FINAL REPORT

EFFECTS OF WATER CLARITY AND OTHER FACTORS ON AQUATIC LIFE OF GRAND LAKE, COLORADO

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Prepared For
Northern Colorado Water Conservancy District

February 28, 2014

EXECUTIVE SUMMARY

This project evaluated the current state of knowledge regarding effects of water clarity and other factors on aquatic life in Grand Lake, Colorado. Existing data and reports were compiled along with a review of scientific literature. Gaps were addressed with field sampling of key components of the reservoir's aquatic life and with laboratory analyses to determine food web structure and evaluate factors limiting for aquatic life at Grand Lake. Data from the present study were combined with existing data on Grand Lake and comparable data from other coldwater reservoirs in Colorado to evaluate the relationship between clarity and other factors on aquatic life of Grand Lake. The food web of Grand Lake is dominated by an extremely abundant Mysis shrimp population that competes with sport fish for zooplankton. Growth and condition of most sport fish in Grand Lake are fair to poor. We believe that the relatively modest changes in water clarity induced by the pumping of water from Shadow Mountain Reservoir have not adversely affected fish populations. Direct effects of turbidity or suspended solids on fish health have not been observed at the levels found in Grand Lake. The data suggest that pumping from Shadow Mountain Reservoir has an enriching effect that should be beneficial to Grand Lake's fish populations. Reducing nutrients and zooplankton pumped into Grand Lake to improve water clarity could result in declines in *Daphnia* and sport fish growth and production.

INTRODUCTION

Clarity of lakes has both aesthetic and ecological aspects. This project focused on ecological aspects. Humans often equate water clarity with water quality and even ecosystem health. Indeed, reduced water clarity can be symptomatic of environmental degradation, for example, cyanobacteria blooms and hypoxia resulting from eutrophication that can be harmful to aquatic life. High turbidity levels can alter plant and algal production, impair vision and foraging of fish (De Robertis et al. 2003), and can even be lethal at extremely high levels. However, health of aquatic life and some beneficial uses of water, such as recreational fishing, may be enhanced by some factors that can reduce water clarity to intermediate levels by providing cover for young fish and increasing productivity of the system (Ney 1996; Stockner et al. 2000; Anders and Ashley 2007).

At Grand Lake, Colorado, water clarity has been affected by Colorado-Big Thompson system operations. Water pumped into Grand Lake from downstream has different physicochemical and biological characteristics than water in Grand Lake (WQP 2013), contributing to a reduction in water clarity, particularly in certain years and seasons (Boyer and Hawley 2012). However, Grand Lake has also experienced dramatic changes resulting from introductions of nonnative species for sport fishery management, some occurring after the completion of CBT. The introduction of Mysis shrimp *Mysis diluviana* has had a strong negative influence on the lake's food web, with consequences for both water clarity and the health of other aquatic life. The purpose of this study is to examine effects of 1) pumping/water clarity and 2) other factors including Mysis shrimp on aquatic life at Grand Lake, with an emphasis on zooplankton and fish.

STUDY SITE

Grand Lake is located at 2,550 m ASL in Grand County, Colorado near the southwest border of Rocky Mountain National Park. Grand Lake is the second largest (208 ha) and deepest (81 m) natural lake in Colorado (Nelson 1988). Colorado River cutthroat trout *Oncorhynchus clarkii pleuriticus* were probably native to the lake but were thought to be hybridized with rainbow trout *Oncorhynchus mykiss* by the early 1900s (Wiltzius 1985). The lake is currently stocked with kokanee *Oncorhynchus nerka* and rainbow trout; brown trout *Salmo trutta* and lake trout *Salvelinus namaycush* are naturally reproducing. Since the 1940s the lake has been part of the Colorado-Big Thompson Project (CBT). The CBT's Alva B. Adams Tunnel was completed on the eastern end of the lake in 1944 and was opened in 1947 (Table 1). The tunnel is used to shuttle water pumped from Granby Reservoir (beginning in 1951) and through Shadow Mountain Reservoir and Grand Lake to northeastern Colorado. Mysis shrimp were introduced into Grand Lake (and many other western U.S. waters) in 1969 with a goal of increasing sport fish growth (Martinez 1991). Unexpectedly, these introductions harmed rather than helped sport fish populations as Mysis shrimp preyed on zooplankton populations but were relatively immune to predation by fishes (Nesler and Bergersen 1991; Chipps and Bennett 2000).

METHODS

We used a combination of field sampling, laboratory analyses and comparative analysis. Data from the present study were combined with existing data on Grand Lake and comparable data from other coldwater reservoirs in Colorado to interpret conditions at Grand Lake and to evaluate the relationship between water clarity and other factors on aquatic life of Grand Lake.

Biological sampling

We sampled zooplankton quantitatively at each of three sites (Figure 1) during June-August 2013 using 153 µ and 500 µ mesh Wisconsin nets (June, August) or Clarke-Bumpus metered plankton sampler (July) towed vertically from 10 m to the surface (Table A1). We also collected zooplankton for stable isotope analysis with both 153 µ and 500 µ mesh nets, by towing the nets horizontally just below the surface. We were unable to capture enough plankton biomass in June for stable isotope analysis.

Mysis shrimp were sampled at night at the time of the New Moon on June 10, 2013 and August 7, 2013 using a net of the same configuration used by Colorado Parks and Wildlife for their standardized Mysis shrimp monitoring statewide (Martinez et al. 2010). This net had a 1.0-m diameter (0.785 m^2) opening and 500 µ mesh. Sampling began about 45 min after sunset and was performed at 8 sites, stratified by depth and quadrant of the lake (Figure 1). Two samples each were collected from within 0-20 m, 20-40 m, 40-60 m, and >60 m depth strata. The net was towed vertically with a windlass at about 1.0 m/s from 1 m above the bottom (or 60 m if depth> 60 m) to the surface. One sample was preserved in 70% ethanol for enumeration and measurements. A second sample was frozen for stable isotope analysis.

Fish were sampled from the catch collected by CPW in July, and supplemented with sampling we conducted during August 7-8, 2013. We also collected samples of fingerling and catchable rainbow trout from CPW hatcheries that provide fish for stocking at Grand Lake. Samples were collected from Finger Rock State Fish Hatchery on August 8, 2013, and from Rifle Falls State Fish Hatchery on September 6, 2013. Fish were measured and weighed and dorsal muscle tissue was collected for stable isotope analysis. We collected otoliths from a subset of salmonids (brown, lake, and rainbow trout) sampled from the lake for age determination. Lake trout abundance was estimated by the Summer Profundal Index Netting (SPIN; Sandstrom and Lester 2009) in July. A total of 36 variable mesh gill nets was set across 10-m depth strata.

Laboratory

Preserved zooplankton were identified to genus or species and life stage. Samples were counted in a Sedgwick-Rafter cell or plankton wheel (Lind 1979). Sample counts were converted to individuals/L based on abundance and the volume of lake water sampled. A subsample of up to 25 individuals from each sampling date and site was measured. Mysis shrimp samples were counted and counts converted to individuals/m^2. A subsample of 25 individuals from each sampling date and site was measured from the tip of the rostrum to the tip of the telson.

Samples for stable isotope analysis were dried at 60°C to constant weight and then pulverized to a fine powder in a mortar and pestle. Samples of this material were sent to the Stable Isotope Laboratory at Cornell University for determination of C:N ratio, $\delta^{13}C$, and $\delta^{15}N$. We normalized isotopic signatures for lipid content using the method of Post et al. (2007). Food web structure was evaluated on the basis of relative carbon and nitrogen isotope signatures of nodes in the web, and expected trophic fractionation when prey are consumed ($\Delta\delta^{15}N \approx 3$, $\Delta\delta^{13}C \approx 0.5$ per trophic level, Vander Zanden et al. 2007; McCuchan et al. 2003).

Otoliths of salmonids were embedded in epoxy resin, sectioned perpendicular to the sulcus and polished to a thickness of 0.8-1.0 mm. Age was determined by microscopic examination of annular marks. Growth was computed by fitting a von Bertalanffy growth function to the sizes-at-age determined from otoliths (Quist et al. 2012). Body condition was estimated by relative weight, W_r, an index of plumpness and well-being in fish (Pope and Kruse 2007).

Comparative analysis

We combined data from the present study on Grand Lake with existing data on water quality and food webs of 15 coldwater lakes and reservoirs in Colorado (Table 2) including Big Creek Lake, Blue Mesa Reservoir, Carter Reservoir, Dillon Reservoir, Eleven Mile Reservoir, Granby Reservoir, Grand Lake, Horsetooth Reservoir, Mc Phee Reservoir, Ruedi Reservoir, Shadow Mountain Reservoir, Taylor Park Reservoir, Turquoise Reservoir, Twin Lakes, and Vallecito Reservoir. Data gathered included surface temperature, Secchi depth, zooplankton (*Daphnia*) density, Mysis shrimp density, and fish growth obtained from our own research and databases of Northern Water, Colorado Parks and Wildlife, USBR and other sources. These data allowed us to put measurements obtained from Grand Lake in the context of findings at other important coldwater systems in Colorado.

Effects of pumping

We assumed that pumping water from Shadow Mountain Reservoir into Grand Lake could reduce water clarity when the source water was higher in dissolved and suspended substances than the water in Grand Lake itself. We differentiated between two clarity-reducing effects: reduced light penetration caused by light attenuating substances in the water such as dissolved and particulate organic matter, and increased light scattering from particulate matter in the water such as algal cells, fine detrital particles, and suspended inorganic material. We reviewed the scientific literature on effects of water clarity on lakes. Our focus was on evaluating potential direct and indirect effects of reduced water clarity on aquatic life, primarily fish. We also considered the effects of other characteristics of pumped water such as nutrients, organic matter and zooplankton, which could have an enriching effect on the Grand Lake food web.

RESULTS AND DISCUSSION

Biological sampling

The density of total zooplankton increased from < 1.00 plankters/L in June to > 200 plankters/L in August (Table 3). All taxa increased over the summer, but cyclopoid copepods were by far the most numerous zooplankton taxon sampled, increasing from 0.7 plankters/L in June to about 190 plankters/L in August. Catch composition was very different between 153 µ and 500 µ nets (Table A2, Figure A1), with the 500 µ net missing virtually all *Bosmina* and most copepods. Density of all *Daphnia* spp, the zooplankton preferred by fish, was very low all summer, and only exceeded 1 plankter/L in August (1.468 plankters/L) when the surface temperature was > 17.0 °C. These results appear to be fairly typical for the lake. The mean *Daphnia* density measured in NCWCD monitoring at Grand Lake during 2005-2013was just 0.6 ± 0.5 *Daphnia*/L. We believe the low *Daphnia* density at Grand Lake is primarily due to the presence of a very large Mysis shrimp population that can access the epilimnion throughout most of the year, and not the result of low system productivity.

The density of Mysis shrimp was very high, at about 800 mysids/m^2 in June and August (Table 4). Mysis shrimp areal and volumetric densities were more variable across sites and depths in June compared to August. In August Mysis shrimp areal density was highest in the 40-60 m depth stratum and was about half that at all other depth strata. On a volumetric basis, Mysis shrimp density was highest in the shallowest stations, and lowest in depths > 60 m where dissolved oxygen on the bottom was lowest. These are the first estimates of Mysis shrimp density measured at Grand Lake, so there are no historical data to which to compare. However, Mysis shrimp density at Grand Lake was higher than all other waters in the comparative analysis (below).

Body condition of sport fish was fair to poor for all species sampled. Relative weight (W_r) was generally below the norm (100) for each species (Figure 2). Mean W_r was 82, 81, 94, and 83 for brown trout, kokanee, lake trout and resident rainbow trout. The range of W_r for lake trout was greatest (W_r = 55-120), with some individuals in good to excellent condition but many others in fair to poor condition. Surprisingly little historic data were available on the fish populations at Grand Lake. The best information available was collected by Jon Ewert (CPW), who conducted periodic surveys at Grand Lake to monitor the status of the fishery beginning in 2005. Relative weights of brown trout and lake trout were similar to 2013 in 2005-2012, with lake trout generally in somewhat better body condition than brown trout (Table 5).

Consistent with differences in body condition, the growth rate of brown trout was poorer than lake trout. Growth of brown trout (Figure 3) was fair and was similar to that measured in Dillon Reservoir, where size and condition of brown trout is unacceptable to many anglers and has required extraordinary management measures by CPW in 2012-2013 to improve growth. Few brown trout in Grand Lake achieve even intermediate size ("preferred", Hyatt and Hubert 2001). Alternatively, lake trout growth in Grand Lake was fair to good, with some fish achieving "memorable" size within 10 years (Figure 3). No historic data on fish growth at Grand Lake were available. Growth of lake trout in Grand Lake was modest compared to the state's premier lake trout fishery at Blue Mesa Reservoir. However, an abundance estimate performed by CPW and CSU in July 2013 (Jon Ewert, CPW, unpublished data) suggested that lake trout abundance (N=2,491, CL=2008-2738) and density (12.9 fish/ha) were relatively high in Grand Lake.

We determined carbon and nitrogen isotopic signatures of zooplankton, Mysis shrimp, suckers, hatchery rainbow trout, resident rainbow trout, brown trout, and lake trout. In aggregate, the signatures suggested several patterns. The signatures of Mysis shrimp suggested that zooplankton are not their only prey resource (Figure 4). Because of the extremely low density of preferred zooplankton prey (*Daphnia*) in Grand Lake, it is likely that Mysis shrimp must supplement their diet with detrital material and algae with lower carbon and nitrogen signatures than zooplankton. Kokanee, which are typically the most planktivorous sport fish species, also must have relied on other prey besides zooplankton. Although not sampled, we believe that based on experience in other Colorado waters kokanee are probably consuming chironomid larvae and pupae.

The carbon and nitrogen signatures of brown trout and lake trout increased with fish size (Figure 4). The largest sizes of both species had similar isotopic signatures that strongly suggested that hatchery rainbow trout and kokanee contributed significantly to the diet and growth of these fish. Fingerling kokanee and rainbow trout have been stocked in fairly consistent numbers during 2003-2013 (Figure 5), supporting the notion that hatchery prey are important for some lake trout and brown trout at Grand Lake. Signatures of smaller lake trout suggested that they consumed Mysis shrimp, zooplankton, kokanee, and perhaps chironomid larvae. Smaller brown trout diet was probably composed of invertebrates not sampled, such as chironomid larvae.

Comparative analysis

At 208 surface ha, Grand Lake was the second smallest water body in our dataset (Figure 6). This may explain why the lake was not included in statewide coldwater reservoir surveys conducted by CPW in the 1990s and 2000s (Martinez et al. 2010). Grand Lake is also unusual because water level fluctuations are much less than in the other systems. Although most of the systems in our set are manmade reservoirs, Big Creek Lake and Twin Lakes were originally natural water bodies that were subsequently modified for water supply, as at Grand Lake. Grand Lake's surface elevation (2,550 m ASL) is similar to the average elevation of waters in the dataset (Figure 6), which ranged 1655-3009 m ASL.

Average (July-September) Secchi depth at Grand Lake (3.35 m) was slightly lower than the average for all waters in the dataset (3.86 m; Figure 6). Generally, waters with the highest Secchi depth were also waters with high summer *Daphnia* densities and lowest Mysis shrimp abundance (Figure 6). However, Twin Lakes had relatively clear water but very low *Daphnia* density, and Shadow Mountain Reservoir had high *Daphnia* density and turbid water, suggesting that both top-down and bottom-up factors control water clarity in Colorado coldwater reservoirs, including Grand Lake. Determining the relative importance of top-down/bottom-up effects on clarity at Grand Lake is difficult with the present observational data because the transport of substances, including inorganic material, from Shadow Mountain Reservoir may mask some food web effects on clarity.

Water temperature at Grand Lake was similar to other reservoirs at similar elevation (Figure 7). Surface temperature reached its annual maximum (~18 °C) in the first week of August (Figure 7). Comparison with surface temperatures measured in 1940-1942, prior to completion of the CBT, suggest that pumping and transfers through the Adams Tunnel have not affected the lake's surface temperature during the growing season (Figure 8). The thermal regime at Grand Lake is favorable for Mysis shrimp. Mysis shrimp have a thermal preference of 6-12°C (Boscarino et al. 2010), and avoid water temperatures > 17 °C (Johnson and Martinez 2012). The temperature of Grand Lake's epilimnion exceeds this threshold for only about one month or less during late July- early August (Figure 8), allowing Mysis shrimp to prey on epilimnetic zooplankton for most of the year.

Density of Mysis shrimp measured in Grand Lake in 2013 was higher than the average Mysis shrimp density measured at 10 other Colorado reservoirs containing the species (Figure 6). The relatively favorable thermal regime and extremely abundant Mysis shrimp population are very likely responsible for the lake's exceptionally low *Daphnia* density (Figure 6). Only Twin Lakes and Dillon Reservoir had lower *Daphnia* density, partially due to their relatively oligotrophic status.

Effects of pumping- clarity

Extensive water quality monitoring by NCWCD and others has documented changes in water clarity of Grand Lake associated with pumping water from Granby Reservoir into Shadow Mountain Reservoir and Grand Lake (WQP 2013). Post-CBT Secchi depths have ranged 1.2 to 5.7 m. Unfortunately, few water clarity (Secchi depth) data exist prior to the 1990s and only a single observation exists from prior to operation of the CBT (9.2 m in 1941; Boyer and Hawley 2012). Nor are there substantive data available on the status of fish populations in Grand Lake before the Adams Tunnel became operational. This lack of "pre-treatment" data makes inference about how pumping has affected aquatic life in Grand Lake more difficult but results of studies in the literature provide insights.

The limnological literature shows that reduced light penetration (and increased scattering) can have wide-ranging effects on aquatic life in lakes (Table 6). Fundamentally, light attenuation limits the depth of the photic zone (~ 3 x Secchi depth; Horne and Goldman 1994), where photosynthesis exceeds respiration. Thus, the maximum depth where rooted macrophytes, benthic algae and phytoplankton can persist is set by water clarity. Reduced clarity can then affect the distribution and production of herbivorous insects and littoral zooplankton. Reduced light penetration may also favor phytoplankton over macrophytes in competition for light. Very low light penetration can even shift the composition of the phytoplankton assemblage toward cyanobacteria (Mur et al. 1977; Huisman et al. 1999), which then can limit production of grazers and other consumers.

Because of the shape and composition of Grand Lake's basin, most of the lake bottom with suitable depths (<10 m) and substrate for rooted macrophytes occurs in the southwest corner of the lake. It is in that area of the lake that changes in water clarity should have the most readily observable effects on the density and distribution of rooted macrophytes. Rooted macrophytes can provide habitat for various fish food organisms so this region of the lake may be an important foraging area for fish that consume certain invertebrates. If turbidity reduces the biomass of macrophytes it could affect production of fish food organisms. However, this area comprises a relatively small fraction of the lake's area, and such indirect effects of fish food production should be small and difficult to demonstrate. There are more direct potential effects of reduced clarity on visual-foraging consumers that would affect the entire lake.

Both light intensity and scattering affect predators by reducing their visual field and increasing energy spent foraging. Many fish species, including salmonids, rely on vision for detecting their predators and prey (Confer et al. 1978; Mazur and Beauchamp 2003). Turbidity reduces their visual range and reaction distance (Vinyard and O'Brien 1976; Vogel and Beauchamp 1999) and thus reduces the ability of predators and prey to detect each other (Ferrari et al. 2010; Chivers et al. 2012). Predators have an easier time detecting prey in clear water, and prey species may change their behavior (e.g., forage less) to avoid predators in clear water. In more turbid water visual predators and prey detect each other at closer distances, making prey easier to capture, but increasing the search time of predators.

Because prey fish feed on smaller prey than piscivores, they detect their prey at relatively shorter distances. Hence, their foraging success is less affected by turbidity than for piscivores (Vinyard and O'Brien 1976). Turbidity ranging 0.95-11 NTU had no effect on weakfish *Cynoscion regalis* consumption of Mysis shrimp (Grecay and Targett 1996). Planktivorous salmon feeding was unaffected by a turbidity range of 0-40 NTU (De Robertis et al. 2003). Other studies have demonstrated that prey fish may actually forage more under moderate turbidity (~10-100 NTU) than they would in clear water, partly because it is not advantageous to reduce foraging when evading predators is unlikely. Abrahams and Kattenfeld (1997) found that planktivorous minnows were more likely to forage in turbid water (11-13 NTU) than in clearer water. Likewise, Gregory and Northcote (1993) found that invertebrate-eating juvenile salmon increased their foraging when turbidity increased to 35 NTU, and was impaired only when turbidity approached 150 NTU. Juvenile steelhead *Oncorhynchus mykiss* showed reduced growth rate at 25-50 NTU (Sigler et al. 1984) but others have found conflicting results (Swenson and Matson 1976). Regardless, the average turbidity measured at Grand Lake during the 2011, 2012 growing seasons (1.99 NTU; range 0.60-3.90 NTU; n = 104) was well below the level that the literature suggests would adversely affect foraging or growth of prey fish such as kokanee and rainbow trout.

Turbidity may affect foraging by piscivores more than by prey fish because piscivores can detect their prey at much longer distances in clear water compared to prey fish so the reduced visual field caused by turbidity is more significant to piscivores. Mazur and Beauchamp (2003) found that reaction distance of lake trout was unaffected by low turbidity (0.08 - 0.55 NTU) but decreased by about 15% when turbidity increased to 1.50 NTU, and by about 30% when turbidity increased to 3.18 NTU, but little more at 7.40 NTU (Vogel and Beauchamp 1999) (Figure 9). Reaction distance of cutthroat and rainbow trout changed little at 0.08 – 1.50 NTU (Barrett et al. 1992; Vogel and Beauchamp 1999). Overall, these studies suggest that lake trout reaction distance may be reduced by turbidity more than for rainbow and cutthroat trout. Whether such changes affect the feeding and growth of piscivores is harder to evaluate because predators can search more to compensate for a reduced visual field, and studies suggest that their capture success may actually increase under more turbid conditions.

Jönsson et al. (2013) found that although encounter rate and duration were reduced by turbidity (3.2-7.5 NTU) capture success of piscivores increased with turbidity. This may help explain why predation by adult cutthroat trout on juvenile salmonids did not differ between clear (0.5 – 2.4 NTU) and turbid (12-87 NTU) treatments (Gregory and Levings 1996). Abrahams and Kattenfeld (1997) found that predation on planktivorous minnows did not decline in turbid (11-13 NTU) water and Chivers et al. (2012) found that minnows were less able to recognize and respond to predators in turbid water (31 NTU, making piscivory more successful.

While turbidity can have indirect effects on fish health by limiting feeding, suspended solids associated with turbidity can have direct effects on fish health via physical injury and physiological stress (Michel et al. 2013). Although turbidity is not always a good surrogate for the quantity and nature of suspended solids that can affect fish health (Davies-Colley and Smith 2001; Bilotta and Brazier 2008), studies often use turbidity as a benchmark. Sigler et al. (1984) found that juvenile steelhead trout died when chronic turbidity ranged 100-300 NTU. In New Zealand, acute exposure at up to 20,000 NTU had no effect on several aquatic insects, crayfish and fish (Rowe et al. 2002). The lethal turbidity levels for two sensitive fish species were 3,050 NTU and 20,235 NTU, and much higher for others. In a review of more than 70 studies, Newcombe and MacDonald (1991) found that salmonids were most sensitive to suspended solid concentrations at the egg-fry life stages. Lethal and sublethal effects were rarely demonstrated below 20 mg/L and most reported effects occurred at orders of magnitude higher TSS. During 2005-2011 TSS averaged about 2 and 3 mg/L and never exceeded 13 mg/L in surface water of Grand Lake and Shadow Mountain, respectively (WQP 2013). The literature suggests that adverse health effects of turbidity inducing substances on fish occur at substantially higher turbidities and TSS than have been observed at Grand Lake.

Effects of pumping- enrichment

Pumping affects more than turbidity at Grand Lake. Monitoring has shown that water that enters Grand Lake from Shadow Mountain Reservoir has higher nutrient and organic matter concentrations (WQP 2013; McCutchan 2013). Phytoplankton and zooplankton are also transported from Shadow Mountain Reservoir to Grand Lake during pumping. Thus, to understand the potential effects of pumped water on the aquatic life of Grand Lake it is also necessary to examine the effects of substances in the water pumped into Grand Lake that can affect system productivity.

Many connote the term eutrophication with degraded water quality, and assume that “cleaner” (clearer) water will be beneficial for all forms of aquatic life (Ney 1996). This perception is inaccurate. Generally speaking and below some threshold, the productivity of fish populations is inversely related to indicators of oligotrophy such as water clarity (Oglesby 1977; Olem and Flock 1990; Figure 10). Thus, lake management goals of clear water and productive fish populations can be conflicting. Increasing nutrient and chlorophyll concentrations decrease clarity but increase fisheries production until the assimilative capacity of the system is exceeded and decomposition of unconsumed primary production results in degraded habitat (e.g., hypoxia) (Stockner et al. 2000). At low to intermediate trophic states, reducing nutrient loading to encourage clearer water deprives the food web of resources that could contribute to higher growth and abundance of fishes.

Colorado’s reservoir fisheries are primarily supported by energy produced in the pelagic zone (Johnson and Goettl 1999; Johnson and Martinez 2000). Based on the lake’s steep-sided basin morphometry, we would expect pelagic production to be the primary energy source for Grand Lake also. Nutrient inputs can stimulate increased production of phytoplankton, and provided a suitable N:P ratio, the phytoplankton produced can provide more resources for grazing zooplankton including *Daphnia*. Several studies have demonstrated a very strong linkage between *Daphnia* density and the growth of sport fish in Colorado (Martinez and Wiltzius 1995; Johnson and Martinez 2000; Johnson and Martinez 2012). At Grand Lake *Daphnia* density was among the lowest of the reservoirs we examined, and growth and body condition of most sport fish were fair to poor. Mysis shrimp undoubtedly contribute to the reduced *Daphnia* density at Grand Lake but nutrients transported from Shadow Mountain Reservoir could be moderating the effects of Mysis shrimp on *Daphnia* and fish.

In fact, nutrient supplementation has been proposed as a management tool to mitigate effects of Mysis shrimp predation on *Daphnia* and thereby increase sport fish production in other lakes with Mysis shrimp and salmonid sport fisheries (Caldwell and Wilhelm 2011). Not enough is known about the food web to advocate for purposeful nutrient additions at Grand Lake, but we do believe that reducing nutrient loading would be detrimental to fish populations. Surface TP at Grand Lake averaged about 11 µg/L during 2005-2011 (WQP 2013), and was nearly always below the 25 µg/L interim water quality standard for TP in coldwater lakes and reservoirs. During 2008-2011 total nitrogen at the surface averaged about 250 µg/L and rarely exceeded the 426 µg/L interim water quality standard for TN (WQP 2013). These relatively low nutrient concentrations occurred despite that fact that TP and TN loading are approximately five times higher than they would be without pumping from Shadow Mountain Reservoir (Boyer and Hawley 2012). A large number of studies suggest that fish production would decrease with lower nutrient concentrations (Figure 10). For example, Plante and Downing (1993) found that salmonid (including brown trout and kokanee) production increased with TP up to about 100 µg/L, and lake trout growth and size structure increased with nutrient additions to an oligotrophic Arctic lake (Lienesch et al. 2005). Thus, nutrient inputs to Grand Lake from Shadow Mountain Reservoir are probably beneficial to food web production. The specific effects of nutrients on fish production at Grand Lake are difficult to predict because they depend on algal nutrient limitation status, the effects of Mysis shrimp and the conversion efficiency of phytoplankton to fish. Maintaining a relatively high N:P ratio would favor edible algae and a higher conversion efficiency. Reducing nutrient inputs would likely result in declines in *Daphnia* and sport fish growth and production.

Direct transport of *Daphnia* from Shadow Mountain Reservoir is also likely compensating for Mysis shrimp predation, and is probably beneficial to fish production in Grand Lake. Although the system-level impact of this zooplankton subsidy was not quantified, monitoring data show that *Daphnia* density in the water flowing into Grand Lake from Shadow Mountain Reservoir is much higher than that measured in the water column of Grand Lake (Figure 11). Management alternatives aimed at improving water clarity in Grand Lake that reduce or eliminate the enriching effects of Shadow Mountain Reservoir nutrients and zooplankton will likely be detrimental to the growth and production of Grand Lake's fish populations.

CONCLUSIONS

The relatively modest changes in turbidity in Grand Lake caused by pumping may allow prey fish to forage more freely, improving their opportunity for feeding and growth. While piscivores such as lake trout and brown trout may need to devote more energy to searching for prey, they may experience a higher probability of capturing the prey which could offset search costs. Direct effects of turbidity or suspended solids on fish health have not been observed at the levels found in Grand Lake.

The food web of Grand Lake is dominated by an extremely abundant Mysis shrimp population. Predation by Mysis shrimp suppresses zooplankton populations that are essential to productive sport fisheries in Colorado's coldwater lakes and reservoirs. Growth and body condition of most sport fish in Grand Lake are fair to poor and satisfactory body condition of large lake trout and brown trout are probably only sustained by annual stocking of kokanee and rainbow trout. Although no pre-CBT fish data exist, we believe that changes in water clarity induced by the pumping of water from Shadow Mountain Reservoir have not adversely affected fish populations. In fact, the data suggest that pumping from Shadow Mountain Reservoir has an enriching effect that should be beneficial to Grand Lake's fish populations. Reducing nutrients and zooplankton pumped into Grand Lake to improve water clarity could result in declines in *Daphnia* and sport fish growth and production.

RECOMMENDATIONS

Important areas for future research to better understand the influences of pumping on aquatic life in Grand Lake include:

- Investigations to quantify the indirect effects that Mysis shrimp predation upon herbivorous zooplankton have on water clarity.
    - Has the Mysis shrimp population reduced system-wide grazing on phytoplankton, resulting in poorer water clarity than would exist in the absence of Mysis shrimp?
    - Would reductions in Mysis shrimp biomass result in improved water clarity, and if so, how might such reductions be accomplished?
- Importance of zooplankton pumped into Grand Lake from Shadow Mountain Reservoir
    - Does the biomass of *Daphnia* pumped into Grand Lake represent a meaningful food subsidy supporting growth of sport fish?
- Long-term effects of subsidies of nutrients and organic matter from Shadow Mountain Reservoir to Grand Lake.
    - Will continued inputs of organic matter and ungrazed phytoplankton exceed the assimilative capacity of Grand Lake, resulting in increased hypoxia in the hypolimnion?
    - How do water residence time and seasonal timing of pumping influence food web benefits derived from subsidies (e.g., effects on particle settling vs. uptake by food web vs. flushing)?
- Effects of climate on the food web
    - Will a warmer climate increase the epilimnetic thermal refuge for *Daphnia*, reducing predation by Mysis shrimp and contributing to increased grazing and food for planktivorous fish?
    - How will climate change interact with human population growth to alter the timing and quantity of water transfers through Grand Lake?
- Effects of nutrient stoichiometry on phytoplankton, zooplankton and water clarity.
    - How will changes in climate and land use in the watershed affect N:P and nutrient inputs to Three Lakes system, and how will such changes affect water clarity?

  - How might changes in N:P ratios in Grand Lake's inflows affect phytoplankton community composition and edibility for primary consumers that are the food of sport fish?
  - Is nutrient management aimed at maintaining an N:P ratio that improves grazing on phytoplankton a means to improve water clarity and fisheries production?
- Effects of increased clarity on aquatic life in Grand Lake
  - Given the overwhelming influence that Mysis shrimp appear to have on the food web, what evidence is there to expect modest changes in water clarity (i.e., 4 m Secchi depth standard) would enhance the health of aquatic life?
  - Would changes to water management aimed at improving water clarity necessitate reductions in the subsidies of nutrients and plankton that support fish growth in Grand Lake and that compensate for the effects of Mysis shrimp?
  - Would the removal of such subsidies actually intensify competition for zooplankton by Mysis shrimp and fish in Grand Lake, and result in further reductions in growth and condition of fishes?

ACKNOWLEDGMENTS

This study was funded by Northern Colorado Water Conservancy District. We appreciate the cooperation and assistance of Jon Ewert, Jesse Lepak, Doc Capwell and Mitch Espinoza of Colorado Division of Parks and Wildlife.

LITERATURE CITED

Abrahams, M. & Kattenfeld, M. 1997 The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behaviour Ecology and Sociobiology 40:169–174.

Anders, P.J. and K.I. Ashely. 2007. The clear-water paradox of aquatic ecosystem restoration. Fisheries 32:125-128.

Barrett, J.C., G.D. Grossman, and J. Rosenfeld. 1992. Turbidity-induced changes in reactive distance of rainbow trout. Transactions of the American Fisheries Society 121:437-443.

Bilotta and Brazier. 2008. Understanding the influence of suspended solids on water quality and aquatic biota. Water Research 42:2849-2861.

BOR (U.S. Department of Interior Bureau of Reclamation). 2012. Colorado-Big Thompson Project West Slope Collection System Grand County, Colorado: Preliminary Alternatives

Development Report. Bureau of Reclamation, Great Plains Region, Eastern Colorado Area Office, Loveland, Colorado.

Boyer, J-M., Hawley, C. 2012. Operational and water quality summary report for Grand Lake and Shadow Mountain Reservoir. Prepared by Hydros Consulting Inc. (Boulder, CO) for Grand County, Northern Water and U.S. Bureau of Reclamation.

Caldwell, T.J. and F.M. Wilhelm. 2011. The life history characteristics, growth and density of *Mysis diluviana* in Lake Pend Oreille, Idaho, USA. Journal of Great Lakes Research 38(S2):58-67.

Chipps, S.R., Bennett, D.H. 2000. Zooplanktivory and nutrient regeneration by invertebrate (*Mysis relicta*) and vertebrate (*Oncorhynchus nerka*) planktivores: Implications for trophic interactions in oligotrophic lakes. Transactions of the American Fisheries Society 129: 569-583.

Chivers, D.P., F. Al-Batati, G.E. Brown, and M.C.O. Ferrari. 2012. The effect of turbidity on recognition and generalization of predators and non-predators in aquatic ecosystems. Ecology and Evolution 3:268-277.

Confer, J.L., G.L. Howick, M.H. Corzette, S.L. Kramer, S. Fitzgibbon and R. Landesberg. 1978. Visual predation by planktivores. Oikos 31:27-37.

Davies-Colley, R.J., and D.G. Smith. 2001. Turbidity, suspended sediment and water clarity: a review. Journal of the American Water Resources Association 37:1085-1101.

De Robertis, A., C. H. Ryer, A.Veloza, and R. D. Brodeur. 2003. Differential effects of turbidity on prey consumption of piscivorous and planktivorous fish. Canadian Journal of Fisheries and Aquatic Sciences 60:1517-1526.

Ferrari, M.C.O., K.R. Lysak, and D.P. Chivers. 2010. Turbidity as an ecological constraint on learned predator recognition and generalization in a prey fish. Animal Behaviour 79:515-519.

Grecay, P.A. and T.E. Targett. 1996. Effects of turbidity, light level and prey concentration on feeding of juvenile weakfish *Cynoscion regalis*. Marine Ecology Progress Series 131:11-16.

Gregory, R.S. and T.G. Northcote. 1993. Surface, planktonic, and benthic foraging by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) in turbid laboratory conditions. Canadian Journal of Fisheries and Aquatic Sciences 50:233-240.

Gregory and Levings 1996. The effects of turbidity and vegetation on the risk of juvenile salmonids, *Oncorhynchus* spp., to predation by adult cutthroat trout, *O. clarkii*. Environmental Biology of Fishes 47:279-288.

Horne, A.J. and Goldman, C.R. 1994. Limnology, Second edition. McGraw-Hill, Inc. New York, NY.

Hyatt, M. and W.A. Hubert. 2000. Proposed standard-weight (Ws) equations for kokanee, golden trout, and bull trout. Journal of Freshwater Ecology 15:559-563.

Hyatt, M. and W.A. Hubert. 2001. Proposed standard-weight (Ws) equation and length-categorization standards for brown trout (*Salmo trutta*) in lentic habitats. Journal of Freshwater Ecology 16:53-56.

Huisman, J., Jonker, R.R., Zonneveld, C., Weissing, F.J. 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. Ecology 80:211-222.

Johnson, B. M. and J. P. Goettl, Jr. 1999. Food web changes over fourteen years following introduction of rainbow smelt into a Colorado reservoir. North American Journal of Fisheries Management 19:629-642.

Johnson, B. M. and P.J. Martinez. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:115 131.

Johnson, B.M. and P.J. Martinez. 2012. Hydroclimate mediates effects of a keystone species in a coldwater reservoir. Lake and Reservoir Management 28:70-83.

Jönsson, M., L. Ranåker, P.A. Nilsson, and C. Brönmark. 2013. Foraging efficiency and prey selectivity in a visual predator: differential effects of turbid and humic water. Canadian Journal of Fisheries and Aquatic Sciences

Lienesch, P. W.; McDonald, M. E.; Hershey, A. E.; O'Brien, W. J.; Bettez, N. D. Effects of a whole-lake, experimental fertilization on lake trout in a small oligotrophic Arctic lake. Hydrobiologia 2005, 548, 51-66.

Lind, O. T. 1979. Handbook of common methods in limnology, second edition. C. V. Mosby Company, St. Louis, MO.

Martinez, P.J. 1991. Kokanee studies. Federal Aid Project F-79, Colorado Division of Wildlife, Fort Collins, CO.

Martinez, P.J., M.D. Gross, and E.M. Vigil. 2010. A compendium of crustacean zooplankton and Mysis diluviana collections from selected Colorado reservoirs and lakes, 1911-2009. Special report 82, Colorado Division of Wildlife, Fort Collins, CO.

Martinez, P.J., and W.J. Wiltzius. 1995. Some factors affecting a hatchery-sustained kokanee population in a fluctuating Colorado reservoir. North American Journal of Fisheries Management 15:220-228.

Mazur, M.M., and D.A. Beauchamp. 2003. A comparison of visual prey detection among species of piscivorous salmonids: effects of light and low turbidities. Environmental Biology of Fishes 67:397-405.

McCutchan, J. H. Jr, W. M. Lewis Jr, C. Kendall, and C. C. McGrath. 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378-390.

McCutchan, J.H., Jr. 2013. Sources and characterization of particles affecting transparency in Grand Lake and Shadow Mountain Reservoir: 2012 preliminary report. Center for Limnology, University of Colorado, Boulder, CO.

Michel, C., H. Schmidt-Posthaus, and P. Burkhardt-Holm. 2013. Suspended sediment pulse effects in rainbow trout (*Oncorhynchus mykiss*) — relating apical and systemic responses. Canadian Journal of Fisheries and Aquatic Sciences 70:630-641.

Mur, L.R., H.J. Gons, and L. Vanliere. 1977. Some experiments on competition between green-algae and blue-green bacteria in light-limited environments. FEMS Microbiology Letters 1:335-338.

Nelson, W.C. 1971. Comparative limnology of Colorado-Big Thompson Project reservoirs and lakes. Colorado Division of Game, Fish, and Parks, Fort Collins, CO.

Nelson, W.C. 1988. High lake research and management in Colorado. Special Report 64, Colorado Division of Wildlife, Fort Collins, CO.

Newcombe, C.P., and D.D. MacDonald. 1991. Effects of suspended sediments on aquatic ecosystems. North American Journal of Fisheries Management 11:72-82.

Ney, J. J. 1996. Oligotrophication and its discontents: effects of reduced nutrient loading on reservoir fisheries. American Fisheries Society Symposium 16:285-295.

Nesler, T.P. and E.P. Bergersen. 1991. Mysids in fisheries. American Fisheries Society Symposium 9, Bethesda, Maryland.

Oglesby, R.T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. Journal of the Fisheries Research Board of Canada 34:2271-2279.

Olem, H. and G. Flock, eds. 1990. Lake and reservoir restoration guidance manual, second edition. EPA 440/4-90-006, United States Environmental Protection Agency, Washington, DC.

Plante, C. and J.A. Downing. 1993. Relationship of salmonine production to lake trophic status and temperature. Canadian Journal of Fisheries and Aquatic Sciences 50:1324-1328.

Piccolo, J.J., and W.A. Hubert. 1996. Standard weight equation for lake trout. North American Journal of Fisheries Management 13:401-404.

Pope, K. and C. Kruse. 2007. Condition. Pages 423-472 In Guy, C.S. and M.L. Brown. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, MD.

Post, D. M., C. A. Layman, D. A. Arrington, G. Takimoto, J. Quattrochi, and C. G. Montana. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. Oecologia 152:179-189.

Quist, M. C., M. A. Pegg, and D. R. DeVries. 2012. Age and growth. Pages 677-731. In Zale, A. V, D. L. Parrish, and T. M. Sutton, editors. Fisheries techniques, third edition. American Fisheries Society, Bethesda, MD.

Rowe, D.K., A. M. Suren, M. Martin, J.P. Smith, B. Smith, and E. Williams. 2002. Lethal turbidity levels for common freshwater fish and invertebrates in Auckland streams. National Institute of Water and Atmospheric Research, Hamilton, New Zealand.

Sandstrom, S. J. and N. Lester. 2009. Summer profundal index netting protocol; a Lake Trout assessment tool. Ontario Ministry of Natural Resources. Peterborough, Ontario. Version 2009.1.

Sigler, J.W., T.C. Bjornn, and F.H. Everest. 1984. Effects of chronic turbidity on density and growth of steelheads and coho salmon. Transactions of the American Fisheries Society 113:142-150.

Simpkins, D. G., and W. A. Hubert. 1996. Proposed revision of the standard-weight equation for rainbow trout. Journal of Freshwater Ecology 11:319-325.

Stockner, J.G., E. Rydin, and P. Hyenstrand. 2000. Cultural oligotrophication: causes and consequences for fisheries resources. Fisheries 25:7-14.

Swenson, W.A. and M.L. Matson. 1976. Influence of turbidity on survival, growth, and distribution of larval lake herring (*Coregonus artedii*). Transactions of the American Fisheries Society 105:541-545.

Vander Zanden, M.J., S. Chandra, S. Park, Y. Vadeboncoeur and C. R. Goldman. 2007. Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. Canadian Journal of Fisheries and Aquatic Sciences 63:2608-2620.

Vinyard, G.L. and J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. 33: 2845–2849.

Vogel, and Beauchamp. 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Canadian Journal of Fisheries and Aquatic Sciences 56:1293-1297.

Willis, D. W., B. R. Murphy, and C. S. Guy. 1993. Stock density indices: development, use and limitations. Reviews in Fisheries Science 1:203-222.

Wiltzius, W. J. 1985. Fish culture and stocking in Colorado, 1872-1978. Colorado Division of Wildlife, Fort Collins, CO.

WQP (Water Quality Program) 2013. WY2005 – WY2011 lake & reservoir sites water quality report. Northern Colorado Water Conservancy District, Berthoud, Colorado.

Table1 Chronology of events related to changes in water clarity and the food web at Grand Lake, Colorado.

Year	Event	Source
1941	9.2 m Secchi depth measured	BOR 2012
1944	Adams Tunnel completed	NCWCD
1945	Shadow Mountain Dam completed	NCWCD
1947	Adams Tunnel opened, water transfers begin	NCWCD
1951	First water pumped from Granby to Shadow Mountain	NCWCD
1951	Kokanee introduced into Granby (first place in State)	Martinez 1991
1953	Maximum Secchi depth 4.6 m	BOR 2012
1957	CBT completed	NCWCD
1961	Lake trout introduced into Granby	Martinez 1991
1969	Mysis introduced into Grand Lake	Douglas Silver
1971	Mysis introduced into Granby	Martinez 1991
1985	Windy Gap Project completed	NCWCD

Table 2. Characteristics of lakes and reservoirs included in the comparative analysis. "Natural lake" includes water bodies that were natural prior to modifications for water supply.

Water body	Code	Natural lake?	Mysis?	Year built/ altered	Elevation (ft)	Area (ac)	Capacity (ac-ft)
Big Creek Lakes	BCL	YES	YES	-	8996	351	-
Blue Mesa Reservoir	BMR	NO	NO	1965	7519	9180	940700
Carter Reservoir	CTR	NO	YES	1952	5759	1443	112230
Dillon Reservoir	DIL	NO	YES	1963	9022	3442	257269
Eleven Mile Reservoir	ELE	NO	NO	1932	7418	3400	97779
Granby Reservoir	GBR	NO	YES	1949	8281	7255	539790
Grand Lake	GDL	YES	YES	1947	8366	515	68600
Horsetooth Reservoir	HST	NO	YES	1949	5430	1900	156735
Mc Phee Reservoir	MCP	NO	NO	1984	6924	4470	381,195
Ruedi Reservoir	RUE	NO	YES	1968	7779	996	102369
Shadow Mountain Reservoir	SHM	NO	YES	1946	8367	1337	17,354
Taylor Park Reservoir	TAY	NO	YES	1937	9327	2009	106200
Turquoise Reservoir	TUR	NO	YES	1968	9873	1788	129432
Twin Lakes	TWN	YES	YES	1984	9199	1834	95988
Vallecito Reservoir	VAL	NO	NO	1941	7665	2720	129700

Table 3. Density (n/L) of *Daphnia* spp (DAP), *Bosmina* spp (BOS), cyclopoid copepods (UCY), and calanoid copepods (UCA) at three sites on Grand Lake sampled in June, July and August 2013.

Date	Site	DAP	BOS	UCY	UCA	Sum
06/10/13	ATW	0.008	0.004	0.426	0.039	
	MID	0.012	0.000	1.192	0.071	
	9A5	0.004	0.000	0.474	0.036	
	MEAN	0.008	0.001	0.697	0.049	0.755
	SD	0.004	0.002	0.429	0.019	
07/18/13	ATW	0.932	0.381	19.807	0.894	
	MID	0.213	15.446	14.659	0.340	
	9A5	0.199	2.692	17.697	1.246	
	MEAN	0.448	6.173	17.388	0.827	24.836
	SD	0.419	8.114	2.588	0.457	
08/07/13	ATW	2.368	3.158	162.229	10.263	
	MID	1.579	1.184	187.490	11.052	
	9A5	7.894	2.763	220.252	27.235	
	MEAN	3.947	2.368	189.990	16.183	212.489
	SD	3.441	1.044	29.092	9.580	
All	MEAN	1.468	2.848	69.358	5.686	79.360
	SD	2.159	3.114	104.803	9.099	

Table 4. Summary of Mysis shrimp sampling performed with a 1.0 m diameter, 500-µm mesh plankton net at Grand Lake, Colorado on June 10, 2013 and August 7, 2013.

Month	Station	Stratum (m)	Depth at station (m)	Time of tow	Sample number	Catch: No. per haul	No. per m^2	No. per m^3
June	8	00-20	11	21:58	GDL061013005	81	103.2	10.3
	5	00-20	14	22:35	GDL061013009	992	1263.7	97.2
	7	20-40	24	21:19	GDL061013001	1665	2121.0	96.4
	1	20-40	33	23:32	GDL061013015	138	175.8	5.9
	6	40-60	47	21:36	GDL061013003	918	1169.4	26.0
	2	40-60	56	23:06	GDL061013013	124	158.0	2.9
	4	>60	84	22:13	GDL061013007	762	970.7	16.2
	3	>60	85	22:48	GDL061013011	493	628.0	10.5
					MEAN=	646.6	823.7	33.2
					SD=	550.2	700.8	39.9
					N=	8.0	8.0	8.0
August	8	00-20	16	21:17	GDL080713003	444	565.6	37.7
	5	00-20	13	21:36	GDL080713005	435	554.1	55.4
	7	20-40	28	20:55	GDL080713001	516	657.3	25.3
	1	20-40	31	22:11	GDL080713008	535	681.5	23.5
	6	40-60	48	21:02	GDL080713002	844	1075.2	23.4
	2	40-60	46	21:58	GDL080713007	1045	1331.2	30.3
	4	>60	84	21:26	GDL080713004	478	608.9	10.1
	3	>60	85	21:42	GDL080713006	432	550.3	9.2
					MEAN=	591.1	753.0	26.9
					SD=	227.7	290.0	14.9
					N=	8.0	8.0	8.0

Table 5. Mean total length and body condition (W_r) of lake trout and brown trout sampled in six surveys on Grand Lake, Colorado. Data from 2013 collected by CPW and CSU; previous years data collected by Jon Ewert (CPW).

	2005	2008	2009	2012	2013	
Date of survey	06/22	07/08	07/08	06/25	07/17	08/08
LAKE TROUT (n)	14	11	12	10	87	1
Mean size (in)	12.6	16.5	13.2	13.2	16.5	18
Body condition	102	87	86	80	94	95
BROWN TROUT (n)	35	31	35	28	37	46
Mean size (in)	12.9	12.3	11.3	11.5	326	300.2
Body condition	98	85	83	82	85	81

Table 6. Potential physical and biological effects of pumping from Shadow Mountain Reservoir on the clarity and production of Grand Lake. "High" levels of these factors have not occurred to date.

Level	Reduced light penetration	Increased light scattering	Increased substances in water
Low to moderate	Shallower photic zone	Reduced visual field for predators and prey	Nutrients: subsidy taken up by pelagic food web
	Reduced macrophyte distribution: reduced invertebrate production	Increased foraging time for prey and predators	Organic matter: subsidy to detritivores, increased biomass of macroinvertebrates including Mysis
	Competitive edge to phytoplankton over macrophytes	Reduced success evading predators Increased capture success by predators	Plankton: subsidies of phytoplankton and zooplankton in pumped water to consumers
High	Phytoplankton competition for light: shift in algal community composition toward cyanobacteria, reduced food for zooplankton	Reduced encounter rates with prey, increased activity and reduced growth	Organic matter: Increased biological oxygen demand in hypolimnion Inorganic particles: inhibition of zooplankton grazing, gill abrasion in fish, sedimentation and smothering

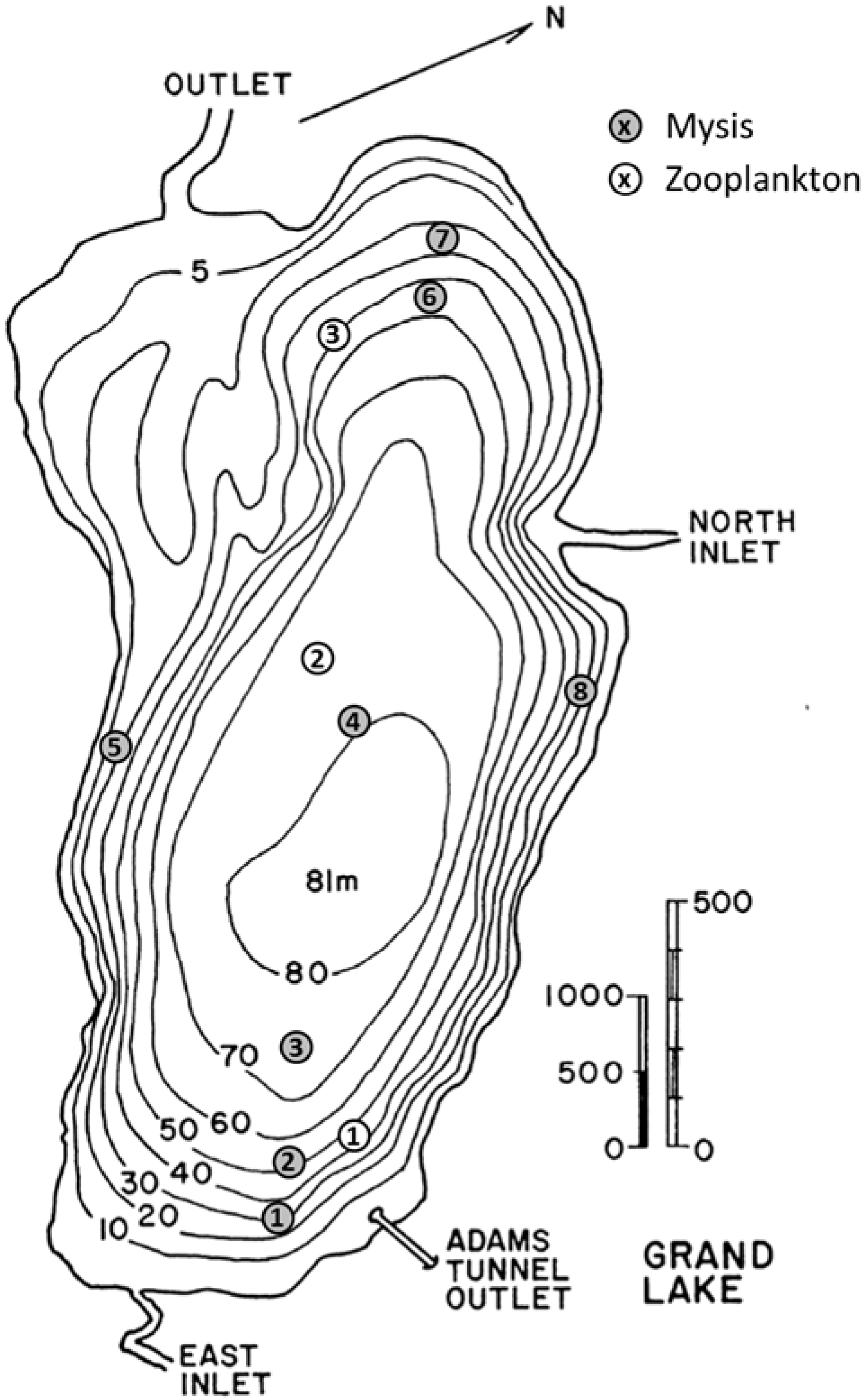

Figure 1. Bathymetric map (meters) of Grand Lake, Colorado (Nelson 1971) showing approximate locations of Mysis shrimp and zooplankton sampling sites used by CSU during summer 2013.

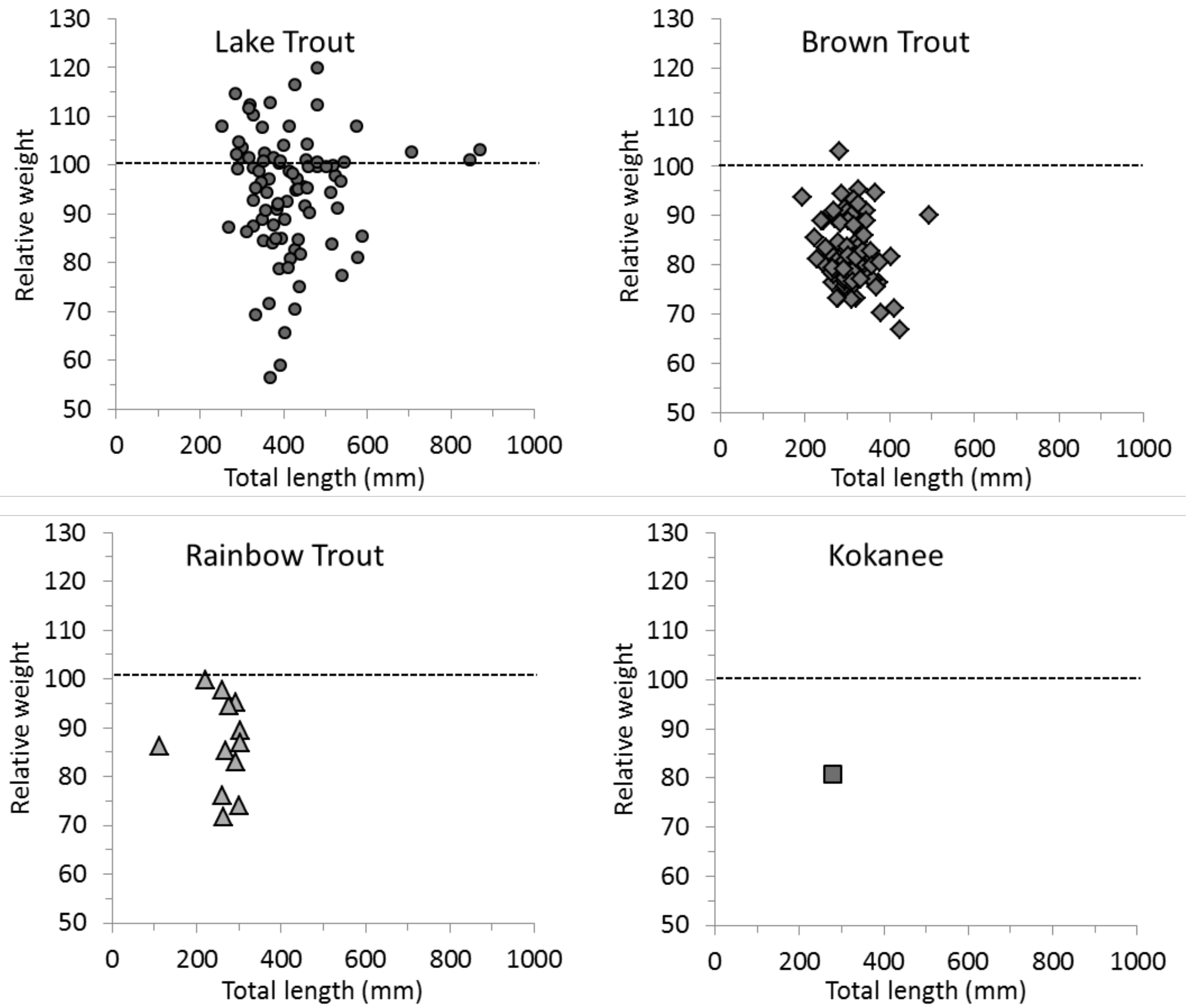

Figure 2. Relative weight, an index of body condition, of lake trout (Piccolo et al. 1996), brown trout (Hyatt and Hubert 2001), rainbow trout (Simpkins and Hubert 1996) and kokanee (Hyatt and Hubert 2000) sampled at Grand Lake during July, August 2013. Relative weight of 100 is considered normal, greater than 100 is better condition, and less than 100 is poorer condition.

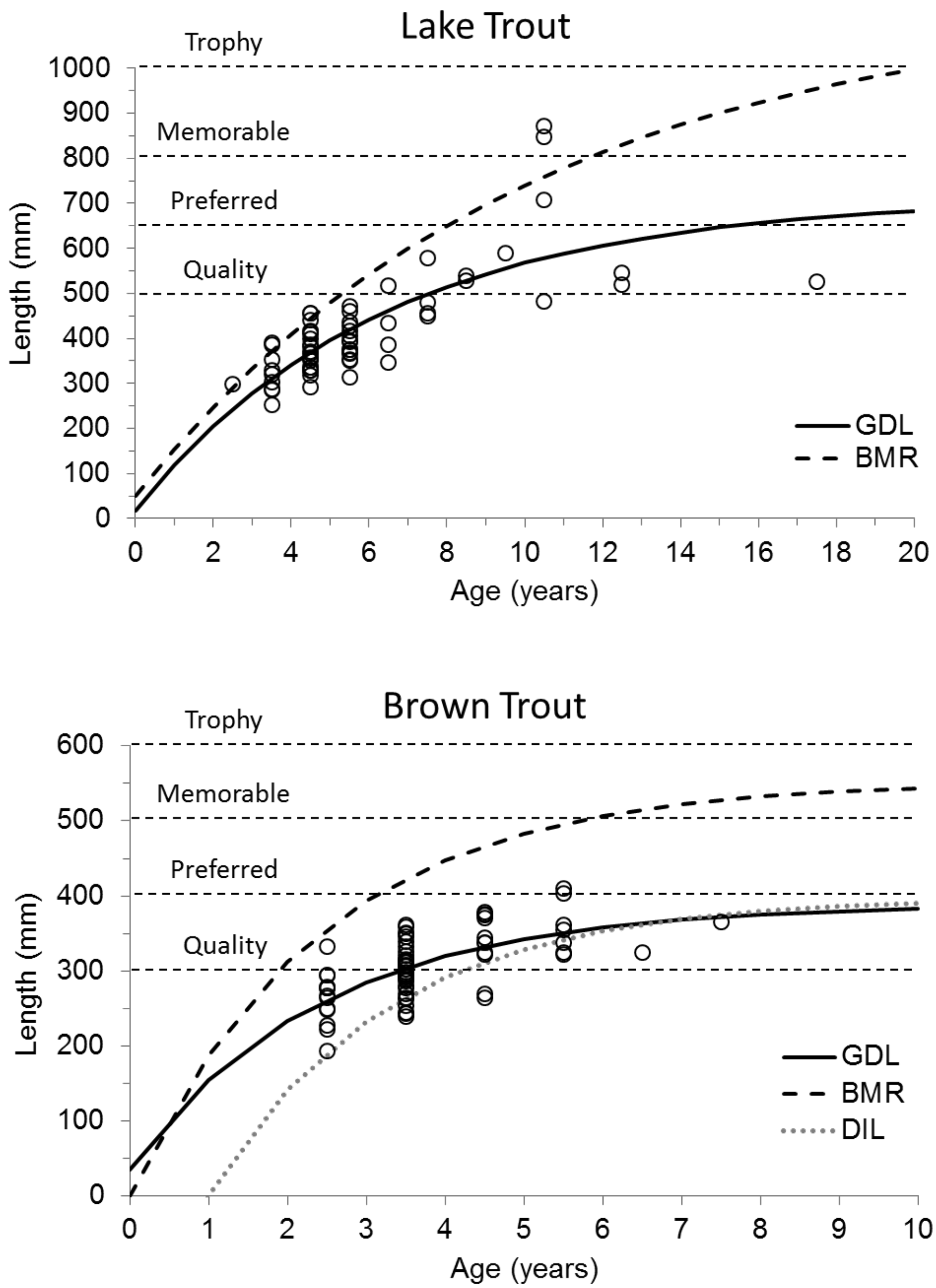

Figure 3. Length at age of lake trout and brown trout from Grand Lake compared to Blue Mesa and Dillon reservoirs. Size categories are from Willis et al. (1993).

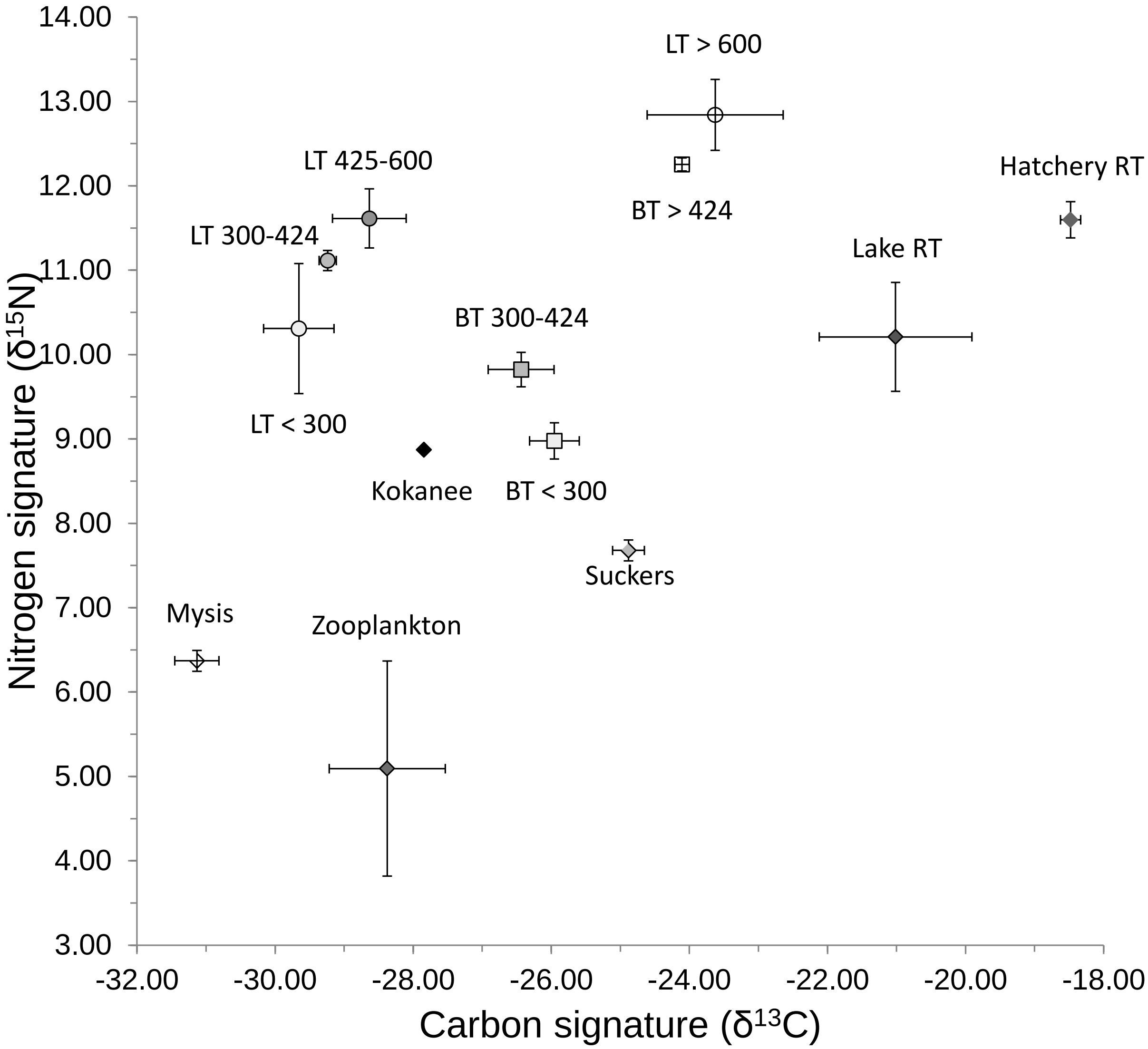

Figure 4. Mean (±2SE) stable carbon and nitrogen isotope signatures of fish and some invertebrates sampled from Grand Lake, Colorado and rainbow trout fingerlings from two Colorado Parks and Wildlife hatcheries during summer 2013.

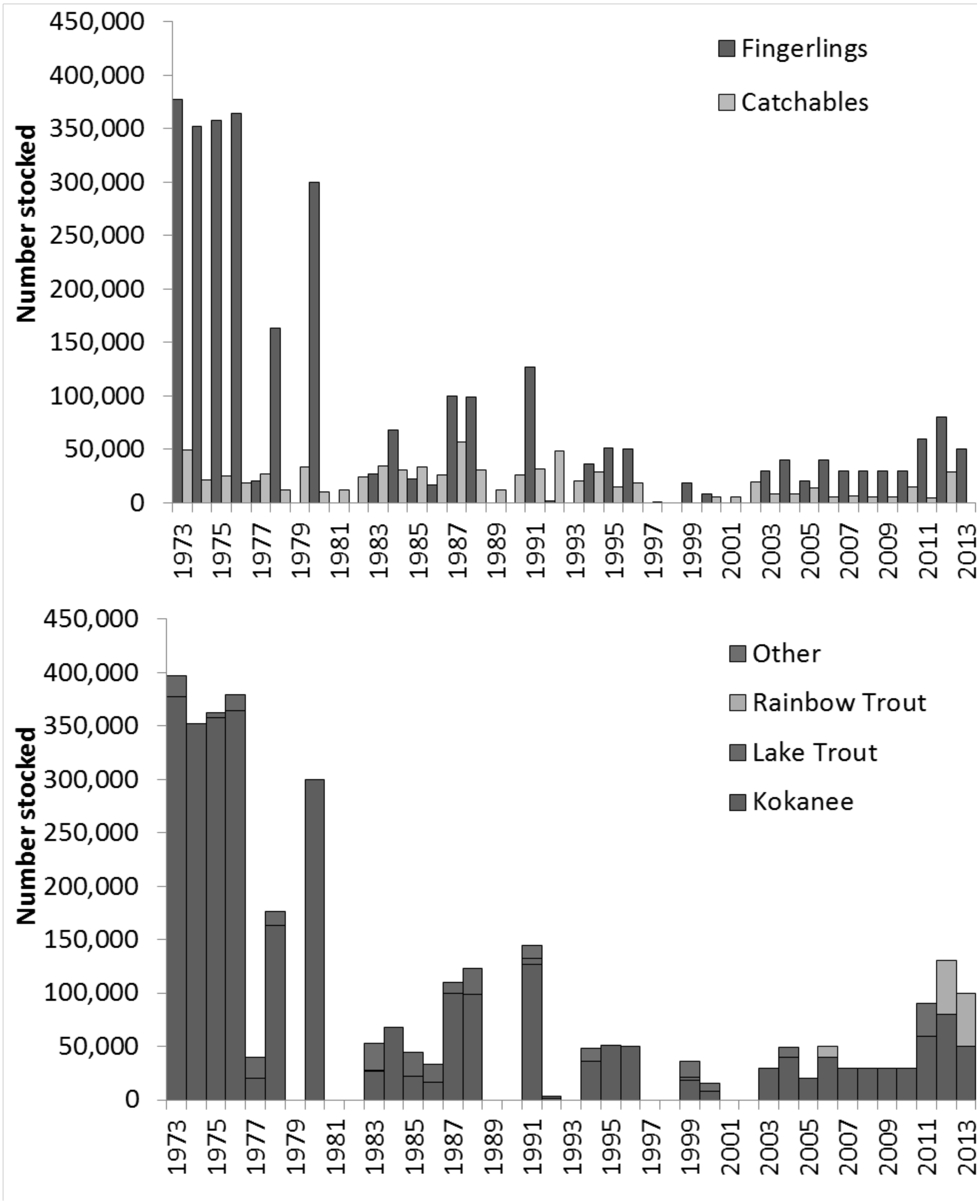

Figure 5. Upper panel: number of fingerlings (mostly kokanee, lake trout, and rainbow trout) and catchables (mostly rainbow trout), and lower panel: all species stocked into Grand Lake by Colorado Parks and Wildlife since 1973.

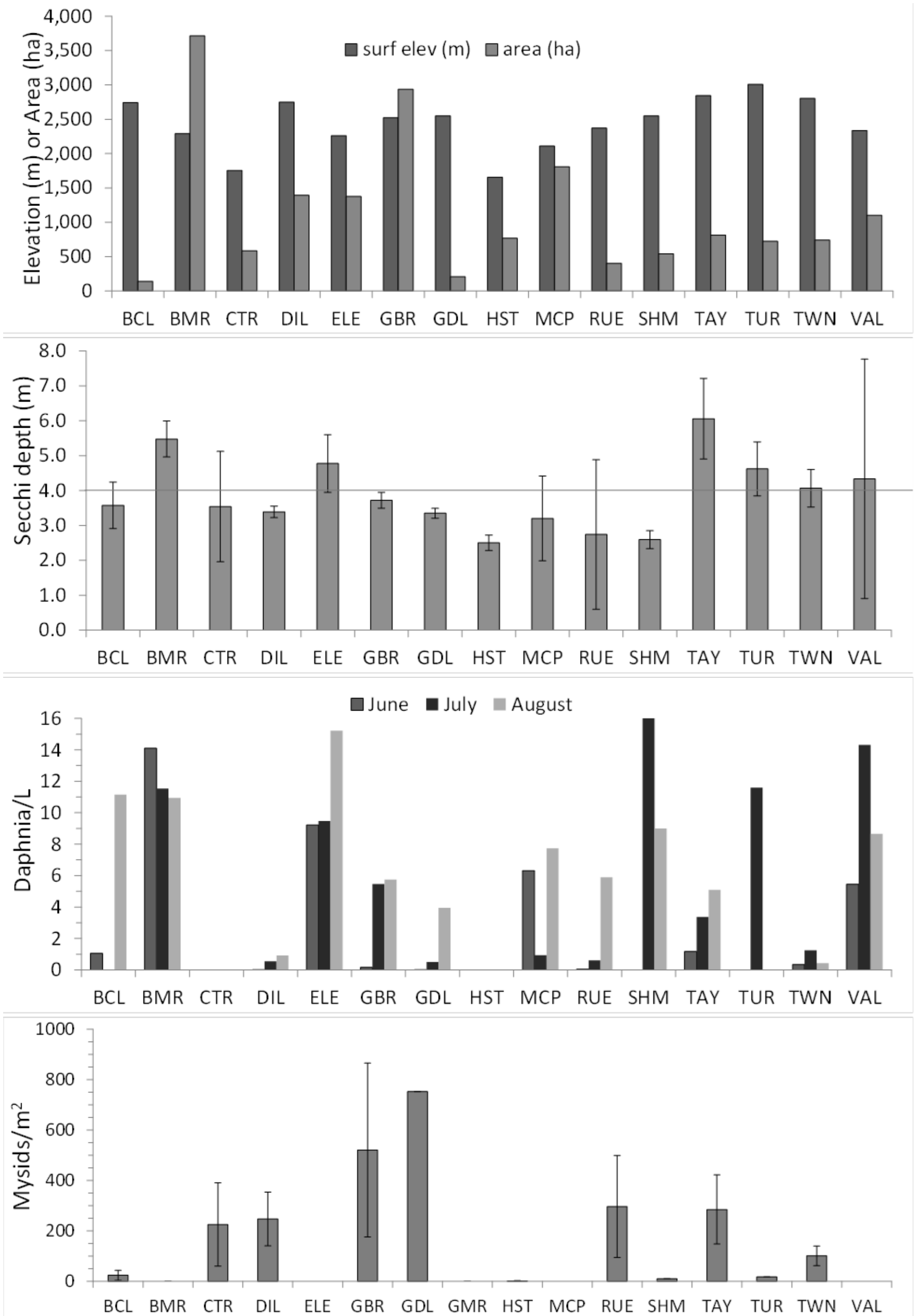

Figure 6. Some characteristics of 15 coldwater lakes and reservoirs in Colorado.

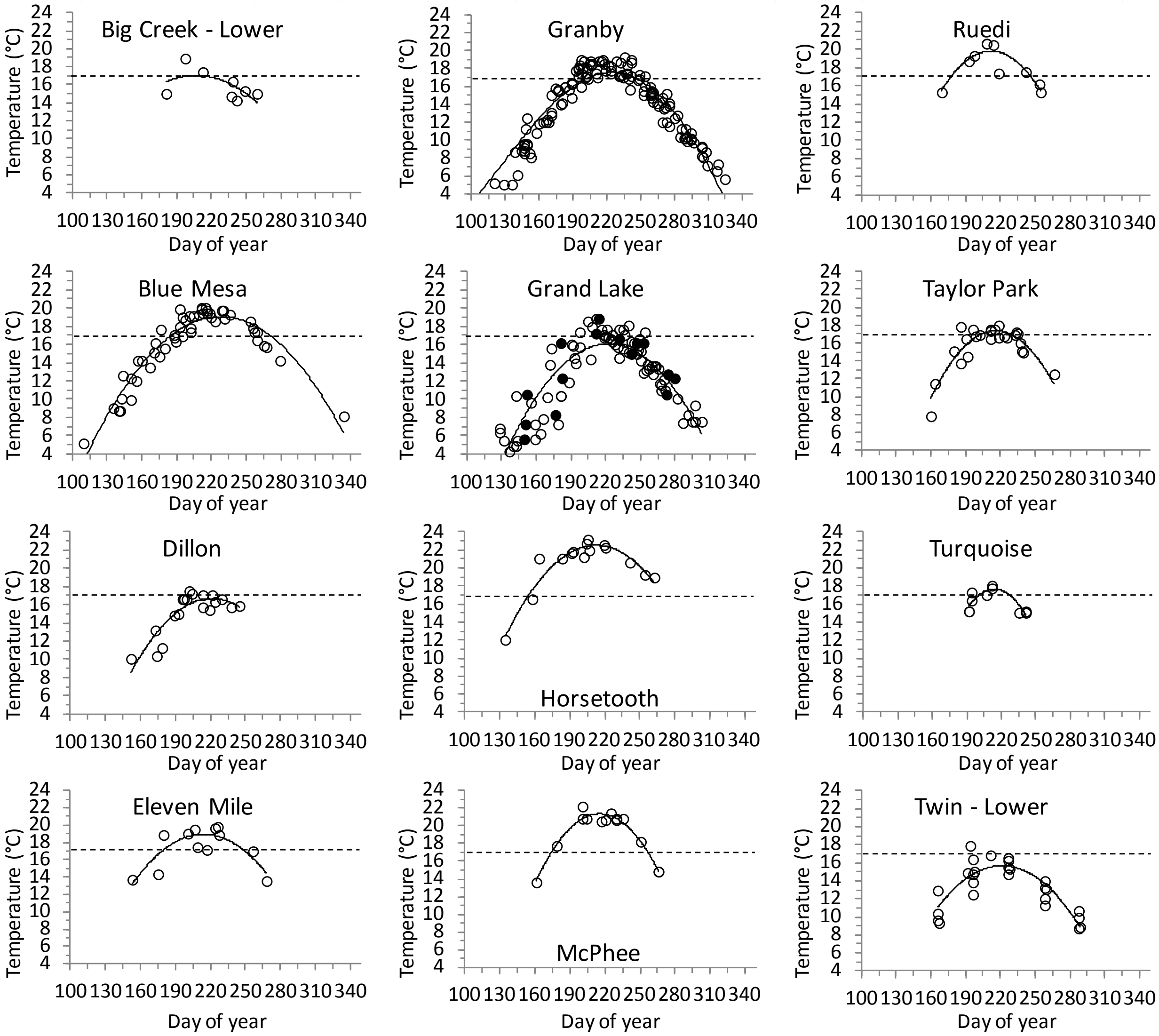

Figure 7. Surface temperature (1-m) of 12 Colorado reservoirs. Parabolas fitted simply to visualize differences among waters. Horizontal dashed lines represent the upper thermal limit of Mysis shrimp.

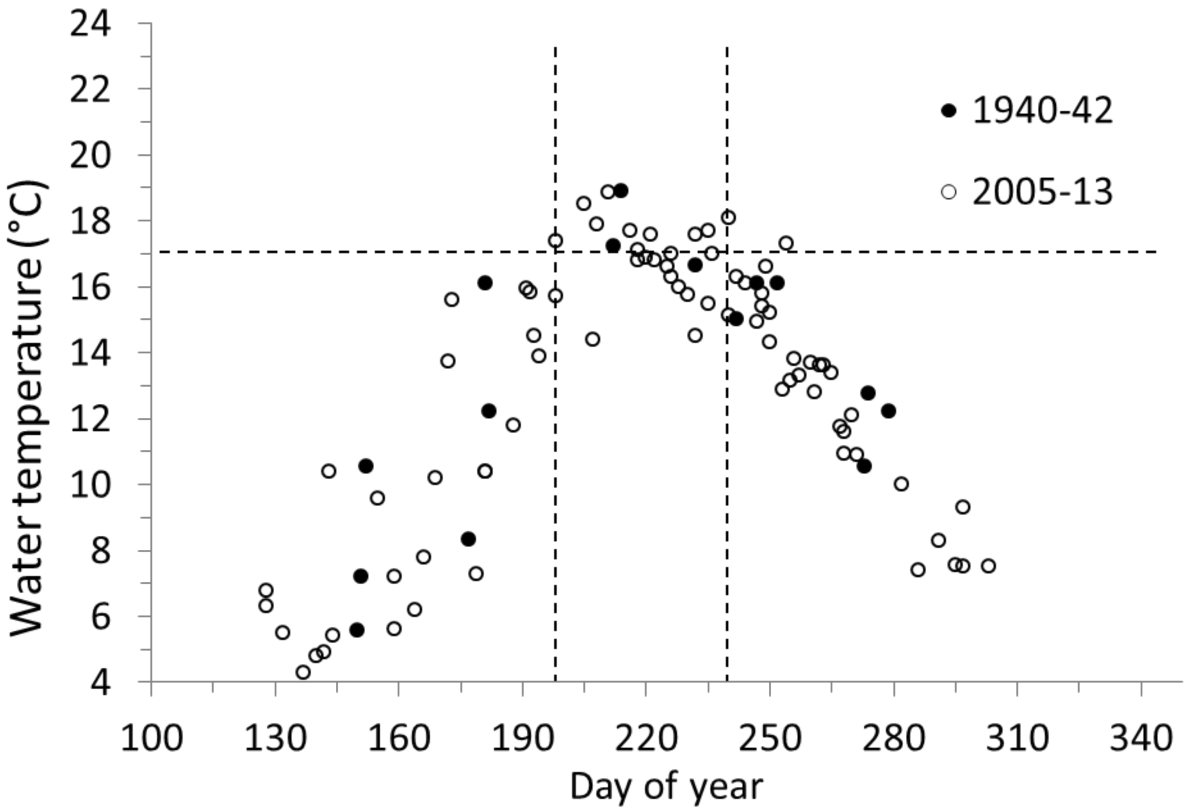

Figure 8. Surface temperature of Grand Lake measured during two time periods, before and after the completion and operation of the Adams Tunnel. Horizontal line represents the upper thermal tolerance of Mysis shrimp; vertical lines represent the approximate time period when surface temperatures are high enough to prevent Mysis shrimp access to the epilimnion.

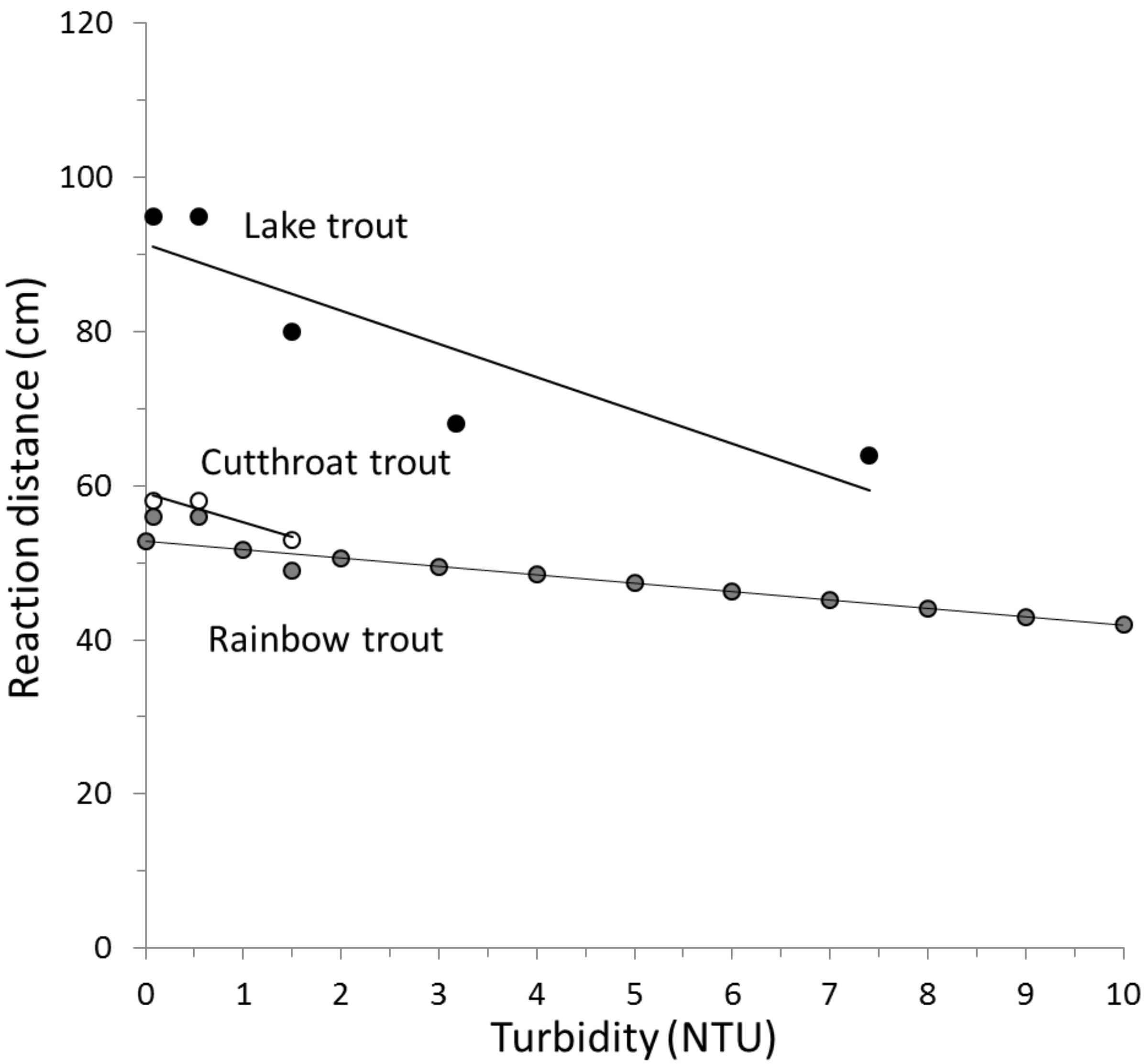

Figure 9. Reaction distance of lake trout (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003), cutthroat trout (Mazur and Beauchamp 2003), and rainbow trout (Barrett et al. 1992, Mazur and Beauchamp 2003) as a function of turbidity.

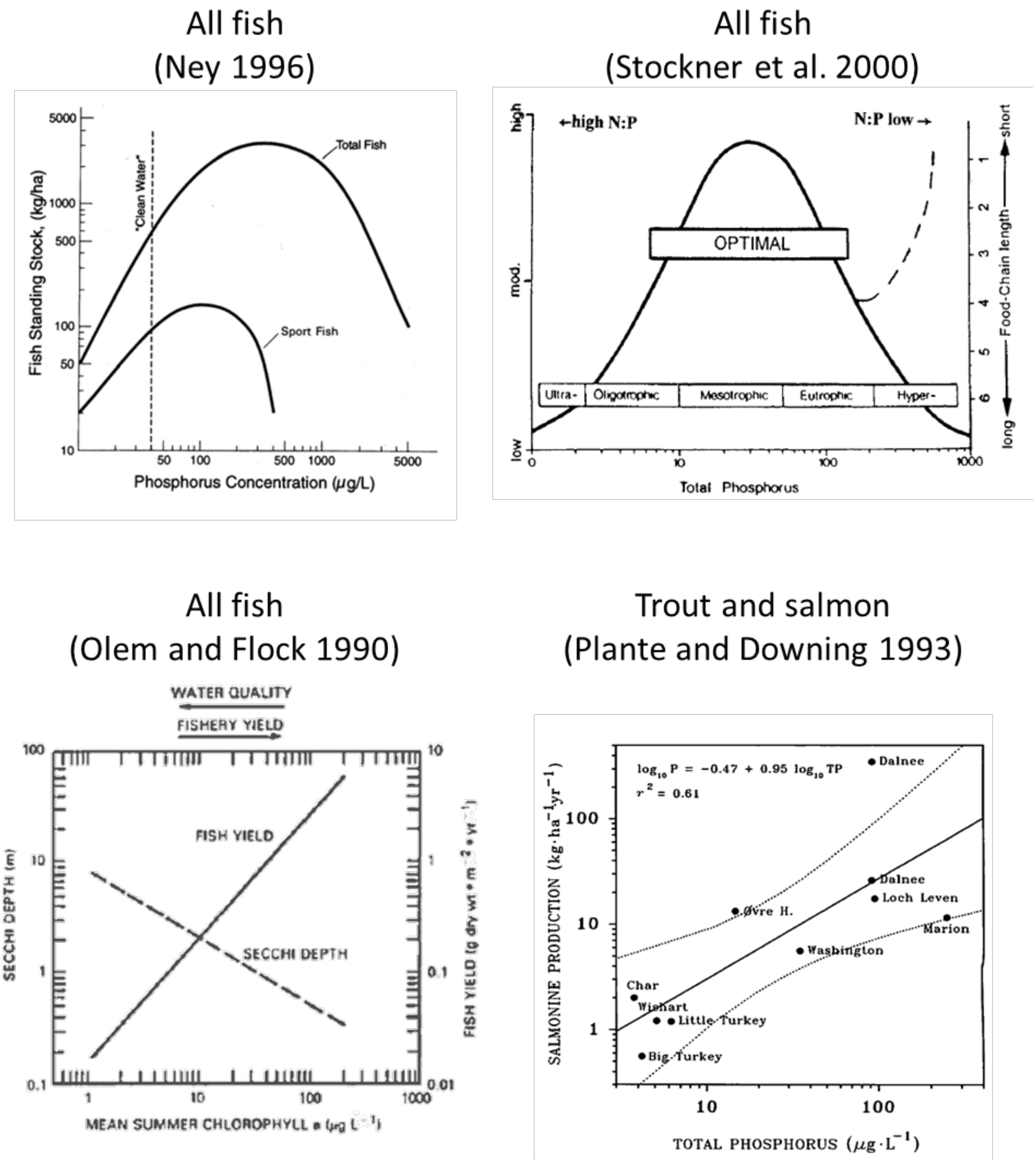

Figure 10. Effects of lake trophic conditions on fish production and yield.

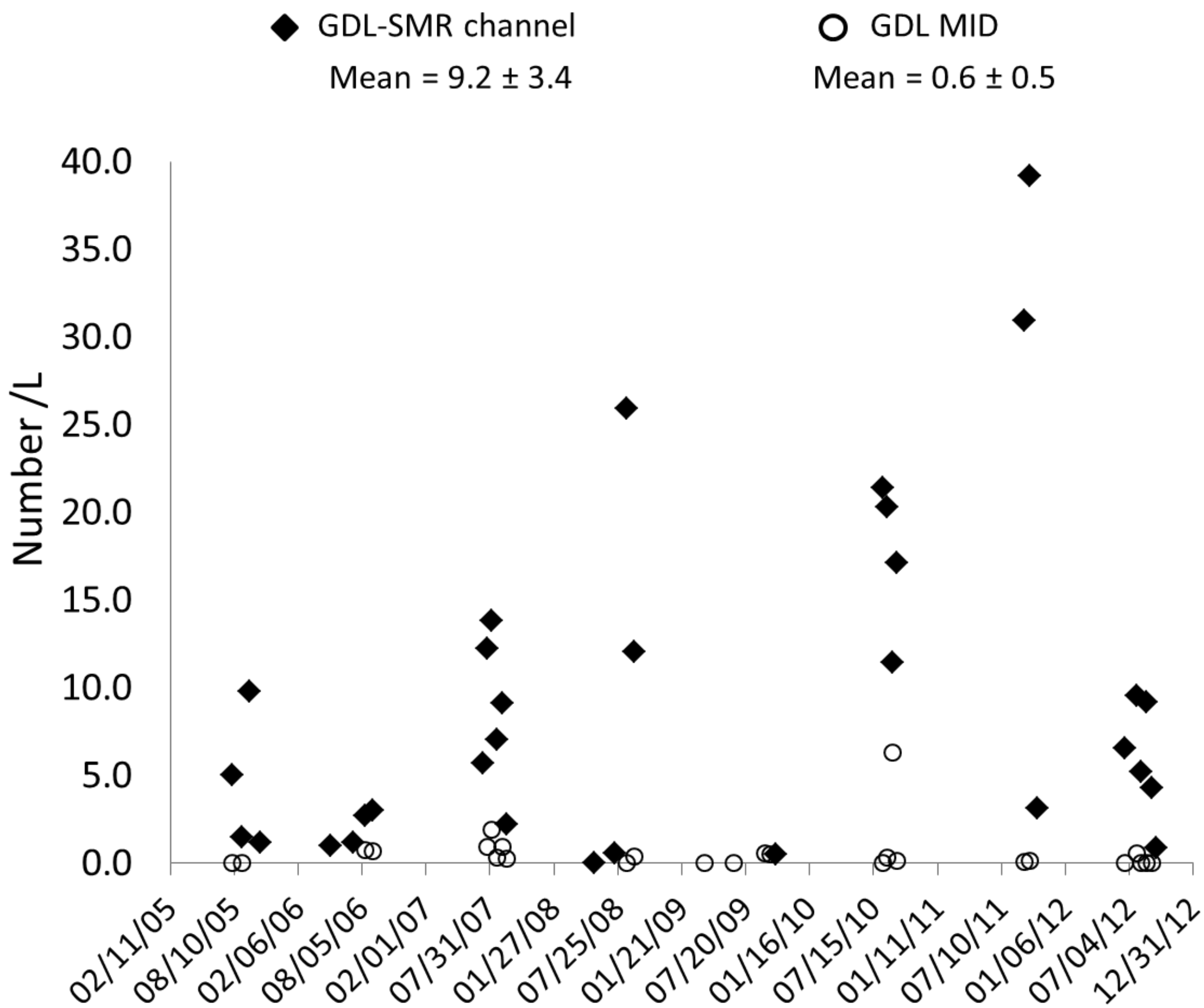

Figure 11. *Daphnia* density in the channel between Grand Lake and Shadow Mountain Reservoir, and at the mid-lake station (5-10 m) on Grand Lake.

APPENDIX

Table A1. Summary of zooplankton sampling performed at three stations and three dates at Grand Lake, Colorado.

Date	Sample number	Sampling gear	Mesh (µ)	Station	Depth sampled (m)	Max depth (m)
06/10/13	GDL061013001	Wisconsin net	153	GL-ATW	00-10	72
06/10/13	GDL061013002	Wisconsin net	153	GL-ATW	00-10	72
06/10/13	GDL061013005	Wisconsin net	153	GL-MID	00-10	83
06/10/13	GDL061013006	Wisconsin net	153	GL-MID	00-10	83
06/10/13	GDL061013008	Wisconsin net	153	GL2009A5	00-10	72
06/10/13	GDL061013009	Wisconsin net	153	GL2009A5	00-10	72
06/10/13	GDL061013004	½ m cone	500	GL-ATW	Surface	83
06/10/13	GDL061013007	½ m cone	500	GL-MID	Surface	83
06/10/13	GDL061013010	½ m cone	500	GL2009A5	Surface	72
07/18/13	GDL071813004	Wisconsin net	153	GL-ATW	Surface	45
07/18/13	GDL071813006	Wisconsin net	153	GL-MID	Surface	82
07/18/13	GDL071813012	Wisconsin net	153	GL2009A5	Surface	74
07/18/13	GDL071813003	Clarke-Bumpus	153	GL-ATW	0-10	45
07/18/13	GDL071813005	Clarke-Bumpus	153	GL-MID	0-10	82
07/18/13	GDL071813011	Clarke-Bumpus	153	GL2009A5	0-10	74
07/18/13	GDL071813001	¼ m cone	500	GL-ATW	Surface	45
07/18/13	GDL071813008	¼ m cone	500	GL-MID	surface	82
07/18/13	GDL071813010	¼ m cone	500	GL2009A5	surface	74
07/18/13	GDL071813002	Clarke-Bumpus	500	GL-ATW	0-10	45
07/18/13	GDL071813007	Clarke-Bumpus	500	GL-MID	0-10	82
07/18/13	GDL071813009	Clarke-Bumpus	500	GL2009A5	0-10	74
08/07/13	GDL080713001	Wisconsin net	153	GL-ATW	00-10	43
08/07/13	GDL080713004	Wisconsin net	153	GL-MID	00-10	85
08/07/13	GDL080713007	Wisconsin net	153	GL-NW	00-10	.
08/07/13	GDL080713002	Wisconsin net	153	GL-ATW	surface	43
08/07/13	GDL080713005	Wisconsin net	153	GL-MID	surface	85
08/07/13	GDL080713008	Wisconsin net	153	GL-NW	surface	.
08/07/13	GDL080713003	Mysis net	500	GL-ATW	surface	43
08/07/13	GDL080713006	Mysis net	500	GL-MID	surface	85
08/07/13	GDL080713009	Mysis net	500	GL-NW	surface	.

Table A2. Length distributions of seven zooplankton taxa sampled on July 18, 2013 with 153 µ and 500 µ mesh Clark-Bumpus metered plankton sampler at three stations in Grand Lake, CO

	Mesh Size: 153 µ								Mesh Size: 500 µ						
	Cladoceran					Copepod			Cladoceran					Copepod	
Length Class in mm	Unidentified *Daphnia* spp.	*Daphnia galeata mendotae*	*Daphnia pulicaria/pulex*	*Daphnia rosea*	*Bosmina longirostris*	Unidentified cyclopoid	Unidentified calanoid	Length Class in mm	Unidentified *Daphnia* spp.	*Daphnia galeata mendotae*	*Daphnia pulicaria/pulex*	*Daphnia rosea*	*Bosmina longirostris*	Unidentified cyclopoid	Unidentified calanoid
0.1					4			0.1							
0.2					36	1		0.2					3	1	
0.3	1				15	8	2	0.3	4	2			5	5	
0.4					11	18	6	0.4	2	1			1	2	
0.5		3		2	4	15	7	0.5						3	
0.6		3		2		16	11	0.6						3	
0.7		1	1	1		11	5	0.7							
0.8						4	6	0.8							
0.9						1	6	0.9						1	
1.0		1		1		1	5	1.0							
1.1				1			12	1.1							
1.2				1			6	1.2							
1.3								1.3			1	1			
1.4		2						1.4		1					
1.5								1.5				2			
Total	1	10	1	8	70	75	66	Total	6	4	1	3	9	15	0
Mean Length	0.3	0.8	0.7	0.8	0.3	0.5	0.8	Mean Length	0.3	0.6	1.3	1.4	0.3	0.4	--

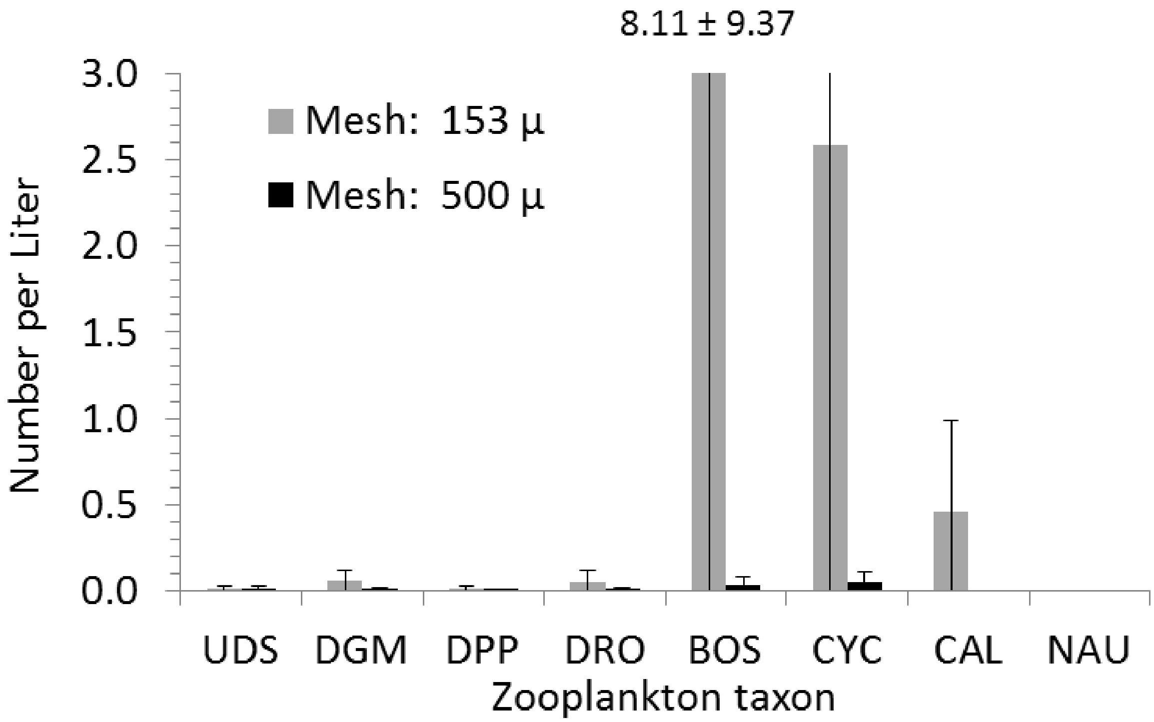

Figure A1. Density (± 2SE) of eight zooplankton taxa sampled on July 18, 2013 with a 153 µ and 500 µ mesh Clarke-Bumpus metered plankton sampler at three stations on Grand Lake, CO. UDS isunidentified *Daphnia* species, DGM is *Daphnia galeata mendotae*, DPP is *Daphnia pulex/pulicaria*, DRO is *Daphnia rosea*, BOS is *Bosmina longirostris*, CYC is cyclopoid copepod, CAL is calanoid copepod, and NAU is copepod nauplius.