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Eradication of an invasive cyprinid (*Gila bicolor*) to achieve water quality goals in Diamond Lake, Oregon (USA)

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Abstract

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We used a case study of whole-lake fish removal to demonstrate the importance of the fish community to nutrient cycling in Diamond Lake, Oregon, USA, to meet regulated water quality standards for pH, dissolved oxygen and nuisance algae. The cyprinid tui chub (*Gila bicolor*) was removed through a process beginning with netting and ending with a whole-lake and tributary rotenone treatment in September 2006. The lake was stocked with rainbow trout in spring 2007. Between 2007 and 2009, lake transparency increased 250%, accompanied by decreases in epilimnetic pH, total nitrogen, and total organic carbon. Mean concentrations of total phosphorus and ortho-phosphorus remained unchanged in epilimnetic waters. Chlorophyll *a*, phytoplankton biovolume, *Anabaena* biovolume, and *Anabaena* cell density declined. *Daphnia pulicaria*, a large herbivorous cladoceran virtually absent for 10 years, returned in abundance, and benthic biomass increased more than 12-fold. The project successfully demonstrated that water quality and fishery goals can be met through eradication of the invasive cyprinid. Fish populations need to be considered in some lakes to achieve water quality standards.

Key words: biomanipulation, internal loading, rotenone, total maximum daily load, tui chub

Improving water quality in water bodies through the Total Maximum Daily Load (TMDL) program has been a major component of efforts to improve water quality in the United States. Many resources for improving lakes have been directed toward reducing watershed (external) loads of phosphorus and nitrogen. However, many lakes cannot meet water quality goals because of in-lake biological factors not often recognized in traditional watershed-based TMDL programs (Havens and Schelske 2001). One source of internal loads is fisheries with a high proportion of planktivores, detritivores, or omnivores relative to the capacity of the lake to support large populations. This was the case for Diamond Lake, which had a fishery dominated by the invasive cyprinid tui chub (*Gila bicolor*). As the population of the cyprinid increased, the lake experienced intense blooms of *Anabaena,* elevated pH levels, and other common symptoms of eutrophication (Jones et al. 2007). The rainbow trout (*Oncorhynchus mykiss*) fishery eventually could no longer be sustained as the tui chub population expanded.

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TMDL analysis for Diamond Lake suggested that the water quality problems could be attributed, in large part, to the excretion products of the tui chub or indirect effects of fish on microbial processes (Eilers et al. 2005). Efforts to suppress the well-established population of tui chub by introducing large predacious salmonids such as chinook salmon (*Oncorhynchus tshawytscha*) proved unsuccessful (USDA 2004). This was attributed to the high fecundity of the female tui chub, which can lay up to 40,000 eggs per year (Bird 1975). The Oregon Department of Fish & Wildlife (ODFW) concluded that not enough tui chub could be removed by mechanical methods (Jackson and Loomis 2004); consequently, they collaborated with other agencies and groups to develop an Environmental Impact Statement (EIS) to scope management options. The preferred option selected in the final EIS (USDA 2004) was a plan to eradicate all fish in the lake through rotenone application.

Rotenone, a naturally derived piscicide, has been used in the United States since 1934 (Krumholz 1948). Investigators later identified a link between fish eradication using rotenone and other favorable biological and chemical responses in lakes (Hrbáček et al. 1961). Since then, research on the effects of this and other types of biomanipulation has expanded considerably (Shapiro et al. 1975, Carpenter 1988, Hansson et al. 1998, Kasprzak et al. 2002). Biomanipulation has been successful to varying degrees, with failures often attributed to inadequate control of planktivorous and omnivorous fish or failure to reduce external loading of nutrients to acceptable levels (Mehner et al. 2004). Earlier trials of piscivore introduction at Diamond Lake were ineffective and supported the argument that only complete eradication of tui chub would satisfy the project goals. Although managers were reasonably confident that rotenone application would eradicate tui chub, uncertainty remained as to whether the treatment would be equally successful in achieving the water quality goals of lower epilimnetic pH, lower chlorophyll *a*, and reduction in cyanobacteria. This uncertainty prompted managers to support efforts to monitor biological and water quality components through the planning, implementation, and posttreatment phases of the project. This study reports monitoring results from the Diamond Lake Restoration Project, a large, whole-lake biomanipulation experiment, focusing on posttreatment responses (pretreatment conditions are described in greater detail elsewhere; Eilers et al. 2007).

Study site

Diamond Lake is a moderately large, relatively shallow lake located in the Oregon Cascade Range (Table 1). The lake was created during the eruption of Mt. Mazama (Sherrod 1991), which dammed a stream with tephra (7627 yr BP; Zdanowicz et al. 1999). The lake is dimictic with relatively brief stratification in July and August and ice cover typically from mid-December to May. Diamond Lake remained fishless until about 1910 when it was stocked with rainbow trout (Dimick 1954). The lake has 2 permanent surface inlets and numerous intermittent tributaries, but none are suitable for trout reproduction; consequently, the trout fishery is maintained by stocking with hatchery fingerling fish. This recreational fishery thrived until the 1940s when it was discovered that tui chub, native to an adjacent basin, had been introduced to Diamond Lake (Dimick 1954). This resulted in an impaired trout fishery, and the lake was successfully treated with rotenone in 1954 (Bauer 1976). The lake was restocked with trout in 1955, and a popular recreational fishery was restored (Bauer 1964). This second phase of the trout program was maintained until 1992, when once again tui chub were found in the lake (USDA 2004). The trout fishery began to decline by 1994, and the ODFW initiated a public process in 1994 to restore the lake to meet their fish management plan objectives. However, it was the intense blooms of *Anabaena* beginning in 2001 that prompted both state and federal management agencies to support another attempt to remove the cyprinids (Jones et al. 2007). Additional information regarding the lake history and the setting are found in Eilers et al. (2001, 2007) and USDA (2004).

Methods

Most of the methods conform to standard limnological protocols (Wetzel and Likens 2000) and are presented, in part, elsewhere (Eilers et al. 2007). Additional details are provided below.

Field methods

Water quality in Diamond Lake was assessed by sampling the primary site located over the deep portion of the lake

Table 1.-Morphometry and water budget for Diamond Lake, OR.

Attribute		Water Budget[c]	Annual Budgets[c] Water (%)	P (kg)	N (kg)
Elevation (m)	1580	Inflows			
Lake Area (ha)[a]	1226	Streams	58	2037	1083
Depth (maximum, m)[a]	14.8	Precipitation (on-lake)	32	163	3089
Depth (mean, m)[a]	6.9	Groundwater	10	448[d]	512[e]
Volume ($10^6 m^3$)[a]	84.0	Outflows			
Residence Time (yr)[b]	1.6	Stream	81	1282	26,574
Annual Precipitation (cm)[b]	140–165	Evaporation	14	--	--
Topographic Watershed Area (km^2)[b]	136	Groundwater	5	68	1415

[a]Eilers et al. 2007.
[b]Johnson et al. 1985.
[c]Eilers et al. 2005.
[d]Includes 76 kg from anthropogenic sources.
[e]Includes 341 kg from anthropogenic sources.

(43°10′10.99′N; 122°9′6.37′W). *In situ* measurements were made primarily using an In-Situ Troll 9000 sonde equipped with sensors for pressure, temperature, conductivity, pH, and dissolved oxygen. Light extinction was measured by percent difference between light intensity at the lake surface and in the water column with a LI-COR model LI-250A underwater quantum sensor. Field measurements and sample collection were typically conducted between 10:00 and 14:00 h.

Water samples were collected at discrete depths using a peristaltic pump attached to high-grade Tygon tubing, weighted at the opening. The samples were placed in Nalgene bottles and stored in a cooler until shipment to the labs. Samples for analysis of silica, nitrate + nitrite (reported here as nitrate), ammonia, and ortho-phosphorus were filtered. Silica aliquots were kept refrigerated before shipping, whereas the nutrient samples typically were frozen. Before 2007, samples were filtered with Whatman® GF/C glass microfiber 47 mm filters using a manual Nalgene pump filtration system. In 2007, Geotech 0.45 μm in-line capsule filters were used with the peristaltic pump. Split samples were used to evaluate differences between filtration methods, of which none were found. Water samples were collected for biochemical oxygen demand (BOD_5) during and after the treatment to assess rates of fish decomposition.

Analytical laboratory

The primary analytical laboratory used for analysis of nutrients was the Cooperative Chemical Analytical Laboratory (CCAL) at Oregon State University, Corvallis. Analytical methods used for analyses are summarized on the CCAL website (http://ccal.oregonstate.edu/).

Biological sampling

The water quality monitoring program included collection of phytoplankton, zooplankton, and benthic macroinvertebrates. Taxonomic analyses of phytoplankton samples from Diamond Lake were conducted by Aquatic Analysts Inc., Friday Harbor, Washington. Phytoplankton samples were preserved in Lugol's solution, subsamples were permanently mounted on slides, and measured transects were scanned at 1000× magnification using a phase-contrast compound microscope. Counting was generally limited to 100 cells per sample. Biovolume estimates were calculated for each algal unit (for filamentous algae, the biovolume unit was standardized to 100 μm length of filament) based on measurements of average algal length and diameter. Sampling of phytoplankton and algal toxins associated with public health concerns was initiated in 2001 (these data are reported elsewhere; Jones et al. 2007). Phytoplankton were collected and shipped to PhycoTech Inc., St. Joseph, Michigan (http://www.phycotech.com/) and GreenWater Laboratory, Palatka, Florida (http://www.greenwaterlab.com/), for comparison. Because of the considerable uncertainty among taxonomists regarding species identification for *Anabaena* (St. Amand et al. 2007), we reported *Anabaena* to genus only.

Macrophyte distribution and canopy height were measured in summers 2002, 2007, and 2009 by conducting hydroacoustic surveys over fixed transects. Distance between transects ranged from 75 to 100 m among surveys. The data were acquired using a BioSonics DTX digital echosounder equipped with a 200 kHz split-beam transducer. Data were processed using Visual Analyzer 4.1 software. Each data file was analyzed twice using different threshold settings, once to identify the bottom and once to identify the tops of the macrophytes. A "depth to bottom" and a "depth to top" of macrophytes were identified at 2 sec intervals along the survey (1 Hz GPS and 5 Hz SONAR, thus an average of 2 positions and 10 sonar measurements). The height of the macrophyte canopy was calculated at each location and gridded (10 m grid) using a kriging algorithm. Slight discrepancies were present between the 2 threshold analyses methods in areas with no macrophytes, so a high-pass filter was used in the analysis for macrophytes deemed present only when the difference in depths between the 2 measurements was >20 cm.

Zooplankton were collected by vertical tows of a plankton net from a depth of 12 m. The net had a 20 cm opening with a 30 cm reduction collar and a mesh size of 64 μm. Zooplankton samples were analyzed by ZP Taxonomic Services Inc., Lakewood, Washington. Volume of water sampled with the vertical net tow may have been overestimated, particularly during periods of high phytoplankton density. These results should be viewed as semiquantitative.

The benthic macroinvertebrate data collected by ODFW were based on triplicate samples collected with a petite PONAR (152 × 152 mm) dredge from 23 sites, stratified by habitat type. The samples were sieved through a 500 μm mesh. Most samples were aggregated in major taxonomic groups, although some samples were retained for analysis to species level. When identified to species, samples with more than 500 organisms were subsampled using a Caton gridded tray with a 500 μm wire mesh and 30 grids to expand raw samples. Samples reported for 2006 were analyzed by Third Rock Consultants, Lexington, Kentucky (http:www.thirdrockconsultants.com/), and samples from 2007–2009 were analyzed by ABR Inc., Forest Grove, Oregon (http://www.abrinc.com), and ODFW.

Samples of trout from trap net data were used to determine growth rates and condition. Population estimates of tui chub abundance before treatment (1995–2003) were developed using trap net data and comparison of trout-to-chub capture ratios generated from repeated trap net sampling (Jackson et al. 2003). The Oneida trap nets have internal stretch mesh (1.75 cm) that created a capture bias, reducing the likelihood of capturing chub <60 mm in length. The size range of typical young-of-the-year (YOY) tui chub was <31 mm, and maximum size of adults was about 240 mm. Tui chub calculations also yielded number of fish per size class. The estimates of mass (wet weight) of tui chub were generated by using length–weight relationships (Bird 1975; ODFW unpublished data). Estimates of the proportion of tui chub in the lake in 2006 were derived from shoreline surveys following treatment. Sections of shoreline were walked by crews who counted the number of fish per section. The number of fish was expanded to the entire lake perimeter. An estimate of fish biomass present in the lake at the time of the treatment was generated based on the increase in total phosphorus in the 2 month period following treatment. The estimate accounted for changes in natural inputs of phosphorus during that period and other fluxes, as shown in the Supplemental Information.

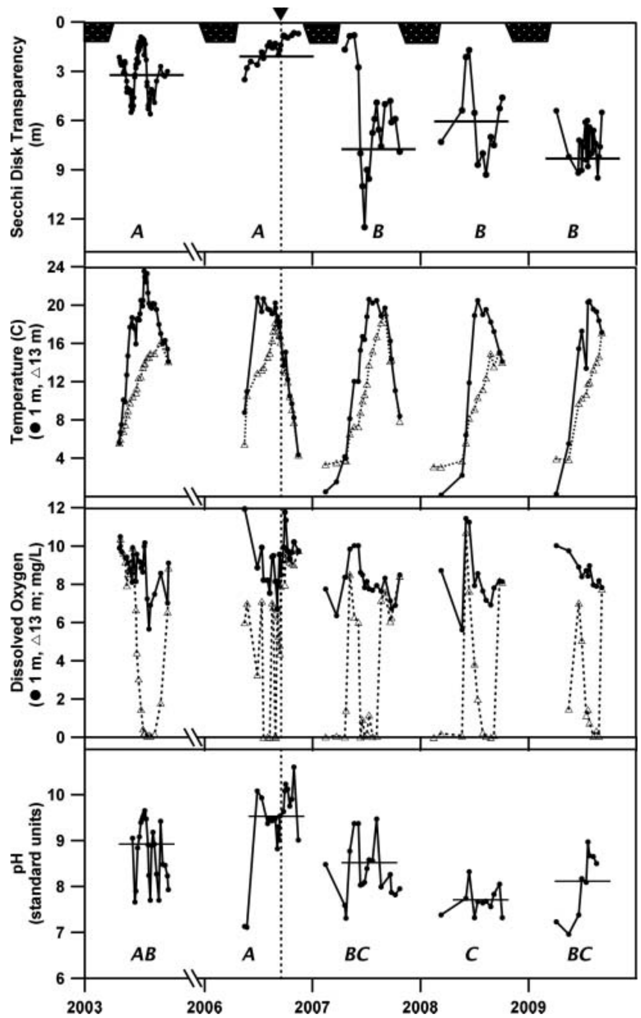

Figure 1.-Temporal variation in field measurements collected at the primary monitoring site. Surface values are presented for data collected at a depth of 1 m and bottom values represent samples collected at or near 13 m. The polygons at the top of the figure indicate the period of approximate ice cover. Mean values during summer (Jun–Sep) are shown as horizontal lines. Statistically significant differences ($P = 0.05$) among years are indicated by letters using results from Kruskal-Wallis one-way AOV.

Fish eradication

Fish eradication involved a series of actions including lake drawdown, netting operations to remove live chub, rotenone application, and lake refill. The lake stage was lowered 2.65 m from November 2005 to July 2006, which reduced the amount of rotenone required for the project by 40% and ensured that no discharge from the lake would occur immediately after the rotenone application. During July and August 2006, commercial gill netting was conducted in the lake to reduce biomass that would decay in the lake following treatment. The headgate controlling the outflow was closed on 5 September 2006, and the lake and the permanent tributaries were treated with rotenone from 13–15 September 2006. Following application and verification of a successful treatment, a portion of the dead fish were gathered along the shoreline and removed. Rainbow trout of various strains were stocked in Diamond Lake starting in June 2007 and continued annually. The lake achieved full pool on 12 July 2007. Additional details regarding the rotenone application and related activities are provided in Finlayson B, Eilers JM, Truemper H, Jul 2011, unpubl.

Data processing

Data were reviewed for internal consistency and checked against standard metrics for quality using blanks and duplicates. All data were retained in the dataset for plotting time-series graphs, but statistical comparisons among years were based on samples collected between 1 June and 30 September of a given year. Statistical analyses were made using Statistix 9 by Analytical Software. Comparisons among years were evaluated using the Kruskal-Wallis test.

Results

In situ *measurements*

Maximum surface temperature (1 m) was approximately 20 C for 2006–2009, although the mean surface temperature was slightly lower (not significant) for June–September 2007–2009 compared to 2006 (Fig. 1). Mean summer Secchi disk transparency increased from 1.9 m in 2006 to 7.6 m

Table 2.-Recent trout stocking rates, fish growth, and condition factors.

			Trout Stocking			
			Fingerlings[c]		Larger Fish[d]	
Year	Growth Rate[a] (mm/d)	Condition Factor[b]	Number	Biomass (kg)	Number	Biomass (kg)
1960–1991	NA	1.43 (1.21–1.89)	395,800 (292, 400–500, 400)	3989 (2953–5054)	0	0
1992–2004	NA[e]	1.04 (0.87–1.23)	400,100	4041	4997	795
2006[f]	NA	NA	0	0	24,026	3886
2007	1.32	1.51	100,000	990	84,453	37,174
2008	1.33	1.30	200,100	2081	85,786	31,365
2009	1.12	1.26	346,600	4303	0	0

[a]Growth rate computed during spring–fall, generally from Jun through Oct.
[b]Condition factor (K) is a dimensionless value based on the relationship between fish fork length (L, in cm) and weight (W, in grams), where: $K = \frac{100 \times W}{L}$
[c]Fingerlings defined as fish generally between 75 and 100 mm.
[d]Other fish include larger fish generally about 200–300 mm.
[e]Growth rate not measured, although rate was observed to approach zero.
[f]Year of treatment.

in 2009. The maximum transparency for the study period of 12.5 m occurred in July 2007. Depth of light extinction (1% of surface irradiation) increased from a mean of 5.8 m in 2006 to 11.9 m in 2008. Dissolved oxygen at the surface declined from 113% in 2006 to 104% in 2008, but increased again in 2009 to 109% (Table 2). Surface (1 m) field pH declined from a summer mean of 9.5 in 2006 to 7.8 in 2008, with a slight increase to 8.2 in 2009 (Fig. 1). Concentrations of dissolved oxygen in the hypolimnion continued to show a pattern of anoxia in the winter, restoration of saturated conditions in the spring, and anoxia in the summer both before and after treatment. Conditions during the drawdown and treatment in 2006 reflect the destabilization of the lake with lowering of the lake stage by 2.65 m. During summer 2006, the chemocline oscillated repeatedly, causing abrupt shifts between anoxia and saturation in the deeper waters.

Water chemistry

Concentrations of total and ortho-phosphorus showed no significant change in the years following treatment (Fig. 2). Total phosphorus increased substantially in the weeks after the rotenone treatment, but concentrations in the surface waters returned to pretreatment levels in 2007. Substantial spikes in total and ortho-phosphorus occurred in 2008 following a late ice-off. Summer stratification in 2008 was relatively brief, and an early turnover in August caused another increase in surface concentrations of phosphorus as anoxic hypolimnetic waters mixed throughout the lake.

Concentrations of total nitrogen showed an initial spike following treatment and then steadily declined in subsequent years (Fig. 2). Concentrations of nitrate were generally low throughout the study period, except during fall 2007 and spring 2008 when nitrification of ammonia was evident (Fig. 2). Concentrations of total organic carbon declined significantly in 2007–2009 (Fig. 2). Alkalinity and pH also declined following treatment.

Degradation of fish in the lake was assessed by measuring BOD_5 several times from September 2006 through March 2007. Shortly after treatment in September 2006, BOD_5 was 2.3 mg/L, increased to a maximum of 6.7 mg/L on 11 November 2006, and declined to <2.0 mg/L (the detection limit) by 20 March 2007.

Biological responses

Concentrations of chlorophyll *a* declined from a mean of 15.3 ug/L before treatment to 2.7 ug/L in 2007. However, chlorophyll increased in 2008 (Fig. 3). Phytoplankton biovolume showed a pattern similar to chlorophyll for 2006–2008; 2009 values were 46% lower than the previous low measured in 2007. Summer biovolume and cell density of *Anabaena* declined by more than 95% in years following treatment (Fig. 3). Other taxa of cyanobacteria, including *Microcystis aeruginosa, Gloeotrichia echinulata*, and *Aphanizomenon flos-aquae*, were occasionally present in low densities from 2007–2009. The diatom assemblage in the years preceding the treatment was characterized by spring blooms of *Synedra* spp., transitioning into lower densities of *Asterionella formosa* and summer dominance by *Fragilaria crotonensis*. This was followed by a bloom of *Synedra* continuing until treatment. In the years following treatment, the dominant diatom taxa included *Aulocoseria granulata* and *Tabellaria fenestrata.* The most atypical period for phytoplankton assemblages during posttreatment was in June 2008, in which a pulse of *Cryptomonas erosa*

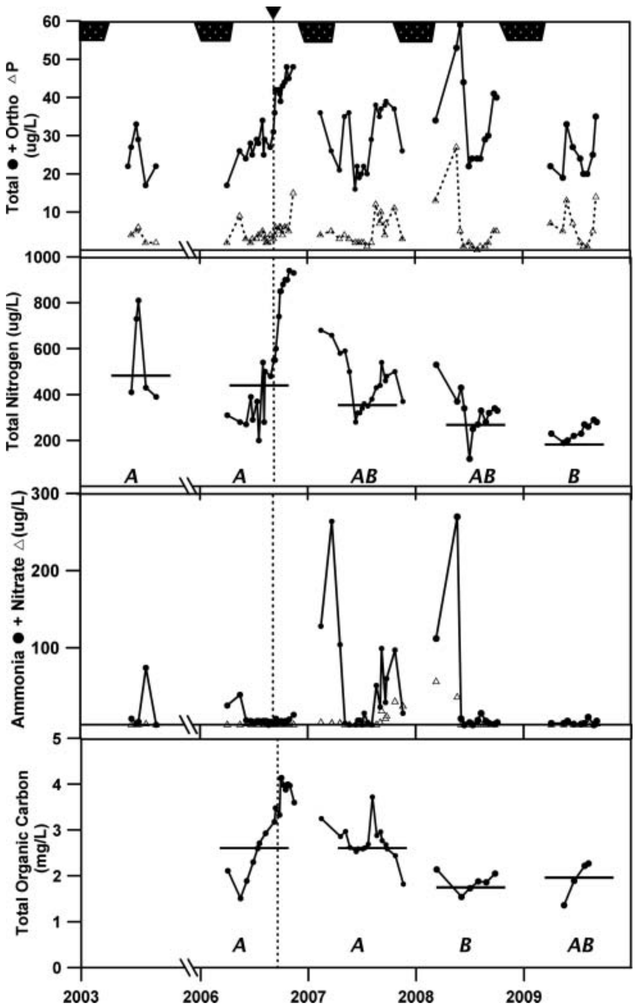

Figure 2.-Temporal variation in analytical chemistry collected at a depth of 1 m at the primary monitoring site. Surface values are presented for data collected at a depth of 1 m and bottom values represent samples collected at or near 13 m. The polygons at the top of the figure indicate the period of approximate ice cover. Mean values during summer (Jun-Sep) are shown as horizontal lines. Statistically significant differences (P = 0.05) among years are indicated by letters using results from kruskal-Wallis one-way AOV.

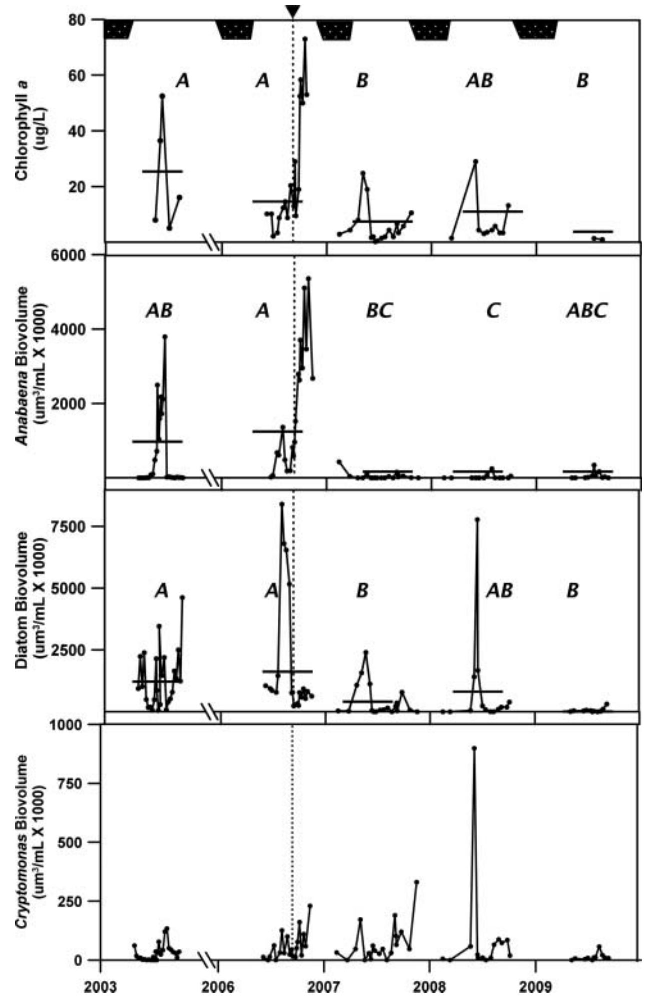

Figure 3.-Temporal variation in selected phytoplankton-related metrics for samples collected at 1 m. Surface values are presented for data collected at a depth of 1 m and bottom values represent samples collected at or near 13 m. The polygons at the top of the figure indicate the period of approximate ice cover. Mean values during summer (Jun-Sep) are shown as horizontal lines. Statistically significant differences (P = 0.05) among years are indicated by letters using results from kruskal-Wallis one-way AOV.

was followed by an intense bloom of *Stephanodiscus astrea minutula*.

Prior to treatment, cladocerans were often the most abundant zooplankton group, but the dominant taxa were smaller-bodied organisms such as *Bosmina longirostris* and *Chydorus sphaericus*. Following treatment, *Daphnia pulicaria*, and to a lesser extent *D. rosea*, showed a major increase, peaking at 78,000 individuals/m^3 in July 2007 (Fig. 4). This was also concomitant with the maximum transparency measured in the lake (Fig. 1). From 2007–2009, *D. pulicaria* averaged 87% of the total cladocerans sampled from June to October. The copepods showed a substantial increase in abundance in 2007 but then returned to densities found in the pretreatment period. The copepods were typically represented largely by cyclopoid copepodites and copepod nauplii both before and after treatment. The rotifers showed a major increase in abundance in 2007 and 2008 but by 2009 also seemed to have returned to pretreatment densities. Rotifer taxa were dominated by *Keratella cochlearis*, *Kellicottia longispina*, and *Asphlanchna priodonta* prior to treatment, but *K. longispina* nearly disappeared from the assemblage after treatment. The biomass of benthic invertebrates increased from 2.3 g/m^2 in 2006 to 38.3 g/m^2 in 2009 (Fig. 4). The benthic community before treatment consisted largely of chironomids; after treatment, a far more diverse assemblage of amphipods, hirudinea, molluscs, and nondipteran insect larvae was present.

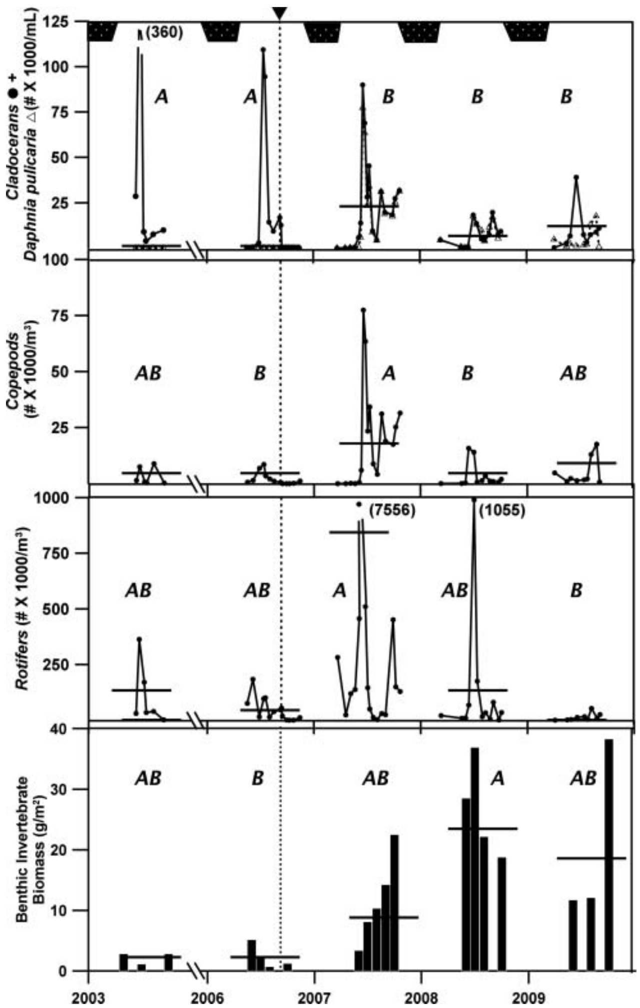

Figure 4.-Temporal variation in selected zooplankton and benthic macroinvertebrate metrics. The benthic samples collected prior to 2006 represent those collected in 2005 rather than 2003, for which data are not available. Mean values for these biological parameters are based on all data for the open-water period. The polygons at the top of the figure indicate the Period of approximate ice cover. Statistically significant differences (P = 0.05) among years are indicated by letters using results from Kruskal-Wallis one-way AOV.

Subsequent posttreatment trap netting and electrofishing did not yield any tui chub through 2009; however, another small invasive cyprinid historically present, the golden shiner (*Notemigonus crysoleucas*), was discovered in the lake in July 2008. Through 2009, more than 3400 golden shiners were removed using boat electrofishing and netting. Various strains of rainbow trout were stocked in Diamond Lake beginning spring 2007, and annual stocking of rainbow trout continues (Table 2). Growth rates and condition factors have remained high through the posttreatment period, although both metrics declined slightly from 2008 to 2009.

The fishery at the time of the rotenone treatment was composed of more than 99.9% tui chub based on a posttreatment shoreline survey of the accumulated fish. The trout-to-chub ratio used to estimate the tui chub population prior to any removal attempts generated 2 estimates: a maximum value of 23 million chub (of catchable size) and a value of 7.6 million chub accepted by ODFW and used in the rotenone project EIS. Based on the 7.6 million chub estimate, about 174 tonnes (wet weight) of chub could have been present in the lake; based on the 23 million estimate, 540 tonnes. Two activities before treatment, trap netting and gill netting, removed 30.2 tonnes of tui chub. As in previous years, some tui chub likely swam downstream through the outlet. Another 15.8 tonnes of fish were collected from the lakeshore after treatment. The computation of fish biomass based on the increase in concentrations of total phosphorus in the lake yielded an estimate of 204 tonnes (Supplemental Information). That, combined with pretreatment netting and posttreatment collection, yield an estimate of 250 tonnes of fish ($\sim$200 kg/ha at full pool) in the lake in summer 2006. This may be a conservative estimate of fish biomass because it assumes that all the fish had decomposed fully in 2 months and that all phosphorus from fish decay had mixed fully throughout the lake. However, the estimate based on the increase in phosphorus concentrations does not address other factors such as phosphorus release from macrophyte senescence or from nonfish organisms killed in the treatment. This estimate compares with the total mass of fish killed in the 1954 rotenone treatment of 363 tonnes (Bauer 1976); however, the estimate reported by Bauer was based on counts of floating fish following treatment and did not include an estimate of fish that sank.

Other measured responses due to treatment included changes in the distribution and canopy height of aquatic macrophytes. Macrophyte coverage declined from 41% of the lake area in 2002 to 27.8% in 2007. The area from 0–3 m depth was temporarily denuded of macrophytes by desiccation during the drawdown. By September 2009, macrophyte coverage had increased to 33.4%, with colonization of the shallows still lagging. Average canopy height increased in 2009.

Discussion

Before the rotenone treatment, Diamond Lake was a eutrophic water body, featuring repeated cyanobacteria blooms, elevated pH, low transparency, low density of large cladocerans, and a sparse benthic fauna. Although aesthetic problems contributed to reduced recreational use of the lake, 3 factors that drove the decision to remove the tui chub were the severely impaired trout fishery, water quality violations, and human health considerations associated with high densities of cyanobacteria. The short-term response of the lake to eradication of tui chub was a major release of nutrients from the decomposing fish, which supported a developing bloom of *Anabaena*. Although most freshwater taxa of cyanobacteria generally favor warm conditions (Paerl and Huisman 2008), the density of *Anabaena* increased despite water temperatures declining to ice-on conditions. The decomposition of fish carcasses continued to support a major diatom bloom in spring 2007. The bloom of *Synedra* likely provided food for *D. pulicaria*, which exhibited a surprisingly rapid recovery from near-zero densities before treatment to densities up to 78,000 individuals/m^3 in July 2007. Similar zooplankton responses to rotenone treatments have been observed by others (Shapiro and Wright 1984), although this has not been a universal response to rotenone treatments (Faafeng and Brabrand 1990 as cited in Hansson et al. 1998). Density of *D. pulicaria* declined following the initial peak but has remained moderately high through much of the posttreatment period. Recovery of benthic abundance and diversity proceeded at a slower pace than the recovery of zooplankton, which is consistent with the longer life cycles for many of these benthic invertebrates. However, by summer 2008, benthic biomass had returned to values observed before the introduction of the tui chub and in 2009 exceeded levels since monitoring began in 1946 (Eilers et al. 2007). The dramatic resurgence of large cladocerans and benthic macroinvertebrates illustrates the degree to which both of these trophic groups had been consumed by tui chub.

Removal of tui chub brought pH into compliance with water quality standards and greatly reduced *Anabaena* density. Concentrations of phosphorus (P) in the water column remained largely unchanged, except for the release of P during decay of tui chub, yet chlorophyll declined substantially. Drenner and Hambright (2002) in a review of biomanipulation studies found that the regression slope of total P versus chlorophyll was lower in lakes with planktivores and piscivores compared with lakes containing only planktivores. The Diamond Lake results seem consistent with their observation in that chlorophyll declined without a change in concentration of P. This may have occurred as an indirect effect associated with an alteration of microbial cycling or as a direct effect of increased nutrient supply from fish excretion (Vanni 2002). For example, 357 tonnes of tui chub (an average of the low and high modeling estimates) would be expected to release 2570 kg P and 31,500 kg N during the summer (90 d), assuming excretion rates for tui chub are similar to bluegills (Mather et al. 1995). An approximate loading of P from external sources (derived from Table 1) for the same period would be about 650 kg P. Thus, the internal load of P associated with tui chub may have been 4 times the external load. Diamond Lake is an excellent candidate for translocation of nutrients by fish from the littoral to the pelagic zone because of the high proportion of macrophyte cover. The release of P following the rotenone treatment also illustrates the important role that fish exhibit in sequestering nutrients. The amount of P released during the decay of fish exceeded the P present in the water column prior to treatment and reinforces observations by others regarding the role of fish and nutrient sequestration (Kitchell et al. 1975).

The project had the immediate effect of causing macrophyte loss in the nearshore area as a consequence of desiccation during the drawdown. By summer 2009, recolonization of the littoral zone had begun, and canopy height of macrophytes in deeper water increased, possibly in response to increased transparency. Increased macrophyte growth appears to be a common response in successful rotenone and related biomanipulation projects (Hansel-Welch et al. 2003). Diamond Lake is sufficiently deep to stratify, yet is shallow enough to support macrophyte growth on more than 40% percent of the lake area. The temporary reduction of 13% macrophyte coverage apparently did little to prevent the dramatic improvement in water quality. Through 2009, an additional 5% of the lake area had been recolonized with macrophytes. The macrophyte recovery is expected to continue, providing additional competition for nutrients with the phytoplankton and additional habitat for invertebrates. A number of authors report higher rates of success with biomanipulation projects in shallow lakes compared to deep lakes (Reynolds 1994, Drenner and Hambright 1999, Mehner et al. 2004). Diamond Lake has characteristics of both shallow lakes (high coverage of macrophytes) and deep lakes (stratification), although the apparent lack of association between changes in macrophyte abundance and lake response would seem to place it in the class of deep lakes relative to biomanipulation projects. However, this distinction between shallow and deep lakes may be unwarranted for Diamond Lake given the brief period of stratification and high areal coverage of macrophytes.

Seldom do natural resources management activities involve only a single action. Here we observed a partial lake drawdown, netting of tui chub, a rotenone application, lake refill, and subsequent restocking with trout. Some of these potentially confounding effects can be addressed by noting specific responses during the sequence of events. For example, the drawdown that occurred from November 2005 to August 2006 destabilized the lake and likely promoted greater interaction of the sediment and water column during summer 2006. Unlike previous years when *Anabaena* was often dominant in summer, the diatom *F. crotonensis* was dominant. *Anabaena* did not become dominant until total P increased from 30 μg/L to nearly 50 μg/L with the death and decomposition of the tui chub. The magnitude of the drawdown was large with respect to lake volume (40%) and decreased the lake hydraulic residence time and increased the rate of nutrient transport from the lake. However, during the refill from November 2006 to July 2007, the hydraulic residence time increased and nutrient export decreased, yet water quality improved. It seems that the drawdown–refill had no significant role in the lake recovery.

The removal of tui chub by netting preceding the rotenone treatment resulted in changes to the zooplankton community, but the community composition was still dominated by small-bodied cladocerans until spring of 2007. This is not surprising given that the mass of fish removed by netting was less than 10% of the mass of tui chub based on the average of the low and high fish modeling results. Others have shown that successful biomanipulation requires removal of a high percentage of the fish biomass (Hansson et al. 1998, Meijer et al. 1999, Mehner et al. 2004). Restoration of high quality water with the removal of tui chub raises the issue of whether the water quality improvement resulted from the reduction of fish biomass and excretion of nutrients by fish, or whether the reduced predation of large cladocerans allowed the resurgent population of *D. pulicaria* to graze down the cyanobacteria. The effects based on this treatment alone are difficult to separate, but other researchers have shown that herbivorous zooplankton cannot suppress cyanobacteria in eutrophic lakes because of interference with feeding (Webster and Peters 1978, Gliwicz 1990, DeMott et al. 2001) or through effects of cyanotoxins (Hansson et al. 2007, Dao et al. 2010). In nearby Odell Lake, annual blooms of *Anabaena* continue despite high densities of herbivorous copepods and cladocerans (J. Eilers, unpub. data). In another area lake, abundant populations of *D. pulicaria* coexist with high densities of *A. flos-aquae* by grazing diatoms and other more edible taxa (Kann 1997), a behavior also observed by Epp (1996) for *D. pulicaria* in several New York lakes. In Diamond Lake, the first notable *Anabaena* bloom did not occur until 2001, the same period when tui chub abundance appeared to increase substantially. However, the density of *D. pulicaria* had already plummeted to less than 1% of the zooplankton individuals by 1995 (Eilers et al. 2007), which should have allowed the phytoplankton to grow to bloom proportions several years earlier than observed if the blooms were kept in check by the large cladocerans. We conclude that improvement in water quality in Diamond Lake following rotenone treatment cannot be attributed to consumption of cyanobacteria by *Daphnia*.

The moderately high rate of external loading of P to Diamond Lake of 5.9 kg/d (0.17 g P m^2 yr) compared to 28.6 kg/d estimated for excretion of tui chub at 357 tonnes made it susceptible to biomanipulation effects. Consequently, it is important to monitor the fisheries, other trophic groups, and water quality to minimize a repeat of the degraded conditions observed from 2001–2006 and to document the sustainability of the treatment. The previous treatment was effective from 1955 to circa 1990, and hopefully that longevity can be duplicated with this treatment. Currently, golden shiners are present in the lake. Although this taxon was present in the 1980s and 1990s, past experience suggests that this cyprinid cannot exploit the lake habitats to the degree achieved by tui chub. Regardless, research has shown that biomanipulation projects require continued monitoring to ensure long-term success (McQueen 1998).

Earlier investigators did an excellent job of defining the watershed sources of nutrients to Diamond Lake (Lauer et al. 1979). However, because understanding of nutrient loading from fish and other biota to lake nutrient cycles was in the early stages of development, they did not account for fish-related sources that may have been of a similar magnitude to those from the watershed. However, the same reasoning cannot explain why lake restoration projects requiring reduction of fish biomass to achieve water quality goals remain a rarity in the United States. Although research supporting the effects of fish on water quality has been available for decades (Hrbáček et al. 1961, Shapiro et al. 1975, Andersson et al. 1978, Brabrand et al. 1990), the regulatory process in the United States and elsewhere has been slow to incorporate these findings into lake restoration programs. Diamond Lake is one of the first projects of its kind in the United States to achieve water quality goals through invasive fish eradication and be approved under the TMDL process (http://www.epa.gov.owow/NPS/Success/state/pdf/or_diamond.pdf). A number of other lakes on the Oregon 2010 303(d) list were assigned based on Harmful Algal Bloom Health Advisories, where fishery related issues potentially contribute to the cyanobacterial blooms (A. Schaedel, ODEQ, pers. comm. 2011). Other states such as Maine have recognized the importance of modification of nutrient cycling associated with the introduction of white perch (*Morone americana*) to a number of lakes on their TMDL list (Halliwell and Evers 2008). Efforts are currently underway to determine if removal of white perch by trap netting can yield improvements in water quality on East Pond, Maine (http://www.main.gov/dep/blwa/doclake/biomanipulation/index.htm). Others have shown that removal of gizzard shad (*Dorosoma cepedianum*) can yield nutrient removal rates comparable to those from extensive wetland treatment systems in Lake Apopka, Florida (Schaus et al. 2010). Although we support efforts to reduce nonpoint sources of pollution through better stewardship of the land, such techniques alone will not succeed in providing the desired improvements in water quality to some lakes until the effects of fish on water quality are also addressed.

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