Lake and Reservoir Management

Hydroclimate mediates effects of a keystone species in a coldwater reservoir

Brett M. Johnson [a] & Patrick J. Martinez [b][c]

[a] Department of Fish, Wildlife and Conservation Biology, 1474 Campus Delivery, Colorado State University, Fort Collins, CO, 80523

[b] Colorado Division of Wildlife, 711 Independence Ave., Grand Junction, CO, 81505

[c] US Fish and Wildlife Service, 764 Horizon Drive, Grand Junction, CO, 81506-8721

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Brett M. Johnson[1,*] and Patrick J. Martinez[2,3]

[1]Department of Fish, Wildlife and Conservation Biology, 1474 Campus Delivery, Colorado
State University, Fort Collins, CO 80523
[2]Colorado Division of Wildlife, 711 Independence Ave., Grand Junction, CO 81505
[3]Current address: US Fish and Wildlife Service, 764 Horizon Drive,
Grand Junction, CO 81506-8721

Abstract

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Many reservoirs exhibit interannual variations in water content resulting from climatic variability. Hydroclimatological factors may also affect physicochemical conditions such as thermal stratification and dissolved oxygen concentrations, which in turn have important implications for reservoir biota. We investigated the interplay among water budget, climate, and food web interactions involving a keystone planktivore, *Mysis diluviana*, occurring at Lake Granby, Colorado, during 1954–2009. A popular kokanee (*Oncorhynchus nerka*) fishery has been maintained at this 2938 ha montane reservoir, but survival and growth of kokanee has varied widely, with spawning adults ranging in size from 272 to 449 mm total length and population size varying by an order of magnitude (21–269 fish/ha). The kokanee population was strongly affected by *Mysis*, through competition for food (*Daphnia*) and because *Mysis* probably enhanced lake trout recruitment and predation on kokanee. Physicochemical conditions in the reservoir, driven by hydroclimatologic factors, mediated the effects of *Mysis* on *Daphnia*, kokanee, and presumably lake trout by controlling habitat suitability, distribution, and survival of *Mysis*. Effective fishery management in reservoirs requires an improved understanding of the complex interactions among hydroclimate, reservoir conditions, and food web dynamics.

Key words: *Daphnia*, food web, kokanee, *Mysis*, reservoir management

Two intriguing characteristics of reservoirs distinguish them from many natural lakes: (1) their inherent variability, and (2) the degree to which they can respond to anthropogenic factors (Thornton et al. 1990). Reservoirs in the arid western United States are exemplary, with annual water level fluctuations that can exceed 20 m even in large ($\geq 10^3$ ha) reservoirs (Johnson and Goettl 1999, Baldwin et al. 2003), and interannual variation in storage is closely tied to climatic conditions. Sport fisheries are often subsidized or sustained by fish stocking, and fishery quality varies with stocking success, which can be linked to reservoir conditions (Bowles et al. 1991, Martinez and Wiltzius 1995, Johnson and Goettl 1999). Effective management of reservoir fisheries requires an understanding of the relative roles of anthropogenic and natural factors in ecosystem dynamics.

Kokanee (*Oncorhynchus nerka*) is a popular sport fish in coldwater reservoirs throughout the western United States and Canada (Rieman and Myers 1992, Martinez et al. 2009). These fish are proficient zooplanktivores, efficiently channeling a reservoir's pelagic production into desirable fish biomass (Koski and Johnson 2002). The introduction of opossum shrimp (*Mysis diluviana*, formerly *M. relicta*; Rudstam and Johannsson 2009) into many western reservoirs in the 1970s and 1980s proved detrimental to kokanee, as *Mysis* displayed effective predator avoidance behavior and became a competitor for food rather than a supplemental food item for kokanee (Nesler and Bergersen 1991). Depending on thermal conditions, *Mysis* can contribute to the decline of kokanee populations through "middle out" control (control of food web from an intermediate trophic level; Stein et al. 1995) of food web interactions (Chipps and Bennett 2000). This disruption of a trophic cascade has *Mysis* outcompeting kokanee for zooplankton prey, but *Mysis* are undeterred by depletion of their preferred prey

*Corresponding author: brett.johnson@colostate.edu

because they are omnivorous, subsisting on phytoplankton and detritus when zooplankton are scarce (Northcote 1991, Chipps and Bennett 2000). Further, abundant *Mysis* populations seem to foster lake trout (*Salvelinus namaycush*) recruitment by alleviating a trophic bottleneck for juvenile lake trout (Bowles et al. 1991, Martinez et al. 2009, Ellis et al. 2011). Few other sport fish in western lakes and reservoirs are effective predators of *Mysis*. Unfortunately for kokanee, as lake trout grow they become piscivorous, with salmonids making up the bulk of the diet when available (Johnson and Martinez 2000, Ruyzicki et al. 2003, Martinez et al. 2009). Many formerly robust kokanee fisheries across the western United States have collapsed, succumbing to the combined effects of *Mysis* and lake trout (Martinez et al. 2009). Fishery managers striving to restore kokanee in western reservoirs require an understanding of how these complex food web interactions involving *Mysis* (and lake trout) may be mediated by environmental conditions.

It has been proposed that reduced reservoir content allows faster spring warming and a warmer epilimnion, which provides a thermal refuge for *Daphnia* and alleviates competition between kokanee and *Mysis* (Martinez and Wiltzius 1995). This thermal relationship and its mediating effect on *Mysis* impacts to zooplankton have been similarly proposed for some lakes (Schoen 2007, Koksvik et al. 2009). An exciting implication of the hypothesis for reservoirs suggests that dam operations offer a means to manipulate entire food webs to channel energy flow away from *Mysis* and their beneficiaries, such as lake trout, and foster increased productivity of kokanee. Further, a link between content and warming would suggest that reservoirs are more sensitive to the effects of climate change than lakes because reservoir content itself is usually strongly linked to climate. Testing the warming hypothesis is problematic because experimental manipulations of reservoir content are unlikely in arid and semiarid regions; however, long time series of observational data can offer some insights into these ecosystem dynamics and potential explanatory mechanisms.

This study documents 55 years of observations of kokanee size, reservoir characteristics, and hydroclimatological variables, and 20 years of more detailed limnological information. We used this relatively rare long-term dataset to examine the interplay among water budget, climate forcing, and food web interactions involving a keystone planktivore. Specifically, we address (1) how reservoir content and hydroclimatic factors affect reservoir thermal conditions, and (2) how the preceding affect production dynamics of zooplankton, *Mysis*, and kokanee.

Study site

Lake Granby is a 2938 ha reservoir located at 2524 m a.s.l. in Grand County, Colorado. The reservoir was constructed in 1949 primarily for irrigation; hydrology of the system is complex. Winter snowpack is the primary source of water supply to the reservoir (Matter et al. 2010). Water is also pumped into Lake Granby from 2 downstream reservoirs, Willow Creek and Windy Gap. Water is released from Lake Granby into the Colorado River via a hypolimnetic outlet on the dam but also via a pump that shuttles hypolimnetic water upstream into Shadow Mountain Reservoir and eventually through the Adams Tunnel across the continental divide to Colorado's more populous Front Range. Annual drawdown of the reservoir is about 10 m, from an annual low in March and annual high in July. Average content in July is about 80% of capacity but interannual variation is high, depending on inflow and user demand. The lowest annual maximum surface elevation was about 19 m below full level (50.2% of capacity; Jul 1956), and the lowest annual minimum was 35 m below full level (16.2% of capacity; Apr 1978). In addition to Lake Granby discharge, Windy Gap Reservoir also receives water treatment plant effluent. Thus, water from Windy Gap Reservoir pumped back into Lake Granby supplements Lake Granby's nutrient supply (Lieberman 2008).

The food web is typical of many coldwater, montane reservoirs of the intermountain west. Water level fluctuations preclude a productive littoral zone. Most consumer biomass derives from pelagic primary production and detritivory in the benthos (Johnson et al. 2002). The system is mesotrophic (USEPA 1977) with a trophic state index of about 45 and mean summer chlorophyll *a* concentration of about 4.0 μg/L (Johnson and Martinez 2000, Stevens 2003). Diatoms (*Melosira*, *Synedra*, and *Fragilaria* sp.) are the dominant algal group, with periodic blooms of blue-green algae (*Anabaena* sp.) in summer (Lieberman 2008). *Mysis diluviana* were introduced into Lake Granby in 1971 and developed a dense population by 1978 (Martinez and Bergersen 1991). Mysids consumed cladocerans preferentially, and after *Mysis* became abundant, *Daphnia longiremis*, a deepwater cladoceran, disappeared (Martinez and Bergersen 1991). Stable isotope analysis showed that small lake trout (<426 mm total length [TL]) consumed *Mysis* (Johnson et al. 2002), and diet analysis showed that although kokanee occasionally consumed *Mysis*, their diet consisted primarily of *Daphnia* spp., when present, and copepods, primarily *Diacyclops thomasi* and *Bosmina longirostris* (Martinez and Bergersen 1991).

The fish assemblage in Lake Granby consists predominantly of kokanee, lake trout, rainbow trout (*O. mykiss*), brown trout (*Salmo trutta*), longnose sucker (*Catostomus catostomus*), and white sucker (*Catostomus commersoni*), all nonnative, and one native, mottled sculpin (*Cottus bairdi*; Martinez and Bergersen 1991). Kokanee and rainbow trout do not reproduce naturally in the reservoir, and their populations are sustained by stockings of 0.5–1.5 million fish annually. Lake trout have been stocked sporadically, but the population

is self-sustaining. Predation by lake trout >426 mm TL was implicated in the collapse of the kokanee population in the late 1990s (Johnson and Martinez 2000), and eggs from another source were required to reestablish kokanee in Lake Granby in 1999.

Materials and methods

We compiled data for 2 periods. During 1954–2009, the "period of record," we obtained annual data on climate and reservoir hydrology (a drought index, air temperature, and content) as well as the number of kokanee stocked and size of spawners in the spawning run. During 1990–2009, the "food web period," measurements of temperature and dissolved oxygen profiles, Secchi depth, chlorophyll a concentration (Chl-a), and reservoir inflow were available. Annual zooplankton and $Mysis$ surveys occurred during 1991–2009, and annual hydroacoustics surveys of pelagic fish abundance during 1994–2009.

Reservoir content (total volume) and inflow data were obtained from online resources (Reclamation 2010). Content was converted to a proportion of the reservoir's maximum volume (539,755 ac-ft; Reclamation 2010) for graphing purposes; actual volumes were used in calculations and analyses. We used content in July (C_{Jul}; Table 1) in analyses that examined the effect of reservoir volume because it was highly correlated with mean annual content (C_m; r = 0.870), July was when the reservoir typically reached maximum content for the year, and July is when epilimnetic temperatures typically exceed the thermal tolerance of $Mysis$. Hydraulic residence time (HRT) was computed from mean annual content and total inflow for the year (I_Σ). Inflows included natural inflow (I_n), water received from upstream reservoirs, and water pumped into Lake Granby from Willow Creek (I_{WC}) and Windy Gap (I_{WG}) reservoirs (summed as I_p) downstream. Data on reservoir discharge were not available.

Monthly values for the Palmer Drought Severity Index (PD) were obtained for 2 National Climate Data Center Divisions in Colorado (NCDC 2009a) that either receive water from Lake Granby via a transcontinental diversion (Division 4; PD4) or deliver water to the reservoir as precipitation and runoff (Division 2; PD2). Their mean (PD$_m$) was used in analyses. The PD generally ranges from −6 to +6, with negative values indicative of dry periods; values lower than −4 equate to extreme drought (NCDC 2007). Monthly values were averaged for each year. Air temperature data (daily maximum [T_{max}] and minimum [T_{min}]) were obtained from a weather station on the north shore of the reservoir (NCDC 2009b). Daily values for April–October were averaged to obtain a single, growing season average of T_{max} for each year. We summed growing degree-days (GDD) as GDD = ((T$_{max}$

Table 1.-Description of equation symbols used in analysis of reservoir hydrology, food web and climate interactions at Lake Granby, CO.

Symbol	Description	Units
Chl-a	Chlorophyll a concentration	μg/L
C_{Jul}	Reservoir content (Jul)	ac-ft
C_m	Reservoir content (annual mean)	ac-ft
C_{pre}	Reservoir content previous year (Jul)	ac-ft
D_b	$Daphnia$ spp. biomass (dry)	mg/m^3
D_d	$Daphnia$ spp. density	animals/L
DY	Day of year	—
GDD	Growing degree days (T$_{base}$ = 10 C)	degree-days
HRT	Hydraulic residence time	years
I_n	Inflow, natural sources	ac-ft
I_p	Inflow, pumped from downstream	ac-ft
I_{WG}	Inflow, pumped from Windy Gap Reservoir	ac-ft
I_Σ	Inflow, total all sources	ac-ft
K_N	Kokanee abundance from hydroacoustics	number of fish
K_s	Kokanee stocked (per year)	number of fish
K_{TL}	Kokanee total length (spawners)	mm
M_b	$Mysis$ biomass (dry)	mg/m^2
M_d	$Mysis$ density	animals/m^2
PD$_m$	Palmer Drought Severity Index (mean)	unitless
T_3	Minimum temperature with 3 mg/L dissolved oxygen	C
T_e	Mean temperature of epilimnion	C
T_h	Mean temperature of hypolimnion	C
T_{max}	Maximum air temperature (mean, Apr–Oct)	C
T_Δ	Thermal gradient	C/m^1
Z_{14}	Depth of 14 C isotherm (Jul 15)	m
Z_{17}	Depth of 17 C isotherm (Jul 15)	m
ZP_b	Zooplankton biomass (all species, dry)	mg/m^3
ZP_d	Zooplankton density (all species)	animals/L^1

− T$_{min}$)/2)−T$_{base}$, where T$_{base}$ = 10.0 C, for April–October each year.

Water temperature and dissolved oxygen were measured at a midlake station near the dam and were assumed to represent prevailing conditions of the pelagic zone (Lieberman 2008,

USGS 2009; P. Martinez, Aquatic Biologist, Colorado Division of Wildlife, unpubl. data). We determined the depth of the 14 C (Z_{14}) and 17 C (Z_{17}) isotherms on each sampled day and then standardized to July 15 by linearly interpolating across the sampled dates. We estimated the average temperature of the epilimnion (T_e) and hypolimnion (T_h) during July and August 1990–2009 by determining the vertical thickness of the metalimnion (where temperature changed by ≥ 1.0 C/m). We then averaged all measurements within the epilimnion and hypolimnion during each sampling period. Thermal gradient (T_Δ, in C/m) was computed from the depth range and temperature change in the metalimnion. To compare rates of epilimnetic warming in low water years (<79% full, the long term mean, on July 31) versus high water years (>79% full on July 31), we fit a second-order polynomial to the mean water temperature in the top 10 m of the water column (dependent variable) and day of year (independent variable). We then used the functions to compare expected summer water temperature during dry and wet years. Dissolved oxygen profiles were used to determine the minimum temperature at which 3 mg/L (minimum tolerable level for *Mysis*; Horppila et al. 2003) was available on each sampled day. The annual maximum of these values (T_3) became an indicator of severity of thermal-oxygen stress for *Mysis*.

Chlorophyll *a* (μg/L) data were compiled from online resources (USGS 2009) and Northern Colorado Water Conservancy District (J. Stephenson, Engineer, Colorado Water Conservancy District, unpubl. data). Zooplankton were sampled approximately monthly during June–September using a standardized survey design (duplicate samples, 10 m to surface, at 5 sites). Samples were collected with a 127 mm Clarke-Bumpus metered 153 μm plankton net (De Bernardi 1984, Martinez 1992, Martinez et al. 2010). Sites were chosen to optimize coverage of the reservoir such that each of the 4 tributary arms was sampled as well as a site in front of the dam. Number of zooplankton in each tow was computed from counts in triplicate 1 mL aliquots drawn with a Hensen-Stempel pipette and enumerated in a Sedwick-Rafter cell (Lind 1977). We computed estimates of in-lake plankter density (animals/L) from the mean of the aliquot counts and the volume sampled derived from the flow meter of the Clarke-Bumpus sampler (De Bernardi 1984). Five taxa always comprised more than 95% of zooplankton sampled: *Bosmina longirostris*, *Daphnia galeata mendotae*, *D. pulex*, *Diacyclops thomasi*, and *Leptodiaptomus nudus.*

Mysids were collected in duplicate vertical tows with a 500 μm mesh, 1 m diameter and 3 m long plankton net at each of 10 stations after dark during the new moon in mid- to late summer 1991–2009 (Martinez 1992, Martinez et al. 2010). The net was retrieved at 0.37 m/s, close to the optimal tow speed for the device (Nero and Davies 1982). The dry

biomass of all macrozooplankton (ZP_b) and their density (ZP_d) were computed by summing across species in the Clarke-Bumpus samples. Zooplankton and *Mysis* lengths were converted to dry weight for biomass calculations using published formulae (Dumont et al. 1975, Morgan 1979). Volumetric densities of *Mysis* were converted to an areal basis (per square meter of reservoir surface) by dividing the catch in each tow by the area of the opening of the net, and assuming complete vulnerability (Nero and Davies 1982).

The number of kokanee stocked each year and the total lengths of spawning kokanee during egg collection operations at the reservoir have been recorded since 1954 (Martinez and Wiltzius 1995; Martinez, Aquatic Biologist, Colorado Division of Wildlife, unpubl. data). Hydroacoustic surveys of pelagic fish abundance occurred at night annually in August or September around the new moon using methods described in Johnson and Martinez (2000) and Crockett et al. (2006). Hydroacoustic surveys were performed with an HTI model 243 echosounder and with a down-looking 200 kHz split beam transducer with 15° beam width. Surveys followed a "zig-zag" pattern (MacLennan and Simmonds 1992), with 10 transects (total length: 8569 m) covering all regions of the reservoir >5 m deep. Minimum target strength threshold was set to −55 dB to avoid counting mysids as fish (Gal et al. 1999). Data acquisition and postprocessing were performed using HTI software. Because kokanee are the primary fish species found in midwater in Colorado's coldwater reservoirs (Johnson and Martinez 2000), changes in pelagic fish abundance from hydroacoustics surveys likely reflected kokanee population dynamics.

We used multiple regression to examine relationships among climatic, hydrologic, and biotic variables. Our model selection protocol involved hypothesizing a set of predictors for each response variable. We examined covariance structure among predictors and retained only one of the strongly correlated predictors in the global model to avoid multicollinearity. We then fitted all possible models by multiple linear regression in SAS, used AIC_c (Akaike's Information Criterion, corrected for small sample size bias; Burnham and Anderson 2002) to compare competing models. We adjusted the AIC value from SAS with the correct value of k, where k is the number of estimable parameters in the model (β_0, β_i, σ^2), prior to computing AICc (Stafford and Strickland 2003). To reduce the likelihood of overfitting the data, we restricted the set of plausible models to those with k = n/9 + 2. We computed ΔAIC_c, the difference in AIC_c for a given model standardized to that of the model with the lowest AIC_c. Models with $\Delta AIC_c \leq 2$ were considered to have substantial evidence to support them (Burnham and Anderson 2002). The likelihood of a particular model being

the best in the candidate set was judged from AIC_c weight (Burnham and Anderson 2002).

Results

Hydroclimate and reservoir conditions

Reservoir content was driven by hydroclimatic conditions. July content was inversely correlated with T_{max} ($r = -0.352$, $p = 0.009$) and positively correlated with PD_m ($r = 0.680$, $p < 0.001$) and I_Σ ($r = 0.544$, $p = 0.011$; Table 2). Reservoir content in July has averaged 79.3% since 1954. There have been 4 significant periods of drought since 1954, including 3 severe droughts in 1954–1955, 1963–1964, and 1977, and one extreme drought in 2001–2003 (Fig. 1A). Effects of drought on reservoir content seemed to carry over into the following summer, as evidenced by a high correlation

between C_{Jul} and reservoir content in July of the previous year (C_{pre}; $r = 0.417$, $p = 0.002$; Table 2). There have also been 4 relatively high water periods since 1954, when the reservoir was >79% full in July. These wet periods were approximately 6 years in duration (Fig. 1A). Overall, the best supported model for C_{Jul} was one with PD_m and C_{pre} (AIC_c weight = 0.76, n = 53; Table 3).

Temperature of the epilimnion was not correlated with climate or hydrology ($|r| < 0.35$, $p \geq 0.15$; Table 2; Fig. 2), but the 17 C isotherm was usually deeper in warm, dry years indicated by strong correlations with PD_m ($r = -0.575$, $p < 0.001$) and T_{max} ($r = 0.619$, $p = 0.004$; Table 2). GDD was highly correlated with T_{max} ($r = 0.921$, $p < 0.001$), but with none of the biological variables (Table 4); because GDD did not provide any additional information, it was not included in further analyses. A second-order polynomial described observed daily (day of year [DY])

Table 2.-Correlation coefficients (Pearson's r, associated p values and sample size) among hydrologic, climatic, and thermal characteristics of Lake Granby, CO. Bold indicates correlation coefficients with p < 0.05, and numbers in parentheses indicate sample size for that row.

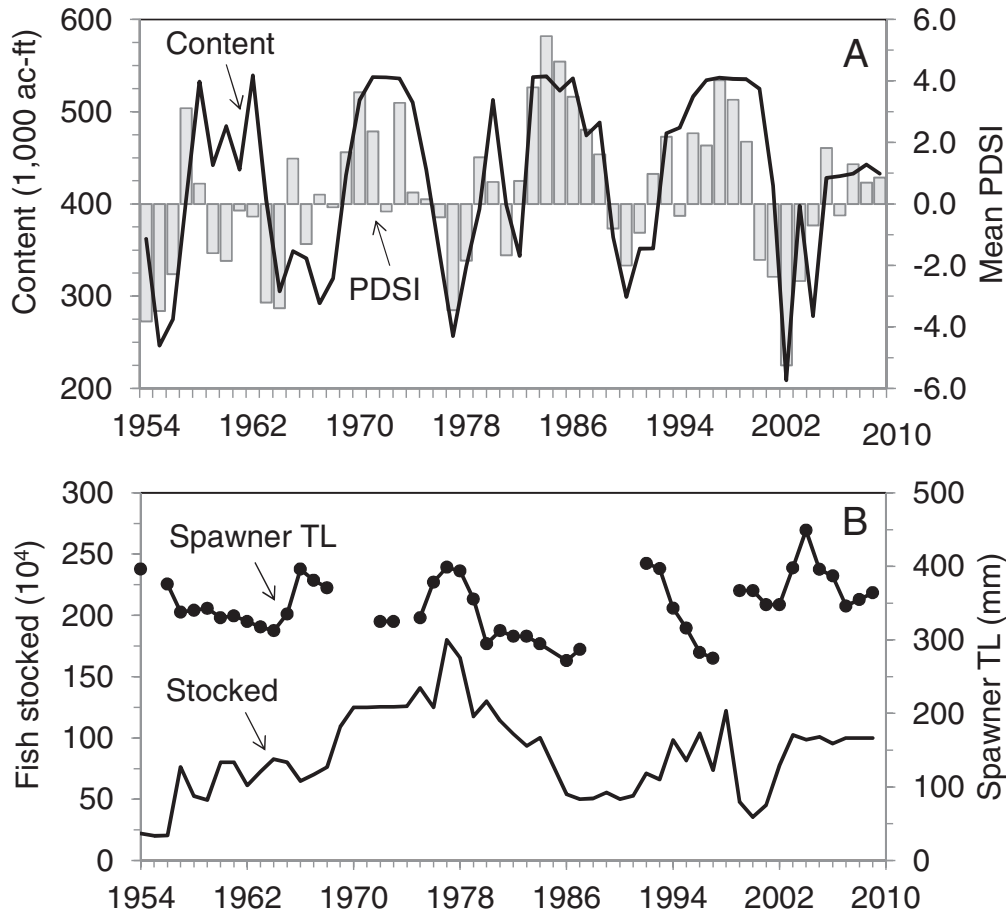|	C_{Jul}	C_{avg}	C_{pre}	I_Σ	PD_m	T_{max}	GDD	Z_{17}	T_e	T_h	T_Δ	T_3
C_{Jul}	**1.00**	**0.870**	**0.417**	**0.544**	**0.680**	**−0.352**	−0.202	−0.326	0.172	**−0.846**	−0.249	−0.010
	—	< 0.001	0.002	0.011	< 0.001	0.009	0.142	0.161	0.481	< 0.001	0.304	0.967
	54	54	53	21	54	54	54	20	19	19	19	19
C_{avg}	**0.870**	**1.00**	**0.666**	0.105	**0.471**	−0.213	−0.066	−0.085	0.156	**−0.778**	−0.002	−0.161
	< 0.001	—	< 0.001	0.651	< 0.001	0.119	0.630	0.723	0.523	< 0.001	0.993	0.511
	54	55	54	21	55	55	55	20	19	19	19	19
C_{pre}	**0.417**	**0.666**	**1.00**	−0.080	0.063	0.003	0.099	0.167	0.346	**−0.630**	0.300	−0.207
	0.002	< 0.001	—	0.729	0.651	0.981	0.473	0.482	0.147	0.004	0.213	0.396
	53	54	54	21	54	54	55	20	19	19	19	19
I_Σ	**0.544**	0.105	−0.080	**1.00**	**0.538**	**−0.491**	**−0.472**	**−0.466**	0.090	−0.427	−0.398	0.230
	0.011	0.651	0.729	—	0.012	0.024	0.027	0.038	0.714	0.068	0.091	0.343
	21	21	21	21	21	21	22	20	19	19	19	19
PD_m	**0.680**	**0.471**	0.063	**0.538**	**1.00**	**−0.575**	**−0.440**	**−0.575**	−0.109	**−0.520**	−0.235	0.157
	< 0.001	0.003	0.651	0.012	—	< 0.001	< 0.001	0.008	0.656	0.022	0.333	0.523
	54	55	54	21	55	55	55	20	19	19	19	19
T_{max}	**−0.352**	−0.213	0.003	**−0.491**	**−0.575**	**1.00**	**0.921**	**0.619**	0.270	0.393	0.413	0.234
	0.009	0.119	0.981	0.024	< 0.001	—	< 0.001	0.004	0.264	0.096	0.079	0.336
	54	55	54	21	55	55	55	20	19	19	19	19
GDD	−0.202	−0.066	0.099	**−0.472**	**−0.440**	**0.921**	**1.000**	**0.585**	0.394	0.118	**0.444**	0.058
	0.142	0.630	0.473	0.027	< 0.001	< 0.001	< 0.001	0.007	0.086	0.619	0.049	0.809
	54	55	55	22	55	55	55	20	19	19	19	19
Z_{17} (20)	−0.326	−0.085	0.167	**−0.466**	**−0.575**	**0.619**	**0.585**	**1.00**	**0.550**	0.242	**0.492**	0.055
	0.161	0.723	0.482	0.038	0.008	0.004	0.007	—	0.012	0.305	0.028	0.817
T_e (19)	0.172	0.156	0.346	0.090	−0.109	0.270	0.394	**0.550**	**1.00**	−0.070	0.289	0.359
	0.481	0.523	0.147	0.714	0.656	0.264	0.086	0.012	—	0.777	0.230	0.132
T_h (19)	**−0.859**	**−0.804**	**−0.630**	−0.394	**−0.537**	0.373	0.108	0.238	−0.131	**1.00**	−0.082	**0.468**
	< 0.001	< 0.001	0.004	0.068	0.015	0.105	0.651	0.313	0.582	—	0.730	0.037
T_Δ (19)	−0.249	−0.002	0.300	−0.398	−0.235	0.413	**0.444**	**0.492**	0.289	−0.053	**1.00**	−0.009
	0.304	0.993	0.213	0.091	0.333	0.079	0.049	0.028	0.230	0.830	—	0.970
T_3 (19)	−0.020	−0.161	−0.207	0.230	0.157	0.234	0.058	0.055	0.359	0.198	−0.009	**1.00**
	0.967	0.511	0.396	0.343	0.522	0.336	0.809	0.817	0.132	0.416	0.970	—

Figure 1.-(A) Content in July (C_{Jul}, solid line; 1000s ac-ft) of Lake Granby, CO, during 1954−2009 and mean values of the Palmer Drought Severity Index (PD_m; bars) during the same period. (B) Number of kokanee stocked at Lake Granby (K_s, solid line) and mean total length of spawners (K_{TL}, closed circles) sampled in egg take operations during 1954−2009.

epilimnion temperatures well in both wet ($T_e = -0.0014 \times DY^2 + 0.6485 \times DY - 56.35$, $r^2 = 0.94$, n = 42) and dry periods ($T_e = -0.0014 \times DY^2 + 0.6273 \times DY - 53.20$, $r^2 = 0.92$, n = 45). Mean temperature of the epilimnion of the reservoir differed by <1.0 C in wet versus dry years over the 75 d summer period (0.9 C in May, 0.4 C in Aug). Depth of the 14 C isotherm was not correlated with any hydroclimatic factors examined (p ≥ 0.100). Two models for Z_{17} were well supported (Table 3): $Z_{17} = T_{max}$ ($\Delta AIC_c = 0.0$, AIC_c weight = 0.47) and $Z_{17} = T_{max} + HRT$ ($\Delta AIC_c = 1.9$, AIC_c weight = 0.18). Depth of the 17 C isotherm decreased from 7.9 m in 1990 to a mean of 3.2 m during 1991–1998 and increased to a mean of 6.2 m for the remainder of the food web period (Fig. 3A).

The hypolimnion was warmer in dry years (Fig. 2); T_h was strongly negatively related to content (C_{Jul}, C_{avg}, and C_{pre}; −0.846, −0.778, −0.630, respectively; p ≤ 0.004), but less so to PD_m (r = −0.520, p = 0.022). Thermal gradient (T_Δ) was steeper when Z_{17} was greater (r = 0.492, p = 0.028). T_3

varied considerably (Fig. 3A) and was not significantly correlated with any climate or hydrology variables examined. However, 2 models for T_3 met selection criteria: $T_3 = -C_{Jul}$ and $T_3 = -C_{Jul} - T_\Delta$ ($\Delta AIC_c = 0.0$, 1.1, respectively; Table 3). The AIC_c weights were low (AIC_c $w_i = 0.28$, 0.17, respectively) indicating that evidence in support of these models was not strong. Still, in extreme water years, T_3 was very different and much higher in the driest year compared to the wettest year (Fig. 2).

Food web

Phytoplankton biomass (as chlorophyll *a* concentration) was affected by inputs from Windy Gap Reservoir, the lowest Chl-*a* observed occurred during 1996–2000 when no water was pumped from Windy Gap Reservoir into Lake Granby, and Chl-*a* increased when pumping resumed after 2002 (Fig. 3B). Correlation between Chl-*a* and I_{WG} was high (r = 0.741, p = 0.002; Table 4). Chlorophyll *a*

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Table 3.-Plausible and favored multiple regression models ($\Delta AIC_c \leq 2.0$ or $\Sigma AICw_i \geq 0.75$; $k \leq n/9 +2$) used to investigate relationships among biotic, climatic, hydrologic, and reservoir thermal variables. Coefficients shown for each model do not include β_0, which was fitted in all cases. See Table 1 for variable names; ΔAIC_c is difference between the Akaike information criterion (adjusted for small sample size) of the given model and the model with the lowest AIC_c; k is number of parameters in the model. AIC_c weight (w_i) indicates the probability of the particular model being the best in the candidate set.

Global model (time span, observations) Plausible models	ΔAIC_c	AIC_c w_i	k	R^2
$C_{Jul} = PD_m - T_{max} + C_{pre}$ (1954–2009, n = 53)				
$C_{Jul} = PD_m + C_{pre}$	0.0	0.76	4	0.60
$Z_{17} = -C_{Jul} + T_{max} - I_\Sigma$ HRT (1991–2009, n = 19)				
$Z_{17} = T_{max}$	0.0	0.47	3	0.38
$Z_{17} = T_{max} + HRT$	1.9	0.18	4	0.42
$Z_{17} = T_{max} - I_\Sigma$	2.5	0.14	4	0.40
$T_3 = C_{Jul} T_{max} I_\Sigma$ HRT $T_h T_\Delta Z_{17}$ (1991–2009, n = 19)				
$T_3 = -C_{Jul}$	0.0	0.27	3	0.39
$T_3 = -C_{Jul} - T_\Delta$	1.0	0.16	4	0.45
$T_3 = -C_{Jul} + Z_{17}$	2.4	0.08	4	0.41
$T_3 = T_h + T_\Delta$	2.4	0.08	4	0.41
$T_3 = -C_{Jul} + T_{max}$	2.5	0.08	4	0.41
$T_3 = -C_{Jul} + T_h$	2.6	0.07	4	0.40
$T_3 = -C_{Jul} + HRT$	2.8	0.07	4	.40
$M_d = C_{Jul} T_{max} K_s$ HRT $Z_{14} Z_{17} T_h T_e T_\Delta T_3$ (1991–2009, n = 19)				
$M_d = C_{Jul}$	0.0	0.17	3	0.26
$M_d = C_{Jul} + Z_{17}$	0.7	0.12	4	0.35
$M_d = C_{Jul} - T_{max}$	1.7	0.07	4	0.32
$M_d = C_{Jul} + HRT$	1.9	0.06	4	0.31
$M_d = -T_3$	2.7	0.04	3	0.14
$D_d = C_{Jul} T_{max} K_s$ HRT $Z_{14} Z_{17} T_h T_e T_\Delta M_d$ Chl-a T_3 (1991–2009, n = 14)				
$D_d = -M_d$	0.0	0.81	3	0.54
$K_{TL} = C_{Jul} T_{max} K_s$ (1954–2009, n = 44)				
$K_{TL} = -C_{Jul} + T_{max}$	0.0	0.61	4	0.41
$K_{TL} = -C_{Jul} + T_{max} + K_s$	2.6	0.17	5	0.41
$K_{TL} = C_{Jul} T_{max} K_s$ HRT $Z_{14} Z_{17} T_h T_e T_\Delta M_d$ $D_d ZP_d T_3$ (1991–2009, n = 15)				
$K_{TL} = D_d$	0.0	0.96	3	0.64

concentration was negatively correlated with HRT ($r = -0.621$, $p = 0.018$). *Daphnia* did not seem to be food limited; *Daphnia* density (daphnids/L) was not correlated with Chl-a ($p = 0.575$), and one of the highest *Daphnia* densities measured occurred during the third lowest Chl-a year (Fig. 3B). Mean *Daphnia* spp. biomass (D_b) over the 19 year period of record was 40.1 mg/m^3 and ranged from 0.10 mg/m^3 in 1997 to 133.3 mg/m^3 in 2006. Highest D_b usually occurred during low water years (e.g., 1992, 65% full; 2004, 52% full). *Daphnia* biomass seemed to vary independent of reservoir content during 2005–2009, when content was quite stable at about 425,000 ac-ft (80% of capacity; Fig. 3C). *Daphnia* density (D_d) was strongly inversely related to *Mysis* density, with peak *Daphnia* density corresponding to years of low *Mysis* density (M_d; Fig. 3A and 2B; $r = -0.624$, $p = 0.004$; Table 4). However, in 2 years (1997, 2001) the lowest D_d occurred the year after a peak in M_d.

Mysis density varied from 30 to 1367 mysids/m^2 with an 18 year average of 467 mysids/m^2 (Fig. 3A). Peak M_d occurred in 1996 (1365 mysids/m^2; SE: 327), 2000 (843 mysids/m^2; SE: 347) and 2007 (1186 mysids/m^2; SE: 321). *Mysis* density and dry biomass (M_b) were higher when Lake Granby water level was higher in July ($r = 0.508$, $p = 0.031$; $r = 0.524$, $p = 0.026$, respectively). *Mysis* density was lowest during low water periods, but there were 2 abrupt declines in M_d when the reservoir was full (1997–1998) and at average content (2009). During the early 1990s, low M_d coincided

with relatively low reservoir volume and unfavorable temperature and oxygen conditions. In 1990 the depth of the 17 C isotherm was the deepest observed (8 m), and the highest annual minimum temperature with >3 mg/L oxygen ranged from 11 C to almost 14 C (Fig. 3A). *Mysis* density increased with improving temperature and dissolved oxygen conditions after 1993, followed by a decline in 1997 that coincided with an abrupt increase in T_3. Then temperature and dissolved oxygen conditions improved again, with corresponding higher M_d until 2002 when several years of high temperature, low dissolved oxygen, and low reservoir content occurred. During 2002–2003, M_d was the lowest on record (<100 mysids/m^2). *Mysis* density rebounded to another peak in 2007, after which it declined again, following another spike in T_3.

Overall, during 1954–2009, the average number of kokanee stocked per year (K_s) was 862,800. The greatest K_s occurred during the 1970s when an average 1.355×10^6 kokanee were stocked per year (Fig. 1B). During the food web years, K_s was typically around 820,000, but during 1999–2001 K_s averaged 429,000 because of low spawner returns and

hence few progeny to restock the system (Fig. 3D). Kokanee eggs from another reservoir were required to "restart" the Lake Granby population after no spawners returned in 1998 (Martinez 2000). In the 2000s, K_s was almost 1.0×10^6 (2003–2009) and kokanee abundance from hydroacoustics (K_N) increased 2- to 3-fold (Fig. 3D). Kokanee abundance decreased during a period when the reservoir was full or near full (1994–2000). However, stocking was not always tied to abundance, and the correlation between K_N and C_{Jul} was not significant (r = −0.006, p = 0.983; Table 4). There was little correlation between K_s and the mean size of spawners (K_{TL}) during 1954–2009 (r = 0.022, p = 0.887; Table 4) or K_N and K_{TL} during 1994–2009, (r = 0.126, p = 0.666; Table 4).

Kokanee growth was strongly affected by *Daphnia* availability and therefore *Mysis* density. During 1991–2009, K_{TL} was highly correlated with both D_b and D_d (r = 0.718, p = 0.001; r = 0.798, p < 0.001; respectively; Table 4) and negatively related to M_d (r = −0.543, p = 0.030). Kokanee growth was best in warm, dry years, with K_{TL} negatively correlated with C_{Jul} (r = −0.578, p < 0.001), C_{pre} (r = −0.501, p < 0.001), and PD_m (p = −0.459, r = 0.002), and positively correlated with T_{max} (r = 0.439, p = 0.003; Table 4). The correlations between C_{Jul} and K_{TL} and between C_{pre} and K_{TL} were strong before *Mysis* were abundant during 1954–1970 (r = −0.694, p < 0.001; r = −0.467, p = 0.012, respectively), suggesting that direct effects of temperature on kokanee growth were important. Of 2 plausible models for K_{TL} during 1954–2009, one ($K_{TL} = -C_{Jul} + T_{max}$, AIC_c weight = 0.61) was better and the other was much less credible with $\Delta AIC_c = 2.6$ (Table 3). The variable C_{Jul} appeared in both models. A more complex global model was possible for K_{TL} during the food web period, but only a single model was supported for that smaller dataset: $K_{TL} = D_d$, AIC_c weight = 0.96. All other models for K_{TL} had ΔAIC_c > 6.

Discussion

Reservoir content and underlying hydroclimatological drivers indirectly mediated food web interactions at Lake Granby through their effects on a keystone species, *Mysis diluviana*. Resulting effects of temperature and dissolved oxygen conditions on *Mysis* density and biomass had important implications for *Daphnia* populations and kokanee growth and survival. The cascading effects of reservoir physicochemical conditions on the food web were not the result of varying reservoir content alone, as had been hypothesized. Instead, climatic conditions controlled both reservoir content and subsequent warming of the reservoir.
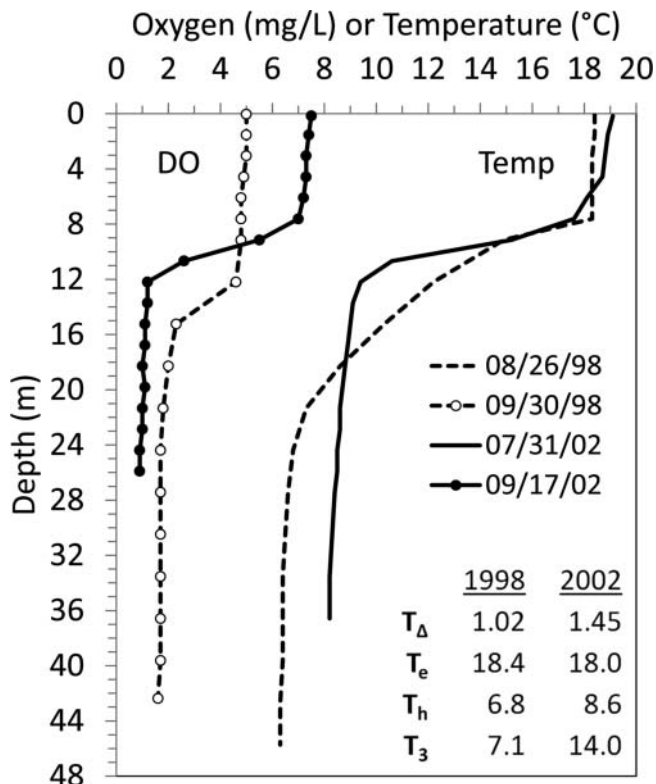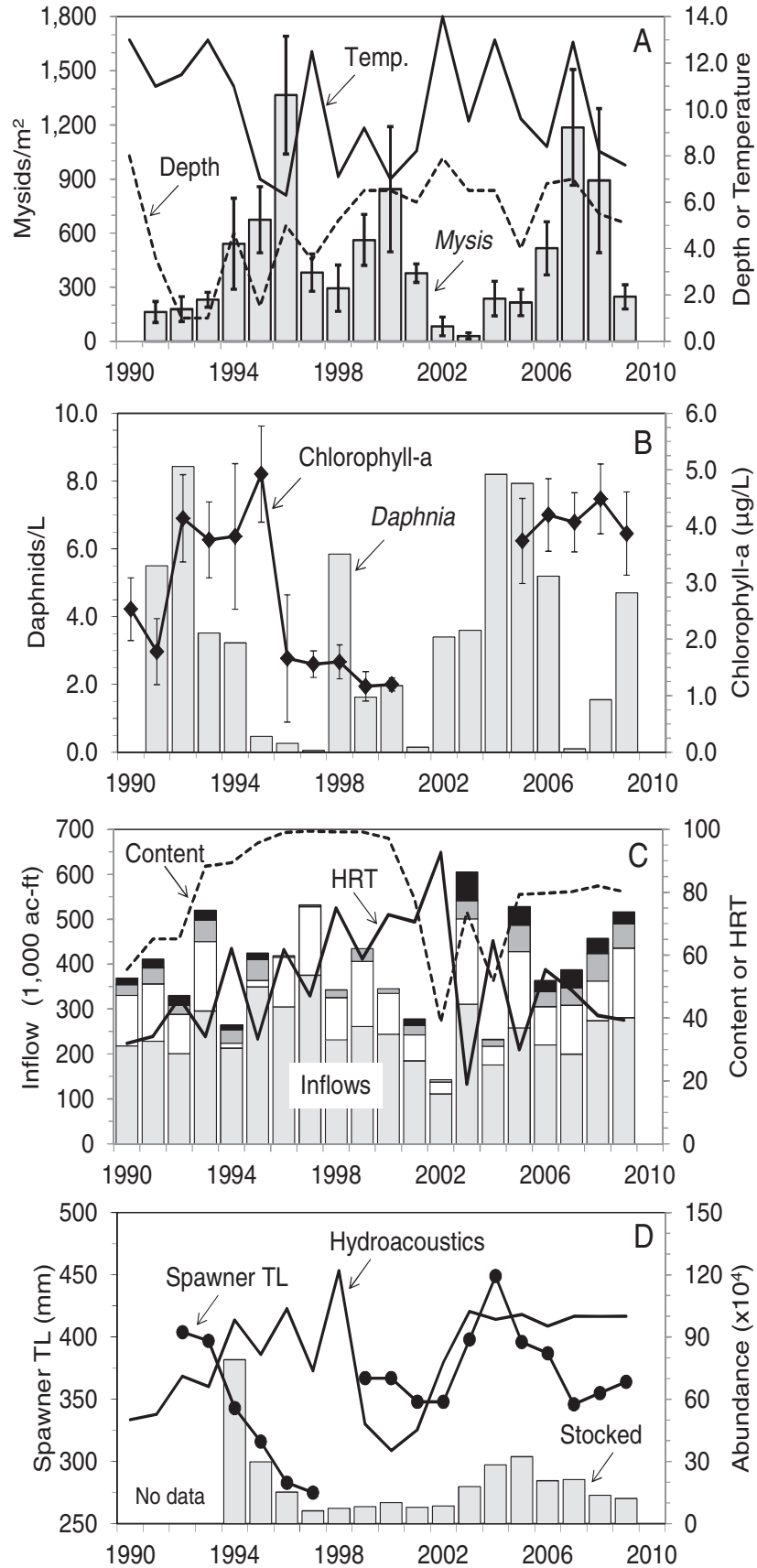

Figure 2.-Dissolved oxygen (DO, left) and temperature (temp, right) profiles from Lake Granby, CO, in a very wet year (1998, 99.2% full in July, dashed lines) and a very dry year (2002, 38.7% full in July, solid lines). Physicochemical descriptors of the water column are also shown (see Table 1 for abbrevations).

Years with little snowpack, and therefore little inflow to the reservoir, also had warm and dry summers. This finding is concordant with a recent longer term analysis (Matter et al. 2010) that found high complementarity between temperature and precipitation patterns in Upper Colorado River Basin and alternating cool–wet and warm–dry climate regimes. Thus, years with high snowpack, runoff, and content in Lake Granby would be expected to be cool years, and Lake Granby is more likely to receive less runoff and be less full in warm (and dry) years.

In general, the reservoir was less full in warm, dry years. While midsummer temperature of the epilimnion could not be explained by any of the hydroclimate variables we examined, the mixed layer was deeper and the hypolimnion was smaller, warmer, and more hypoxic in warm, dry years. *Mysis* were constrained by unfavorable oxygen conditions below and unsuitable temperatures above in these years, and the population experienced several crashes. *Daphnia* proliferated in the thermal refuge of the epilimnion, and kokanee growth was good.

Interannual variability in climate and reservoir thermal conditions is probably responsible for persistence of *Daphnia* and a viable kokanee population in Lake Granby. Periodic warm and dry years prevent *Mysis* from establishing as the dominant planktivore, as they have in some other cooler locations (Nesler and Bergersen 1991; Ellis et al. 2011). The maximum temperature where *Mysis* are observed in nature is 14–18 C (Bowles et al. 1991, Horppila et al. 2003, Boscarino et al. 2007). Although Martinez and Bergersen (1991) did not observe mysids in water >14 C in Lake Granby during 1982, we found that the depth of the 14 C isotherm was uncorrelated with *Mysis* or *Daphnia* density and biomass, suggesting that 14 C is not a hard threshold limiting *Mysis* access to epilimnetic *Daphnia* in Lake Granby. Rather, we found that *Mysis* density was negatively associated with the depth of the 17 C isotherm.

Oxygen in the hypolimnion was also an important factor limiting *Mysis* dominance in Lake Granby, and T_3 was a useful variable for describing oxythermal habitat for *Mysis*. Jacobson et al. (2010) used this same variable (calling it T_{DO3}) as an indicator of oxythermal conditions for several coldwater fishes, including lake trout, in natural lakes of Minnesota. The lower the value of T_3 (or T_{DO3}), the better

the oxythermal habitat is for coldwater organisms because of the larger range of temperatures available with suitable oxygen conditions.

Mysis were driven into warmer water in some years when the hypolimnion became hypoxic and T_3 was higher. The abundance of *Mysis* varied considerably over the past 20 years, and minima occurred during or just after spikes in the minimum temperature offering dissolved oxygen ≥ 3 mg/L. These events would have pushed *Mysis* into waters with minimum temperatures of ~ 13 C during periods in September–October. Such temperatures are below the upper lethal temperature for *Mysis diluviana* (96 h $TL_m = 16.0$ C; Smith 1970) but seem to have been deleterious nonetheless. While *Mysis* were generally more abundant when the reservoir was more full, a major decline in *Mysis* occurred in 1997–1998, in the middle of a multiyear period when C_{Jul} was $>99\%$. However, a period of severe hypoxia occurred during summer 1997, constricting *Mysis* distribution between unsuitable oxygen conditions below and higher than preferred water temperatures above.

The convergence of unfavorable oxygen and temperature conditions has been associated with *Mysis* declines in other systems. Smith (1970) argued that hypolimnetic temperatures above 10 C would be harmful to *Mysis*. In a Finnish lake, deep hypoxia caused habitat shifts in *Mysis*, making them unusually vulnerable to fish predation and consequent population declines (Horppila et al. 2003). Such obligatory habitat shifts, whereby mysids are forced into shallower waters, particularly during daytime, would have increased predation by lake trout, rainbow trout, and kokanee in Lake Granby (Martinez and Bergersen 1991). These shifts also account for the declines in *Mysis* density in 1997–1998 and again in 2002, when another spike in the minimum habitable temperature and reduced *Mysis* density occurred.

Severe drought may create reservoir conditions unsuitable for *Mysis*. *Mysis* density at Lake Granby was lowest during 2002–2003 following the start of a severe multiyear drought in 2001. In 2002 the reservoir was at its lowest level on record, T_3 was the highest observed, and Z_{17} was greater than or equal to that of other years. This low water year was the beginning of a multiyear resurgence of *Daphnia* and increased growth and survival of kokanee, again suggesting that reservoir content played a role in food web dynamics

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← **Figure 3.**-(A) *Mysis* density (M_d, bars, mysids/m^2 ± SE), depth (m) of 17 C isotherm (Z_{17}, dashed line) and the highest annual minimum temperature (C) containing ≥3.0 mg/L dissolved oxygen (T_3, solid line). (B) *Daphnia* spp. density (D_d, bars, daphnids/L) and chlorophyll *a* concentration (Chl-*a*, solid line, μg/L ± SE). (C) Inflow to Lake Granby in thousands of ac-ft (bars: light gray = natural inflow, white = inflow from Shadow Mountain Reservoir, dark gray = inflow pumped from Willow Creek Reservoir, black = inflow pumped from Windy Gap Reservoir), content in July (% of capacity, dotted line), and hydraulic residence time (HRT, solid line, weeks). (D) Mean total length of spawning kokanee (K_{TL}, closed circles), abundance of pelagic fish from hydroacoustics surveys (K_N, bars, fish × 10^4, no surveys during 1990–1993), and number of kokanee stocked (K_s, solid line, fish × 10^4).

Table 4.-Correlation coefficients (Pearson's r, and associated p values) among biotic variables and climatic, hydrologic, and reservoir thermal conditions at Lake Granby, CO. Bold indicates correlation coefficients with p < 0.05. Data for K_{TL}, PD_m, T_{max} were available for 1954–2009; other variables for 1991–2009.

	K_{TL}	K_N	M_b	M_d	D_b	D_d	ZP_b	ZP_d	Chl-*a*
K_{TL}	**1.00**	0.126	−0.384	**−0.543**	**0.718**	**0.798**	0.275	0.015	0.322
	—	0.666	0.142	0.030	0.001	< 0.001	0.302	0.956	0.307
K_N	0.126	**1.00**	0.073	0.020	0.166	0.213	−0.118	−0.273	0.468
	0.666	—	0.796	0.943	0.538	0.427	0.965	0.325	0.147
M_b	−0.384	0.073	**1.00**	**0.909**	−0.356	**−0.527**	−0.011	0.114	0.069
	0.142	0.796	—	< 0.001	0.134	0.020	0.797	0.654	0.815
M_d	**−0.543**	0.020	**0.909**	**1.00**	−0.428	**−0.624**	0.082	0.258	−0.041
	0.030	0.943	< 0.001	—	0.068	0.004	0.745	0.301	0.890
D_b	**0.718**	0.166	−0.356	−0.428	**1.00**	**0.804**	**0.541**	−0.168	0.253
	0.001	0.538	0.134	0.068	—	< 0.001	0.020	0.506	0.363
D_d	**0.798**	0.213	**−0.527**	**−0.624**	**0.804**	**1.00**	0.248	0.046	0.160
	< 0.001	0.427	0.020	0.004	< 0.001	—	0.320	0.858	0.568
ZP_b	0.275	−0.118	−0.011	0.082	**0.541**	0.248	**1.00**	0.224	0.070
	0.302	0.675	0.965	0.745	0.020	0.320	—	0.372	0.812
ZP_d	0.015	−0.273	0.114	0.258	−0.167	0.046	0.224	**1.00**	0.061
	0.956	0.325	0.654	0.301	0.506	0.858	0.372	—	0.9836
Chl-*a*	0.322	0.468	0.069	−0.041	0.164	0.149	0.204	0.011	**1.00**
	0.307	0.147	0.815	0.890	0.575	0.611	0.504	0.971	—
PD_m	**−0.459**	−0.018	0.276	0.278	−0.115	−0.092	−0.154	−0.041	−0.019
	0.002	0.950	0.267	0.264	0.649	0.716	0.556	0.871	0.947
T_{max}	**0.439**	0.055	−0.134	−0.069	0.222	0.139	−0.032	−0.115	0.017
	0.003	0.845	0.596	0.784	0.376	0.583	0.904	0.649	0.953
GDD	0.293	0.030	−0.086	0.032	0.123	0.030	−0.042	−0.065	−0.109
	0.051	0.913	0.725	0.897	0.615	0.904	0.869	0.798	0.688
HRT	−0.347	−0.386	0.176	0.226	**−0.566**	−0.317	−0.068	0.407	**−0.621**
	0.187	0.156	0.483	0.367	0.014	0.200	0.796	0.093	0.018
C_{Jul}	**−0.578**	−0.006	**0.524**	**0.508**	**−0.502**	**−0.542**	−0.411	−0.098	−0.440
	< 0.001	0.983	0.026	0.031	0.034	0.020	0.101	0.698	0.116
C_{pre}	**−0.501**	−0.450	0.377	0.393	**−0.767**	**−0.675**	−0.353	0.205	−0.491
	< 0.001	0.092	0.122	0.106	< 0.001	0.002	0.165	0.414	0.074
I_{WG}	0.324	0.121	−0.170	−0.140	0.376	0.120	0.091	−0.212	**0.741**
	0.220	0.666	0.501	0.580	0.124	0.635	0.728	0.398	0.002
T_3	0.218	0.187	−0.130	−0.170	**0.522**	0.370	< 0.001	**−0.471**	0.149
	0.418	0.506	0.608	0.500	0.026	0.313	0.999	0.049	0.610
Z_{17}	0.073	−0.270	0.077	0.172	0.004	−0.148	0.235	0.262	−0.311
	0.780	0.312	0.754	0.482	0.987	0.546	0.348	0.294	0.240
T_e	−0.143	−0.283	0.050	0.089	−0.050	−0.228	0.110	0.032	−0.468
	0.596	0.306	0.845	0.726	0.844	0.363	0.675	0.899	0.091
T_h	**0.706**	0.024	−0.249	−0.370	**0.650**	**0.679**	0.406	−0.051	0.465
	0.002	0.932	0.319	0.130	0.004	0.002	0.106	0.841	0.094
T_Δ	−0.364	−0.254	−0.293	−0.100	−0.271	−0.222	−0.026	0.298	−0.468
	0.166	0.360	0.236	0.692	0.276	0.375	0.920	0.230	0.091

through its effects on *Mysis* abundance and distribution. In Lake Granby, factors that govern *Mysis* dynamics propagate their effects up and down the food web by controlling the predatory and competitive interactions of *Mysis* with zooplankton and fish.

Mysis are capable of controlling *Daphnia* abundance in Lake Granby. The maximum density of *Mysis* in Lake Granby

(1365 mysids/m², 4039 mg dry/m²; 1996) was as high or higher than in many other large western lakes and reservoirs (Morgan 1980, Bowles et al. 1991, Chipps and Bennett 2000, Whall and Lasenby 2009, Ellis et al. 2011). If this population consumed 5% of its biomass per day (Rudstam 1989), that would amount to about 202 mg dry/m²/day compared to the average standing stock of *Daphnia* in Lake Granby in 1996 of about 24 mg dry/m². Thus, *Mysis* predation was

ample to regulate *Daphnia* density in 1996, even if *Daphnia* contributed to only a fraction of the mysid diet. During 1993–1997, while the *Mysis* population was building and *Daphnia* were in decline, daily consumptive demand of the *Mysis* population was 40–4600% of standing stock of *Daphnia*. By 1997 *Daphnia* were virtually eliminated from the reservoir, and no kokanee entered the spawning run to provide eggs in 1998 (Martinez 2000).

Deleterious effects of *Mysis* competition with kokanee can be compounded by a trophic triangle involving the lake trout. Kokanee growth and abundance declined during the buildup of the Lake Granby *Mysis* population during the mid-1990s. *Mysis* abundance drove food availability for kokanee, and ultimately their growth. Reduced growth of kokanee likely made them more vulnerable to lake trout predation, and the kokanee population declined despite increasing stocking. Eventually the kokanee population went "bankrupt" as kokanee mortality increased too quickly to allow a sufficient number of spawners to survive and provide the eggs needed to stock the next generation. Because an abundant *Mysis* population leads to poor kokanee growth, it also seems to facilitate increased lake trout recruitment, growth, and subsequent consumptive demand on the kokanee population (Hansen et al. 2008).

Food web interactions were more important in explaining patterns in kokanee, *Mysis*, and *Daphnia* dynamics than were physicochemical or hydroclimatological variables, suggesting that the latter had indirect effects on the biota of interest. Over the period of record, when kokanee size was the only biotic variable measured, content and air temperature were important predictors. During the years when detailed biological data were available (1991–2009) physicochemical and hydroclimatological variables dropped out of models, and kokanee growth was best explained by *Daphnia* density, which was driven by *Mysis* density. While productivity was an important predictor of kokanee size in 10 Idaho lakes and reservoirs (Rieman and Myers 1992), food web dynamics at Lake Granby do not seem to be regulated by bottom up forces. Neither *Daphnia* nor *Mysis* density was correlated with chlorophyll *a* concentration, an indicator of algal food availability. Thus, nutrient inputs, which covaried with pumped inputs from Windy Gap Reservoir, did not seem to control production dynamics of the system beyond the producer level.

Climatic factors seem to drive hydrology and thermal structure of Lake Granby, with important consequences for food web interactions. Hot, dry periods result in a lower water level, a warmer and less oxygenated hypolimnion, and deeper penetration of intolerable water temperatures for *Mysis* from above. We hypothesize that these conditions may provide a thermal refuge for *Daphnia* in surface waters and also increase the likelihood of obligatory habitat

shifts by *Mysis* out of hypoxic but thermally optimum water into warmer, shallower water with a higher predation risk from fish. When climate patterns and associated hydrologic changes cause physicochemical conditions in the reservoir to align poorly for *Mysis*, precipitous population declines result, as observed in 1997–1998, 2001–2003, and 2008–2009. Both competitors and prey of *Mysis* benefit, responding strongly and rapidly to the opportunity until hydroclimatological conditions moderate and allow *Mysis* to regain their dominance over the reservoir's food web.

Managers seeking to manipulate reservoir conditions to favor a particular food web configuration may be able to overcome climatic forcing by altering withdrawal depth of releases. Such changes to dam operations can affect reservoir stratification patterns and trophic dynamics (Saito et al. 2001, Saito and Koski 2006, Moreno-Ostos et al. 2008, Çalıskan and Elçi 2009), and this sets reservoir thermal dynamics apart from those of natural lakes (Martin and Arneson 1978, Moreno-Ostos et al. 2008). The lack of data on discharge from Lake Granby prevented us from directly evaluating the thermal effects of dam operations there. But in general, thermocline depth of reservoirs can be positively correlated with withdrawal depth, and heat accumulates in the epilimnion during hypolimnetic withdrawals (Moreno-Ostos et al. 2008), as in warm, dry years at Lake Granby. Conversely, withdrawing water from the epilimnion can reduce overall water column temperature and produce a shallower thermocline, as we observed in cool, wet years. As more dams are retrofitted with variable outlet structures to adjust dam outflow temperatures for riverine concerns (e.g., Saito et al. 2001) we are presented with a growing opportunity to learn how hydroclimate and dam operations interact to affect water quality and food web interactions within reservoirs.

Acknowledgments

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