water column from the inflow and outflow areas of ALR were measured on six days during the spring of 2011 while storage wetland was being filled. Concentrations near outflow were consistently higher than at the inlet with a difference of 0.07±0.02 mg-P L^{-1}, n=6). Such an increase would be consistent with a positive benthic flux of SRP in ALR. It would take approximately three months to generate such a water-column increase assuming the diffusive benthic flux measured in May 2011 (table 2); it would take less time if that diffusive flux was enhanced by bioturbation or invertebrate excretion.

Water-column concentrations for DOC ranged 3.5±0.1 mg-C L^{-1} in the reconnected wetland in November 2007 following the levee breaches to 33.9±1.1 mg-C L^{-1} at ALR in June 2011. In fact, the only two DOC measurements made in ALR (26.4±0.5 and 33.9±1.1 mg-C L^{-1}) were the highest observed during the study. By comparison, the overall DOC average for all sampling sites aside from ALR was 6.6±2.4 mg-C L^{-1} (n=45). In his review, Curtis (1998) reported a range of DOC for wetlands of 10 – 50 mg-C L^{-1} that brackets the ALR measurements. Similar to dissolved ammonia and SRP, dissolved silica was consistently higher in post-bloom conditions relative to pre-bloom. Concentrations ranged from 6.7±0.0 mg-Si L^{-1} (n=2) at lake site MDN in May 2009 prior the annual *A. flos-aquae* bloom, to 48.3±0.4 mg-Si L^{-1} at TNC1 in August 2010 following the annual cyanobacterial bloom. Dissolved-nitrate concentrations were consistently low, with detectable concentrations (>0.03 mg-N L^{-1}) only observed after the annual *A. flos-aquae* bloom. In contrast to other sampling dates when 75% of samples contained <0.03 mg-N L^{-1} (that is, below the detection limit), samples collected in November 2007 following the levee breaches exhibited elevated nitrate concentrations that ranged from 0.14 to 0.18 mg L^{-1}. As previously reported in studies of Upper Klamath Lake (Kuwabara and others, 2007), dissolved-ammonium and silica concentrations, like SRP, were higher after the annual *A. flos-aquae* bloom compared to before (table 5) at all lake and wetland sites where comparable data are available. With only two sampling trips to ALR, the importance of SRP inputs to the adjacent lake due to water releases cannot be discussed with certainty. As noted above, water-column SRP was highest in ALR for June 2011. Further investigation of SRP temporal trends in ALR may, therefore, be warranted to assist water-quality managers in the appropriate timing of water releases from ALR.

Benthic Flux of Trace Metals

Information on the flux of trace elements across the sediment-water interface for any part of the Klamath River Basin is limited (Kuwabara and others, 2007). Using calculations based on Fick's law, as for nutrients above, the present study provides among the first dissolved trace metal benthic-flux estimates for the wetland and lake sites following engineered levee breaches. Both dissolved iron and manganese exhibited dramatic concentration differences between overlying waters and porewaters, with that in the deepest porewater sample at 10 cm often being two orders of magnitude higher than in the overlying sample. Calculations based on these gradients yielded flux estimates for iron ranging from -0.08±0.12 mg m^{-2} d^{-1} in the Upper Klamath Lake National Wildlife Refuge in May 2009 to 61±76 mg m^{-2} d^{-1} at site TNC2, also in May 2009. The elevated error estimate about the TNC2 mean flux is a reflection of small-scale (within site) variability in concentration gradients; the triplicate flux estimates were 15.4, 18.5 and 148 mg m^{-2} d^{-1}, all three higher than any other site mean in this study (table 6). As mentioned in the prior section on macronutrient fluxes, the disparity between iron fluxes in the Wildlife Refuge (WET) and sites within the newly reconnected wetlands (TNC1 and TNC2) suggest an ongoing transition for areas inundated in 2007 by the levee breaches. Dissolved-iron fluxes observed at wetland sites in this study (9.39±16.74 mg m^{-2} d^{-1}, n=12) were more variable than for lake sites (5.45±3.81 mg m^{-2} d^{-1}, n=10). Dissolved-iron flux estimates at lake sites were similar to those reported in previous studies (Kuwabara and others, 2009); with higher fluxes at the Williamson River delta site (WMR) than at the Modoc Rim site (MRM, fig. 1). By comparison, maximum iron-flux estimates for oligotrophic Coeur d'Alene Lake, Idaho, were lower than those reported herein (1.1 mg m^{-2} d^{-1}; Kuwabara and others (2000), as determined by core incubations). The maximum diffusive iron flux observed in this study (61±76 mg m^{-2} d^{-1})

generates an areally averaged benthic flux of 668±985 kg d^{-1} that is comparable to the highest measurement of riverine inputs (732 kg d^{-1}) determined during spring high flow in June 2011 (table 4). Furthermore, benthic flux exceeds previous estimates of riverine iron inputs by an order of magnitude (areally averaged at 0.7±0.1 mg m^{-2} d^{-1} during spring high flow and 0.3±0.1 mg m^{-2} d^{-1} during summer low flow; Kuwabara and others (2009)). At ALR, both iron-flux determinations (1.24±0.65 and -0.01±0.01 mg m^{-2} d^{-1}) were well below maximum values mentioned above from the reconnected wetland. All iron benthic fluxes, including those from ALR, are conservative estimates because diffusive porewater flux estimates do not account for bioturbation or bioirrigation by macroinvertebrates, which are likely to enhance solute flux (Kuwabara and others, 2009). Conversely, diffusive iron fluxes could overestimate the transport of bioavailable iron into the water column. Reduced iron species prevalent in the deeper samples could become more particle-reactive (removed from dissolved pool) as they reach an oxidized water column. Elevated dissolved-iron concentration gradients within the newly restored wetland areas may represent remobilized iron in dense, decomposing agricultural remnants, as observed before the levee breaches, but trace-element analysis of bed sediment would be required to confirm this hypothesis.

As with iron fluxes, dissolved-manganese flux estimates were typically positive and ranged from -0.01±0.02 mg m^{-2} d^{-1} in the Wildlife Refuge in November 2007 to 8.78±4.91 mg m^{-2} d^{-1} at WMR in July 2009. The average of all manganese flux estimates for this study (1.1±1.6 mg m^{-2} d^{-1}, n=47 ; table 6) is two orders of magnitude lower than that reported for Lake Coeur d'Alene, Idaho (190±59 mg m^{-2} d^{-1}, n=12), an oligotrophic lake with surficial sediment deposits of iron and manganese oxyhydroxides (Kuwabara and others, 2000; Kuwabara and others, 2003). The maximum diffusive manganese flux observed in this study (8.78±4.91 mg m^{-2} d^{-1}) generates an areally averaged benthic flux of 1,756±983 kg d^{-1} that exceeds by more than an order of magnitude the highest measurement of riverine inputs (19 kg d^{-1}) determined during spring high flow in June 2011 (table 4). As with dissolved-iron benthic flux, dissolved-manganese benthic flux at ALR (0.21±0.15 and 0.05±0.08 mg m^{-2} d^{-1}) were well below maximum values mentioned above from WMR near the mouth of the Williamson River.

In contrast to iron and manganese fluxes, dissolved-copper and dissolved-zinc fluxes were generally negligible or slightly negative (table 6). At observed levels of copper and zinc, neither is anticipated to provide a toxic effect on phytoplankton production (Kuwabara and Leland, 1986; Stauber and Florence, 1987) (table 6). Other metals discussed in the water-column section below (cobalt, nickel, lead, and zinc), like copper, did not exhibit statistically significant concentration gradients near the sediment-water interface, hence the diffusive fluxes would also be negligible.

Dissolved (0.2-µm filtered) Trace Metals in the Water Column

Low trace-metal concentrations in volcanic pumice, that dominates inorganic sediments of Upper Klamath Lake, generate consistently low particulate trace-metal concentrations relative to other lacustrine environments (Martin and Rice, 1981). Although data for dissolved, and hence more biologically available, trace metals in the Upper Klamath Lake are sparse (Kuwabara and others, 2007; Kuwabara and others, 2009), they also reflect a trace-metal-depleted environment in the dissolved phase. Data described herein extend this sparse information base to include dissolved trace-metal concentrations in the wetlands adjacent to Upper Klamath and Agency Lakes. For all dissolved metals, the overlying-water concentrations (collected approximately 1 cm above the sediment water interface by the porewater profilers, see Methods section) compared favorably with surface-grab samples (collected approximately 1 m below the surface; table 7). As previously reported for Upper Klamath Lake, many of those metals (for example, cadmium, cobalt, lead, and zinc) were present at dissolved concentrations below or near detection limits (Kuwabara and others, 2009) (table 7). Concentration gradients across the sediment-water interface for these metals were not observed, and hence diffusive fluxes are not tabulated.

For dissolved copper, concentrations in the water column were well above detection limits (>0.002 μg L^{-1}) but consistently below 3 μg L^{-1} and exhibited a range of 0.05±0.27 μg L^{-1} at the Wildlife Refuge site (WET) in August 2011 to 2.05±0.02 μg L^{-1} in the Agency Ranch wetland (ALR) in June 2011. Elevated dissolved-copper concentrations in ALR is not surprising considering elevated DOC, that represents organic ligands in the ALR water column to enhance copper solubility through chelation (table 7; fig. 2). Samples from the WET site were routinely lowest in dissolved copper for any given date among sites. Temporally, samples during the pre-bloom conditions of May 2009 were lowest in dissolved copper at each site, except for the mid-lake north (MDN) site. Consistently low dissolved-copper concentrations were observed among lake and hydrologically reconnected TNC1 and TNC2 sites near the sediment-water interface. Hence the dissolved-copper benthic fluxes, like those for cadmium, cobalt, lead, and zinc, were also negligible (table 6).

Dissolved iron, an essential micronutrient for primary production, varied greatly in concentration from undetectable (<5 μg L^{-1}) levels at MRM in November 2007 after the levee breaches, to 284±2 μg L^{-1} in Agency Lake Ranch (site ALR) in June 2011. In particular, for all sampling dates, the average dissolved-iron concentrations in sampled wetland sites exceeded those for lake sites. This is not surprising, because for each sampling date the highest iron fluxes were observed in the wetlands, with one exception. Furthermore, dissolved iron in ALR was highest among all sites (table 7). Similar to dissolved Cu, one might expect elevated dissolved iron concentrations at ALR due to visibly elevated DOC that was previously shown to be well correlated with dissolved iron (Kuwabara and others, 2009; table 5, fig. 2). In June 2008 and June 2011, relatively low iron diffusive flux (1.24±0.65 and -0.01±0.01 mg m^{-2} d^{-1}, respectively) at wetland-storage site ALR was associated with the two highest water-column concentrations for dissolved iron (234±19 and 284±2 μg L^{-1}, respectively). We hypothesize that, by those sampling dates, dissolved iron in the water column of Agency Lake Ranch (site ALR), used for water storage, approached chemical equilibrium with the porewater. Soon after, this storage reservoir was drained into Agency Lake to help maintain lake levels. This release would thereby represent an additional source of dissolved iron to the lake. With only two sets of profiler deployments at site ALR, however, more frequent sampling of this storage area is required to rigorously test this hypothesis. Quantifying the sources of DOC and iron from the Wood River wetland may also be useful in timing water storage into and release from ALR. As previously reported (Kuwabara and others, 2009), dissolved iron entering the lake via riverine inputs was well correlated in this study with water-column dissolved organic carbon (DOC) over all sampling dates (significant at the 95% confidence level with r between 0.82 and 0.98, n=6 in summer and 8 in spring sampling when the Williamson River tributary flows). This relationship with DOC was inconsistent for riverine manganese (r between -0.18 and 0.94) or copper (r between 0.36 and 0.99).

Highest concentrations for dissolved manganese, another essential micronutrient, were consistently observed in July 2009 relative to other sampling dates. A maximum concentration difference was observed at lake site MDN in 2009 from undetectable levels (<0.02 µg L^{-1}) before the *A. flos-aquae* bloom to 51.1±2.3 µg L^{-1} post bloom in July. Similar to the lake sites, wetland sites WET and TNC1 displayed an increase in dissolved manganese between pre-bloom and post bloom samplings, with the highest dissolved-manganese concentration observed at WET in July 2009 (53.1±4.1 µg L^{-1}; table 7). Site TNC2, closest to the levee breach, did not display such an increase.

Therefore, variability in dissolved trace-metal concentrations can reflect processes (for example, wind directions and current patterns) that operate over multiple time scales, some much shorter than the frequency of profiler deployments that our manpower permits.

Benthic Chlorophyll

Benthic chlorophyll measurements provide an indication of the settled carbon load to the sediment bed as phytoplanktonic densities cycle through seasonal variations in productivity. Based on the elevated algal biomass generated in the water column of hypereutrophic aquatic systems like Upper Klamath Lake, one might expect a seasonal signal for benthic chlorophyll. This signal was consistently observed at all lake and wetland sites in 2011 where benthic chlorophyll during post-bloom sampling exceeded that during pre-bloom conditions (a seasonal increase of 7.6 ± 6.9 µg cm^{-2}, n = 5), but was inconsistent in other years. This inconsistency may be due to settled, viable cells may be advected away from our sampling sites, perhaps to the lake trench on the western boundary, the only feature of the lake exceeding 10 m in depth. Only a single set of benthic-chlorophyll measurements were made at ALR in June 2011, and were the lowest relative to other wetlands sites sampled on that date (table 8).

Pheophytin increased in the wetlands following the levee breaches. On November 1, 2007, WET, TNC1, and TNC2 sites exhibited benthic chlorophyll concentrations of <0.1 µg cm^{-2}, 1.0±0.6 µg cm^{-2} and 0.2±0.5 µg cm^{-2}, respectively, and pheophytin concentrations of 5.8±3.5 µg cm^{-2}, 1.5±0.8 µg cm^{-2} and 4.0±1.1 µg cm^{-2}, respectively. Moving forward in time to May 26, 2009, benthic chlorophyll concentrations were essentially unchanged at <0.1 µg cm^{-2}, 0.4±1.1 µg cm^{-2} and <0.1 µg cm^{-2} at WET, TNC1, and TNC2, respectively, while pheophytin concentration increased significantly to 101.6±13.9 µg cm^{-2}, 34.0±1.2 µg cm^{-2} and 15.6±1.8 µg cm^{-2} (n=3), respectively. Those pheophytin concentrations have since gradually decreased to 18.1±11.2 µg cm^{-2} (n=7) for wetlands in 2011. Comparative benthic-pheophytin concentrations for other lakes are scarce, but Wolfe (2006) determined a concentration of 5 µg g^{-1} in sediments from Lake Louise, Colorado, which converts to approximately 6 µg cm^{-2} assuming: (1) a typical sediment density of 2.5 g cm^{-3} and (2) a sample depth of 0.5 cm, where the pheopigments are primarily distributed. This value is consistent with studies of oligotrophic Camp Far West Reservoir in California, where a concentration range of 6.5 to 20.2 µg cm^{-2} was observed (J.S. Kuwabara, unpublished data), and with published estuarine concentration ranges from 1 to 24 µg cm^{-2} (Light and John, 1998; Kuwabara and others, 2009).

The ratio of benthic chlorophyll to the sum of pheophytin plus benthic chlorophyll represents a coarse indicator of the reproductive status of the benthic algal community. Because pheopigments represent degradation products of chlorophyll, the fact that only 5 of 42 samples indicate a ratio $\geq$ 0.5 (table 8) suggests the degradation or senescence of phytoplankton cells that settle to the sediment bed, or an active benthic fauna that consumes benthic algae to generate feces rich in pheopigments (Thompson and others, 1981; Light and John, 1998; U. S. Environmental Protection Agency, 2000). Additionally, growth and subsequent settling of phytoplankton augment the benthic carbon source that supports microbial and macroinvertebrate assemblages near the sediment-water interface with feeding and foraging mechanisms, and in so doing, may seasonally enhance the benthic flux of solutes (Kuwabara and others, 1999; Boudreau and Jorgensen, 2001). At ALR, the ratio of chlorophyll to pheophytin plus chlorophyll was 0.10 compared to 0.28 $\pm$ 0.06 (n=3) at the other wetland sites in June 2011.

Benthic Invertebrate Assemblages

Although all lake-dwelling organisms contribute to nutrient cycling (for example, bacteria, phyto- and zooplankton, fish, birds), benthic invertebrates represent an obvious linkage between lake sediments and the water column (Sereda and Hudson, 2011). Aside from their importance in the trophic transfer of energy and solutes from lower trophic levels to higher trophic levels, elevated densities of benthic invertebrates have the potential to increase the benthic flux of solutes (Kuwabara and others, 2009). Benthic invertebrate assemblages may enhance dissolved nutrient (or toxicant) diffusion across the sediment-water interface by: (1) modifying diffusion-layer thicknesses and permeability through bioturbation, (2) enhancing advective flow across the interface through bioirrigation, and (3) excreting or expelling dissolved or particulate solutes directly into the overlying water column (Boudreau and Jorgensen, 2001). Despite these potentially important solute-transport processes associated with benthic invertebrate assemblages, there remains a near absence of data characterizing these assemblages in Upper Klamath Lake.

Benthic sampling for invertebrates revealed that three taxonomic groups were dominant (that is, accounting for 93% of all individual organisms identified): 49.1% were members of the Oligochaeta (worms), 36.9% were from the Chironomidae (midges), and 7.0% from the Hirudinea (leeches). There was both high spatial (among habitats and sites) and temporal (among months and years) variability in the distribution of invertebrates (table 3).

Open-water sites (WMR and MRM), located along the eastern shore of Upper Klamath Lake (table 3) had high temporal variation in invertebrate distributions both seasonally and among years. During autumn 2007, total invertebrate densities exceeded 10,000 individuals m-2, and chironomids were dominant at both sites. However, during early summer 2008 and late spring 2009 total invertebrate densities were only one-quarter as high as during autumn 2007, and invertebrates were more evenly distributed among the oligochaetes, leeches and chironomids. During late July 2009, total densities were approximately one-third as high as during autumn 2007, and both oligochaetes and leeches dominated the benthos at WMR and MRM. Early May 2010 samples from WMR and MRM had some of the highest invertebrate densities recorded (approximately 28,000 and 19,000 individuals m^{-2}, respectively), and both sites were dominated by oligochaetes. Benthic samples collected during early August 2010 were similar to those collected in late July 2009 relative to total density, with oligochaetes > leeches > chironomids in abundance. During 2011, invertebrate densities remained similar to earlier sample dates for similar times of the year. Densities in late May were slightly over 2 times as high as mid-summer samples collected at the end of July. From early May 2010 through the end of July 2011, oligochaetes dominated the benthos at these two locations.

The mid-lake north site (MDN, table 1) was the only mid lake site sampled during the study. Total invertebrate densities were similar to the two eastern sites for almost all sampling periods; although the assemblages were always dominated by tubificid oligochaetes and leeches. Chironomids were always low or absent in this mid lake type of habitat. Previously sampled lake sites had similar faunal distributions (Kuwabara and others, 2007). In general, total densities were approximately 10,000 individuals m^{-2}; however, similar to the WMR and MRM, total densities of invertebrates were highest during early May 2010 and late July 2011.

Variability in invertebrate distributions among wetland sites was likely a function of location, among year and seasonal effects, and the influence of vegetation on sampling efficiency. Unlike the newly restored wetland sites (TNC1 and TNC2), wetland site location varied from sampling occasion to sampling occasion because of access limitations imposed by varying lake water elevation. Similar to the open-water sites sampled in the autumn of 2007, the WET site also had extremely high densities of invertebrates, and oligochaetes accounted for >93% of the organisms present (table 3). High oligochaete density also was observed during late May 2009. Although the WET sited sampled during July 2009 also had high densities, chironomids and tubificids were co-dominant. The WET sites sampled from early May through the remainder of the study contained similar total numbers of invertebrates, and oligochaetes once again dominated the samples, except for the final sampling the latter part of July 2011. In contrast to the high invertebrate densities in the above samples, relatively few invertebrates were collected from the WET site sampled in June 2008. This site was dominated by Mare’s Tail (Hippuris vulgaris), in contrast to all other WET sites which were either in a stand of hardstem-bulrush and cattail or were adjacent to one. It’s unclear whether there were simply fewer invertebrates or collecting efficiency was very poor.

Substantial changes in invertebrate densities and distributions occurred over the period of study at the sites (TNC1 and TNC2) located within the reconnected wetland (table 3). Approximately one week after the levee breach, relatively few invertebrates were present at either site (mean density of invertebrates between sites was approximately 500 individuals m^{-2}). At that time, the benthos was dominated by oligochaetes, but in contrast to lake and wetland sites which are dominated by the family Tubificidae, the newly flooded sites were dominated by the Enchytraeidae. These enchytraeid worms were likely of terrestrial origin and resident prior to the land being inundated after the levee was breached. Densities of invertebrates at the newly restored wetland sites quickly increased given the consistent water column after the levee breaches. Densities at TNC2, located near the northern portion of the levee breach and adjacent to Agency Lake increased montonically from the initial flooding through August 2010. Densities then decrease slightly during late May 2011. Invertebrate densities at TNC2 during late July 2011 were some of the highest recorded. These extreme densities were a function of an increase in chironomids, principally, the genus Parachironomus. In general, chironomids, followed by tubificids, dominated the benthos at TNC2 during each sampling period; however, leeches also were abundant. Invertebrate densities also increased substantially at TNC1 over the period of study. However, chironomids dominated only during late June 2008 and late July 2009, otherwise, the benthos was overwhelmingly dominated by tubificids. Tubificids were particularly abundant from early May 2010 to the end of the study period.

Due to a lack of precipitation during the period of our study, only two collections were made at ALR, the managed water-storage site located near the northwestern edge of Agency Lake. During the late June 2008 period, total invertebrate densities were very low. Although the fauna was dominated by oligochaetes, only a few tubificids were present, the majority of individuals were Lumbriculus sp., a member of the Lumbriculidae well known for rapid colonization. The next collecting period was at the end of May 2011. Invertebrate densities were among the highest recorded during the study. Practically all of the invertebrates (~ 99%) were oligochaetes, most of which were tubificids.

Changes in the benthic invertebrate composition were expected given the transition of terrestrial to aquatic habitat. Although the WET sites were initially included as control sites, they were dominated by hardstem-bulrush and cattails, and represent a very different habitat than is currently present at the newly restored wetland sites (TNC1 and TNC2). As a result, there was little expectation that over 4 years the newly restored wetland sites would be similar to the WET sites in benthic invertebrate species composition. Nevertheless, a rapid change in composition did occur during the period of study (table 3). The observed change appears to be following a trajectory that is leading to newly restored wetland sites having a greater similarity in the benthic composition to wetland sites than to lake sites. The development of aquatic, benthic invertebrate assemblages may provide a food source to help reestablish fish populations in the reconnected wetland.

Methods

After engineered levee breaches on October 30, 2007 adjacent to Upper Klamath Lake, OR, three lake sites and four sites in adjacent wetlands were sampled between November 3, 2007 to August 10, 2011, temporally spanning the annual cyanophyte bloom of *Aphanizomenon flos–aquae*. The three lake sites included a mid-lake site in the northern lake component (hereafter referred to as site MDN), a site within the Williamson River plume (WMR), and third off Modoc Rim (MRM, table 1). The four wetland sites included one in the established wetlands of the Upper Klamath National Wildlife Refuge (WET), two others in the newly restored wetlands ~500 m and 100 m from a levee breach (TNC1 and TNC2, respectively), and an ephemeral wetland used for water storage to maintain summer lake levels (ALR, table 1). Lake sites were selected to coordinate with existing lake monitoring and wetland sites were selected to provide land-use contrasts for wetland types (that is, established refuge, restored wetland after long-term agricultural use, and seasonal inundated wetland for water storage). Due to consistent low precipitation in the basin during our study, water availability at site ALR permitted sampling only once.

Nonmetallic porewater profilers, designed for nutrient and trace-metal sampling (U.S. Patent 8,051,727 B1 issued November 8, 2011; Kuwabara and others (2009)), were deployed in triplicate at each sampling site. In addition to water just above the sediment-water interface (approximately 1 cm), samplers collected interstitial water from five depths within the top 10 centimeters of the sediment, with fritted polypropylene probes at depths of approximately 1, 2, 3.3, 5.5, and 10 cm, to characterize dissolved-solute vertical gradients using six independent sampling circuits. Each sampling circuit collected filtered (0.2 µm) water into 50-mL acid-washed, all-plastic syringes. After being lowered onto the sediment, the device was tripped mechanically to begin sample collection and then retrieved approximately 24 hours later. In contrast to passive sampling by dialysis, samples are slowly drawn through a series of filters into a 60-mL all-plastic, valved syringe. Dye experiments indicated that this extended sampling period with low flow rates avoided short-circuiting of samples between depths and along device surfaces. After retrieval, the sample syringes were closed with a valve, double-bagged in argon, and refrigerated in darkness for sample processing, splitting, and later chemical analyses.

Flux calculations, based on Fick's Law, assumed that the benthic flux is diffusion controlled with solute-specific diffusion coefficients (Li and Gregory, 1974; Applin, 1987; Lead and others, 2000; Rebreanu and others, 2008). For DOC, the lower value (i.e., 2×10^{-6} cm^2 s^{-1}) was used of the average range (i.e., $(2 - 3) \times 10^{-6}$ cm^2 s^{-1}) for DOC diffusivity reported by (Lead and others, 2000) to provide a conservative estimate. Benthic fluxes (J_i in mg m^{-2} d^{-1}), were calculated using the equation:

$J_i = D_{i,T}(\varphi)(dC/dz)$, where

$D_{i,T}$ is the diffusion coefficient in cm^2 s^{-1} of solute i at temperature T in degrees Celsius,

φ is the sediment porosity in dimensionless units, and

dC_i/dz is the concentration gradient for solute i in the vertical (or z) direction in mg/cm^4, with calculated flux values converted to meter and day units. Porewater and overlying water concentrations from each profiler were fit to an exponential gradient model as described by Klump and Martens (1981).

Diffusive fluxes can be enhanced by bioturbation, bioirrigation, metabolic cycling, wind resuspension, and potential groundwater inflows (Reddy and DeLaune, 2008; Kuwabara and others, 2009). Hence, the calculated benthic flux of dissolved solutes based on porewater profiles is a conservative estimate that provides lower bounds indicating the potential importance of such internal-solute sources. Tabulated results include standard deviations about mean values for the number of replicates specified in the tables (e.g., triplicate profiler deployments in table 1).

At each profiler-deployment site, dataloggers provided water-column profiles of ancillary parameters (pH, salinity, temperature, dissolved oxygen, and oxidation-reduction potential), monitored at 15-second intervals. Sampling methods have been previously described (Kuwabara and others, 2003, 2009), but details are provided below. At each site, the following samples were collected, unless otherwise noted.

Biological Parameters

1. Benthic chlorophyll *a*. Upon completion of water-column sampling, surficial sediment (that is, the top centimeter of bed material) was collected for benthic chlorophyll *a* analysis from a fresh Ekman grab at each profiler-deployment site, and stored refrigerated in a plastic Petri dish within a sealed plastic bag. Each dish was subsampled in triplicate for benthic chlorophyll *a.* The surficial sediment for each replicate (0.785 cm^2) was collected on a glass-fiber filter and buffered with 1 milliliter of a supersaturated magnesium carbonate suspension (10 g L^{-1}). Water was removed from the buffered samples by vacuum at less than 5 pounds per square inch (psi) to avoid cell lysis. Samples were then frozen on dry ice and later at -80 degrees Celsius in darkness for preservation until analyzed spectrophotometrically (before 2007-2010) or by fluorometer (2011 samples) within 3 months (Thompson and others, 1981; Franson, 1985).

2. **Benthic invertebrate sampling.** After water-column sampling was completed at each sampling site, three additional Ekman grabs (15×15 centimeter cross section by approximately 10 cm deep) were collected to determine the spatial and temporal distribution of benthic invertebrates. In most instances, these three grabs were composited into a single sample per site. However, replicate grabs collected at TNC2 during November 2007, as well as grabs collected at TNC1 on the remaining sampling dates were processed separately. These individual (un-composited) benthic grabs were processed separately to obtain an estimate of small-scale (within-site) variability. Samples were sieved in the field (500-micrometer mesh) and fixed with 10% buffered formalin. They were later transferred to 70% ethanol. Invertebrates were sorted at 10× magnification and identified to the lowest practicable taxonomic level. Samples were stained with Rose Bengal to facilitate sorting and/or randomly subsampled when necessary.

Chemical Parameters

1. **Dissolved nutrients.** Nutrient samples were filtered (0.2-µm polycarbonate membranes) and immediately refrigerated in darkness. Unlike trace-metal samples, nutrient samples were not acidified. Concentrations were determined for dissolved (0.2-µm filtered) nitrate (EPA method 353.1), ammonia (EPA method 350.1), orthophosphate (SRP; EPA method 365.2), and silica (EPA method 370.1) by batch automated spectrophotometry (Aquakem 250, Thermo Scientific).
2. **Dissolved organic carbon (DOC).** Dissolved organic carbon samples were also collected in duplicate in baked 60-milliliter glass bottles with acid-washed fluoroethylene-polymer caps and filtered (0.7-µm baked glass-fiber filter) for analysis by high-temperature catalytic combustion (Vandenbruwane and others, 2007). Potassium phthalate was used as the standard. Low-DOC water (blanks less than 40 µg-C L^{-1}) was generated from a double-deionization unit with additional ultraviolet treatment (Milli-Q Gradient, Millipore Corporation).
3. **Dissolved trace elements.** Water-column samples were collected in duplicate in 250-mL acid-washed high-density polyethylene bottles, filtered (0.2-µm polycarbonate membrane) using clean technique (Fitzwater and others, 1982), and acidified (pH 2) to provide dissolved trace-metal information for the saline waters by inductively coupled plasma mass spectrometry (ICP-MS;Topping and Kuwabara, 1999; Topping and Kuwabara, 2003). Porewater samples were filtered in-line and acidified before analysis by above water-column methods.

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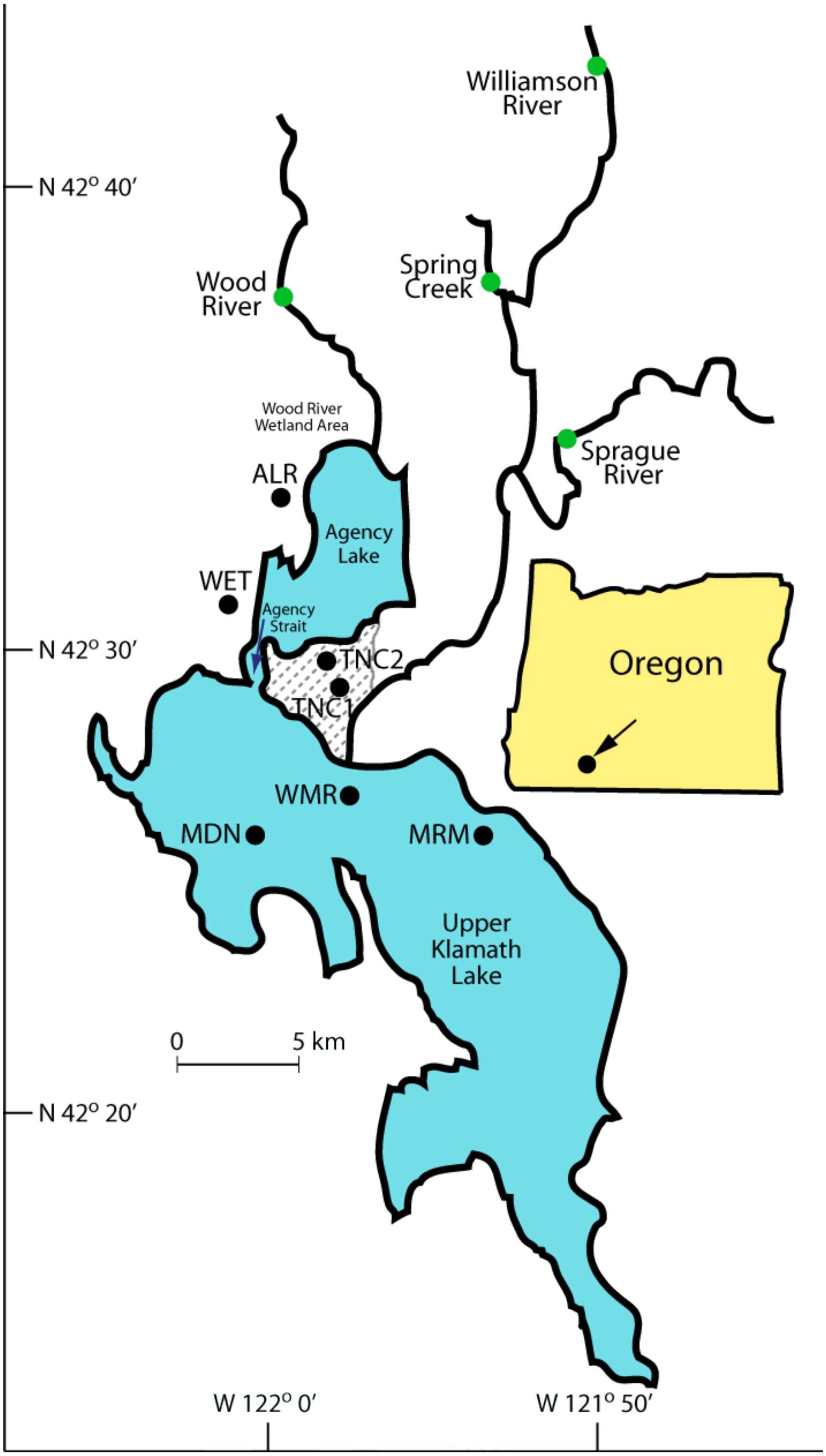

Figure 1. Lake, wetland and tributary sampling locations for this study. The diagonally hatched area, containing sites TNC1 and TNC2, represents an approximation of the zone inundated by the engineered levee breaches on October 30, 2007.

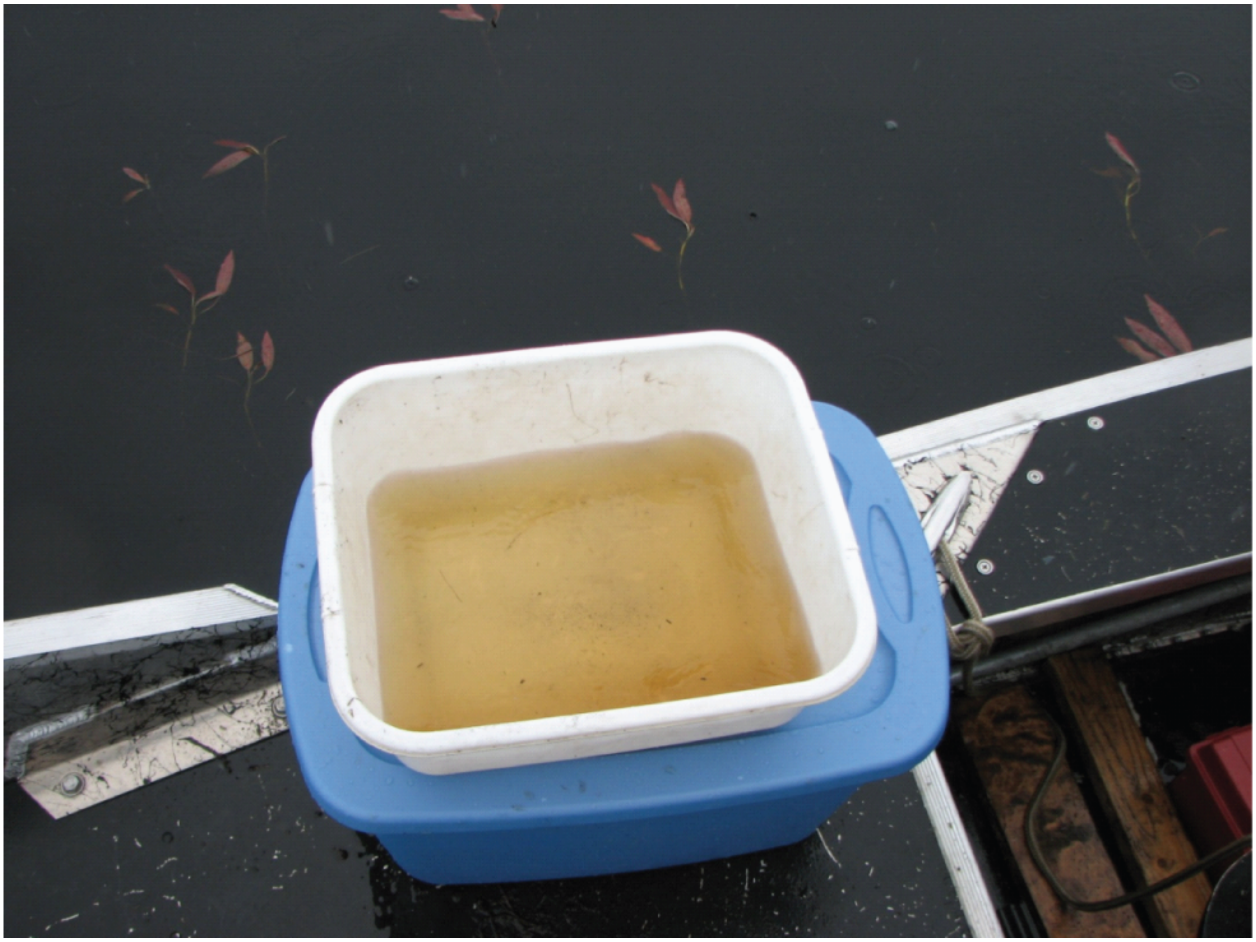

Figure 2. The wetland storage site (ALR) is not continually submerged, and hydrologic connection to adjacent Agency Lake is intermittent. Therefore, water-column chemistry at ALR contrasts other wetland and lake sites in this study in many ways. For example, the "tea" colored water column depicted here was only seen at ALR in this study.

Tables 1–8

A Microsoft® Excel file of tables 1–8 is available at *http://pubs.usgs.gov/of/2012/1057*.

Table 1. Location of water-quality sites used in this study (see also fig. 1), including ranges for ancillary parameters.

Table 2. Summary of dissolved-macronutrient fluxes for soluble reactive phosphorus (SRP), dissolved nitrate, ammonia, silica, and organic carbon in Upper Klamath Lake and adjacent wetlands, Oregon

Table 3. Density and percent composition of benthic invertebrates collected at profiler deployment sites.

Table 4. Riverine flux estimates for dissolved macro- and micronutrients into Upper Klamath Lake, OR.

Table 5. Dissolved-nutrient concentrations for soluble reactive phosphorus (SRP), dissolved nitrate, ammonia, silica and organic carbon (DOC) in the water column at profiler deployment sites.

Table 6. Benthic flux of dissolved trace elements in Upper Klamath Lake and adjacent wetlands, OR.

Table 7. Dissolved trace metal concentrations in the water-column of Upper Klamath Lake and adjacent wetlands, OR.

Table 8. Benthic chlorophyll and pheophytin concentrations in surficial sediments (μg cm^{-2}) of Upper Klamath Lake and adjacent wetlands.

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