

## Trophic Economics of Lake Trout Management in Reservoirs of Differing Productivity

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**Abstract.**—Because of their potential to reach large size, lake trout *Salvelinus namaycush* are managed as trophy fish in many reservoirs in the western United States. In Colorado, restrictive harvest regulations for lake trout were enacted in reservoirs exhibiting a range of productivities. Annual stockings of kokanee (lacustrine sockeye salmon *Oncorhynchus nerka*) and rainbow trout *O. mykiss* sustained sport fisheries, but stocked fish also dominated the prey fish assemblages in these systems. Hydroacoustic surveys suggested that lake trout management allowed an imbalance to develop between prey fish biomass and the biomass of piscivorous lake trout. Piscivorous fish biomass was, on average, 60% of total pelagic fish biomass. Bioenergetics modeling confirmed the imbalance: annual lake trout consumption was near or exceeded annual pelagic prey fish supply (standing stock plus production); the degree of imbalance was greater in less productive reservoirs. Annual subsidies to the food web, in the form of stocked sport fish, were necessary to allow the imbalance between predator and prey populations to persist, especially in the least-productive systems. Though highly sensitive to the size at which hatchery fish are consumed, the per capita costs to sustain lake trout growth at observed levels would total about US\$200 per lake trout in the more productive reservoirs and \$300–600 per lake trout in the less productive reservoirs. The cost of maintaining high lake trout biomass in these stocked systems may be a difficult management strategy to justify and sustain, either economically or socially.

Trophic economics is a term coined by Ney (1990) to describe the relationship between prey resource supply and consumer demand. Ney's theses were that (1) sport fish production is often limited by food supply, (2) a variety of methods exist to quantify predator–prey relationships in fisheries, and (3) fishery managers' actions should maintain some balance between predator consumption demand and prey supply. Failure to manage within the constraints dictated by ecosystem productivity and sport fish food supply threatens the ecological integrity of the ecosystem and results in expensive and ultimately unsustainable management programs.

In practice, trophic economics has been an underlying tenet of fishery management for decades. Swingle (1950) was perhaps the first fishery scientist to attempt to balance piscivorous sport fish and their prey in ponds for the purpose of manipulating growth rates and size structure of large-mouth bass *Micropterus salmoides* and bluegills *Lepomis macrochirus*. More recently, trophic eco-

nomics concepts have been successfully applied to important management questions of carrying capacity and stocking policy on the Laurentian Great Lakes (Stewart et al. 1981), in limits to sport fish production in southeastern U.S. reservoirs (Ploskey and Jenkins 1982), and to the effects of harvest restrictions on predator consumption demand (Johnson et al. 1992; Luecke et al. 1994; Johnson and Martinez 1995). Although predicting future states of managed fisheries is complicated by well-known recruitment stochasticity (Magnuson 1991), quantifying existing relationships between predator demand and prey supply is important because ultimately the persistence of predator and prey populations will depend in part on their relative biomasses, or the balance between predation rate and prey supply.

Balance may be an unfortunate term because it implies that managers should strive to achieve a stable equilibrium between predator and prey populations. Contemporary ecologists and managers are becoming more aware of the nonequilibrium dynamics of communities, particularly when systems are subjected to anthropogenic disturbance (Pimm 1991; Meffe and Carroll 1994). Managers of west-

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ern reservoirs should be especially cognizant of this variability because of the vagaries of managing human-made environments with nonnative predator and forage species (Wydoski and Bennett 1981). In practice, balance is a dynamic system attribute, the value of which changes with recruitment, growth, and survival patterns of managed populations. Hence, as Ney (1990) argues, managing for a balance between predator demand and prey supply is a dynamic, adaptive process requiring periodic monitoring. Fishery managers can respond to unbalanced systems by applying standard fishery management tools: adjusting stocking rates and manipulating harvest mortality by means of regulations.

In this paper, we assess trophic economics of four reservoir sport fisheries by quantifying pelagic predator and prey fish biomass, prey fish production, and the consumption demand (food consumed by a predator population growing at physiological maximum) and realized consumption (biomass actually consumed by predator population) exerted by piscivorous lake trout *Salvelinus namaycush* on their prey. The four reservoirs exhibited a wide range of productivities and, thus, different capacities to support top predators. Next, because most of the prey fish in our study reservoirs were of hatchery origin, we evaluate the fiscal economics of sustaining the consumption by a lake trout population on a stocked forage base. Finally, we examine fishery management strategies with respect to observed predator and prey biomasses and the economic and social costs associated with maintaining the observed predator-prey systems.

### Management Context

This study was conducted using data from four of Colorado's largest and most important coldwater lentic fishery resources: Blue Mesa Reservoir (Gunnison County), Lake Granby (Grand County), Taylor Park Reservoir (Gunnison County), and Twin Lakes (Lake County). Each of these reservoirs has been managed, in part, to produce large lake trout. Lake trout are a popular nonnative sport fish, and because of their long life span, many can attain large size (>20 kg) if prey fish resources are sufficient and they are protected by harvest regulations (Luecke et al. 1994). Lake trout are also the dominant apical predators in many Colorado mountain reservoirs. Most of these systems are oligotrophic to mesotrophic with a rather limited capacity for sport fish production. Unlike other regions of North America where lake trout oc-

TABLE 1.—Size, number, and cost of hatchery fish stocked in study reservoirs during 1994. Subcatchable and catchable trout consisted mainly of rainbow trout but also included small numbers of cutthroat trout and brook trout.

Measure	Blue Mesa Reservoir	Lake Granby	Taylor Park Reservoir	Twin Lakes
<b>Kokanee fry</b>				
Length (mm)	51	38	76	
Number/ha	380.0	334.5	264.4	
Kg/ha	0.38	0.15	1.06	
Total cost (\$)	211,216	108,028	45,695	
<b>Subcatchable trout</b>				
Length (mm)	122	66	51	178
Number/ha	226.7	16.8	5.1	50.4
Kg/ha	5.2	0.04	0.005	2.0
Total cost (\$)	298,251	9,380	628	29,351
<b>Catchable trout</b>				
Length (mm)		259	267	229
Number/ha		27.6	90.8	75.4
Kg/ha		5.3	19.1	10.0
Total cost (\$)		60,826	58,274	56,575

<sup>a</sup> 1994 US\$.

cur, coldwater reservoir fish assemblages in Colorado are not species rich, in part due to zoogeographic constraints that resulted in no native, specialized lacustrine fishes. The longnose sucker *Catostomus catostomus* and white sucker *Catostomus commersoni* are the only nongame species common in these reservoirs; mottled sculpins *Cottus bairdi* and johnny darters *Etheostoma nigrum* are present in some reservoirs, but they are not abundant.

Because natural reproduction of salmonids other than lake trout is negligible in most Colorado reservoirs, large numbers of juvenile salmonids are stocked each year. In 1994,  $3.8 \times 10^6$  kokanee (lacustrine sockeye salmon *Oncorhynchus nerka*) and rainbow trout *O. mykiss* (as well as small numbers of cutthroat trout *O. clarki* and brook trout *Salvelinus fontinalis*) were stocked in the four study reservoirs alone (Table 1). Three sizes or types of stocking are typically employed to manage the state's coldwater lentic fisheries: kokanee fry (51 mm total length, TL), subcatchable rainbow trout (120 mm TL), and catchable rainbow trout (260 mm TL). Managers rely on the smallest and, hence, least-expensive fish in productive systems where stocked fish can be expected to grow rapidly and recruit to the fishery by exploiting a no-cost reservoir food supply. Catchable-sized fish are typically used where rapid and efficient angler exploitation are expected and where the recipient system has insufficient food resources to allow fry

TABLE 2.—Harvest regulations for lake trout in the study reservoirs since 1970. Size restrictions are given in English units. Metric equivalents are as follows: 15 in = 381 mm, 20 in = 508 mm, 22 in = 559 mm, 26 in = 660 mm, 34 in = 864 mm, and 36 in = 914 mm.

Regulation period	Daily bag limit : size restriction for			
	Blue Mesa Reservoir	Lake Granby	Taylor Park Reservoir	Twin Lakes
1970–1971	4:none	4:none	4:none	4:15 in minimum
1972–1973	4:none	4:none	4:none	2:20 in minimum
1974–1976	2:15 in minimum	2:15 in minimum	2:15 in minimum	2:15 in minimum
1977–1984	2:none	2:none	2:none	2:15 in minimum
1985–1987	1:20 in minimum	1:20 in minimum	1:20 in minimum	1:20 in minimum
1988–1989	1:20 in minimum	1:20–30 in protected slot	1:20 in minimum	1:20 in minimum
1990–1992	1:22–34 in protected slot	1:22–34 in protected slot	1:22–34 in protected slot	1:22–34 in protected slot
1993–1995	1:22–34 in protected slot	2:26–36 in protected slot, only 1 >36 in	1:22–34 in protected slot	1:22–34 in protected slot
1996–2000	8:none	4:26–36 in protected slot, <sup>a</sup> only 1 >36 in	3:only 1 >26 in	1:22–34 in protected slot

<sup>a</sup> Protected slot relaxed during July–September due to high expected hooking mortality.

or subcatchables to grow to a harvestable size. Thus, because the cost of hatchery fish increases with size at stocking, unproductive reservoirs require the most expensive hatchery products to sustain a fishery.

The paucity of nongame fishes and intensive stocking in Colorado reservoirs have produced pelagic prey fish assemblages that are dominated by stocked kokanee and rainbow trout. Not surprisingly, preferred prey for lake trout in Colorado include rainbow trout and kokanee, themselves popular sport fishes.

Lake trout biomass has been fostered in the four reservoirs by stocking and restrictive harvest regulations (Table 2). Over the past two decades, lake trout have been stocked sporadically in Blue Mesa Reservoir, more regularly in Lake Granby, and nearly annually in Twin Lakes. Restrictive bag limits (two fish/d) and minimum size limits (mostly 15 in [381 mm]) were in effect on all study reservoirs starting in 1974. In 1985, the bag limit was reduced to one fish/d, and the minimum size limit increased to 20 in (508 mm). During 1988–1995, a variety of closed slot regulations were implemented, with the most restrictive regulations at Lake Granby. This trend raised concern with some biologists about the sustainability of the trophy lake trout management strategy and about the economic and recreational tradeoffs that were required to produce trophy lake trout fisheries at the expense of a sport fish forage base. If effective, these regulations will have increased the biomass and, hence, realized consumption of large lake trout.

Yet, none of the regulation changes were enacted with respect to productive capacity of the reservoirs or the relationship between predator consumption demand and prey supply (Johnson and Martinez 1995). Further, no fishery assessments aimed at evaluating trophic balance have occurred until the present study.

## Methods

*Reservoir productivity.*—Because basin morphometry, siltation, and water level fluctuations preclude significant primary and secondary production in the littoral zone, food webs in many reservoirs are sustained primarily by pelagic production (Kimmel et al. 1990; Hayes et al. 1993; Martinez and Wiltzius 1995). A wide variety of variables have been used as indicators of lake productivity (Downing and Plante 1993), here defined as the inherent capacity of a system to produce fish biomass. We evaluated several abiotic and biotic indicators of reservoir “productivity”: length of growing season, morphoedaphic index (MEI; Ryder 1965; Henderson et al. 1973), midsummer Secchi disk depth, midsummer chlorophyll concentration, crustacean zooplankton density, density of opossum shrimp *Mysis relicta*, and fish biomass density.

Length of the growing season was defined as the number of days that reservoir surface temperature exceeded 10°C. The MEI was computed from mean depth (at full pool) and conductivity ( $\mu\text{S}/\text{cm}$ ; total dissolved solids =  $0.62 \times$  conductivity; APHA 1995) obtained from the National Park Ser-

vice (M. Malick, Curecanti National Recreation Area, unpublished data), Weiler (1982), Uglund et al. (1994), and La Bounty and Sartoris (1993). Midsummer chlorophyll-*a* concentrations were determined for July–August from 0–10-m integrated water column samples in 1994 in Blue Mesa Reservoir, Lake Granby, and Taylor Park Reservoir. Concentrations were measured by methanol extraction (Holm-Hansen and Riemann 1977; Marker et al. 1980) and a calibrated Turner model 450 fluorometer. Data for Twin Lakes were from 0–15-m composite samples (S. Campbell, U.S. Geological Survey, unpublished data).

Crustacean zooplankton density was estimated from oblique 0–10-m tows at three to five locations in each reservoir with a Clarke-Bumpus metered plankton sampler with 153- $\mu$ m net. Crustacean zooplankters in two or three 1-mL subsamples were identified to species or genus, counted, and measured. Reservoir densities were computed by expanding subsample counts to the volume sampled (Martinez 1992). Because many planktivorous fishes strongly select for *Daphnia* spp. (O'Brien 1987) and kokanee select large *Daphnia* spp. (Martinez and Bergersen 1991; Stockwell and Johnson 1997), we also computed density of daphnids that were more than 1.0 mm in length. We measured density of opossum shrimp with a 1.0-m-diameter, 3-m-long net constructed of 500- $\mu$ m nitex and towed vertically at a rate of 0.3 m/s. Sampling was conducted at least 30 min after sunset during the new moon in midsummer 1991–1994 at 10 stations per reservoir in two depth strata, with two replicate hauls per station (Martinez 1992).

**Stock assessment.**—Lake trout length at age for Blue Mesa Reservoir (P. J. Martinez, unpublished data), Taylor Park Reservoir (Weiler 1982), and Twin Lakes (Nesler et al. 1993) was determined from otoliths. Growth rates were derived by fitting a von Bertalanffy growth function (Hilborn and Walters 1992) to the mean lengths at age ( $R^2 \geq 0.96$  in each reservoir). Current age data were unavailable for Lake Granby, so based on body condition and productivity indices, we assumed that growth of Lake Granby lake trout was intermediate between Blue Mesa and Taylor Park rates. For population level analyses, size and abundance data for large (>425 mm) fish from hydroacoustic surveys were parsed into age-classes according to mean lengths at age determined from otoliths. We assumed lengths at age were normally distributed, a common and parsimonious assumption in length-frequency analysis (MacDonald 1987). Fish that

fell in a size-class at the exact midpoint between two successive ages were divided equally into the two age-classes. Some fish were probably underaged and others overaged in each age-class; however, the bias should have been small if lengths of successive age-classes were distributed symmetrically. Although the error in assigned ages probably increased with fish size, abundance and annual growth increment decreased with age, making errors in estimated ages less consequential to our consumption estimates. Lake trout biomass was computed from reservoir-specific length–weight regressions ( $R^2 \geq 0.97$ ; Martinez 1995) that converted hydroacoustic estimates of numbers of fish in each length-class into biomass.

Experimental gill nets were used to assess species composition and size structure of fishes in each reservoir. Three standardized (Powell 1981) vertical nets measuring 3  $\times$  60 m, each composed of two mesh sizes (12.5, 19, 25, 32, 38, and 51 mm, square measure), were fished overnight at three locations in Blue Mesa Reservoir during June, August, and October, and at a midlake station in Taylor Park Reservoir during June and August 1994. At Lake Granby, a combination of vertical (configured as above) and horizontal gill nets (2 m  $\times$  46 m; 6 meshes, ranging from 19 to 76 mm) were fished overnight during May, July, and October 1994. Experimental horizontal gill nets (configured as above) were fished overnight on 20–21 July 1994, in Twin Lakes.

Hydroacoustic surveys were conducted with a Hydroacoustics Technology, Inc. (HTI) model 240 split-beam echosounder and bow-mounted transducer (15°, 200 kHz). The acoustic system was fully calibrated. The transmitter was set to a pulse width of 0.3 ms, at 5 pings/s. Receiver gain was set to –6 decibels (dB). The acoustic signal was monitored with a Hitachi V-212 oscilloscope, and a dot matrix printer continuously recorded the echogram. Data were stored on digital audiotape for subsequent analyses with HTI signal-processing software.

Transects followed a zig-zag survey design (Gunderson 1993; Martinez 1994); the number and total length of transects surveyed was proportional to reservoir surface area; 15 transects and 24.4 km were surveyed in Blue Mesa Reservoir, and 4 transects and 6.7 km were surveyed in Taylor Park Reservoir. Hydroacoustic surveys were performed well after sunset during the new moon at Blue Mesa, Granby, Taylor Park, and Twin Lakes reservoirs during August 1–3, September 28, August 4, and July 19, respectively, in 1994.

Minimum target strength threshold was set to  $-55$  dB to avoid counting mysids. Fish distributions were sufficiently dispersed to analyze for abundance by echo counting. Fish densities and target strengths were analyzed separately in three depth strata: 2–10 m, 11–20 m, and  $>20$  m. Fish density (fish/m<sup>3</sup>) was computed by totaling tracked targets detected in each depth stratum and dividing this by the volume of that stratum that was acoustically sampled. Elevation–capacity relationships (U.S. Department of Interior, Bureau of Reclamation, unpublished data) were used to compute the total reservoir volume in each stratum, which was multiplied by fish density to obtain lakewide abundance of pelagic fishes. In situ target strength measurements were range-weighted and converted to fish length with the equation in Love (1977). No lake trout were caught shallower than 20 m in gill-net sampling during 1994–1996, so we assumed all lake trout in Blue Mesa Reservoir occurred in the  $>20$ -m depth stratum during the hydroacoustic survey. Biomass of prey-sized fish was computed from abundance using length estimated from target strength and length–weight regressions for each species and reservoir. Prey fish production (kg·ha<sup>-1</sup>·year<sup>-1</sup>) was computed from maximum individual prey body weight and prey population biomass using the approach of Downing and Plante (1993).

*Consumption estimates.*—We used the bioenergetics modeling package of Hanson et al. (1997) to estimate consumption by piscivorous lake trout by size-class. Model assumptions are detailed in the software's documentation (Hanson et al. 1997); details about the lake trout component can be found in Stewart et al. (1983). Simulations were run for 365 d, and consumption was fit to the estimated annual growth increment while accounting for energy loss each fall due to spawning (average for both sexes: 6.8% of individual mass per year; Stewart et al. 1983). In addition to demographic data described earlier, the following information was required to perform these simulations: mortality rate, thermal history, diet composition and prey energy content, and lake trout energy content. Mortality rates were not available so we performed simulations using two instantaneous annual mortality schedules:  $Z = 0.693$  ( $S$  [survival] = 50%/year) and  $Z = 0.288$  ( $S = 75\%$ /year). Although few studies exist, this range encompasses survival rates of lake trout reported in the literature (Fabrizio et al. 1997) and was supported by a catch curve analysis performed on data from Blue Mesa Reservoir (where missing age-classes were fewest;

$S = 57\%$ /year). The higher mortality estimate was considered the nominal rate in simulations and probably produced a conservative underestimate of the potential prey biomass consumed by lake trout.

Temperature and dissolved oxygen profiles were obtained periodically with a Yellow Springs Instruments model 58 meter as part of routine limnological sampling (Lee 1994; Johnson et al. 1995a; Martinez 1995). We assumed lake trout occupied water of 4°C under ice cover and that during the stratified, ice-free season, they behaviorally thermoregulated to the temperature nearest 10°C, provided that dissolved oxygen concentrations exceeded 3 mg/L. Temperatures at which lake trout were captured in vertical gill nets during summer 1994–1997 in Blue Mesa Reservoir (Johnson et al. 1997) averaged 9.8°C ( $N = 40$ ), supporting our assumption of behavioral thermoregulation. Resulting thermal histories were comparable with those for lake trout in other waters (Stewart et al. 1983; Yule and Luecke 1993).

Stomach contents of lake trout sampled from anglers' creels and in gill nets during April–October 1994–1997 were preserved in 10% formalin until they could be examined in the laboratory. The proportion of the stomach contents (by volume) consisting of fish and macroinvertebrates was estimated by eye. Prey organisms were identified to the lowest taxonomic level possible; however, results varied with the state of digestion. Mean diet composition was computed for four size-classes:  $<425$  mm, 425–600 mm, 601–900 mm, and  $>900$  mm. The latter three groups corresponded to important life stanzas for lake trout in these fisheries: the onset of piscivory up to the lower end of a typical closed slot limit, the size-class that is protected by a commonly applied closed slot limit, and the size beyond the upper slot limit.

In simulations, we entered the diet composition estimated from stomach samples and assumed wet weight energy content of prey to be 3,641 J/g for invertebrates (Rudstam 1989) and 7,528 J/g for fish prey (Yule and Luecke 1993). Lake trout energy content was modeled as a function of body weight (Hanson et al. 1997). The bioenergetics model computed the proportion of the maximum possible consumption rate that was actually achieved ( $pC_{\max}$ ) to match the observed growth in each population, accounting for allometric effects of body size on consumption rate, the thermal regime, and diet composition. The proportion of maximum consumption that a fish achieves is an

TABLE 3.—Biological productivity indicators in four Colorado montane reservoirs (Martinez 1995). Chlorophyll *a* is reported as the mean of integrated 0–10-m (0–15-m in Twin Lakes) samples taken in midsummer 1994. Mean densities of *Daphnia* spp. and other zooplankton (mainly *Diatylops bicuspidatus thomasi*) were computed from sampling at three to five stations per lake (with 153- $\mu$  net) during mid-July and mid-August 1991–1994. Mean mysid densities were computed from sampling at 10 stations per lake during mid-July and mid-August 1991–1994. Total fish biomass densities estimated from hydroacoustic surveys conducted during August 1994 (variability estimates were not available; numbers in parentheses indicate total lake volume [ $m^3$ ] sampled in each survey).

Attribute	Blue Mesa Reservoir			Lake Granby			Taylor Park Reservoir			Twin Lakes		
	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>	Mean	SD	<i>N</i>
Chlorophyll <i>a</i> ( $\mu g/L$ )	2.66	0.56	3	5.76	0.43	5	1.66	0.14	5	0.55	0.14	2
<i>Daphnia</i> density (number/L)	13.2	1.20	3	6.52	4.52	4	3.03	2.95	3	1.35	1.85	3
Other zooplankton (number/L)	33.3	3.82	3	28.9	6.81	4	31.5	19.2	3	9.90	4.52	3
Mysid density (number/ $m^2$ )				278	178	4	307	161	4	97.0	19.0	4
Fish biomass (kg/ha)	43.5 <sup>a</sup>			30.7 <sup>b</sup>			12.0 <sup>c</sup>			3.70 <sup>d</sup>		

<sup>a</sup> Lake volume sampled =  $5.264 \times 10^6 m^3$ .

<sup>b</sup> Lake volume sampled =  $1.194 \times 10^6 m^3$ .

<sup>c</sup> Lake volume sampled =  $5.973 \times 10^5 m^3$ .

<sup>d</sup> Lake volume sampled =  $6.990 \times 10^5 m^3$ .

indicator of the ratio of predator demand and prey supply, or relative food availability for piscivores.

We used length–weight regressions for kokanee and rainbow trout (Martinez 1995) to estimate the weight of various-sized hatchery fish consumed by lake trout. The per capita consumption necessary for a lake trout to grow through three piscivorous size-classes at observed rates in each reservoir was computed. This biomass was then apportioned into the number of prey consumed by assuming a lake trout consumed prey 33% of its length (similar to the mean fish prey: lake trout size ratio observed by Yule and Luecke (1993) in Flaming Gorge Reservoir).

The cost of hatchery fish was computed by using a linear cost function derived by the Hatchery Section, Colorado Division of Wildlife: cost =  $\$0.00373 \times SS$ , where SS is total length (mm) at stocking (Martinez 1996). These costs did not include administrative and support services or capital replacement costs (Johnson et al. 1995b). Three sizes and types of stocking were evaluated: kokanee fry (51 mm TL, \$0.19/fish), subcatchable rainbow trout (120 mm TL, \$0.45/fish) and catchable rainbow trout (254 mm TL, \$0.95/fish). To estimate predation costs, the number of prey consumed by lake trout was multiplied by the cost of each hatchery fish based on its size at stocking.

## Results

### Reservoir Productivity

Based on biotic measures, Twin Lakes was the most oligotrophic reservoir, with the lowest chlo-

rophyll concentration, zooplankton and fish densities, and lake trout growth rate and condition. Chlorophyll-*a* concentration was highest in Lake Granby followed by Blue Mesa Reservoir (Table 3). Although chlorophyll concentration was higher in Granby than Blue Mesa, we believe this was due to food web rather than productivity differences. In Granby, high mysid density probably reduced zooplankton density (Martinez and Bergersen 1991), limiting herbivory in the system and allowing primary production to accumulate. Zooplankton density was highest in Blue Mesa despite the highest planktivorous fish density. Zooplankton and mysid densities were comparable in Lake Granby and Taylor Park Reservoir. Granby was probably more productive than Taylor Park because the growing season is about a month longer (Table 4) and chlorophyll concentration and fish density were much higher than at Taylor Park (Table 3). Judging from the length of the growing season, conductivity, zooplankton density, total fish biomass density (Tables 3, 4), and kokanee growth rates (Martinez 1994, 1995, 1996), Blue Mesa was the most productive system in upper trophic levels.

Most abiotic indices appeared to be weakly related at best to biotic characteristics of the reservoirs. Elevation and length of the growing season did not distinguish the more productive Taylor Park Reservoir from the least productive system, Twin Lakes. Reservoir morphometry appeared to have little influence on trophic status: Blue Mesa was the largest reservoir in terms of mean and

TABLE 4.—Physical and chemical characteristics of four Colorado trophy lake trout reservoirs. Lake elevation is maximum surface elevation (m) above sea level (ASL). Growing season is expressed as number of days with water temperatures 10°C or higher (data from Cudlip et al. 1987; Lee 1994; Martinez 1986, 1992, 1994; LaBounty and Sartoris 1993). Secchi depth is mean for June–August (Blue Mesa, Granby, and Taylor Park) or July only (Twin Lakes). Conductivity was obtained for Blue Mesa from M. Malick (National Park Service, unpublished data), for Granby from Ugland et al. (1994), for Taylor Park from Weiler (1982), and for Twin Lakes from LaBounty and Sartoris (1993).

Characteristic	Blue Mesa Reservoir	Lake Granby	Taylor Park Reservoir	Twin Lakes
Elevation (m ASL)	2,292	2,524	2,844	2,804
Surface area (ha)	3,706	2,936	823	1,120
Mean depth (m)	31	23	16	15
Maximum depth (m)	101	66	44	31
Volume (m <sup>3</sup> )	1.16 × 10 <sup>9</sup>	6.65 × 10 <sup>8</sup>	1.31 × 10 <sup>8</sup>	1.73 × 10 <sup>8</sup>
Residence time (years)	0.97	1.77	0.73	0.53
Growing season (d)	129	122	93	112
Secchi depth (m)	4.6	2.5	7.6	5.2
Conductivity (μS/cm)	175	55	126	66
Morphoedaphic index	3.5	1.5	4.9	2.8

maximum depth and volume (Table 4) but was the most productive. Conversely, Twin Lakes was the shallowest reservoir but was the least productive. Secchi disk depth was not correlated with chlorophyll concentration ( $P = 0.26$ ) or zooplankton ( $P = 0.77$ ) or fish biomass density ( $P = 0.51$ ). A commonly used chemical indicator, conductivity, was poorly linked to system productivity (Tables 3, 4). Even MEI, an index of nutrient status corrected for basin morphometry that has been shown to predict fish yields in natural lakes, was not consistent with the other indicators of system productivity (Table 3) and was not correlated ( $P \geq 0.45$ ) with chlorophyll, zooplankton, or fish biomass in our study reservoirs.

#### Stock Assessment

Horizontal and vertical experimental gill nets in Blue Mesa Reservoir (Johnson et al. 1995a), Lake Granby, and Taylor Park Reservoir (Martinez 1995) showed that hydroacoustic targets  $-33$ dB and greater (425 mm) were exclusively piscivores, most of which were lake trout. In Twin Lakes (G. Policky, Colorado Division of Wildlife, unpublished data) some white suckers exceeded the 425-mm threshold size; however, large suckers did not appear in the pelagic zone. Kokanee and rainbow trout made up the great majority of the non-lake trout gill-net catch (Figure 1) in all reservoirs, except in Twin Lakes where rainbow trout constituted 39% of the non-lake trout catch and catostomids made up the remainder. Catches in Twin Lakes probably overestimated relative abundance of the more benthic catostomids because only horizontal gill nets were used there.

Consistent with trends in reservoir productivity, lake trout were heaviest for a given length and grew fastest in Blue Mesa Reservoir; lake trout were leanest and slowest growing in Twin Lakes (Figure 2a). Individual weight at maximum age was about 68% lower in the slowest growing population (Twin Lakes) compared with Blue Mesa, the fastest growing population (Figure 2b). Growth rates of lake trout in Granby and Taylor Park were about midway between the maximum and minimum growth rates. Horizontal gill-net sampling at Blue Mesa in 1997 (B. M. Johnson, unpublished data) captured a broad size distribution of lake trout, consistent with the size structure estimated by hydroacoustics. Older lake trout ( $>13$  years old) were most abundant in Lake Granby.

Blue Mesa Reservoir and Lake Granby showed

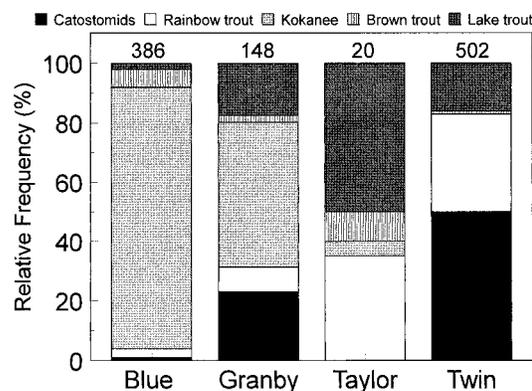


FIGURE 1.—Species composition of the catch in vertical gill nets (Blue Mesa Reservoir = Blue, Taylor Park Reservoir = Taylor), horizontal gill nets (Twin Lakes = Twin), or both (Lake Granby = Granby). Total number of fish sampled is shown above each bar. Nets were experimental, with six mesh sizes ranging from 12 to 76 mm bar. Catostomids were longnose and white suckers.

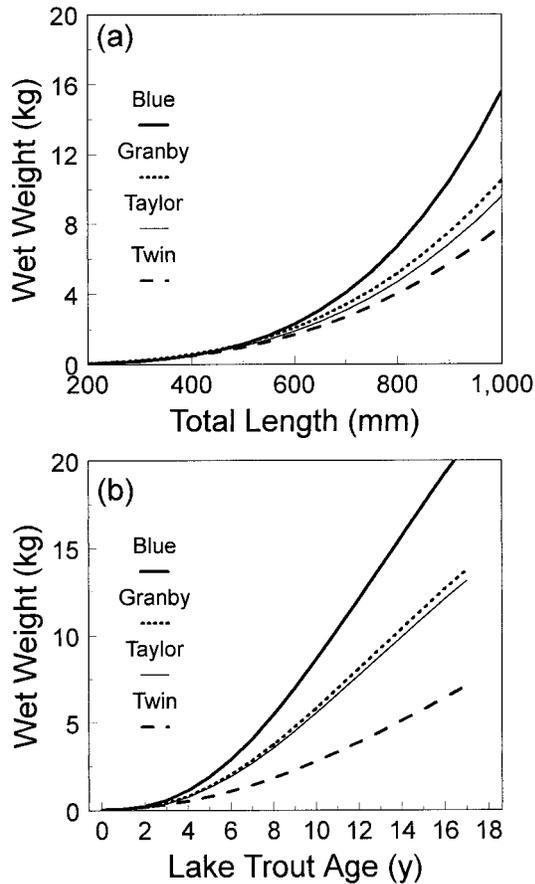


FIGURE 2.—Lake trout (a) length–weight and (b) weight-at-age relationships in four Colorado reservoirs based on otolith analyses (Martinez 1995). Reservoir abbreviations are defined in Figure 1. A von Bertalanffy growth function was fitted to each data set to fill in missing ages and produce the smooth curves shown here.

similar lakewide abundance estimates of all sizes of fish ( $7.47 \times 10^5$  versus  $7.42 \times 10^5$  fish; Table 5). However, prey-sized fish densities were lower on an areal basis in Blue Mesa (182 fish/ha; Figure 3) than at Granby (246 fish/ha). Alternatively, the density of predator fish was higher at Blue Mesa (12 fish/ha) than at Granby (7 fish/ha). Total fish abundance was lower at Taylor Park Reservoir (82 fish/ha; Figure 3) and much lower at Twin Lakes (14 fish/ha). It was not known what proportion of prey-sized fish were actually young lake trout. Biomass density of predators was greater than prey biomass density in the low-productivity reservoirs (Taylor Park and Twin Lakes), and predator and prey biomasses were similar in Blue Mesa and Granby (Figure 3). Predator fish constituted 50, 41, 68, and 78% of the total fish biomass in Blue

Mesa, Granby, Taylor Park, and Twin Lakes, respectively.

#### Consumption Estimates

Only in Lake Granby were lake trout unable to behaviorally thermoregulate to their preferred temperature of  $10^\circ\text{C}$  during late summer due to hypoxic conditions in the hypolimnion. There, lake trout were assumed to have inhabited  $10.5\text{--}11.5^\circ\text{C}$  water from late August through mid-October. The number of days per year when lake trout could inhabit water near their preferred temperature was highest at Blue Mesa (129 d) and Granby (122 d), about 2 weeks less at Twin Lakes, and about a month less at Taylor Park, the highest-elevation reservoir.

The species composition in gill-net samples showed that sport fish should make up a large proportion of the fish encountered by piscivorous lake trout in all reservoirs. This was corroborated by diet information ( $N = 188$  nonempty stomachs) that showed that sport fish made up the majority of the diet of lake trout greater than 425 mm TL during May–October (Figure 4). Identifiable fish in the stomachs of 425–600-mm lake trout were mostly salmonids, of which 33% were identifiable as rainbow or cutthroat trout and 33% were kokanee. Diets of large lake trout ( $>600$  mm) consisted of about 95% salmonids and 5% catostomids. Juvenile lake trout ( $<425$  mm) fed heavily on mysids, crayfish, and other macroinvertebrates until they reached a size large enough to begin exploiting fish prey.

Lake trout were feeding nearest their maximum physiological limit at Blue Mesa Reservoir, where  $pC_{\text{max}}$  averaged 68% for all sizes. Lake trout in Taylor Park Reservoir exhibited an intermediate average  $pC_{\text{max}}$  (60%), and lake trout at Lake Granby and Twin Lakes showed the lowest (53% and 49%, respectively), suggesting that food availability, scaled for temperature, was lower in those reservoirs.

Annual population consumption (kg/ha) by piscivorous age-classes of lake trout increased with reservoir productivity. The Twin Lakes lake trout population consumed the least fish prey, and the Blue Mesa population consumed the most (Figure 5). Prey fish production varied by more than an order of magnitude across reservoirs. Prey fish production was similar at Blue Mesa and Granby ( $11.4$  and  $10.6 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ , respectively), was much lower at Taylor Park ( $2.5 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ), and lowest at Twin Lakes ( $0.6 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ ; Figure 5). Estimated total annual consumption by lake

TABLE 5.—Hydroacoustic survey results in three depth strata showing total volume sampled ( $N = 15$  transects at Blue Mesa,  $N = 10$  transects at Granby,  $N = 4$  transects at Taylor Park, and  $N = 6$  transects at Twin Lakes), total number of fish targets detected (by size), and estimated lakewide abundance of fishes in study reservoirs during summer 1994.

Depth stratum (m)	Volume sampled (m <sup>3</sup> )	Fish targets		Lakewide abundance	
		<425 mm	≥425 mm	<425 mm	≥425 mm
<b>Blue Mesa Reservoir</b>					
2–10	134,097	57	0	56,116	0
10–20	405,329	1,193	86	311,394	26,514 <sup>a</sup>
>20	4,724,364	4,195	602	299,218	53,653
<b>Lake Granby</b>					
2–10	111,715	172	1	336,657	6,951
10–20	321,146	713	33	358,669	18,661
>20	761,128	110	17	18,467	3,172
<b>Taylor Park Reservoir</b>					
2–10	85,757	60	1	40,630	725
10–20	205,197	77	3	11,456	502
>20	306,328	192	47	11,444	2,951
<b>Twin Lakes</b>					
2–10	126,229	4	0	2,565	0
10–20	373,573	15	2	2,354	164
>20	199,157	94	6	9,861	735

<sup>a</sup> Based on gillnetting in 1994–1996. Large targets measured in water shallower than 20 m were not considered to be lake trout.

trout exceeded the sum of prey standing stock in August plus annual production in the two low-productivity reservoirs and was somewhat less than prey stock plus production in the higher-pro-

ductivity systems. Consumption estimates using the lower mortality rate ( $Z = 0.288$ ) were about 19% higher than those computed using the nominal mortality rate, which suggests that our assump-

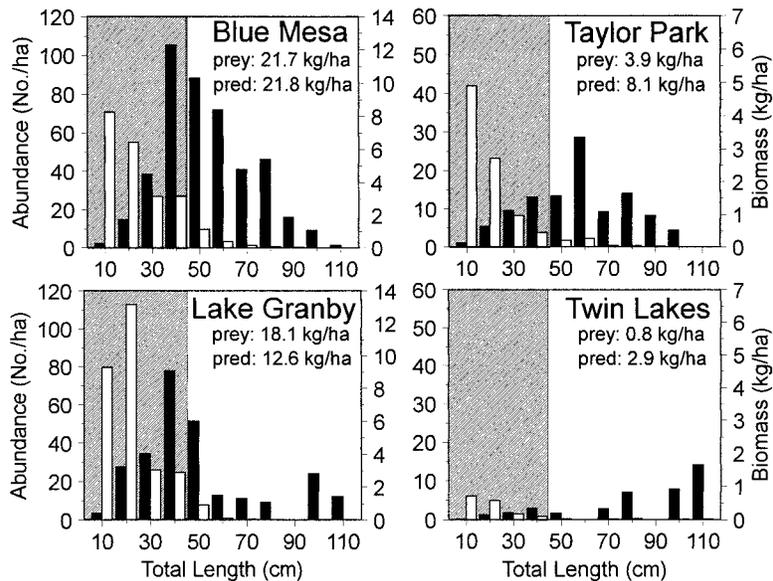


FIGURE 3.—Abundance (open bars) and biomass (black bars) of pelagic fishes estimated from nighttime hydroacoustic surveys conducted during July, August, or September 1994. Biomass (kg/ha) was estimated from size-specific abundances and length–weight regressions for fish 425 mm total length [TL] or less (prey, shaded) and fish greater than 425 mm TL (predators; see text for equations). Note that y-axes differ among lakes.

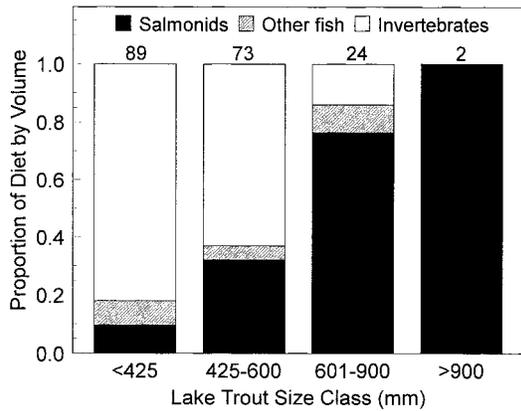


FIGURE 4.—Average proportions of salmonids (black shading; mainly stocked rainbow trout and kokanee), other fish (gray shading; mainly catostomids), and invertebrates (no shading; mainly chironomids, decapods, and mysids) in diets of four size-classes of lake trout. Number of nonempty stomachs is shown above each bar.

tions about mortality were not extremely important to the outcome of analyses.

Per capita costs of lake trout predation were highest in the lower-productivity systems (Figure 6). The cost of stocked prey consumed by a lake trout growing through the three piscivorous size-classes was about \$200/fish in Blue Mesa and Granby, where lake trout were assumed to consume kokanee that were stocked as fry but grew to a length 33% of that of the lake trout. Costs were about \$450/fish in Taylor Park and Twin Lakes, which are stocked with catchable rainbow trout that did not grow before being consumed. Predation costs were sensitive to the size at which the prey was stocked and the size at which it was consumed.

Taking Lake Granby as an example, cost per lake trout growing through a particular size-class was highest (\$100–830/fish) if lake trout fed on the smallest-sized prey (kokanee fry) shortly after stocking (Figure 7). At all lake trout sizes, predation cost declined rapidly as prey size at the time of consumption increased because the number of fish prey eaten declined according to the exponential relationship of length and weight of the prey and the assumed fixed cost of the stocking event. Because of their much higher absolute per capita consumption, the largest lake trout generated the highest cost of prey consumed per lake trout. Harvest regulations that protect lake trout to 600 mm would have a per capita cost as high as \$100/fish if their diet consisted entirely of newly stocked kokanee fry. Per capita costs would be

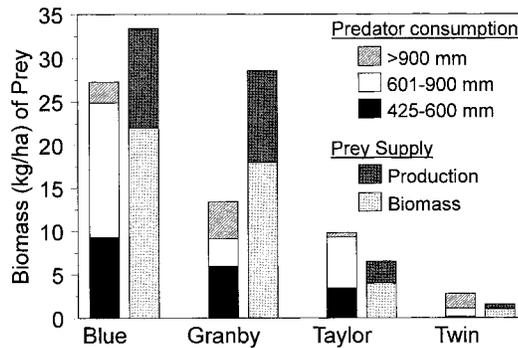


FIGURE 5.—Annual population consumption of salmonid prey by three size-classes of lake trout estimated with a bioenergetics model, and estimates of prey supply (standing stock in August plus annual production of pelagic prey fish) in four study reservoirs (abbreviations defined in Figure 1).

about seven times higher for a 600–900-mm slot limit (about \$700), and about 15 times higher for a 900-mm maximum size limit (\$1,500). Because kokanee fry are only available for a short period, these costs would not accrue over the entire year. Hence, these estimates represent upper limits to predation costs. At a given prey size, catchable trout stocking was the most expensive way to satisfy lake trout consumption (Figure 7).

### Discussion

Abiotic productivity indices that are commonly applied in natural lakes did not correspond well

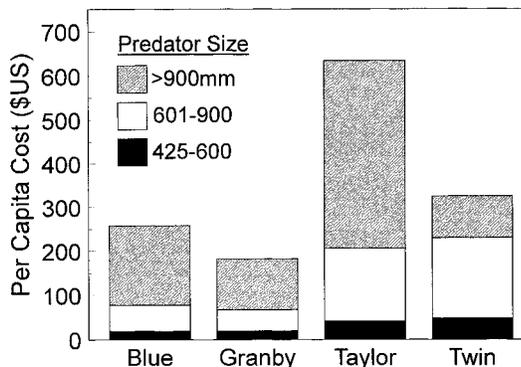


FIGURE 6.—Cost per predator (\$US, 1995) of prey consumed by lake trout growing through three piscivorous size-classes in four reservoirs (abbreviations defined in Figure 1), assuming lake trout consumed prey approximately 33% of the predator’s length. Stocked kokanee fry were the prey base in high-productivity reservoirs (Blue and Granby), and catchable rainbow trout were the prey base in low-productivity reservoirs (Taylor Park and Twin Lakes).

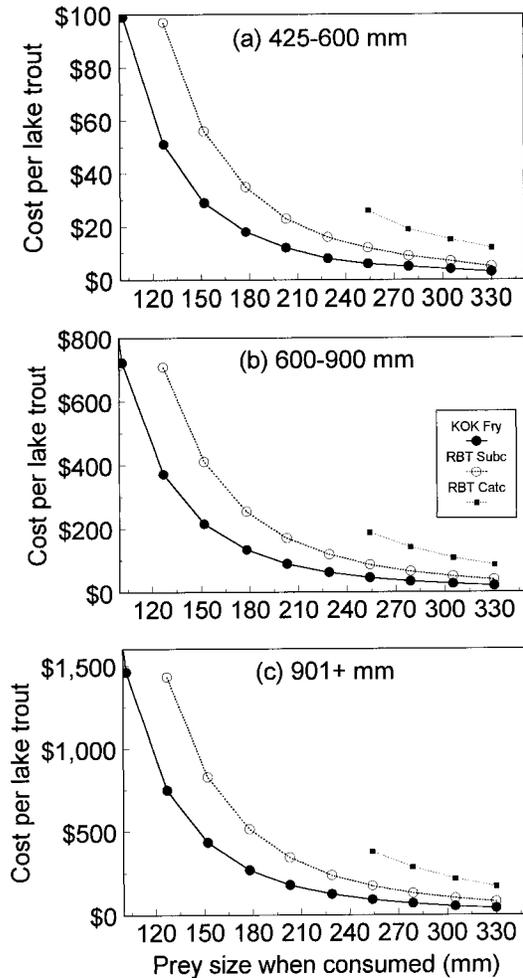


FIGURE 7.—Cost per predator (\$US, 1995) of three types of stocked prey (kokanee [KOK] fry, subcatchable rainbow trout [RBT Subc], and catchable rainbow trout [RBT Catc]) consumed at various sizes after stocking by three size-classes of lake trout in Lake Granby.

with observed biomasses of various trophic levels or the predator-prey relationships in the study reservoirs. This is perhaps due to the overriding influences of hydraulic residence time and elevation, which were inversely related to productivity. Productivity can influence food web structure and ecosystem dynamics (Persson et al. 1996), and energetic arguments have often been invoked to explain how food chain length can increase with increasing productivity (Elton 1927; Slobodkin 1960; Persson et al. 1992). Thus, low-productivity systems may not be capable of sustaining significant piscivore biomass under natural conditions. Although the generality of the argument that pro-

ductivity controls number of trophic levels continues to be debated (Hairston and Hairston 1993), it stands to reason that, given equivalent prey exploitation efficiency by consumers, higher biomasses of prey fish and apical predators could be sustained in more productive systems (Lindeman 1942; Oglesby 1977; Pauly and Christensen 1995).

Despite the trophic implications of the wide range of productivity in our study reservoirs, management actions and fish community structure indicated that high biomass of large lake trout has been a management goal in all four systems. Stocking and restrictive harvest regulations fostered the development of high lake trout biomass and size structure, and estimated piscivorous trout biomass exceeded estimated prey biomass in two of the four reservoirs. Inverted Eltonian pyramids of biomass are not uncommon in pelagic freshwater ecosystems (Diana 1995), where zooplanktivore standing stock may exceed that of zooplankton, which exceeds standing stock of phytoplankton. High turnover rates in lower trophic levels account for this pattern. However, it is unusual to see this pattern continue to top piscivores, as was the case in our study reservoirs. Because of the much greater similarity in body size and, therefore, turnover rates of planktivorous and piscivorous fish (Downing and Plante 1993), we would not expect such a pattern to be stable. A probable interpretation of this apparent paradox is that annual subsidies to the food web, in the form of stocked sport fish, maintain an otherwise unsustainable trophic structure.

Management actions and reservoir productivity also appeared to interact to affect food web structure and dynamics. The proportion of total fish biomass represented by piscivores was generally higher and lake trout growth rate was lower in the reservoirs with the lowest productivity, indicating that protective harvest regulations may have created the greatest imbalance in predator and prey biomasses in those reservoirs. Further, the difference between realized consumption and consumption demand was greatest in the least productive systems. Therefore, lake trout biomass was more limited by food availability in these reservoirs. It would be necessary to stock considerably more prey fish in the low-productivity systems to increase lake trout growth and condition to the level seen in the more productive systems. Because lake trout biomass, growth rate, and condition increased with reservoir productivity, the biomass consumed by each lake trout and by the population

growing through various length intervals also increased with increasing reservoir productivity.

Although size limits are usually set on the basis of fish length, most trophy anglers probably gauge their success by the weight of the fish they catch. If one computes the fish biomass required to grow a lake trout from the onset of piscivory to a "trophy" weight, the pattern of biomass consumed (and costs) versus productivity is quite different because it takes much longer for a lake trout in an unproductive system to attain trophy weight than it does in a productive system. For example, a 7-kg lake trout in Blue Mesa Reservoir would be about 10 years old and would have consumed 39 kg of fish to reach that size. In Twin Lakes, a lake trout of the same weight would probably be 17 years old and would have consumed 50% more biomass (60 kg total), with a proportional increase in cost, to attain trophy weight. Because lake trout in our study lakes and elsewhere (Elrod 1983; Trippel and Beamish 1989; Rieman and Myers 1991) undergo a characteristic trophic ontogeny, regulations that protect lake trout to trophy sizes also protect the most piscivorous segment of the lake trout population. Work at Flaming Gorge Reservoir, Utah–Wyoming (Luecke et al. 1994), showed that the harvest regulation that maximized catches of trophy lake trout also produced the greatest increase in consumption of prey fish populations.

Although the biomass of prey required to sustain lake trout in Taylor Park and Twin Lakes reservoirs was less than the biomass of sport fishes stocked each year, hydroacoustic density estimates suggested that few stocked fish survived to fall. The prey fish biomass required to maintain observed lake trout growth rates at Blue Mesa Reservoir and Lake Granby was near or exceeded the biomass of pelagic prey fish, yet sport fisheries for kokanee and rainbow trout persist there. The discrepancy between predator demand and prey supply could be accounted for by several factors: bias in our hydroacoustic data that either overestimated lake trout biomass or underestimated prey biomass, overestimates of lake trout growth rate, or underestimates of the importance of benthic fishes as prey for lake trout. Our hydroacoustic estimates of lake trout density should be less than or equal to true density because lake trout within about 1 m of the bottom would be acoustically undetectable. Growth rates of lake trout in our study lakes are similar to those found in other western lakes and reservoirs (Yule and Luecke 1993; Ruzycski and Beauchamp 1998). Diet data came only from April–October, but because consumption rates are

exponentially related to temperature, this period should encompass the majority of the annual consumption. Lake trout may in fact be feeding on nongame benthic prey fish during colder months, but their contribution to annual consumption should be small.

Managing for trophy lake trout has important economic costs when the prey base includes hatchery-derived sport fishes. Hatchery fish serve many purposes, and their value can be quantified in many ways (Stroud 1986; Wiley et al. 1993; Johnson et al. 1995b; Schramm and Piper 1995; Loomis and Fix 1999). We made a conservative estimate of the hatchery cost to produce a stocked kokanee or rainbow trout because the cost function we used was a linear function of fish length. This function undoubtedly underestimated production costs of larger stocked fishes, and hatchery administrative and capital replacement costs were not included (Johnson et al. 1995b). We then used the production cost to compute the cost of sustaining lake trout populations on a stocked forage base. The cost of a kokanee or rainbow trout recruited to the fishery would be much higher because only a small fraction of the fish stocked survive to harvestable size. An alternative approach that included the opportunity cost of fish lost to the sport fishery would have yielded higher estimates of the cost to sustain lake trout consumption with hatchery sport fish.

Total predation costs were higher in the more productive reservoirs because these systems support higher lake trout biomass at higher growth rates. However, the actual cost of individual hatchery fish consumed in more productive waters is lower than in unproductive waters. Stocked fishes grow more rapidly in more productive systems, and hence the cost incurred when these fish are consumed by lake trout will decline more rapidly because the prey biomass is determined more by in-lake tissue elaboration that comes at no cost to the hatchery system.

Predation cost was sensitive to assumptions about the size of the prey fish when consumed relative to its size at stocking. Cost was highest when lake trout fed on the smallest stocked prey. Despite their lower per capita cost to produce, small prey (e.g., kokanee fry) have exponentially less biomass per fish than longer prey, and hence predators must consume many more of these small stocked fish to satisfy their energetic requirements. The rapid decline in per capita predation cost with increasing prey size emphasizes the importance of poststocking production of the stocked cohort. However, in unproductive waters, growth of

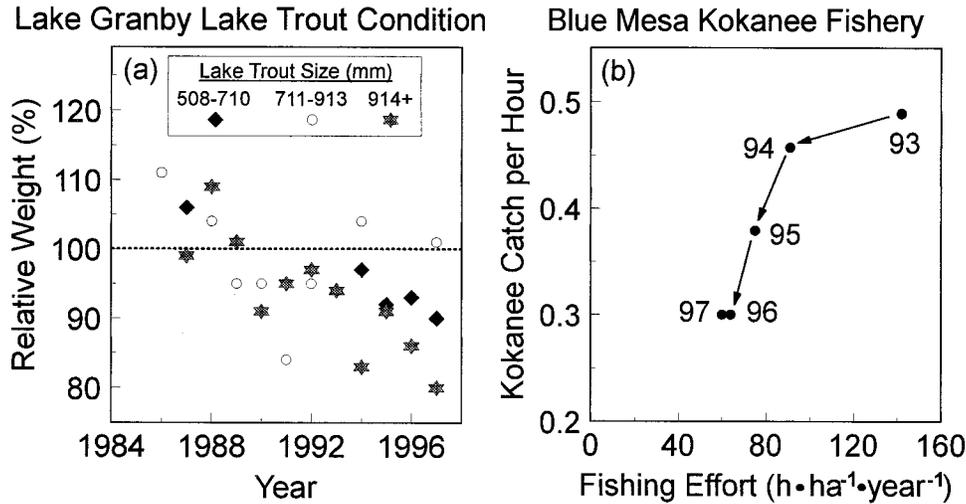


FIGURE 8.—(a) Relative weight of three size-classes (mm, total length) of lake trout in Lake Granby during 1986–1997 and (b) kokanee angler catch rate and fishing effort at Blue Mesa Reservoir from May through October during 1993–1997. Numbers beside data points indicate last two digits of year.

stocked trout and kokanee is poor, larger stocked sizes are required to enhance fisheries for these species, and the size-specific predation cost is high.

There are also important social costs and management tradeoffs associated with managing for trophy lake trout on a sport fish prey base. Recent survey data suggest that kokanee populations are declining in Blue Mesa Reservoir and Lake Granby (Martinez 1994, 1995, 1996). Data do not exist to conclusively link kokanee declines to lake trout predation, and other factors, such as competition with *Mysis relicta* (but see Bowles et al. 1991 and Beauchamp 1996) or entrainment in dam releases, could play a role. However, total lake trout consumption exceeded our estimates of pelagic fish biomass in these reservoirs, strongly implicating lake trout predation as a contributing factor in these kokanee declines. Lake trout predation has been implicated as a threat to prey fish populations (including kokanee) in several other western lakes and reservoirs (Bowles et al. 1991; Rieman and Myers 1991; Yule and Luecke 1993; Beauchamp 1996; Carty et al. 1997; Ruzycski and Beauchamp 1998). In Lake Granby, relative weights (Piccolo et al. 1993) of large lake trout have decreased by about 2% per year since 1986, concomitant with the decline of a major kokanee fishery (Figure 8a). Kokanee population declines are disturbing because of the implications for fishing participation, kokanee propagation programs, and the sustainability of lake trout and kokanee fisheries.

Creel surveys in Oregon and Idaho (Rieman and Maiolie 1995) and in Colorado show a strong relation between kokanee density and total fishing effort. In Blue Mesa Reservoir, fishing effort has declined each year from about 520,000 angler-hours/year in 1993 to about 230,000 angler-hours/year in 1997 (Figure 8b), concurrent with a decline in the kokanee population. When the kokanee population was strong in Lake Granby, angler effort averaged 150,000 h during the summers of 1975–1985 (Martinez and Bergersen 1991) but dropped to about 90,000 h for the entire year after the decline of the kokanee population in 1986 (Martinez and Bergersen 1991; M. Jones, Colorado Division of Wildlife, unpublished data). Reductions in fishing pressure occurred in both systems in spite of an apparently burgeoning lake trout population in Blue Mesa Reservoir and several widely publicized fish over 15 kg that were caught by anglers from both reservoirs in 1995. In considering the tradeoffs of managing for a trophy piscivore fishery at the expense of a put-grow-and-take fishery, it does not appear that fishing effort lost from kokanee fisheries is compensated for by increases in lake trout angling. Unless lake trout anglers spend inordinately more money per angler-day than kokanee and rainbow trout anglers, managing for lake trout at the expense of kokanee and rainbow trout fisheries is not economically justifiable.

Socially, this management strategy is questionable because the state's limited hatchery production is used to support a piscivore fishery in which

a minority of anglers participate but that all license buyers must support. Anglers and angler groups petitioning for restrictive harvest regulations in Colorado in effect command a highly disproportionate allocation of the state's hatchery production by increasing predation demand as piscivore numbers and size structure are enhanced (Martinez 1995). Further, recent recommendations to consider user-pay scenarios for hatchery-sustained fisheries (Bennett et al. 1996) should also include an analogous evaluation of the predation cost on hatchery salmonid prey bases in fisheries where numbers or size structure of piscivores increase as a result of piscivore management. This kind of evaluation would provide a basis for discussion of fishery trade-offs and user-pay considerations for trophy piscivore management.

We believe efforts by fish managers to portray trophy-sized piscivores as the most valuable component in reservoir fisheries has led to the misconception of many anglers that restricted harvest or catch and release is the only way to manage piscivores (Martinez 1995). Although it is true, based on our analyses, that trophy piscivores are the most costly fish in the state's coldwater reservoirs, their actual value relative to the reduction or loss of other valued fishery components (put-grow-and-take species and kokanee egg supplies) has largely been ignored in past angler education efforts. We foresee confusion and conflict among anglers as managers who promoted catch and release of large piscivores as "conservation" eventually succumb to the necessity of liberalizing lake trout regulations to retain other valued fishery components (Martinez 1995).

In Colorado, the debate over the appropriateness and sustainability of trophy piscivore management using hatchery salmonids as prey has intensified as hatchery production of prey fish and body condition of lake trout have declined. Continuing declines in kokanee populations at Blue Mesa Reservoir and Lake Granby are especially alarming because the spawning runs in these populations are the primary egg sources for the statewide hatchery program, and kokanee are semelparous and short-lived. Chronic shortages in the kokanee egg supply in the western United States (Martinez 1995) preclude satisfying hatchery needs with eggs from other sources. Further, lake trout predation has frustrated efforts to reestablish kokanee in Flathead Lake through stocking (Carty et al. 1997). Although harvest regulations for lake trout in Blue Mesa and Granby were liberalized in 1996, the changes may have come too late. The kokanee

egg supply in 1996 was so limited that the number of Colorado kokanee fisheries stocked in 1997 dropped from 27 to 10, focusing primarily on those waters where stocking had a chance to enhance future egg takes. If kokanee populations in our study lakes crash, it may be impossible to rehabilitate them, which would be a misfortune to the anglers and lake trout that exploit them.

### Conclusions

Balancing predator demand with prey supply has historically been an implicit, but challenging goal of fishery management. We found that system productivity indices alone may not be good indicators of the status of predator and prey fish populations in highly managed, montane reservoirs. Yet, fishery attributes relevant to trophic economics, such as the balance between biomass and production of prey and the biomass and consumption of predators, are difficult to measure. Thus, growth is often used by managers as an indicator of balance of the predator-prey system in the fisheries under their stewardship. If growth rates are low, then stocking of that species may be reduced or harvest restrictions may be relaxed in the hopes of bringing the population back below the system's carrying capacity. However, more direct and immediate measures of balance allow managers to respond to unsustainable trophic conditions before radical declines in prey population abundance and predator growth and condition occur. Such measures can be obtained by quantifying the biomass of predator and prey fishes; a wide variety of techniques are available. Production is the best measure of prey supply and should be computed to assess the predation rate that the prey population can sustain. Prey production can be estimated from P/B ratios or as a function of prey size and population biomass. Coupled with growth and diet information, predator abundance data can be input to bioenergetics models to quantify the predation pressure exerted on prey fish populations. Sustainability of the fishery management policy can then be evaluated by comparing the balance between prey production and predator consumption.

If successful, trophy harvest regulations and other management actions aimed at enhancing predator biomass and size structure will increase consumption demand by the target population. When predator consumption exceeds prey production, declines in prey population abundance and predator growth are inevitable. To sustain such unbalanced systems, the food web must be subsidized (e.g., by stocking prey fish). This can be an ex-

pensive enterprise. When the prey populations of piscivorous sport fish must be regularly stocked, fiscal economics become an important management consideration, and managers must evaluate the costs borne by all license buyers to sustain a piscivore fishery enjoyed by a relatively small segment of the angling public.

#### Acknowledgments

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