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Biological effects of repeated fish introductions in a formerly fishless lake: Diamond Lake, Oregon, USA

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With 10 figures and 4 tables

Abstract: Biological responses to a formerly fishless lake in the Cascade Range, Oregon (USA) were assessed through monitoring of recent changes and paleolimnological techniques to assess earlier changes. We used unpublished fisheries reports, sediment cores, and available published and unpublished water quality data to evaluate changes to the lake. Diamond Lake has undergone four periods of fish introductions in the 20th century. Rainbow trout (*Salmo gairdneri*) were annually released from 1910–2006, except for 1949 and 1954. Tui chub (*Gila bicolor*), an omnivorous cyprinid, were introduced in the late 1930s and the late 1980s, presumably as discarded live bait. Diamond Lake was treated with rotenone in 1954 which successfully eradicated the tui chub. The introductions of trout caused relatively modest changes in water quality and lake biota, whereas the introductions of tui chub caused major increases in cyanobacteria, changes in diatom community composition, reduction in transparency, increases in the proportion of rotifers, major reduction in benthic standing crop, and virtual elimination of amphipods, gastropods, and other large-bodied invertebrates. The unintended biomanipulations demonstrate the importance of an omnivorous cyprinid in promoting a series of biological responses throughout the lake food web.

Key words: fish stocking, paleolimnology, community effects, biomanipulation, food webs.

Introduction

Fisheries management plays an important role in many freshwater lakes throughout the world by attempting to enhance or maintain commercial and recreational fisheries. Earlier approaches in fisheries management considered water largely as a medium for the fish, not realizing the potential interactions from alteration of trophic food webs and potential consequences to water quality and other aspects of lake biota. Progress is being made to understand and quantify the interactions between fisheries, other aquatic biota, and water quality (Håkanson & Boulion 2002, Håkanson et al. 2003). Quantifying these effects are difficult because of the variability among lakes, the variety of species involved in the potential interactions, and the uncertainty in extrapolating results from small-scale studies to large lakes.

We report on changes observed in a formerly fishless lake in Oregon (U.S.A.). The fish introductions to

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the lake have involved two periods of intentional introductions of rainbow trout (*Salmo gairdneri*) and two inadvertent introductions of a minnow (tui chub, *Gila bicolor*), separated by a rotenone treatment. The tui chub are believed to have been introduced as discarded bait fish. These unintended experiments provide an opportunity to examine how the lake responded to two series of similar fish treatments. The lake responses include changes in phytoplankton and zooplankton community composition, zoobenthic community composition, and several metrics of water quality.

Study site

Diamond Lake is located in the Umpqua National Forest near the crest of the Cascades Range of Oregon, USA. The subalpine lake is dimictic with a single basin. The lake stratifies in July and August and typically is ice-covered from December to April. Diamond Lake derives most of its surface inflow from two small streams on the south end of the lake, but substantial inputs are derived from precipitation on the lake surface with supplemental inputs from groundwater sources (Table 1). The lake is located between two currently dormant volcanic peaks, Mt. Thielsen and Mt. Bailey, and is 20 km north of Crater Lake, a caldera. Diamond Lake appears to have been formed following the eruption of Mt. Mazama (the current location of Crater Lake), in which ejecta and tephra blocked Lake Creek, the current outlet of Diamond Lake (Sherrod 1991). Pumice and fractured basalt in the area promote rapid infiltration of snowmelt and rainfall, resulting in vertical flowpaths and about 90 percent less surface inflow to the lake than would be predicted on the basis of precipitation inputs for the size of the topographic watershed. The surface discharge that enters the lake is largely from spring-fed streams. The inputs are cold (3 to 7 °C), highly enriched in phosphorus (50 to 70 μg L^{-1} PO_4-P), and nearly depleted in nitrogen (TN < 25 μg L^{-1}). The high phosphorus inputs are derived primarily from weathering of the basalts and andesites. The forested catchment captures most of the available nitrogen, resulting in streams that are N-limited. Anthropogenic inputs of N and P from the watershed are less than 5 percent of total nutrient loads. Diamond Lake has moderate TP concentrations and relatively low nitrogen concentrations (Table 2). The high primary production in summer (a maximum of 406 mg C m^{-2} hr^{-1} measured in July 2001; J. Salinas, pers. comm.) contributes to elevated pH and supersaturation of dissolved oxygen.

Diamond Lake historically was fishless because of natural barriers to fish passage on the North Umpqua River. However, in 1910 (or possibly as late as 1913) the state fisheries management agency introduced trout into the lake (Bauer 1976). The trout thrived in the productive lake, a response that stimulated the Oregon Game Commission to construct a station for collecting trout eggs, hatching the stripped eggs, and reintroducing fry back into the lake. Stocking was necessary to maintain the trout population because of the absence of suitable spawning sites for trout reproduction. Excess trout fingerlings derived from the eggs of trout from Diamond Lake were used for stocking elsewhere in the state. Trout fishing became very popular at the lake, which stimulated the construction of a resort in 1923; 102 summer cabins were constructed from 1924 to 1955 on the west shore of the lake under a lease program from the Forest Service. The Umpqua National Forest, which is responsible for managing all lands within the watershed, has constructed 585 campsites around the lake to accommodate the large demand

Table 1. Morphometry and hydrologic characteristics of Diamond Lake.

Attribute		Water Budget[c]	
Elevation (m)	1580	Inflows	Percent
Lake Area (ha)[a]	1226	Streams	58
Depth (maximum, m)[a]	14.8	Precipitation	32
Depth (mean, m)[a]	6.9	Groundwater	10
Volume ($10^6 m^3$)[a]	84.0	Outflows	
Residence Time (yr)[b]	1.6	Stream	81
Annual Precipitation (cm)[b]	140–165	Evaporation	14
Topographic Watershed Area (km^2)[b]	136	Groundwater	5

[a] Eilers et al. (2003); unpubl. report
[b] Johnson et al. (1985)
[c] Eilers et al. (2004); unpubl. report

Table 2. Representative surface water chemistry for Diamond Lake for 2001–2003[a].

	Spring[b]				Summer[c]			
	n	Min	Mean	Max	n	Min	Mean	Max
pH	7	7.5	8.2	9.0	30	7.6	8.8	9.6
TP (μg L^{-1})	7	10	20	30	12	10	24	40
PO_4-P (μg L^{-1})	7	1	4	5	14	0	3	6
TN (μg L^{-1})	7	202	288	402	12	430	807	1511
NO_3-N (μg L^{-1})	7	0	1.4	1.9	12	0	1.6	5.4
NH_3-N (μg L^{-1})	7	0	16	30	12	1	31	74
SiO_2 (mmoles L^{-1})	2	0.20	0.24	0.29	8	0.22	0.26	0.29
Chlorophyll-*a* (μg L^{-1})	6	1.8	5.2	8.2	14	2.7	24	63

[a] Eilers et al. (2004); unpubl. report
[b] April–May
[c] July–August

for camping, particularly in the 1960s and 1970s when visits to the lake numbered up to 800,000 annually. Wastes from these campgrounds and the resort are collected and treated outside the watershed. Additional information regarding watershed and lake history is described in Eilers et al. (2001).

Tui chub, a minnow native to the Klamath drainage east of Diamond Lake, was first sighted in the lake in 1940 (Dimick 1954). Trout production first began to decline in the 1940s and trout survivorship and growth declined rapidly by 1950 (Dimick 1954). Early attempts to deal with the abundant tui chub involved conducting aggressive netting and using shoreline applications of rotenone. These attempts failed because of the high population growth rate associated with this species. In response, the Oregon Game Commission lowered the lake stage by 2.5 m in 1954 and treated the lake with 91 tonnes of powdered rotenone (Bauer 1976). The lake was re-stocked with rainbow trout in 1955. Trout production became abundant following 1962 when the current strain of Oak Springs rainbow trout was substituted for the less successful Kamloops strain of rainbow trout (Bauer 1964). Trout production began to decline again in the late 1980s, and the presence of tui chub was documented in 1992. The tui chub population expanded to about 25,000 fish ha^{-1} (excluding young-of year, YOY) by 2002. The stocking of fingerling trout was discontinued in 1996 when trout survivorship and growth rates plummeted. The lake began to experience severe blooms of cyanobacteria in 2001 to the extent that the density of *Anabaena flos-aquae* reached 575,000 cells mL^{-1}, values exceeding those recommended for recreational contact (Chorus 2001). The cyanobacteria populations have remained high through 2006, although cell densities have remained lower than the peak values observed in 2001 (Jones et al., in press). The taxonomy of the *Anabaena* taxa present in Diamond Lake and other lakes in the region is being reviewed and may be revised based on DNA analyses currently in progress. The loss of the trout fishery, combined with the perceived health threat associated with the cyanobacteria blooms, prompted resource agencies to treat Diamond Lake with rotenone in September 2006.

Methods

The evaluation of changes in Diamond Lake is based on observational data starting in the 1940s, responses to the rotenone treatment in 1954, monitoring data from 1971–1977, 1992–2006, and paleolimnologic data from analyses of two sediment cores (Table 3). The fisheries data are derived from annual reports from the Oregon Game Commission (OGC) and its successor agency, the Oregon Department of Fish & Wildlife (ODFW). The earlier data were summarized by Bauer (1976). The trout harvest values were derived from annual creel census data collected by the agencies. These data also included estimates of fishing pressure and catch per unit effort. Samples of trout from trap net data were used to determine growth rates of stocked trout and fish condition. The abundance of tui chub were derived from trap net data and comparison of trout-to-chub capture. The Oneida trap nets have internal stretch mesh (1.75 cm). The trap nets targeted the adult tui chub; size range of typical YOY tui chub were less than 31 mm and maximum size of adult chub was about 240 mm. Information on utilization of open-water habitat by tui chub was derived from hydroacoustic analysis of the lake conducted in spring 2003 using a BioSonics echosounder linked to a 200 kHz split-beam transducer. The hydroacoustic survey was done in the pelagic zone with fixed transects and was repeated during day and night periods to assess diel movements of fish. Fish lengths were derived from target-strength data using Love's equation (1971).

Table 3. Summary of data sources and methods used to assess changes in Diamond Lake.

Class of Data	Early (1910–1955)	Mid (1955–1991)	Recent (1992–2004)
Fisheries	Lake stocking records (unpubl. data)	Creel census & CPUE netting data (ODFW, unpubl. data)	Hydroacoustics (J. Eilers) + netting (ODFW, unpubl. data)
Macrobenthos	Petersen dredge samples (Oregon Game Commission, annual reports; Bauer 1976)	Petersen dredge (Bauer 1976, Lauer et al. 1979)	PONAR dredge (J. Eilers, unpubl. data; ODFW, unpubl. data)
Zooplankton	none	none	Vertical tows (A. Vogel, unpubl. data)
Phytoplankton	No sampling (see paleo)	Community composition + density (Lauer et al. 1979)	Community composition, chlorophyll, density, toxins (J. Sweet, unpubl. data)
Water Quality	Secchi disk (Oregon Dept. Fish & Wild., unpubl. data)	Secchi disk, nutrients (Lauer et al. 1979)	Secchi disk, nutrients, major ions (J. Salinas, unpubl. data)
Diatoms (paleo)		Meyerhoff et al. (1978)	Eilers et al. (2001)
Cyanobacteria (paleo)			Unpubl. data (A. St. Amand)

Benthic macroinvertebrate data were collected by OGC/ODFW from 1946 to 1979, 2002, and from 2004–2006. Benthic invertebrate data were also collected by the U.S. Environmental Protection Agency (EPA) from 1971–1977 (Lauer et al. 1979). The data from the earlier period by OGC/ODFW were collected from single grab samples at 17 to 37 sites using a Petersen dredge. The sample results were stratified to reflect different lake habitat and sample depths. Samples were pooled, passed through a 500 µm sieve, sorted in the field, and reported in major taxonomic groups. Mass of invertebrates was based on displacement of water samples and reported as wet weight. The data collected by EPA were based on multiple samples collected with a standard PONAR dredge (230 × 230 mm) from each of four sites, pooled, and reported by site. Organisms were reported to the lowest practical taxonomic level, usually species, and were reported as organisms per unit area. The most recent data collected by ODFW were based on triplicate samples collected with a petite PONAR (152 × 152 mm) from 23 sites, stratified by habitat type. The samples from each site were pooled and sieved through a 500 µm mesh. Most samples are aggregated in major taxonomic groups as per earlier OGC/ODFW data, although some samples are retained for analysis to species by contract taxonomists. All benthic invertebrate data reported here are from samples collected in October of each year.

Zooplankton data were derived largely from vertical tows in the deepest area of the lake using a mesh size of 64 µm. Taxonomy for 1992 and 1993 was conducted by Dr. J. Lee, Oregon State University and taxonomy thereafter was performed by a co-author (Dr. A. Vogel). Population densities were normalized by the volume of water passed through the net. Volume of water filtered was based on distance of the tow and the net diameter. No corrections were made for filtration efficiency. Samples were first split with a Folsum plankton splitter until an approximate subsample size of 400 total individual arthropods and 100 individuals of the most abundant species were reached. If the initial split did not achieve both of these criteria, then increasingly larger splits were enumerated until both criteria were met, or until the entire sample was counted. All rotifers and protozoans in the split were completely enumerated as well unless their numbers significantly exceeded 400 individuals; in which case, a separate rotifer sub-split was made to count these organisms. Crustacean lengths were measured following the protocols described in Edmondson & Winberg (1971), in which cladocerans from the top of the head (helmet included) to the posterior edge of the carapace excluding any tail spine and copepods from the end of the cephalothorax to the end of the caudal rami. The sample size for the measurements of crustacean length was 150 individuals per sample. Long-term zooplankton abundance was determined by a sediment core collected by the senior author and digested to remove extraneous organic matter and analyzed by Dr. J. Beaver. The results are reported in individuals per gram of sediment (dry weight).

Phytoplankton data from 1971–1977 were reported by Lauer et al.(1979) and data from 1992 to 2006 were collected from over the deepest area of the lake by several investigators (J. Salinas, R. Raymond, and J. Eilers), but all samples reported here were analyzed by J.W. Sweet (Aquatic Analysts). Phytoplankton samples were preserved in Lugol's solution, sub-samples 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. Gaps in the phytoplankton record were supplemented by collection and analysis of two sediment cores. The first core, collected in 1996, provided a reconstruction in water quality changes in Diamond Lake based, in part, on changes in diatom community composition (Eilers et al. 2001). A second sediment core collected by the senior author in 2000 was used to reconstruct changes in cyanobacteria abundance based on deposition rates of preserved akinetes using methods described in Eilers et al. (2004). Intensive sampling of phytoplankton and algal toxins, associated with public health concerns, was initiated in 2001 and these data are reported elsewhere (Jones et al., in press).

Reliable water quality data on Diamond Lake were first reported by Lauer et al. (1979) for the period 1971–1977. Water quality sampling was re-initiated by the Umpqua National Forest (USDA-Forest Service) in 1992 with samples collected from 1992–2002 by J. Salinas, in 2001–2003 by J. Eilers, from 2004–2005 by R. Raymond, and in 2006 by R. Miller. Additional water quality sampling funded by ODFW was initiated in 2003 and is scheduled to continue. Sampling from 1971–1977 consisted of collecting water quality data from several sites approximately monthly through the open-water period (May–Oct). Sampling from 1992–2006 through the Umpqua National Forest program consisted primarily of sampling at the deepest location of the lake three times during the summer, although additional sampling during spring and fall was added for selected years. Sampling of the two primary tributaries was included most years. The frequency of water quality sampling in 2001 was more intensive because of the severity of the cyanobacteria bloom. In 2006, ODFW initiated a comprehensive sampling program of water quality, fisheries, benthic macroinvertebrates, zooplankton, and phytoplankton in response to what is considered a long-term management need as stipulated in the Environmental Impact Statement associated with the decision to eradicate the tui chub (Umpqua National Forest 2004). Water quality data for analysis of nutrients from 1992–2006 has been generated by the Cooperative Chemical Analytical Laboratory, Oregon State University, Corvallis.

Results

Fisheries

Trout production from 1910 to the 1930s (T1) and from 1962 to the 1980s (T2) was very high and supported a major sport fishery. Within less than eight years following initial sightings of tui chub, the trout fishery had been decimated and major changes had been experienced by the benthic macroinvertebrates, crustacean zooplankton, and phytoplankton communities as described below. Tui chub, a relatively small cyprinid, were not a direct threat to trout, but rather caused the collapse of the trout fishery by eliminating most of its available food base. The trout were primarily stocked as fry through 1961 and then as fingerlings starting in 1962 (Table 4). The fry and fingerlings primarily survived largely on zooplankton. Once the trout had

Table 4. Stocking and harvest history of trout in Diamond Lake.

Year	Trout Caught	Stocking History: Fry (~25 mm)	Fingerlings (~75 mm)	Legals (>150 mm)	Notes
1910–37	15,000 to 50,000/yr	1,000,000			Trout up to 4.5 kg common
1938–45		2,000,000			Trout up to 3.6 kg caught; tui chub observed 1940
1946	12,800	4,000,000			An estimated 68 million tui chub
1947	37,500	3,300,000			harvested with seine nets or killed by
1948	27,900	2,000,000			shoreline treatments with rotenone
1949	9,700		None		
1950–53	5900[a]			43,750	
1954	362	None; lake treated with rotenone			~32 million tui chub killed (~360 tonnes)
1955	Closed	440,000	146,600		Kamloops strain of rainbow trout
1956–61	42,450[a]	844,000			trout caught averaged 33 cm stocked;
1962–69	265,700[a]		450,000[a]		Strain of trout changed to Oak Springs strain yielding a 10-fold increase in
1970–78	263,000[a]		380,000[a]		trout caught
1979–88	NA[b]		390,000[a]		
1989	167,000		400,000		
1990–91	NA[b]		412,000		
1992	NA[b]		425,000	5,000	Tui chub found in lake
1993	NA[b]		356,000	14,000	
1994	56,400		425,000	5,000	
1995	NA[b]		412,000	7,500	
1996	70,100		350,000	10,000	
1997	42,000		400,000	7,700	
1998	12,500		400,000	7,500	
1999	5,100		430,000	14,000	
2000	20,000		59,000	53,000	
2001	13,000		50,000	46,000	Lake closures begin with intense *Anabaena* blooms
2002	6800[c]		90,000	65,000	Includes some chinook (*Oncorhynchus tshawytscha)*
2003	7800[c]		90,000	99,000	~30 million tui chub present; includes some chinook
2004	2300[c]		90,000	112,000	
2005	2800[c]			52,000	
2006	19,700			24,000	Lake treated with rotenone, Sept.

[a] Average
[b] Records incomplete, not available
[c] Number recorded in creel survey; actual number is greater

reached a length of about 125 mm, they generally began consuming benthic organisms, particularly amphipods, gastropods, and non-dipteran insect larvae. All four of these major taxonomic groups were depleted rapidly by the cyprinids.

The tui chub population expanded in each introduction (C1 and C2) to reach the apparent carrying capacity of the lake, which was about 25,000 fish/ha (excluding YOY). Efforts to control tui chub by stocking predacious salmonids (*Salmo gairdneri* [3 different strains] and *Oncorhynchus tshawytscha*) failed, in large part, because of the high fecundity of tui chub. An adult female chub can produce 40,000 eggs annually (Bird 1975) and near their peak level of abundance, results in about 21 billion eggs deposited during the early summer. Attempts to reduce the tui chub biomass by netting prior to 1954 and again after 2000 also failed because of the large percentage of small

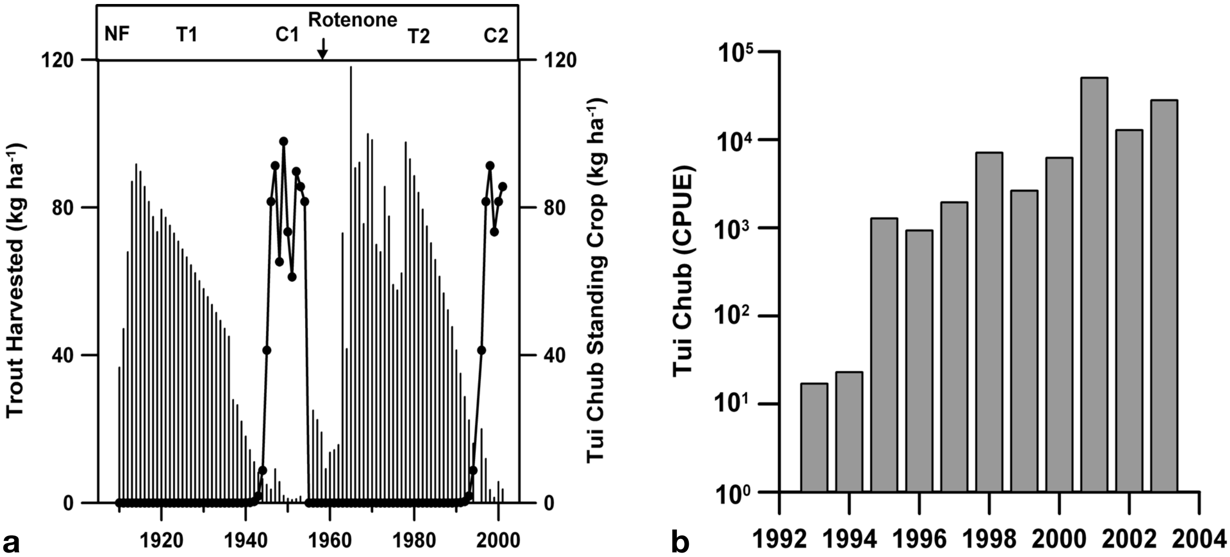

Fig. 1. Trout harvest records **(a)** for Diamond Lake based on data from 1946–2003 (bars). Harvest records for pre-1946 are estimated based on annual agency reports. The standing crop of tui chub (circles) is based on estimates derived from ratios to tui chub:trout and catch-per-unit-effort (CPUE) of tui chub **(b)** in net samples. The various periods of the dominant fisheries are listed across the top as NF (no fish), T1 (first trout fishery), C1 (first tui chub invasion), rotenone treatment in 1954, T2 (second trout fishery), and C2 (second invasion of tui chub). This nomenclature is repeated on other selected figures.

fish present at any one time and the inability to net in the macrophyte beds where the chub congregate. The stocking of fingerling trout continued through 2004, although an increasing emphasis was placed on stocking legal-size trout when the trout survivorship and growth rates began to decline in 1992. The abundance of the tui chub has been far more difficult to quantify than the trout, in part, because of the tui chub's preference for macrophyte cover. This heavy utilization of the shallow macrophyte areas makes netting more difficult and greatly reduces the effectiveness of hydroacoustic methods for fish enumeration. The hydroacoustic data were helpful in confirming the use of the pelagic zone by tui chub, primarily at night.

Reasonable estimates of the relative abundance of the chub population are derived from the ratio of chub to trout captured in net sets which are compared to trout harvest (Fig. 1).

Benthic macroinvertebrates

The success of the trout fisheries in Diamond Lake was attributed largely to the former abundance of the benthic macroinvertebrates (Bauer 1976). The composition of the macroinvertebrate community was first reported in 1946, several years after chub were known to be present in the lake (Fig. 2). Nevertheless, the dominant organisms (dominant taxa shown in parentheses) in the lake were Gammaridae (*Hyalella azteca*), Chironomidae (*Chironomus decorus* and *Tanytarsus* sp) with substantial densities of Hirudinea (*Helobdella stagnalis*), Gastropoda (*Valvata humeralis*), and non-

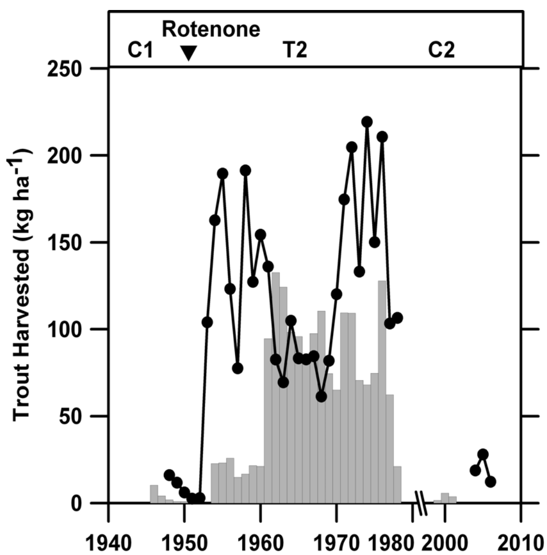

Fig. 2. Trout harvested (bars) in relation to standing crop of benthic macroinvertebrates (•) in Diamond Lake from 1946 to 2006. The original sample results from the benthic sampling are no longer available, but the composite results are based on averages from 35 sample sites collected in October (up to 1979; 22 sites in 2004–2006) of each year and should have low uncertainty. The dominant fish management feature for the period is shown across the top (see Fig. 1a).

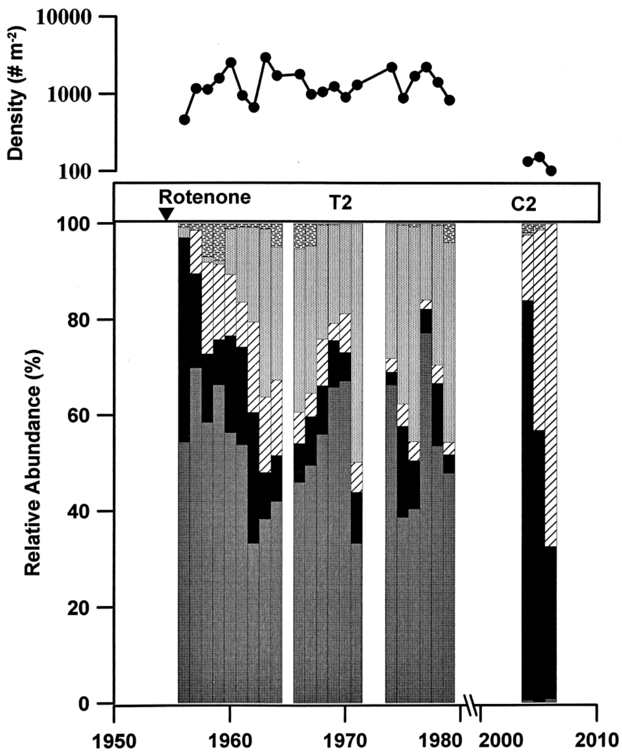

Fig. 3. Relative abundance of benthic macroinvertebrates (based on number of individuals) from Diamond Lake collected during October from 1957–1979 and 2004–2006 in Diamond Lake, where ▒ = amphipods, ■ = chironomids, ▧ = annelids, ▒ = gastropods (mostly), and ▒ = others (largely non-dipteran insect larvae). Shown across the top are density of benthic macroinvertebrates for the same samples.

dipteran insects (*Caenis, Ischnura, Agraylea*) (Fig. 3). The benthic community changed rapidly with the increase of the tui chub population in the 1950s, resulting in a dramatic reduction in standing crop of benthic macroinvertebrates. The surviving organisms were predominantly Chironomidae and Annelida. Following the rotenone treatment in 1954, the benthic community was once again dominated by Gammaridae, and was well represented by the taxonomic groups first reported in the 1940s. After the re-introduction of tui chub, benthic organisms were sampled in 2002 and systematically in 2004–2006, revealing a community that was once again dominated by Chironomidae and Annelida. Whereas portions of the lake in the late 1950s to at least 1977 had supported densities of *Hyalella azteca* (a preferred trout prey) of over 1000 m^{-2}, samples collected from 2002–2006 typically yielded only one to several individuals among all 22 sample sites.

Zooplankton

The zooplankton community was sampled from 1992 through 2006, following the second introduction of tui chub (C2). During this period, the zooplankton community changed from one with large cladocerans (daphnids), to one dominated by rotifers and smaller-bodied crustaceans (Fig. 4). Among the cladoceran taxa that remained, the average size of individuals showed an apparent decrease. For example, the average size of *Daphnia* decreased from 1.68 mm (± 0.54) in June 1992 to 0.95 mm (± 0.30) in August 2002 (Fig. 5).

Phytoplankton

A general sense of the increase in phytoplankton abundance associated with the recent expansion of the tui chub population is the decrease in average lake transparency from 6 m to 3 m during the second invasion of tui chub (Fig. 6). Once the tui chub started to become dominant in the 1990s (see Fig. 1b), transparency progressively declined. The one exception was for 1994, which was based on three Secchi disk measurements from a single month. Phytoplankton community

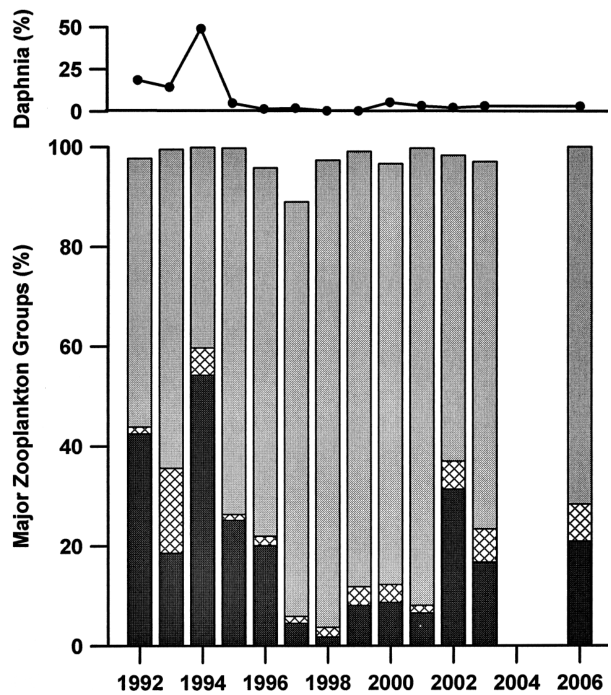

Fig. 4. Relative abundance of major zooplankton groups (based on number of individuals) in Diamond Lake from 1992 to 2006, where ■ = Cladocera, ▩ = Copepoda, and ▒ = Rotifera. *Daphnia* spp. as a percentage of all zooplankton individuals is shown on the top.

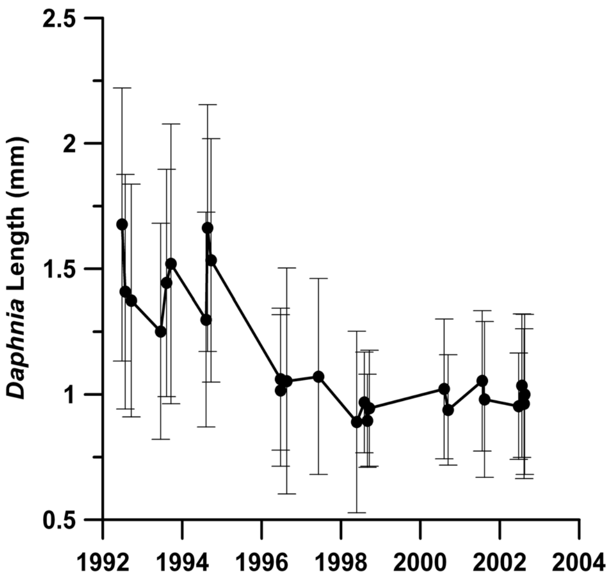

Fig. 5. Average length of *Daphnia* in Diamond Lake from 1992 to 2003. The standard deviations of at least 150 measurements per sample are shown as vertical bars.

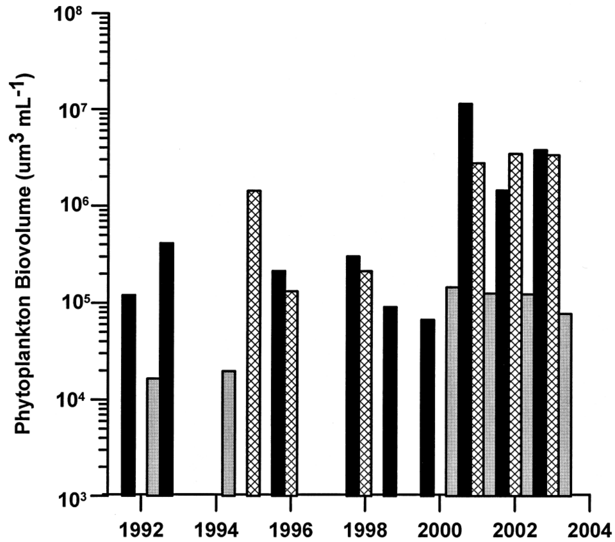

Fig. 7. Recent changes in dominant and persistent phytoplankton taxa in Diamond Lake (■ = *Anabaena*, ▩ = *Fragilaria crotonensis*, ▦ = *Cryptomonas* spp.).

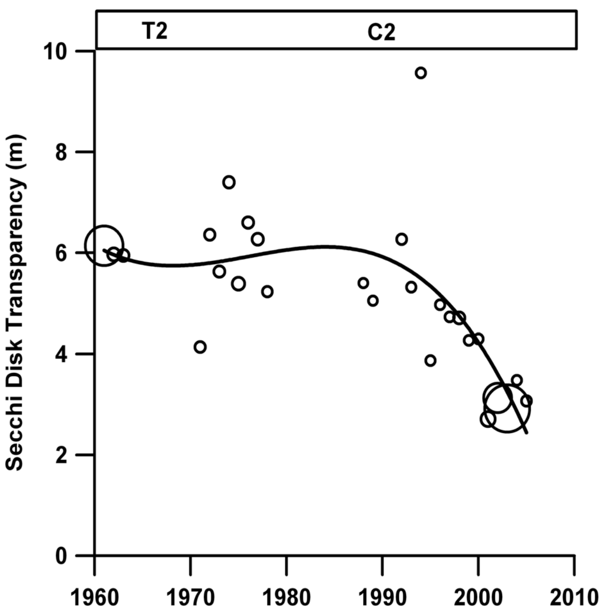

Fig. 6. Average annual Secchi disk transparency from 1961 to 2004 for Diamond Lake. The line represents a polynomial fit of the observed data and the diameter of the circles reflects the sample size associated with the annual mean value, ranging from 3 to 72.

composition was characterized from 1971–1977 and again from 1992–2006. In both periods, diatoms were abundant in the spring and often into summer and fall, whereas cyanobacteria were present in the latter part of the summer. Although *Anabaena* spp. were moderately abundant in Diamond Lake before the tui chub became dominant, it was not until 2001 when the tui chub abundance peaked (based on CPUE, Fig 1b) that the *Anabaen*a populations increased dramatically (Fig. 7). The lake began to experience severe blooms of cyanobacteria in 2001 to the extent that the density of *Anabaena flos-aquae* reached 575,000 cells mL^{-1}, values exceeding those recommended for recreational contact (Chorus 2001). The cyanobacteria populations remained high through 2006, although cell densities remained lower than the peak values observed in 2001 (Jones et al., in press). This increase in *Anabaena* was also accompanied by increases in *Fragilaria crotonensis*, and other diatom taxa including *Aulocoseria ambigua, Synedra radians*, and *Asterionella formosa*.

To reconstruct gaps in the diatom and cyanobacteria data, sediment cores were collected in 1996 (Eilers et al. 2001) and again in 2002 to analyze for changes in zooplankton, diatom community composition, and cyanobacterial akinetes. The ^{210}Pb activity shows a typical profile observed in relatively undisturbed sediment cores (Fig. 8). The sediment accumulation rate (SAR) shows an increase from about 160 g m^{-2} yr^{-1} near the base of the datable core to about 350 g m^{-2} yr^{-1} at the top of the core. The peak SAR observed in 1931 (± 12.5 yr) indicates an increase in SAR, which is consistent with the corresponding decrease in the adjacent pollen profile. The overall pollen profile corroborates the general magnitude of the overall increase in SAR profile. The sediment record of zooplankton remains (largely cladocerans) shows a peak in 1954

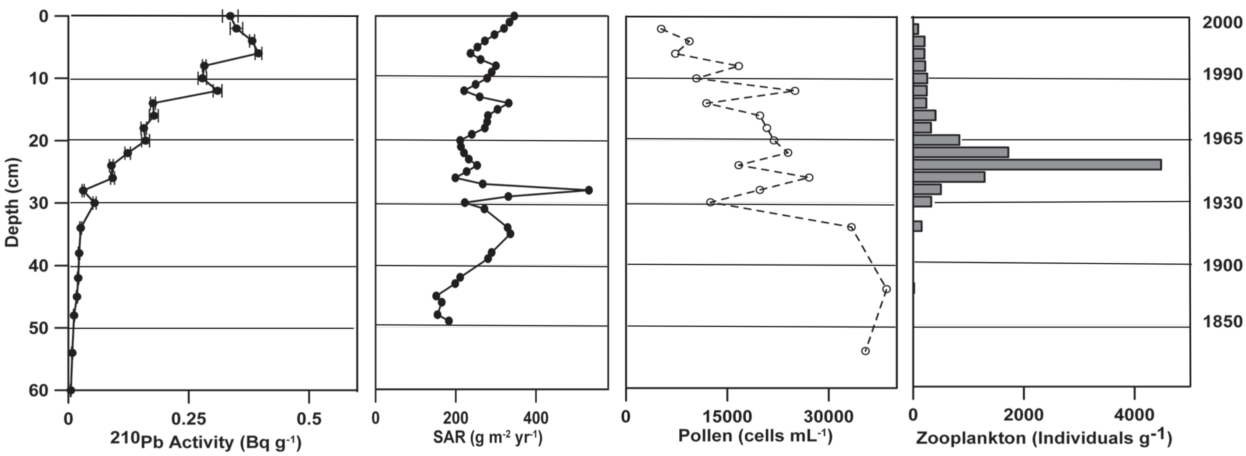

Fig. 8. Analytical results from the sediment dating of the core collected in May 2001 showing **(a)** ^{210}Pb activity per dry weight, **(b)** sediment accumulation rate (SAR) as mass (dry weight), **(c)** pollen density in wet sediment, and **(d)** zooplankton density expressed as dry weight.

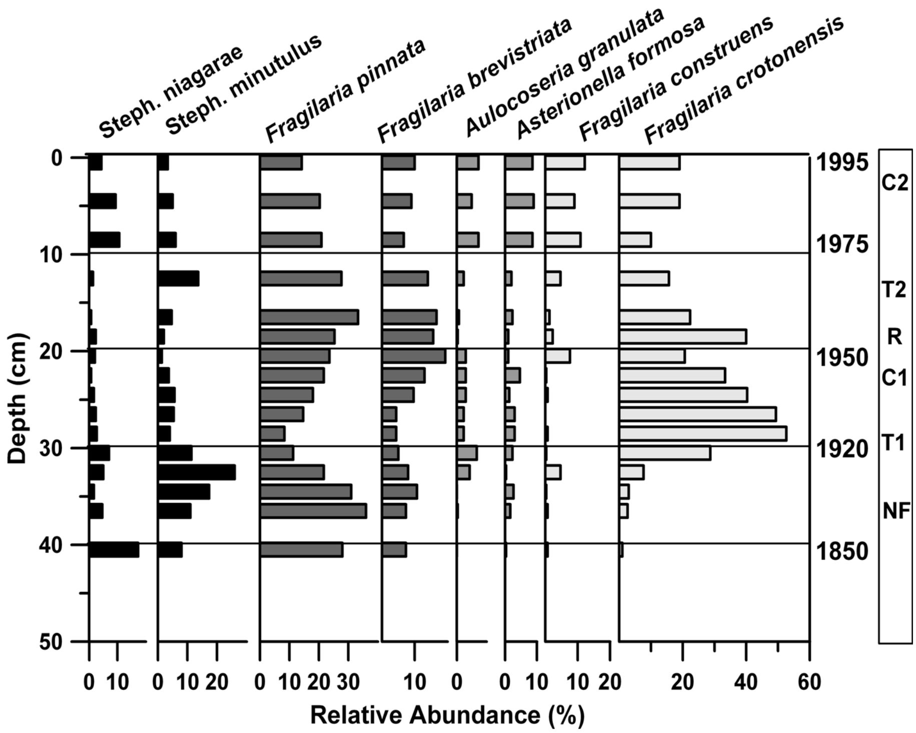

Fig. 9. Dominant diatom taxa in the sediments of Diamond Lake (modified and reprinted with permission from Eilers et al. (2001).

(± 3.6 yr) which could represent either a record of the zooplankton killed during the rotenone treatment in 1954 or perhaps a large increase in cladocerans following the rotenone treatment.

The diatom community composition prior to the introduction of fish changed from a mixed community of epiphytic, epibenthic, tycoplanktonic, and planktonic forms to one dominated by *Fragilaria crotonensis* and other taxa indicative of more nutrient-rich conditions (Fig. 9). The macrophyte community has not been routinely monitored in Diamond Lake, but there are reports of changes in macrophytes that warrant reporting. The relatively shallow depth, soft substrates, and modest winds of Diamond Lake provide excellent opportunity for macrophytes to proliferate throughout much of the lake. A hydroacoustic analysis of macro-

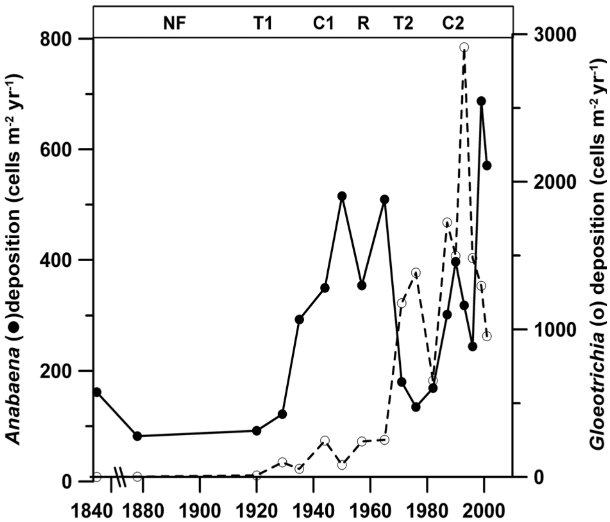

Fig. 10. Changes in deposition rate of cyanobacterial akinetes for **(a)** *Anabaena* and **(b)** *Gloeotrichia* deposition in Diamond Lake.

phyte distribution in 2002 showed that macrophytes extended to a depth of at least 6 m. However, previous surveys during the 1970s showed that macrophytes extended to a depth of 8 m (Lauer et al. 1979). Dramatic changes in the macrophyte community were reported in the early 1950s prior to the rotenone treatment and again in 2001. In both cases, fisheries biologists reported that large mats of *Potamogeton* were dislodged from the substrate and were floating throughout the lake. There was no sampling of the phytoplankton in the 1950s to verify that the cyanobacteria blooms were severe, however the sediment akinete data demonstrate that major *Anabaena* blooms were occurring at that time (Fig. 10).

Discussion

Studies of the effects of biomanipulation often deal with addition of piscivores in an attempt to improve lake water quality (Carpenter et al. 1985, Reynolds 1994, Hansson et al. 1998, Horpilla et al. 1998, Kasprzak et al. 2002, Mehner et al. 2002, 2004, Cowx & Gerdeaux 2004). In Diamond Lake, we have a series of unintended biomanipulations with the addition of the same two species of fish for a total of four additions, punctuated in the middle by total eradication of all fish. Potential confounding effects often associated with anthropogenic activities in lake watersheds are minimal in this case and can be discounted in assessing the lake response to the fish additions. This "unnatural experiment" provides insight into biological responses from repeated introductions that might not be evident in a single treatment and reinforces some of the typical observations associated with introduction of planktivorous and omnivorous fish.

The data from the sediment cores provides our best insight into the early responses of Diamond Lake to fish introductions. The first addition of trout circa 1910 to the previously fishless lake caused a measurable response in diatoms in the 1920s, which is indicative of a slight enrichment of the lake. Additional evidence of increasing lake enrichment associated with the first introduction of the trout was the appearance of a nitrogen-fixing cyanobacterium, *Gloeotrichia*, circa 1930. An alternative explanation for the increase in phytoplankton following the introduction of trout is that the consumption of zooplankton by the trout could have effectively reduced herbivorous zooplankton, thus reducing grazing pressure on the phytoplankton. Although the diatoms were sensitive to the first fish introductions as illustrated by the large increase in *Fragilaria crotonensis*, the response of the diatoms to subsequent fish introduction was more subdued. This may indicate that the lake has shown a long-term shift to a more eutrophic state. In contrast to the response of the diatoms, the dominant cyanobacteria in the lake showed dramatic fluctuations to both sets of tui chub introductions. Major increases in *Anabaena* did not begin until the late 1930s or early 1940s, about the period when the first tui chub were introduced. *Anabaena* showed a brief decline following the rotenone treatment in 1954, but did not decline to pre-fish levels until the 1970s. During the mid 1960s through the 1970s, trout yield was high so there does not appear to be an association between trout production and cyanobacteria responses in the lake. One explanation for the observed pattern in cyanobacteria following the first rotenone treatment is that the addition of phosphorus to the sediment from the fish carcasses provided a supply of nutrients for 10 to 20 years. An estimated 200 tonnes of tui chub were allowed to decay in the lake and the phosphorus burden derived from the decaying chub could have taken years to dissipate. Similar effects have been observed with delayed responses of lakes to reduction of external loading of phosphorus from sewage treatment plants (Larsen et al. 1979).

Zooplankton responses to the fish introductions can be inferred from the data collected in 1992 to 2006 which shows a rapid reduction in the percentage of *Daphnia* after 1994 when the tui chub population was expanding rapidly. Large-bodied cladocerans remain absent in the lake, whereas a healthy zooplankton community would have been required to support the rapid growth rates of fingerling trout observed in the periods when tui chub were absent. The cyanobacteria data in the 1960s and 1970s suggest that return of the zooplankton following the rotenone treatment was inadequate to maintain sufficient grazing pressure on the phytoplankton. We assume large-bodied cladocerans were abundant in the lake during this period based on the rapid growth of stocked trout fingerlings. Thus, high phytoplankton growth in this period appears to have been supported by high nutrient supply.

Benthic macroinvertebrates declined rapidly following the introductions of tui chub. Although trout were abundant in the lake, their numbers were limited by controlled stocking, high fishing pressure, and migration through the outlet. In addition, the benthic standing crop was monitored from 1946 through 1979 (trout condition factor was used instead of macroinvertebrate data starting in 1980), and when the macroinvertebrate food base declined, trout production declined. Managers responded by reducing the number of stocked trout fingerlings. Thus the trout stocking density was carefully limited to protect its primary food source. In contrast, the tui chub were able to reproduce in Diamond Lake and effectively exploit both the crustacean zooplankton and benthic macroinvertebrates to the point where the stocked trout exhibited poor growth and survival.

The increase in cyanobacteria density, reduction in large cladocerans and decrease in macroinvertebrate standing crop were observed with both introductions of tui chub. The most likely cause for the cyanobacteria blooms associated with the fish introductions appears to be related to the stimulatory effects of the tui chub waste products rather than reduction of phytoplankton grazing pressure associated with the loss of the large cladocerans. *Daphnia* were greatly reduced by 1995, yet cyanobacteria density did not exhibit a major increase until 2001, which was also the year that tui chub abundance (based on CPUE) peaked. The apparent direct stimulatory effect of the phosphorus release from the tui chub appears similar to the effects of roach (*Rutilus rutilus*) reported by Tarvainen et al. (2002).

Habitat appears to have played an important role in contributing to the success of the tui chub in Diamond Lake. The lake is relatively shallow and over one-third of the lake has abundant macrophyte growth. This habitat is highly preferred by tui chub, but the trout favor the pelagic zone. The trout in Diamond Lake have shown little ability to use tui chub as a food source, based on analysis of experimental stocking of various salmonids and examination of stomach contents. Consequently, the tui chub were able to effectively seek food in the littoral zone during the day and migrate into the pelagic zone at night. Another consequence of the chubs' behavior is the possible effect it has on translocation of nutrients from the littoral zone to the pelagic zone. The diel migration of tui chub observed in Diamond Lake is similar to that observed for roach (Hölker et al. 2002) and dace (Gauthier & Boisclair 1997), but without the predation risks experienced in these other settings.

Diamond Lake was treated with rotenone again in September 2006 in another attempt to restore the trout fishery and reduce the number and duration of lake closures associated with cyanobacteria blooms. Recovery paths from biomanipulation efforts are notoriously difficult to correctly forecast (Pace et al. 1998, Vanni 2002, Simon & Townsend 2003, Mehner et al. 2004). Nevertheless, past experience suggests that the changes that have a high probability of occurring in Diamond Lake post-treatment include: (1) a major increase in benthic production and a return to a more diverse benthic fauna, (2) a reduction in *Anabaena* density, (3) a decrease in pennate planktonic diatoms, and (4) a decrease in the proportion of rotifers and an increase in the density and proportion of larger cladocerans. It is unclear whether the cyanobacteria densities will decline rapidly following the treatment, or whether the lake will experience a more prolonged recovery as observed in the 1960s and 1970s. Efforts were made in 2006 to reduce the biomass of tui chub by netting 30.8 tonnes of chub prior to the treatment and collecting another 15.8 tonnes of dead fish following the treatment. It is hoped that this will reduce the phosphorus available in the lake and lead to a more rapid improvement in the lake water quality than may have been possible without this action.

The probability of tui chub or other unwanted fish species being re-introduced into Diamond Lake following the planned rotenone treatment in 2006 is considered by some to be high (UNF 2004). Should this occur, we anticipate an increase in cyanobacteria, a decrease in benthic biomass, and an increase in the relative abundance of rotifers. However, it is less clear if the recovery trajectory in Diamond Lake will remain the same as occurred following the 1954 treatment or become increasingly resistant to recovery because of increased nutrient loading to the sediment. Lake response to disruptions in trophic structure appears to increase in more fertile lakes (Pace et al. 1998), suggesting that Diamond Lake may become more sensitive to various perturbations.

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