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Food Web Changes over Fourteen Years Following Introduction of Rainbow Smelt into a Colorado Reservoir

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Abstract.—Rainbow smelt *Osmerus mordax* were introduced into Horsetooth Reservoir, Colorado, in 1983 to increase prey availability for walleyes *Stizostedion vitreum.* The introduction was highly successful. Rainbow smelt abundance reached at least 0.4 fish/m^3 within 6 years, and walleye growth improved by 50%. Zooplankton sampling provided the first clues that the Horsetooth Reservoir food web was undergoing dramatic changes in response to the rainbow smelt introduction. During 1989–1994 the abundant rainbow smelt population apparently reduced April and May crustacean zooplankton concentrations from historical levels of 40–80 organisms/L to less than 1.0 organism/L, and a switch occurred in the cladoceran species composition. Standardized sampling with beach seines and gill nets indicated that after 1988 walleye recruitment ceased. Efforts to bolster walleye recruitment by fry stocking in 1992 and 1993 also failed. A recent decrease in rainbow smelt density allowed a resurgence of zooplankton and a shift in predominance back to a large-bodied cladoceran (*Daphnia pulex*) in 1995 and 1996. Fish sampling in subsequent years corroborated declines in rainbow smelt abundance and walleye condition. Although hybrids of striped bass *Morone saxatilis* × white bass *M. chrysops* have been stocked in recent years, in part to control an overabundant rainbow smelt population, hydroacoustic surveys and bioenergetics modeling suggested that, during 1994–1996, walleye predation alone could have been a significant mortality factor limiting the rainbow smelt population biomass. Thus, we expect further declines in rainbow smelt biomass with possible negative consequences for piscivore growth rates and predation rates on prey-sized sport fish. To manage for balance of prey supply and predator demand, regular estimates of the zooplankton, rainbow smelt, and piscivore populations must be obtained.

Food webs in many western U.S. reservoirs have low species diversity and are trophically simple (Wydoski and Bennett 1981). Few of the native, riverine fish species are well-adapted to the lacustrine conditions imposed when a river is impounded. In Colorado, pronounced water level fluctuations limit benthic production pathways, and hence most fish production in reservoirs is sustained by a pelagic (planktonic) food web (Jones et al. 1994). Establishing sport fisheries in these systems has relied on stocking of nonnative

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piscivores, and often on introducing prey species as well. The challenge to reservoir fishery managers is to create a relatively stable predator–prey system that ideally would provide a self-sustaining sport fishery.

Fishery managers have sought to stock prey species that would be prolific, stable in abundance, vulnerable to sport fish predation, nonmigratory, and relatively innocuous to other species (Ney 1981). Prey fishes that exploit pelagic production are logical choices in highly fluctuating western reservoirs because they are efficient at transferring energy of primary production to higher trophic levels. No species native to Colorado has met these criteria, and managers have introduced a variety of nonnative prey species with mixed success, including opossum shrimp *Mysis relicta,* emerald shiners *Notropis atherinoides,* spottail shiners *N. hudsonius,* and rainbow smelt *Osmerus mordax* to sustain reservoir sport fisheries.

Rainbow smelt were introduced into Horsetooth Reservoir, Colorado, in 1983 to enhance growth of walleye *Stizostedion vitreum* and smallmouth bass *Micropterus dolomieu.* The rainbow smelt introduction was very effective; within a few years rainbow smelt became the most abundant fish in the reservoir. In this paper we document a 14-year study of the direct and indirect effects of the rainbow smelt introduction on the reservoir's food web and evaluate the sustainability of the sport fishery supported by the rainbow smelt prey base.

Methods

Study site.—Horsetooth Reservoir is located 5 km west of Fort Collins, Colorado, at an elevation of 1655 m. It is approximately 11 km long and 1 km wide and has a mean depth of 25 m and maximum depth of 70 m. The reservoir was constructed in 1949 to store water diverted eastward across the Continental Divide for irrigation and domestic water supply. The city of Fort Collins operates a water treatment facility adjacent to the reservoir and has monitored intake water quality (turbidity, dissolved oxygen, and water chemistry) since 1981 (Jassby and Goldman 1996). At maximum storage the reservoir has a surface area of 755 ha, but normal water level fluctuations are on the order of 10–30 m per year. This dramatic fluctuation precludes growth of aquatic macrophytes and the reservoir lacks a true littoral zone (Edmonds and Ward 1979).

Horsetooth Reservoir has been managed as a two-story fishery since the early 1950s. The coldwater component has consisted primarily of rainbow trout *Oncorhynchus mykiss* (25,000–50,000 catchables stocked per year) and lesser numbers of brown trout *Salmo trutta,* lake trout *Salvelinus namaycush,* and kokanee *Oncorhynchus nerka.* The coolwater assemblage, in order of decreasing abundance, is made up of smallmouth bass, walleye, the hybrid of striped bass *Morone saxatilis* × white bass *M. chrysops* (hereafter hybrid striped bass), white bass *M. chrysops,* and yellow perch *Perca flavescens.* Currently, only smallmouth bass, walleye, and white bass are known to reproduce in the reservoir.

In recent years, the Horsetooth Reservoir walleye population was self-sustaining; no walleye were stocked during 1980–1992. Walleye appeared to have drastically reduced yellow perch abundance by the late 1960s, and walleye growth rates declined to unacceptable levels (Jones 1985). In April 1983 approximately 20,000 spawning rainbow smelt were captured at Lake Sakakawea, North Dakota, and stocked in Horsetooth Reservoir. Additionally, 2,000 gravid adults from Rampart Reservoir in Colorado were introduced in May 1983. Declining abundance of small walleyes, noted in standardized sampling, prompted managers to stock 5–6 million walleye fry (prolarvae, 2–3 d old) that were the progeny of eggs collected from Horsetooth Reservoir during mid-April of 1992 and 1993. Fingerling walleyes (50–85 mm) numbering 55,000, 48,500 and 132,700 were stocked in mid-July in 1994, 1995 and 1996, respectively.

Zooplankton.—Zooplankton were sampled at mid-lake stations (Goettl and Johnson 1996) at least monthly from April to September 1987–1996 with a metered Clarke-Bumpus sampler having a 127-mm diameter opening and 120-μm-mesh net (Lind 1979). During 1987–1993, oblique tows were made at one station in each of four depth strata: six tows at 0–5 m, four at 5–10 m, two at 10–20 m, and at 20–30 m. Zooplankton were generally rare or absent below 5 m; therefore, only samples from the 0–5-m strata were used to produce density estimates. During 1994–1996, five tows were made from 0 to 10 m at each of three stations. To reduce osmotic distortion, samples were put on ice prior to being preserved in a 5% formalin solution (Nelson 1970).

For analysis, each sample was diluted to a known volume and stirred to assure homogeneity. A 1-mL aliquot was removed with a Hensen-Stempel pipette and placed in a Sedgwick-Rafter cell for counting under a compound microscope. Counts were expanded to in-lake densities from dilution factors and volumes sampled (Lind 1979). When possible, at

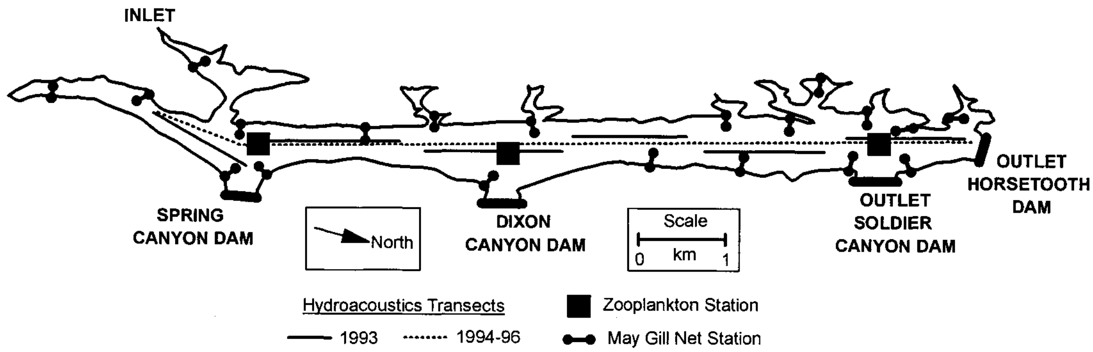

FIGURE 1.—Locations of zooplankton sampling (Nelson 1970) and standardized May gill-net sampling stations (Jones 1985) and transects used in hydroacoustic surveys of Horsetooth Reservoir.

least 50 plankters of each genus were measured to the nearest 0.1 mm using a digitizing pad and personal computer. If fewer than 50 organisms of a given taxon were present in a sample, the mean was established from as many measurements as possible. *Daphnia* spp. were measured from the top of the helmet to the base of the tail spine; copepods were measured from the tip of the metasome to the end of the urosome, excluding setae (Thomas 1989).

Rainbow smelt.—Rainbow smelt used for stomach analysis were captured by trawling, electrofishing, beach seining, and gill netting. From 1986 to 1988, age-0 fish were fixed in 10% formalin for 24 h and transferred to 80% alcohol. Adult fish were always iced in the field and frozen upon return to the laboratory, as were age-0 fish after 1988.

The relative density and reproductive success of the rainbow smelt was monitored with a midwater trawl (6×6-m mouth) fished at night in a stepped-oblique manner (Kirn and LaBar 1991) on approximately August 25 each year from 1983 through 1992 and in1994 (Jones et al. 1994); in 1993, 1995, and 1996 trawling was conducted in October to coincide with hydroacoustic surveys. A random subsample of rainbow smelt captured in the trawl hauls was measured each year (Goettl and Johnson 1998). Nonparametric correlation analysis (Spearman's R) was used to compare rainbow smelt density with zooplankton density and size, and walleye catch per unit effort (CPUE) and body condition (response variables with and without a 1-year time lag).

Hydroacoustic surveys were conducted at night with a BioSonics 420-kHz, dual-beam scientific echosounder on Horsetooth Reservoir in 1993–1996. Reservoir surface elevation, surface area, and volume on the days of hydroacoustic surveys were obtained from U.S. Bureau of Reclamation, Eastern Colorado Projects Office, Loveland, Colorado. These data were used to scale hydroacoustic abundance estimates. Acoustic data were analyzed by BioSonics, Inc., of Seattle, Washington. The 1993 survey was conducted on October 25 and consisted of six 20-min transects (Figure 1) beginning at the north end of the reservoir, approximately 100 m south from the dam. In 1994–1996 surveys were conducted on August 24, October 25, and October 2, respectively, and were performed using a single continuous transect along the north–south axis of the reservoir, covering the same basic area as in 1993.

The acoustic system was fully calibrated in 1994 and again in 1996. In addition, target strength (TS) measurements were conducted in 1994–1996 using a standard target (ping pong ball). The results were consistent with the calibration data. The transmitter was set to a pulse width of 0.4 ms, at 5 pings/s. Receiver gain was set to zero.

Data were analyzed by both echo integration and dual-beam TS analysis in the 2-m depth strata. A noise threshhold of 0.07 volts root mean square (-68 decibels) was used during data analysis, and TS was estimated from transects exhibiting predominantly single-target conditions. Fish densities were calculated by two different methods. In 1993, an overall assumption of -50 decibels mean TS was used to scale the echo integration. In later years, the in situ measurements of TS from each year in each 2-m stratum were used to scale the echo integration from that depth stratum. Biomass estimates were generated from estimated density (fish/m^2 of surface area), mean lengths of rainbow smelt in trawl samples, and a length–weight regression from Goettl and Johnson (1994), where W = wet weight (g) and L = total length (mm):

$$\log_{10}(W) = -6.750 + 3.696 \log_{10}(L), \quad (1)$$

for which $r^2 = 0.93$, and $N = 319$.

Production is a better measure of a prey population's ability to sustain a given level of predation than is its biomass. Production can be estimated using an allometric principle that scales annual production to body size. This approach estimates a production: biomass (*P/B*) ratio from mean body weight (Banse and Mosher 1980), where *P* is annual production, *B* is mean biomass (g wet/m^2) of the population over the year. One then solves for annual production given estimated mean annual biomass. This approach yielded estimates of planktivorous fish (rainbow smelt and alewife *Alosa sapidissima*) production in Lake Ontario that compared favorably with a more direct, independent estimate (Sprules and Stockwell 1995). Production to biomass ratios for rainbow smelt in each of the Laurentian Great Lakes ranged from 1.10 to 1.54 (Lantry and Stewart 1993). We used *P/B* ratio of 1.54 and biomass estimated from hydroacoustic surveys to compute a plausible upper limit of total rainbow smelt production at Horsetooth Reservoir.

Walleye.—Age-0 walleyes were sampled with beach seines in the littoral zone during the summer with 30-m-long, 2-m-deep, 10-mm bar mesh monofilament gill nets in the fall. Walleyes age-1 or older were sampled on approximately May 25 each year between 1983 and 1996 in a standardized manner that consisted of 20 six-panel experimental gill nets set overnight (Jones et al. 1994) and 10 15-min electrofishing stations (1983–1993). The gill net sites were not randomly selected; rather, they were distributed at sites (Figure 1) believed to represent suitable walleye habitat in 1983. The same types of nets were set in the same locations in each of the succeeding 13 years. Night electrofishing (pulsed DC) was conducted at 10 sampling stations covering a variety of habitat types that were uniformly distributed around the reservoir. These same stations were sampled each year until 1993.

Annual estimates of walleye spawning population size were available from spawning operations conducted by Colorado Division of Wildlife personnel in early April 1992, 1993, 1994, 1995, and 1996. Up to 90 multifilament gill nets were set parallel to and normally less than 2 m from shore in a night of sampling; sets took 985, 696, 859, 522, and 571 walleyes greater than 350 mm total length in 1992, 1993, 1994,1995, and 1996, respectively. Walleyes captured during this sampling were marked with year-dependent finclips. Fish were also marked with numbered Floy t-bar tags during 1993–1995. Recapture samples were obtained during each subsequent spawning run during 1993–1996; Chapman's modified Petersen population estimate and an associated asymmetrical confidence interval were computed for each estimate (Ricker 1975).

Data from walleyes sampled in standardized experimental gill nets during May 1983–1996 were analyzed for interannual trends in relative abundance, population size structure, and individual body condition (relative weight). Relative abundance of walleyes was estimated from CPUE, which was computed separately for five size-classes: 150–300 mm, 300–450 mm, 450–600 mm, 600–750 mm, and 750–900 mm. Experimental gill-net sampling was standardized in 1983 so sampling effort, net types, and sites were identical each year. Annual CPUE is reported as number of walleyes caught per standard overnight set.

Population size structure was assessed by plotting length-frequency histograms of all walleyes captured each year. Because gill nets are highly size-selective and walleye vulnerability to gill nets changes with size, abundance trends could only be evaluated within size-classes. Relative weight (W_r) was computed as

$$W_r = W/W_s \cdot 100 \quad (2)$$

where *W* is observed weight (g) and W_s is standard weight. Standard weight was computed from the revised formula of Murphy et al. (1990):

$$\log_{10}(W_s) = -5.453 + 3.180 \cdot \log_{10}(L), \quad (3)$$

where W_s is in grams and *L* is total length in millimeters. Walleye with $70 > W_r > 150$ were deemed outliers and were excluded from the length–weight and condition analyses. Relative weights were also computed separately within the five size-classes used for the CPUE analyses above.

We used estimates of abundance, growth, water temperature, and diet in a bioenergetics model (Hanson et al. 1997) to compute the biomass of rainbow smelt consumed by the adult walleye population during 1993, 1994, and 1995. Abundance of adult walleyes (and associated confidence limits) was obtained from mark–recapture experiments (above); we assumed a total annual mortality rate of 40% (Baccante and Colby 1996). Annual growth increment (length) of Horsetooth Reservoir walleyes was derived from recaptures of tagged fish (Goettl and Johnson 1998). There was no effect of year on slopes of length–weight regressions (analysis of covariance [ANCOVA], $P = 0.260$), and although intercepts were statistically different among years (ANCOVA, $P = 0.043$), differences were not biologically meaningful (<1%). Therefore, a single length–weight regression (parameters significant at $P < 0.01$), derived from experimental gill net samples during 1993–1995 ($N = 79$, 98, and 161 walleyes, respectively), was used to convert total length (L, mm) to wet weight (W, g):

$$\log_{10}(W) = -4.950 + 2.989 \cdot \log_{10}(L), \quad (4)$$

for which $r^2 = 0.97$, and $N = 338$.

Seasonal depth distribution of the walleye population was unknown, so we bounded the range of consumption estimates by performing simulations at two temperature extremes corresponding to the warmest (2-m depth) and coolest (30-m depth) temperatures available throughout the year. High and low temperature scenarios were obtained from mean monthly water temperatures recorded during 1986–1992 at the two depths. Diet sampling was infrequent in 1992–1995, but rainbow smelt were a high proportion of the walleye diet: 90% rainbow smelt, 8.5% invertebrates, 1.5% unidentified fish ($N = 163$ walleyes; Goettl 1993, Goettl and Johnson 1998). Energy densities of these prey were 4,402 (Lantry and Stewart 1993), 1,762 (Hanson et al. 1997), and 4,184 J/g wet (Hanson et al. 1997), respectively.

Results

Zooplankton

There was a significant parabolic trend in the April–May mean density of *Daphnia* ($r^2 = 0.86$, $N = 10$, $P = 0.001$) during 1987–1996, and *Daphnia* density was negatively correlated with rainbow smelt abundance in the previous year ($R = -0.62$, $P = 0.05$, $N = 10$). The springtime density of the most common crustacean zooplankton in Horsetooth Reservoir declined between 1988 and 1989 (Figure 2). Associated with the change in *Daphnia* density was a change in *Daphnia* species. *D. pulex* was the sole representative of the genus during 1987 and 1988 (Goettl and Johnson 1998). In 1989 a combination of *D. pulex* and *D. galeata mendotae* was found throughout the sampling season. *D. pulex* was predominant in May, June, and August; *D. galeata mendotae* was most abundant in July; and the two were equal in September. After 1989, *D. pulex* were observed only in September 1991 when they made up about half the *Daphnia* observed.

For the first time in 4 years, *D. pulex* reappeared in September of 1995 and was the most common (>99%) daphnid in 1996. Although *D. pulex* composed only a trace (0.006 organisms/L) in 1995, it appeared to have been an indication of changes to come with the decline in rainbow smelt densities. Striking increases in *Daphnia* density occurred in May and June of 1994–1996. April densities remained low but showed an increase in the last 2 years. Copepod density followed a somewhat similar increase in spring of the last 3 years. *Daphnia* density was negatively correlated with the density of rainbow smelt in the previous year ($R = -0.62$, $N = 10$, $P = 0.054$).

Mean length of *Daphnia* (Table 1; Figure 2) followed a similar parabolic trend with time, as did *Daphnia* density, but the relationship was more variable ($r^2 = 0.46$, $P = 0.06$, $N = 12$). *Daphnia* length was negatively correlated with rainbow smelt density ($R = -0.69$, $P = 0.01$, $N = 12$). A general decrease in size of *Daphnia* was apparent during 1986–1991, concurrent with its declining density. However, there were a few unexplained deviations from the overall trend. In July and September 1990, *Daphnia* were very large, and in August and September 1991 they were unusually small. After 1991 there was a steady increase in size of *Daphnia*. The mean lengths of *Daphnia* in 1996 were among the largest recorded at Horsetooth Reservoir (Nelson 1970; Goettl and Johnson 1998). The mean size of copepods sampled in the course of this study was normally between 0.6 and 0.9 mm and showed no density-related change.

Rainbow Smelt

Rainbow smelt in Horsetooth Reservoir were primarily planktivorous. Stomach analyses in 1984 and 1987 indicated that diet of age-0 rainbow smelt (<75 mm) was volumetrically about 50% *Leptodiaptomus* and about 50% *Daphnia* and *Diacyclops* (Jones 1985; Goettl and Thomas 1989). As rainbow smelt increased in length from 75 to 100 mm the importance of *Daphnia* increased and utilization of copepods decreased. Rainbow smelt longer than 100 mm consumed mostly *Mysis* and *Daphnia*; *Mysis* predominated the diet of the largest (>125 mm) rainbow smelt (Jones 1985; Goettl and Thomas 1989). Rainbow smelt appeared to eliminate *Mysis* because the crustacean was not found in the reservoir after 1987 nor in rainbow smelt stomachs after 1988 (Goettl and Johnson 1994).

Rainbow smelt occasionally consumed fish, but

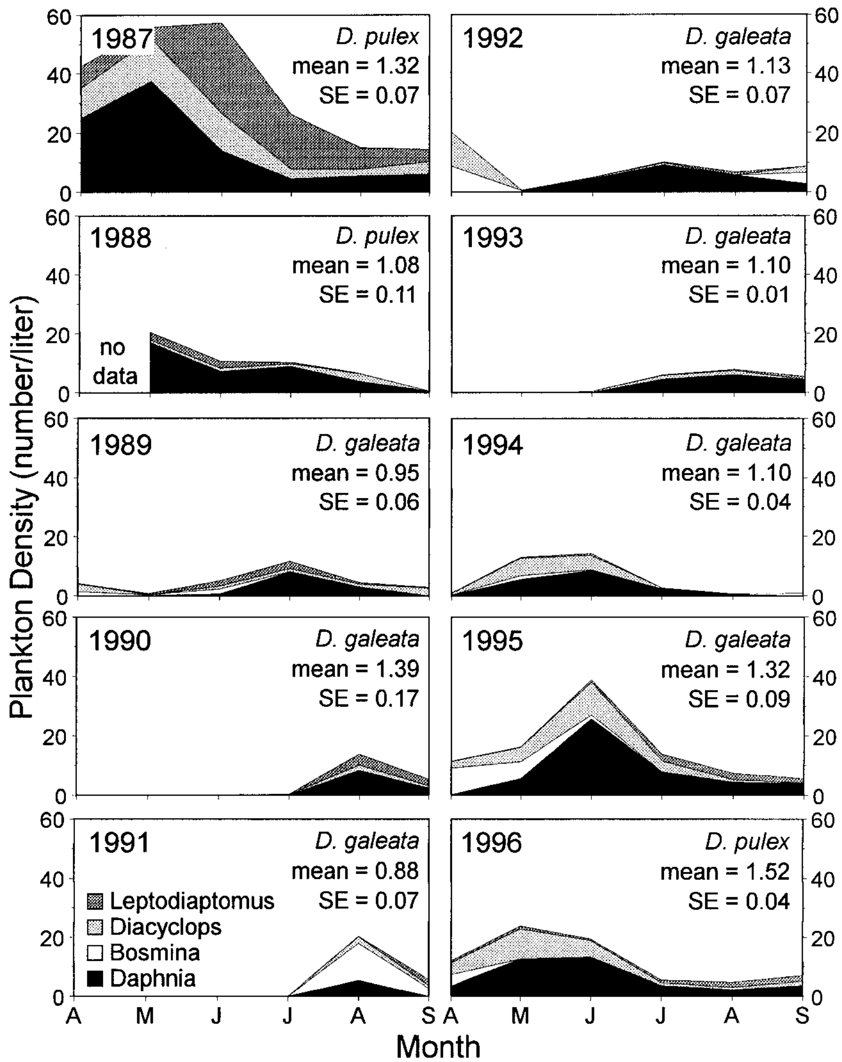

FIGURE 2.—April–September density (plankters/L) of four zooplankton taxa in 0–5 m stratum in 1987–1993 and 0–10 m stratum 1994–1996. Densities determined by the mean of mid-reservoir samples during 1987–1993 and the mean of five means of 0–10-m stratum samples from each of the three distinct basins of Horsetooth Reservoir during 1994–1996. Mean lengths (mm) and standard errors (SE) of daphnids and the predominant *Daphnia* species each year are shown in the upper right of each panel.

TABLE 1.—Mean size (mm) of *Daphnia* (*D. pulex* and *D. galeata mendotae* combined) during April–September, 1985–1996, in Horsetooth Reservoir. Dashes indicate insufficient sample size.

Month	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
Apr	–	–	1.19	–	–	–	1.12	–	–	1.12	1.19	1.37
May	–	–	1.14	–	–	–	0.85	1.19	–	1.06	0.97	1.54
Jun	1.30	–	1.30	1.21	–	–	–	1.28	–	1.21	1.17	1.53
Jul	1.37	1.59	1.46	–	0.86	1.71	0.94	1.16	1.11	1.14	1.40	1.44
Aug	–	1.40	1.57	1.16	1.06	1.15	0.70	1.18	1.08	1.11	1.52	1.59
Sep	1.23	1.32	1.25	0.87	0.92	1.32	0.79	0.85	1.12	0.95	1.53	1.63
Mean	1.30	1.44	1.32	1.08	0.95	1.39	0.88	1.13	1.10	1.10	1.30	1.52

TABLE 2.—Number of standardized midwater trawl hauls (*N*), mean number and SE of age-0 and adult (age-1 or older) rainbow smelt captured per hour of trawling effort, 1983–1996.

		Age-0		Adults	
Year	*N*	Fish/h	SE	Fish/h	SE
1983	7	0		2.3	1.2
1984	5	4.8	1.2	0	
1985	5	62.6	19.3	0	
1986	5	51.4	14.7	13.2	7.9
1987	8	491.5	110.1	1.0	0.7
1988	7	2,045.1	414.6	49.1	8.4
1989	4	26,309.0	20,839.7	195.0	46.3
1990	6	189.0	113.6	383.3	152.9
1991	6	2,786.7	747.9	66.0	13.9
1992	8	1,356.0	269.5	9.8	2.6
1993	8	319.5	142.6	49.7	9.9
1994	8	2,656.0	1,012.2	17.5	11.9
1995	8	196.5	50.4	1.5	0.8
1996	8	260.0	118.9	4.0	2.0

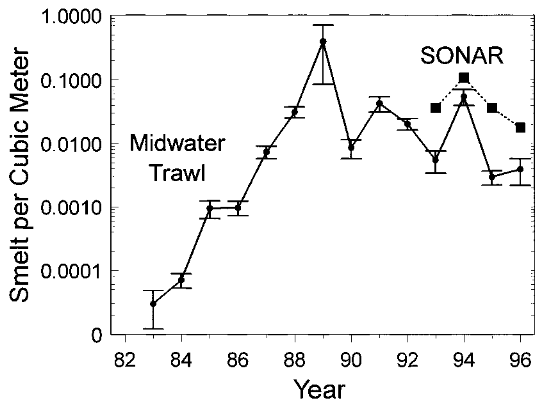

FIGURE 3.—Rainbow smelt density (fish/m^3) estimated by midwater trawl (solid line, ± SE) and hydroacoustically (dotted line) during 1985–1996. Surveys in 1993, 1995, and 1996 were conducted in October; all others were in late August.

no walleyes were found in rainbow smelt stomachs. The first incidence of piscivory by rainbow smelt was observed in 1987 when one adult rainbow smelt was observed to have eaten one larval rainbow smelt (Thomas 1989). Cannibalism became apparent again in April 1989 when large rainbow smelt (>170 mm) consumed larval rainbow smelt exclusively. Approximately 1 month later, 25 rainbow smelt (85–105 mm) were eating only immature dipterans. The next week, age-1 rainbow smelt were consuming zooplankton, mostly *Daphnia. Bosmina* was first noticed as an important diet item in July 1989. Age-2, and older rainbow smelt (148–163 mm) were consuming age-0 rainbow smelt (50–70 mm) exclusively in October 1989.

Rainbow smelt diet observations were less frequent in years after 1989; however, adult rainbow smelt stomach contents were monitored late in April each year through 1995 in an attempt to document predation on walleye fry. The only fish found in rainbow smelt stomachs were rainbow smelt (Goettl and Johnson 1996). Sampling later in the year reconfirmed the importance of zooplankton such as *Daphnia*, *Leptodiaptomus*, *Bosmina* and *Diacyclops* (listed in order of importance). *Daphnia* was the only item found in the stomachs of 435 rainbow smelt captured by the midwater trawl on August 24, 1994. Rainbow smelt (N = 131) captured by midwater trawl on October 27, 1995, had consumed about 60% *Daphnia*, and *Diacyclops* made up most of the remaining volume.

Midwater trawling tracked rainbow smelt density and size during 1984–1996. Rainbow smelt density increased by almost four orders of magnitude within 6 years after the introduction (Table 2; Figure 3), reaching a peak abundance of 0.4 smelt/m^3 in 1989. Abundance decreased nearly as dramatically after 1989, to a low of about 0.003 smelt/m^3 by the end of the study. Mean length of age-0 rainbow smelt in late summer was highest before abundance peaked and showed a declining trend during 1988–1994 (Table 3). Mean length of adult rainbow smelt in summer and fall was also highest before population abundance peaked, and was consistently lower during 1992–1996 (Table 3).

Hydroacoustic surveys provided estimates of rainbow smelt abundance and biomass during 1993–1996. In situ target strengths were believed to be more accurate in 1994–1996, and abundance estimates using in situ TS are independent of changes in acoustic-system performance. An average value of −50 decibels was believed to be more accurate in 1993, based on correspondence of TS estimates with size structure of rainbow smelt sampled in midwater trawls (Table 3). Mean lengths of sampled rainbow smelt in October 1995 and 1996 (62.0 mm, 65.8 mm, respectively) were greater than in August 1994 (41.5 mm) but lower than in October 1993 (78.9 mm; Goettl and Johnson 1998).

Based on hydroacoustics, estimated rainbow smelt density was about three times lower in 1993 than in 1994 (34,075/ha versus 107,909/ha), but biomass was much higher in 1993 (25.4 kg/ha versus 6.7 kg/ha) because of a larger mean size at the

TABLE 3.—Mean total lengths (mm), SEs, and sample sizes (N) of age-0 and adult rainbow smelt captured in standardized midwater trawl hauls in late summer and fall at Horsetooth Reservoir, Colorado.

Trawl date	Age-0 Mean	Age-0 SE	Age-0 *N*	Adult Mean	Adult SE	Adult *N*
Summer						
Aug 29, 1985	68.7	1.4	42			[a]
Sep 3, 1986	67.1	1.1	50	143.3	3.0	9
Aug 17, 1988	53.9	0.85	15	110.2	6.4	4
Aug 28, 1989	52.1	0.65	62	111.4	1.0	36
Aug 20, 1990	49.7	1.1	21	97.9	0.82	107
Aug 27, 1991	41.8	0.61	73			[a]
Aug 30, 1993	45.7	0.54	62	91.6	0.81	62
Aug 24, 1994	41.1	0.33	398	101.8	1.7	35
Fall						
Nov 2, 1988			[a]	135.6	2.7	9
Oct 26, 1992	59.8	1.0	75	111.4	1.7	19
Oct 25, 1993	74.0	0.93	56	105.6	0.82	62
Oct 25, 1995	60.8	0.85	80	118.1	2.7	11
Oct 2, 1996	63.3	0.45	256	113.3	2.6	9

[a] None sampled.

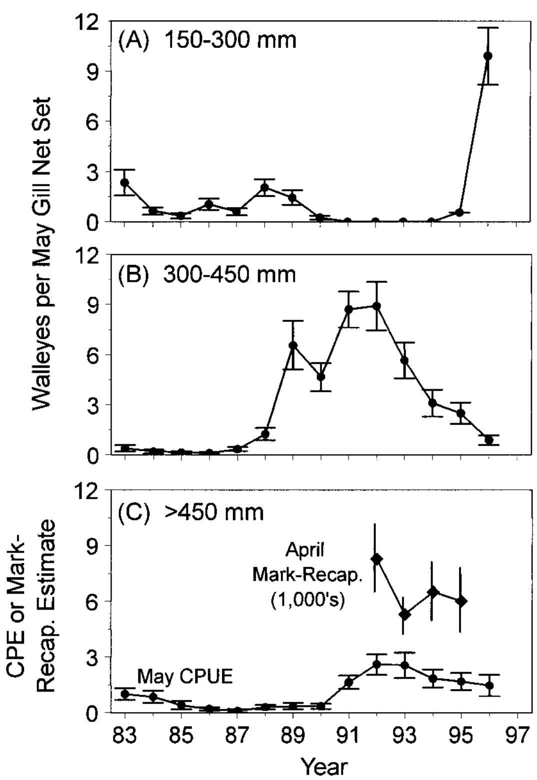

FIGURE 4.—Mean (±SE) number of walleyes **(A)** 150–300 mm, **(B)** 300–450 mm, and **(C)** exceeding 450 mm long captured per standardized overnight gill-net set in Horsetooth Reservoir during May of 1983–1996 (solid circles). April mark–recapture estimates (±95% confidence limits) of walleyes exceeding 450 mm were computed during 1992–1995 (diamonds).

time of the 1993 survey. Biomass was intermediate in 1995 at 12.8 kg/ha, and lowest in 1996 at 6.1 kg/ha. Although trawl and hydroacoustic estimates of rainbow smelt density followed a similar temporal trend (Figure 3), hydroacoustic estimates were generally about 10 times higher than trawl-derived density estimates. We estimated metric tons of rainbow smelt production in Horsetooth Reservoir to be roughly 26 in 1993, 7 in 1994, 13 in 1995, and 6 in 1996.

Walleye

After adjusting for growth, trends in CPUE (Figure 4) of immature walleyes (150–300 mm, ages 1 and 2; Jones et al. 1994) showed that a large natural year-class was produced in 1987. Age-0 walleyes (<150 mm) were readily captured in daytime seine hauls in summer 1987 and 1988 and were sampled in gill nets in October 1988 (Goettl and Johnson 1994). Recruitment of walleyes appeared to fail after 1988; no age-0 walleyes were captured during 1989–1993, and very few or no fish in the 150–300-mm size-class were captured during 1990–1994, despite stocking of 5–6 million walleye fry during 1992 and 1993. Gill-net sampling in May 1995 detected age-1 walleyes (mean length 183 mm, $N = 10$) for the first time since 1990. Immature walleyes were captured again in May 1996, but all were older than age-1 (mean length 256 mm, $N = 189$). These fish were presumably survivors of the stocked 1994 year-class because no age-0 representatives of this year-class were found in nighttime beach seining during summer 1994. Based on seining in summer 1995 and

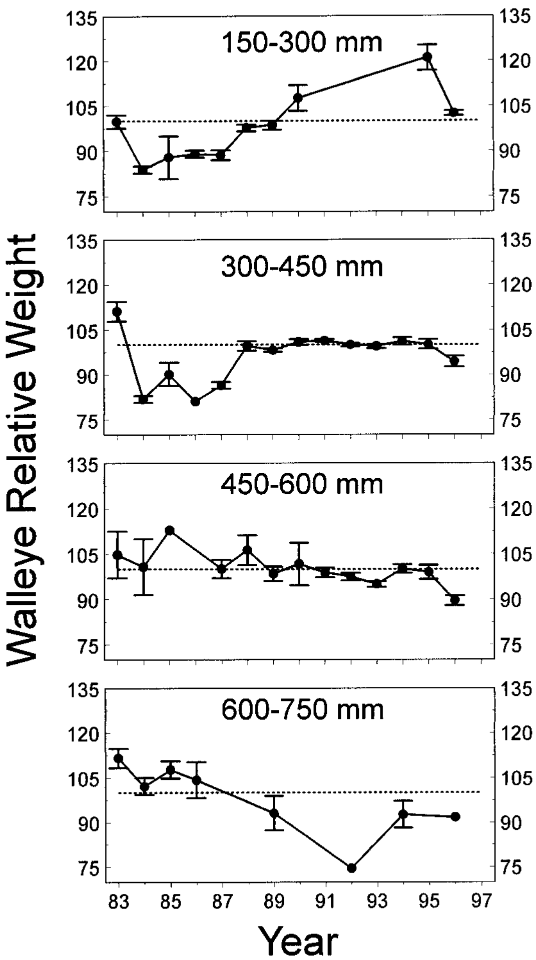

FIGURE 5.—Mean (±SE) relative weight of walleyes 150–300 mm, 300–450 mm, 450–600 mm, and 600–750 mm long captured in standardized overnight gillnet sets in Horsetooth Reservoir during May of 1983–1996. Dotted lines show a relative weight of 100.

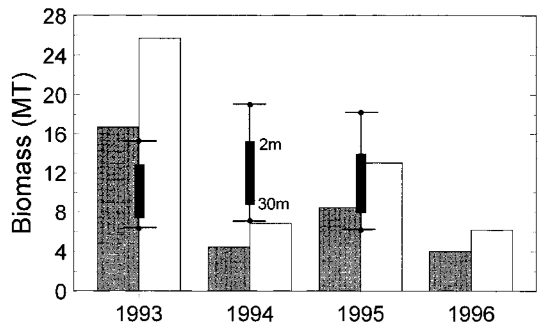

FIGURE 6.—Fall biomass (shaded bars) of rainbow smelt in Horsetooth Reservoir estimated from hydroacoustic surveys in 1993–1996 and production (open bars) estimated from a production: biomass ratio (P/B) of 1.54 (from Lantry and Stewart 1993). Black vertical lines represent the range of total annual consumption demand by adult walleyes during 1993–1995, assuming fish experienced water temperatures at 2 and 30 m. Uncertainty in consumption attributable to walleye abundance is represented by circles and horizontal lines showing consumption using the upper and lower 95% confidence limits on walleye abundance at the two temperature regimes.

gillnetting in May 1996, few of the walleye fingerlings stocked in 1995 survived.

CPUE data suggested an increase in abundance of large (≥450 mm) walleyes during 1990–1992, followed by gradually decreasing abundance thereafter (Figure 4). No fish larger than 750 mm total length were sampled in 1995, and none larger than 600 mm were sampled in 1996. Walleye CPUE was not correlated with rainbow smelt density ($P > 0.3$). Mark–recapture estimates ranged from about 5,300–8,300 large walleyes and generally declined during 1992–1995. Variability was high for both mark–recapture and CPUE estimates of abundance of adult walleyes but taken together, these data suggest a decline in adult walleye abundance during the mid-1990s. Relative weight of small (150–300 mm) walleyes increased steadily after the rainbow smelt introduction, reaching a high of about 120 in 1995. Relative weight of intermediate-sized walleyes (300–600 mm) remained fairly stable at about 100 before and after smelt were introduced, until 1996 when W_r of all walleyes (150–600 mm) declined from the 1995 maxima (Figure 5). Relative weights of 150–300 mm and 300–450 mm walleyes, lagged by 1 year, were positively correlated with rainbow smelt density ($R = 0.92$, 0.71; $N = 9$, 13; $P = 0.0005$, 0.006, respectively). Relative weights of walleyes 600 mm or longer followed a decreasing trend after 1983.

Bioenergetics simulations projected that the adult walleye population consumed between 6.2 and 19 metric tons per year during 1993–1996 (Figure 6), depending on walleye abundance and the temperatures they experienced. Hydroacoustic survey estimates of total rainbow smelt biomass (standing stock in fall) in the reservoir were 16.7 (October 1993), 4.4 (August 1994), 8.4 (October 1995), and 4.0 metric tons (October 1996; Figure 6). Thus, annual consumption demand by adult walleyes was about half of the biomass of rainbow smelt in the reservoir in fall 1993 and about the same as rainbow smelt biomass in fall of 1994–1996. Estimated walleye consumption was also a large fraction of rainbow smelt production, especially in 1994 and 1995.

Discussion

In 1987, after 4 years of rainbow smelt residency in Horsetooth Reservoir, Thomas (1989) could not find adverse impacts of rainbow smelt on the food web. He found that rainbow smelt, walleye, and smallmouth bass were partitioning resources, thereby reducing competition, but he cautioned managers from accepting his preliminary findings. In 1987 abundant *Daphnia* and a relatively low rainbow smelt density allowed all species to flourish. The 56 zooplankters/L observed in May 1987 was similar to historical spring densities of 40–80 zooplankters/L, observed well before the rainbow smelt introduction (Reed and Olive 1956; Nelson 1970). Although abundance was lower (20 zooplankters/L) in 1988, walleyes recruited in substantial numbers. These age-0 walleyes were readily sampled by beach seining during summer 1987 and 1988.

Jones et al. (1994) reported that, as of 1991, the rainbow smelt introduction was highly successful at improving food availability for age-1 and older walleyes. Walleyes switched from consuming mostly macroinvertebrates and sport fishes during 1983–1988 to feeding exclusively rainbow smelt in 1989–1991. In years following rainbow smelt introduction, walleye growth rates were about 50% faster than in the years before the introduction. Although optimistic about the success of the rainbow smelt introduction, Jones et al. (1994) suggested that long-term effects on the food web should be monitored for potential negative consequences.

Shifts in the zooplankton community heralded the changes occurring in the Horsetooth food web. Crustacean zooplankton declined sharply in the spring of 1989, concurrent with a dramatic increase in rainbow smelt density, as reflected in midwater trawl catches. The age-0 rainbow smelt catch in 1989 increased to over 26,000/h from a previous high of 2,100 in 1988. We believe this increase in the number of rainbow smelt was responsible for the decline in zooplankton first observed in 1989 and continuing through 1994. No other planktivorous fish were abundant in the system during and after the rainbow smelt increase, and kokanee stocking was discontinued in 1990 because of low zooplankton density and poor stocking success (K. Kehmeier, Colorado Division of Wildlife, personal communication). A switch in the predominant cladoceran also occurred during 1989, when *Daphnia pulex* gave way to *D. galeata* as the most common daphnid in the summer. A large body of empirical and experimental evidence (Brooks and Dodson 1965; Cerny and Bytel 1991; Prazakova 1991; Gliwicz and Lampert 1993; Rudstam et al. 1993) supports that this change in species is indicative of intense planktivory by size-selective fish, which readily eliminate the larger *D. pulex* but not the competitively inferior *D. galeata,* which is able to persist.

We cannot discount the possibility of bottom–up control of the zooplankton assemblage because nutrient and chlorophyll data were unavailable before 1995. However, some of the worst water-quality problems recorded at the city of Fort Collins water treatment plant intake on Horsetooth Reservoir were thought to be due to excessive phytoplankton production and occurred in 1988 and 1989 (Jassby and Goldman 1996), the years of peak rainbow smelt abundance. Intake water quality improved during 1991–1995, as large zooplankton rebounded in the reservoir (Jassby and Goldman 1996). Further, a reversal in the zooplankton–smelt trend in the last years of this study supported our top–down hypothesis of rainbow smelt-mediated changes in the zooplankton assemblage. Five years of declining rainbow smelt abundance apparently resulted in dramatically increased zooplankton density and a marked increase in mean daphnid size beginning in 1995, coupled with a switch back to *D. pulex* as the predominant cladoceran in 1996.

The dramatic reversal in the zooplankton was our first strong indication that the rainbow smelt population was greatly depressed. High variability in trawl and sonar estimates necessitated several years of costly, labor-intensive surveys to overcome uncertainty about rainbow smelt abundance. Responses in condition of age-1 and older walleyes appeared to lag even further behind smelt declines because changes in relative weight were not observed until 1996. Thus, as previously shown in warmwater ecosystems (Mills and Schiavone 1982), easily obtained zooplankton data proved to be a valuable and timely indicator of food web status in Horsetooth Reservoir.

Beyond their strong control over zooplankton, rainbow smelt did not appear to meet one of Ney's (1981) criteria for a good prey fish; i.e., they were not innocuous to other species. Intensive sampling showed that walleye recruitment had ceased after rainbow smelt became abundant. The last walleye year-class to recruit from natural reproduction was in 1988 when springtime zooplankton density was still about 20 plankters/L. After 1988, springtime plankton density was less than 0.1 organisms/L, and no naturally produced walleyes were found. Walleye fry stocking was also unsuccessful in 1992 and 1993. Walleye reproduction failed during a period of the highest adult walleye growth and abundance ever recorded in the reservoir, so the failure probably was not due to reduced reproductive potential. No changes in the reservoir physicochemical environment could account for the lack of walleye recruitment.

Two hypotheses can explain the possible effect of rainbow smelt on walleye recruitment. First, predation by rainbow smelt on larval walleyes may have precluded natural recruitment and foiled fry stockings. Equipped with large teeth, rainbow smelt are known to be piscivorous (Scott and Crossman 1973). Rainbow smelt have frequently been implicated in declines of nongame and game fishes (McLain and Magnuson 1988; Lantry and Stewart 1993), including walleyes (Evans and Loftus 1987). However, direct evidence of predation on game fish is rare, and the only piscivory we observed in Horsetooth Reservoir was cannibalism by adult rainbow smelt on age-0 smelt. No instances of rainbow smelt predation on walleye fry were observed, despite concerted efforts to detect this in April of 1989–1995. Still, given the large number of individuals in the population ($>4 \times 10^6$) we cannot rule out predation on walleye fry as a potential negative consequence of the rainbow smelt introduction.

A second explanation for the walleye recruitment failure is that by restructuring the zooplankton community, rainbow smelt created unfavorable food conditions for newly hatched walleye, which subsequently starved. Postlarval walleyes are dependent upon zooplankton of the appropriate species, density, and size during the first-feeding stage (Houde 1967; Mathias and Li 1982; Johnston and Mathias 1993). The failure of fry stocking in 1992 and 1993 and the success of fingerling stocking in 1994 suggest that the interaction between young walleyes and rainbow smelt occurs at the larval/postlarval walleye stage. Whatever the mechanism, it appears that rainbow smelt may control food web structure from the ''middle out'' (DeVries and Stein 1992), whereby they exert strong, direct top-down control over the zooplankton community and either direct (predation) or indirect (competition) control over their predators by inhibiting predator reproduction. One dilemma for managers is that rainbow smelt can be an excellent prey for adult walleyes and salmonine piscivores (Evans and Loftus 1987), but apparently at the expense of the growth and survival of early piscivore life stages. Hence, it is important, but especially difficult, to balance rainbow smelt supply with piscivore demand.

The reasons for the initial decline of rainbow smelt in Horsetooth Resvoir are unknown. Variation in sampling dates complicated growth assessments, but growth of rainbow smelt appeared to decline after the zooplankton crashed in 1989. Their 1995 and 1996 growth did not reach 1988 levels, even though zooplankton numbers had recovered greatly. Slow-growing age-0 rainbow smelt may have been more vulnerable to cannibalism, which is common in freshwater rainbow smelt populations (Evans and Loftus 1987) and a factor thought to regulate some rainbow smelt populations (He and LaBar 1994).

After its initial decline, biomass of rainbow smelt in Horsetooth Reservoir estimated by hydroacoustics during 1993–1996 was similar to that observed in a hydroacoustic survey of Lake Oahe, South Dakota in 1988 (35.6 kg/ha) and 1989 (5.0 kg/ha; South Dakota Game, Fish and Parks 1990), but higher than estimates for Lake Oahe during 1983–1985 (2.8–8.5 kg/ha; Burczynski et al. 1987).

Based on gill-net CPUE, adult walleye biomass and, hence, consumption demand, increased to its highest level during 1990–1992. This corresponds to the period with the most dramatic decline in rainbow smelt abundance. Our bioenergetics simulations suggested that walleye predation may have had a modest effect on rainbow smelt in 1993. Although estimated walleye consumption actually exceeded rainbow smelt biomass and production in 1994, that may have been an artifact of earlier timing of the hydroacoustic survey. Significant growth of rainbow smelt can occur between August and October (Goettl and Johnson 1998), making biomass (and production) estimates from 1994 difficult to compare with other years when surveys were conducted in October. Mean size of rainbow smelt in August 1994 was 66% smaller than in October 1993, 1995, and 1996. Had the survey been conducted in October 1994, as in other years, rainbow smelt biomass probably would have been between the 1993 and 1995 estimates. Walleye abundance, and hence consumption, was unknown in 1996, but rainbow smelt biomass was at its lowest level since the peak in 1989. It appears that predation could have been an important mortality factor limiting rainbow smelt biomass during 1994–1995, and probably in 1996 as well. During this same period, hybrid striped bass were stocked, in part to attempt to control the previously overabundant rainbow smelt population. We were unable to quantify hybrid striped bass abundance; however, it appears that consumption demand of piscivores was increasing while prey supply was declining. Consequently, we expect potential negative management implications from the growing imbalance in the food web.

Rainbow smelt are short-lived and they exhibit highly variable recruitment (Kircheis and Stanley 1981; Frie and Spangler 1985; Bryan et al. 1995; Kirn and LaBar 1996). Stocking long-lived piscivores to control rainbow smelt abundance may be inadvisable because of the difficulty in matching piscivore demand to prey supply (Kirn and LaBar 1996), especially when alternative prey fishes are not present. A single weak year-class of rainbow smelt could allow piscivores to quickly reduce rainbow smelt abundance after having built up a high predator biomass with an associated large consumption demand and predation inertia (sensu Stewart et al. 1981). As a consequence, piscivore growth rates would decline, and they could jeopardize other components of the sport fishery by increasing predation rates on prey-sized sport fish (e.g., rainbow trout, young walleyes, smallmouth bass, and hybrid striped bass), as was observed in Horsetooth Reservoir before rainbow smelt became abundant (Jones et al. 1994). An alternative approach would be to adjust piscivore fishing mortality with harvest regulations in response to prey population status, restricting harvest when prey are abundant and liberalizing regulations when prey are in serious decline (Forney 1980; Johnson and Martinez 1995).

Balancing predator demand with prey supply is challenging (Jones et al. 1993; Kirn and LaBar 1996; Johnson and Martinez, in press), but tools (e.g., hydroacoustics, bioenergetics and other computer models) that managers have to assess fish standing stocks and to forecast predation demand of piscivorous sportfish are improving (Jones et al. 1993; Mason et al. 1995; Hanson et al. 1997). Inability to forecast prey supply inhibits efforts to sustain desirable sport fisheries in highly managed systems, such as western reservoirs. In our study, zooplankton monitoring provided insights into prey fish dynamics before fish sampling could reliably detect changes in the food web. When both piscivores and their prey are dependent upon periodic management interventions to maintain a trophically balanced and recreationally desirable food web, fishery managers should be prepared to use nontraditional approaches (e.g., zooplankton sampling) and apply emerging technological tools to continuously monitor the status of fisheries. Only then will they be capable of modifying management policy to adapt to inevitable changes in sport fisheries and their food webs.

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