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Some Factors Affecting a Hatchery-Sustained Kokanee Population in a Fluctuating Colorado Reservoir

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Abstract.—The population of kokanees *Oncorhynchus nerka* in Lake Granby, Colorado, is expected to satisfy the competing demands of providing summer harvest for anglers, kokanee eggs for restocking, and prey for trophy lake trout *Salvelinus namaycush*. In the late 1970s, declines in numbers of kokanees harvested and kokanee eggs collected prompted investigations of the influences of stocking rates, reservoir fluctuations, competition with *Mysis relicta*, and lake trout predation. The kokanee population has been maintained mainly by annual stocking of fry (≤30 mm total length, TL) since 1951. When maturing spawners exceeded 367 mm TL, more than 50% of them were harvested in the summer recreational fishery, which reduced the number of kokanees in some fall spawning runs. However, when maturing year-classes were composed mainly of smaller kokanees, proportionately fewer were harvested, and the number of maturing kokanees entering the spawning run increased. Despite a trend of increased stocking from 1951 to 1978, mean kokanee spawner length varied inversely with the reservoir's water volume. In years of low reservoir volume, water temperatures were warmer. This facilitated *Daphnia* population development, which enhanced survival and growth of stocked kokanees. The colder water temperatures of high reservoir volumes were associated with later appearance of *Daphnia*, reduced kokanee recruitment, and smaller kokanees. Kokanee overstocking in the late 1970s resulted in stunting during the 1980s and shifted the predominant age of spawners from age 3 to age 4. Overpopulation also diminished angler perception of fishery quality and eliminated *Daphnia pulex*, the kokanees' primary food supply. The inverse relationship between reservoir volume and mean kokanee size has persisted despite *M. relicta* predation on *Daphnia* and lake trout predation on kokanees, which suggests that thermal and productivity trends in the reservoir will continue to exert a regulatory role in kokanee population dynamics.

Kokanees *Oncorhynchus nerka* represent a major fishery resource in the western USA and Canada (Wydoski and Bennett 1981; Rieman and Myers 1992). The species is especially well suited to life in fluctuating mountain reservoirs because the majority of its life is spent in pelagic environments where crustacean zooplankters, principally *Daphnia* spp., make up the bulk of its diet (Finnell and Reed 1969; Klein 1979). Although introduced kokanees often develop self-sustaining populations (Wydoski and Bennett 1981), many populations are augmented (Rieman and Myers 1992) or maintained entirely by stocking.

In Lake Granby, Colorado, kokanee reproduction appears limited by cold water temperature (for stream spawners) or by lack of suitable substrate (for shoreline spawners). Finnell (1959) documented that both naturally and artificially deposited kokanee eggs in Lake Granby inlet streams failed to hatch. This was attributed to stream temperatures less than 3.3°C, which is below the range of suitable temperatures reported by Combs (1965). Many kokanees collected from Lake Granby in winter retain eggs well after deterioration of their bodies has progressed, which suggests that substrates suitable for egg deposition are lacking. Furthermore, examination of nearly 4,000 kokanees for tetracycline marks in 1981–1986 revealed that 97% were stocked, which demonstrated that the population was not self-sustaining (Martinez and Wiltzius 1991).

Kokanees in Lake Granby historically supported one of Colorado's best reservoir fisheries, and have been the state's most reliable source for kokanee eggs, which are used to meet in-state and out-of-state stocking needs. In the late 1970s, declines in the numbers of kokanees harvested and kokanee eggs collected prompted further study of kokanee ecology and population dynamics in the reservoir (Martinez and Bergersen 1991). The establishment of *Mysis relicta* in the 1970s, reservoir storage trends, kokanee stocking manipulations, and an emphasis on a trophy lake trout *Salvelinus namaycush* fishery in the late 1980s have been implicated as major factors influencing the kokanee population. In this paper, we chronicle the history of kokanee management in Lake Granby and evaluate relationships between kokanee population characteristics, reservoir water level, and the establishment of lake trout and *M. relicta*.

Methods

Data used in our analyses included annual historical records of kokanee mean spawner length, stocking rates, eggs collected, and reservoir volume. Sporadic creel survey, kokanee spawner enumeration, water temperature, and crustacean zooplankton data were also used. These data did not allow testing of the relative importance among factors; rather, our analyses provide information and insight about the influences of each factor.

Lake Granby covers 2,938 ha at a maximum elevation of 2,524 m above sea level. It was constructed in 1949 primarily for irrigation; therefore, it is subject to large seasonal water level fluctuations (Martinez and Bergersen 1991). End-of-month records of reservoir water volume, obtained from the U.S. Bureau of Reclamation, were expressed as a percent of maximum reservoir volume. These data were regressed with mean kokanee spawner lengths and water temperatures. Water temperature data were obtained from Nelson (1971), Nelson (1982), Martinez (1986), Martinez and Bergersen (1991), and W. C. Lee (Colorado Cooperative Fish and Wildlife Research Unit, unpublished data).

Kokanees were introduced in Lake Granby in 1951 (Moore 1953) and have been stocked annually. Since 1954, kokanees have been stocked in the Colorado River at the location where kokanee eggs are collected (0.6–1.2 km upstream of the reservoir, depending on the water level) to ensure that young kokanees imprint and return to supply eggs. Until the mid-1970s, small portions of the annual stocking were released at a few sites around the reservoir to provide a snagging fishery when the fish matured. Through 1980, annual kokanee stocking consisted mainly of fry shorter than 30 mm (all lengths are total length) that were released in May or early June. In 1981–1985, kokanee harvest and spawning-run returns were evaluated from four length-groups: 25, 40, 55, 160 mm (Martinez and Wiltzius 1991). Kokanees stocked since 1985 have been 35–45 mm long.

Information on kokanee abundance and size was collected at the kokanee egg collection site on the Colorado River. Estimates of mean spawner length (in most years) and numbers of eggs collected have been recorded since 1954 and 1962, respectively. Kokanee numbers in annual spawning runs were estimated in 1975–1979 by using spawner sex ratios and body–egg relationships (Wiltzius, unpublished data) and in 1981–1986 by counting subsamples of spawners. Feed-administered oxytetracycline (OTC) was used to mark kokanees stocked in 1970 and in 1981–1985. Bone samples, usually vertebrae from behind the head, were examined under ultraviolet light to fluoresce the OTC bands (Martinez and Wiltzius 1991). In 1992, kokanee spawner ages were determined from otoliths as described by Parsons and Hubert (1988).

Creel surveys were performed in 1975–1979 (Sealing and Bennett 1980) and 1981–1986 (Martinez and Wiltzius 1991) with a stratified random system of counting and interviewing (Neuhold and Lu 1957). Shore anglers and boat anglers were interviewed to determine hours fished and numbers, sizes, and species of fish caught. Estimates of angling effort and harvest were derived as described by Powell (1975).

Crustacean zooplankton were collected with a Clarke-Bumpus metered plankton net (0.12-mm-aperture netting) and processed as described in Martinez and Bergersen (1991). The net was towed obliquely, and we present results for the depth range of 0–10 m, the zone of maximum crustacean zooplankton abundance (Martinez and Bergersen 1991). Mean lengths (in millimeters) of *Daphnia* in collections made in July or August are presented because they represented the period of peak or near-peak *Daphnia* density in Lake Granby (Nelson 1971; Martinez and Bergersen 1991).

Results and Discussion

Effects of Kokanee Stocking Rate

The annual kokanee stocking rate in Lake Granby varied greatly from 1951 to 1992 (Figure 1a). Kokanee stocking increased from 0.5–0.8 million in 1957–1968 to 1.1 million in 1969 due to concerns that reduced numbers of kokanees surviving to maturity (Finnell 1970) resulted in relatively small egg-takes in 1966–1967 (Finnell 1968; Figure 1b). The trend of stocking greater numbers peaked in 1977–1978, when nearly 2 million fry were stocked annually. These high stocking rates were in response to the record low egg-take of 1.8 million in 1976.

Mean lengths of kokanee spawners varied historically between large and small sizes, but in 1980–1986 they were as small as, or smaller than previously reported at Lake Granby (Figure 1c). In addition to being smaller in 1981–1984, kokanee spawners were numerous (Table 1), which contributed to large annual egg-takes of 10.2–16.3 million (Figure 1b). Further, spawning runs dominated by age-3 fish in the 1970s shifted to age-4 dominance in the 1980s and back to age-3 domi-

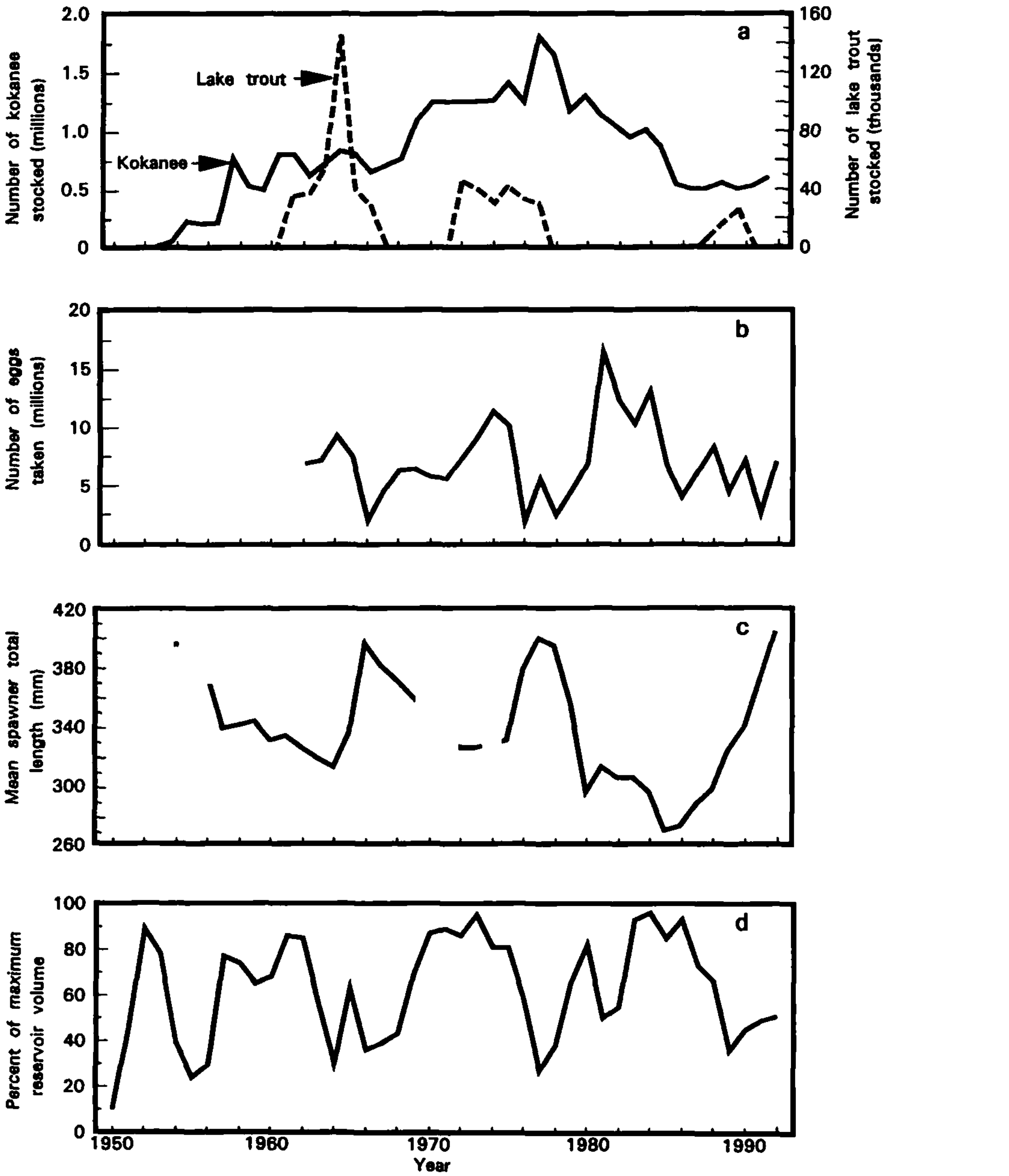

FIGURE 1.—Historic Lake Granby, Colorado, kokanee, lake trout, and reservoir capacity data: (a) number of kokanees and lake trout stocked; (b) number of kokanee eggs collected; (c) mean kokanee spawner length (gaps indicate missing data); and (d) 30 November reservoir volume (expressed as a percent of maximum reservoir volume).

nance in 1992 (Table 2), following several years of reduced stocking (Figure 1a). These phenomena, indicative of kokanee overabundance in the early 1980s, were apparently caused by the high stocking rates in 1977–1978.

Kokanee overpopulation also influenced angler perception of fishery quality. Despite high catches in the early 1980s (Table 1), anglers were dissatisfied with the small size of the kokanees. Although small kokanees continued to be harvested,

TABLE 1.—Creel survey summary and estimates of kokanee numbers harvested, used for supplying eggs, removed from the population, and mean kokanee length in the sport fishery and spawning run in Lake Granby, Colorado, 1975–1986.

Year	Duration of creel survey	Total hours of angling effort (×10³)	Number of kokanees (thousands): Summer reservoir harvest	Used in egg-take operation	Fall snagging harvest	Removed from population	Mean total length (mm): Sport fishery creel	Fall spawning run
1975 (1976)	1 Apr–31 Mar	227.6	68.9	48.8	39.1	156.8	312	330
1976	1 Apr–31 Dec	171.1	44.6	6.9	21.8	73.3	320	379
1977 (1978)	1 May–31 Jan	131.2	43.0	16.7	13.5	73.2	343	399
1978	1 Apr–31 Dec	150.8	23.2	7.4	4.1	34.7	318	394
1979	1 May–31 Dec	130.4	20.8	19.6	12.7	53.1	295	356
1981 (1982)	1 May–24 Jan	125.7	16.1	83.0	21.1	120.2	267	312
1982 (1983)	17 May–14 Jan	141.2	39.1	79.4	55.0	173.5	259	306
1983	16 May–13 Nov	141.1	44.3	67.4	86.7	198.4	259	304
1984	14 May–25 Nov	135.0	24.2	100.0	49.0	173.2	279	295
1985	13 May–24 Nov	137.1	15.7	65.7	13.9	95.3	244	269
1986	12 May–28 Sep	99.0	5.0	28.5	8.5	42.0	234	272

they did not enter the summer harvest in proportion to their abundance. The percent of kokanees harvested during summer in 1975–1986 was positively related to mean spawner length (Figure 2). Mean spawner length is an index of kokanee length in the summer fishery ($r = 0.93$, $P < 0.01$, $N = 11$; Table 1). These relationships indicated that when kokanees were larger, a greater proportion of the maturing year-classes was harvested by anglers, which left proportionately fewer fish to mature and enter the spawning run. Conversely, when the maturing fraction of the population was smaller-sized, as in the early 1980s, a smaller percentage was harvested by anglers, which resulted in proportionately more kokanee reaching maturity. Maturing year-classes represent the largest individuals in the population, and these fish contribute most to the annual harvest (Klein 1979; Rieman and Myers 1990).

During the 1980s, it appeared that kokanee predation was the major factor affecting epilimnetic *Daphnia* populations (Martinez and Bergersen 1991), rather than predation by *M. relicta* as originally suspected by Sealing and Bennett (1980). Martinez and Bergersen (1991) believed the thermal refuge that prevented elimination of *Daphnia galeata mendotae* by *M. relicta* also provided refuge for the larger *D. pulex*, reported by Finnell and Reed (1969) to be the preferred food of kokanees in Lake Granby. Consequently, intense selective predation by overabundant kokanees was deemed responsible for the suppression and virtual disappearance of *D. pulex* throughout the 1980s. *Daphnia pulex* reappeared in Lake Granby in 1990 (Table 3), and we believe this resulted from reduced predation by lesser numbers of kokanees in the reservoir. Additionally, mean size of daphnids in 1991–1992 was markedly larger than previously recorded and was strongly correlated with mean spawner size ($r = 0.94$, $P < 0.01$, $N = 8$), not reservoir volume ($r = 0.17$, $P > 0.1$, $N = 8$). These findings suggest that low kokanee numbers in the early 1990s allowed *D. pulex* to recolonize and daphnids to grow to larger sizes.

Influence of Reservoir Volume

Comparison of mean kokanee spawner length with end-of-month reservoir volume revealed con-

TABLE 2.—Percent composition and mean total lengths (in parentheses) of age-classes in Lake Granby, Colorado, kokanee spawning runs, as determined from tetracycline-marked fish in 1973 and 1986, and from examination of otoliths in 1992.

Year	Number of fish examined	Percent composition of spawning run (mean total length, mm) at age: 2	3	4	5	Undetermined[a]
1973	93	11.8 (307)	85.0 (315)			3.2 (329)
1986	422	0.7 (249)	32.2 (254)	59.1 (262)	4.7 (320)	3.3 (334)
1992	102	11.8 (378)	76.4 (406)	11.8 (434)		

[a] Undetermined ages were known to be greater than age 3 in 1973 and greater than age 5 in 1986.

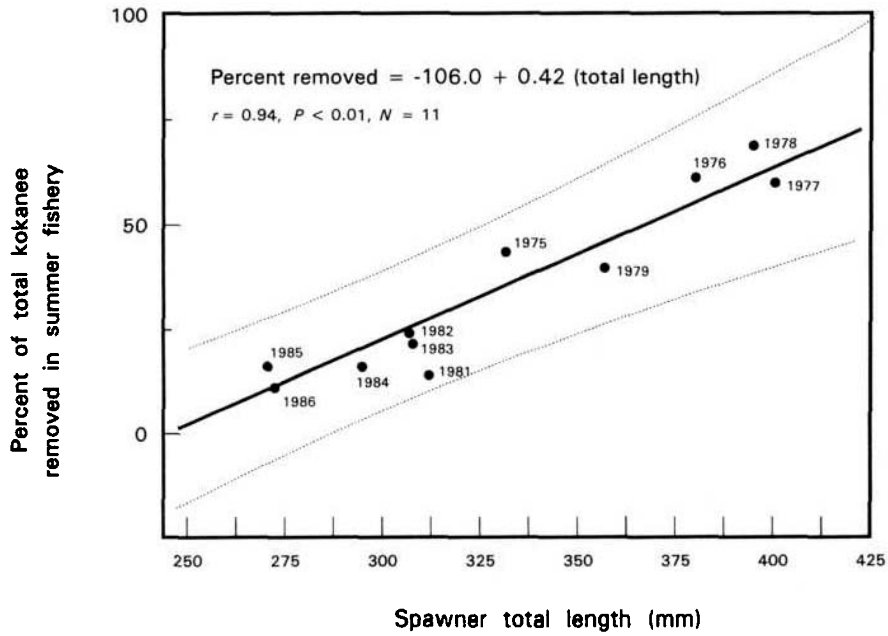

FIGURE 2.—Relation between angler harvest of kokanees and kokanee mean length in the spawning run, 1975–1986. Harvest percentages estimate that portion of the annual kokanee return removed during the kokanee fishing season, May–October, primarily by trolling. The dashed lines denote 95% confidence limits.

sistently negative correlations for all months. The 30 November reservoir volume was chosen as an index due to its high correlation with mean spawner length ($r = -0.66$, $P < 0.01$, $N = 34$) and coincidence with the spawning run. When reservoir volume was near maximum, mean spawner length was consistently smaller than when the reservoir was low (Figure 1c, d). Therefore, the relationship between kokanee size and vulnerability to angling in the summer fishery and its implications for the fall spawning run appear to be linked to reservoir volume.

TABLE 3.—Historic summertime occurrence and mean size of epilimnetic *Daphnia* species, mean kokanee spawner length, and 31 July reservoir volume for Lake Granby, Colorado.

Year	Date of zooplankton sampling	*Daphnia galeata mendotae*	*Daphnia pulex*	Mean length (mm): *Daphnia* spp.	Mean length (mm): Kokanee spawners	Reservoir volume (% of maximum)
1963	31 Jul	Present	Present	0.85[a]	318	68.2
1964	28 Jul	Present	Present	0.93[a]	312	49.3
1965	30 Jul	Present	Present	0.89[a]	335	64.9
1981[b]	23 Aug	Present	Absent	0.87	312	62.2
1982[b]	26 Jul	Present	Absent	0.78	305	57.9
1989[c]	4–7 Aug	Present	Absent	0.77	323	60.1
1991	7 Aug	Present	Present	1.20	371	59.8
1992	29 Aug	Present	Present	1.34	404	58.5

[a] Mean lengths for *Daphnia galeata mendotae* only (from Nelson 1971).
[b] From Martinez (1986).
[c] Unpublished data from G. Bennett and A. Martinez, Colorado Division of Wildlife.

Trends in kokanee size suggest that kokanee growth and survival in Lake Granby were greater during periods of low reservoir volume. Mean water temperature (in the upper 40 m) was cooler when the reservoir was full, as in 1962, but was as much as 30% warmer when the reservoir held about half its maximum volume, as in 1990 (Table 4). In addition, the approximate depth of the 14°C isotherm, the threshold preventing *M. relicta* access to the epilimnion during its nighttime vertical migrations (Martinez and Bergersen 1991), occurred at greater depth when reservoir volume was low. These indicators of thermal conditions were strongly related to reservoir volume ($r = 0.95$, $P = 0.01$, $N = 5$, for mean water temperature and $r = 0.98$, $P < 0.01$, $N = 5$, for depth of the 14°C isotherm; Table 4). We theorize that a reduced water mass in Lake Granby warms earlier in the year, which facilitates development of *Daphnia* populations and results in more favorable conditions for kokanee survival and growth during the remainder of the year.

TABLE 4.—Comparison of 31 July reservoir volumes and mean water column temperatures (0–40 m) and approximate depths of the 14°C isotherm in mid to late July, Lake Granby, Colorado.

Variable	Reservoir volume (percent of maximum)				
	99.9	70.5	59.9	57.8	48.5
Temperature (°C)	9.5[a]	11.4[b]	11.5[c]	12.5[d]	13.7[e]
Depth (m) of 14°C isotherm	3	9	11	11	15

[a] 25 July 1962; from Nelson (1964).
[b] 14 July 1981; from Martinez (1986).
[c] 28 July 1992; P. J. Martinez, unpublished data.
[d] 18 July 1978; from W. C. Nelson, Colorado Division of Wildlife, unpublished data.
[e] 23 July 1990; from W. C. Lee, Colorado Cooperative Fish and Wildlife Research Unit, unpublished data.

Influence of Mysis and Lake Trout

Predation by lake trout and *M. relicta* competition for *Daphnia* have been shown to adversely affect kokanee populations (Beattie and Clancey 1991; Bowles et al. 1991; Spencer et al. 1991). Martinez and Bergersen (1991) concluded that although *M. relicta* delayed seasonal development of *Daphnia* populations in Lake Granby, it was not solely responsible for changes in the kokanee population. Although lake trout preyed on kokanees, they did not prevent kokanee overabundance during the early 1980s (Martinez and Wiltzius 1991).

Mean kokanee spawner length and 30 November reservoir volume were regressed for time periods before and after establishment of lake trout and after establishment of *M. relicta* (which also includes lake trout as a factor) in Lake Granby (Figure 3). These periods were lagged by 9 years following introduction of lake trout (1961) and *M. relicta* (1971) because passage of this length of time would be required before lake trout reached sizes to become predominantly piscivorous (Griest 1976) or *M. relicta* densities posed a competitive threat to kokanees (Nesler and Bergersen 1991). Tests for differences between regression slopes and intercepts followed the method of McCracken (1990).

All regressions were significant ($P < 0.05$), and their slopes were not significantly different ($P > 0.5$; Figure 3), which indicates that the inverse relationship between kokanee length and reservoir volume persisted during the three analysis periods. However, the intercept for the post-*Mysis*–lake trout period was significantly lower ($P \le 0.03$) than the intercepts of the other two regression lines (Figure 3), which indicates that kokanees were shorter following the establishment of *M. relicta.*

If lake trout predation on kokanees or *M. relicta* competition with juvenile kokanees for zooplankton, or both, caused significant mortality of ko-

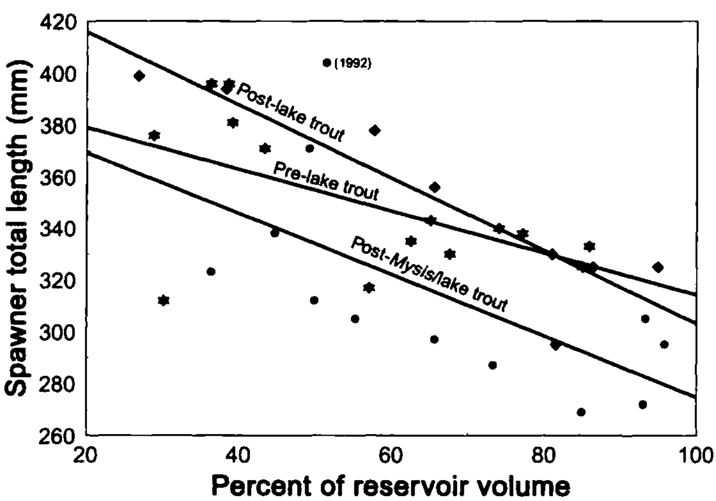

FIGURE 3.—Relation between mean kokanee spawner lengths and 30 November reservoir volume during pre-lake trout (1954–1970, denoted by stars; $r = -0.57$, $P = 0.03$, $N = 14$), post-lake trout (1971–1980, denoted by diamonds; $r = -0.91$, $P = 0.002$, $N = 8$), and post-*Mysis*–lake trout (1981–1992, denoted by dots; $r = -0.64$, $P = 0.03$, $N = 12$) predation periods. Testing for differences in slopes between the three periods showed no significant difference ($F_{2,28} = 0.62$, $P = 0.54$). Differences between intercepts were significant ($F_{2,30} = 5.22$, $P = 0.011$). Pair-wise comparisons for pre- and post-lake trout periods were not significantly different from each other ($P = 0.32$), but they differed significantly ($P = 0.03$ and $P = 0.004$, respectively) from the post-*Mysis*–lake trout period. The largest mean kokanee spawner length at Lake Granby, 404 mm, was recorded in 1992.

kanees, mean spawner length would be expected to increase (Beattie et al. 1988). If only age-0 kokanee survival declined due to *M. relicta* competition for zooplankton, mean spawner length would be expected to remain the same (Bowles et al. 1991). A decline in mean kokanee spawner size might result if *M. relicta* dramatically reduced cladoceran abundance (Morgan et al. 1978); however, *Daphnia* persisted in Lake Granby (Table 3).

The decline in mean spawner length observed at Lake Granby suggests kokanee overpopulation in the 1980s confounded the potentially adverse effects of both *M. relicta* and lake trout. However, mean kokanee spawner length was increasing in the late 1980s and early 1990s, and by 1992, spawners were the longest ever recorded at Lake Granby (Figure 1c). The abnormally large mean spawner length in 1992 (Figure 3), might have been caused by interaction of reservoir volume, reduced kokanee stocking, and enhanced lake trout management. Rieman and Myers (1990) cautioned that unusually large kokanees in a population is a sign that the population may have reached precariously low levels.

Management Implications

Reservoir Volume Fluctuations

The Lake Granby kokanee population appears to exhibit a density-dependent relationship with reservoir volume that is probably a result of variations in reservoir productivity. The initial appearance and duration of the kokanees' preferred food supply, *Daphnia*, also appears to be controlled by reservoir thermal conditions related to reservoir volume. Additionally, the extent of kokanee food competition with *M. relicta* would also be regulated by reservoir volume, which appeared to control the onset, depth, and duration of the thermal refuge where *Daphnia* was protected from predation by *M. relicta*. It is through this theorized cycle of comparatively rich food to comparatively limited food that reservoir volume and thermal conditions are believed to contribute to trends in *Daphnia* and kokanee population dynamics in Lake Granby.

If the *Daphnia* population develops earlier in years of low reservoir volume, then mean *Daphnia* size may be expected to increase in response to the longer growing period. However, kokanees' selectivity for the largest daphnids (Martinez and Bergersen 1991) apparently controls mean *Daphnia* size to a greater extent than do reservoir thermal conditions. When mean *Daphnia* size in the early 1960s was smaller (0.89 mm) than during the early 1990s (1.27 mm), reservoir volumes were nearly equal, 60 and 59%. Consequently, reservoir volume did not appear to be the factor controlling mean *Daphnia* size. The most likely explanation is that during the 1960s, more numerous kokanees (indicated by smaller mean spawner lengths) selectively cropped larger *Daphnia* more effectively than in the 1990s when kokanees appeared to be less abundant. The influence kokanees exert over *Daphnia* species and size composition through selective cropping of *D. pulex* and large *Daphnia* in general suggests that, despite the link between reservoir volume and trends in kokanee size and abundance, kokanees remain a dominant influence on *Daphnia* populations.

Kokanee Length and Density

Although reservoir volume appears to have an overriding effect on kokanee population dynamics in Lake Granby, the magnitude of kokanee stocking and survival can impose trade-offs for managers. Therefore, predictions of density-dependent relationships that influence kokanee growth, length, and fishery quality should influence management goals for population size (Rieman and Myers 1992) and must be taken into account to safeguard kokanee egg supplies.

Kokanee overpopulation and stunting diminishes fishery quality. Often, as kokanee density increases and size declines, catch rates and angler effort decline (Rieman and Myers 1990). Although many 200–250 mm kokanees were present in Lake Granby in the early 1980s, anglers experienced difficulty catching them. Conversely, kokanee populations exhibiting minimum densities and maximum growth may lack compensatory reserve and could be vulnerable to catastrophic events (Rieman and Myers 1992), which jeopardizes egg production for natural deposition or hatchery production.

Kokanee management goals should also consider lake productivity (Rieman and Myers 1992). Martinez and Wiltzius (1991) projected that Lake Granby's kokanee population historically yielded approximately 25,000 kg of kokanees from its maturing year-classes, including those harvested as immature in the summer fishery. Reservoir records indicate that Lake Granby's 30 November volume averaged 65% and 2,500 ha in size. Based on these averages, the reservoir produced about 10 kg/ha of maturing kokanees annually. This value is high relative to kokanee yields reported for 28 lakes and reservoirs in the northwestern USA and British Columbia by Rieman and Myers (1990).

Martinez and Wiltzius (1991) recommended targeting a mean spawner size of 330–340 mm at Lake Granby to provide fishery quality and yield for anglers and also ensure an adequate supply of kokanee eggs. Factors that contribute to reduced kokanee densities and result in larger kokanees should be avoided because overexploitation and excessive piscivory can destabilize even hatchery-sustained populations (Rieman and Myers 1990). For schooling species like kokanee, depensatory mortalities may limit population size to low levels or cause population collapse if piscivores continue to selectively prey upon them after their numbers have declined (Beattie et al. 1988; Bowles et al. 1991).

Lake Trout Management

Sealing and Bennett (1980) recommended that lake trout stocking in Lake Granby be discontinued because of the low lake trout harvest and their adverse effects on the kokanee fishery and egg-take. No lake trout were stocked in Lake Granby from 1978 to 1987, but stocking was resumed in 1988 because managers believed *M. relicta* had so damaged the kokanees' food supply (*Daphnia*) that future management of the reservoir should instead emphasize the lake trout fishery. However, before 1987, Lake Granby's kokanee population did not exhibit signs of collapse, which would have been characterized by unusually large and sparse fish (Rieman and Myers 1990); rather, it exhibited characteristics of overpopulation.

In the 1980s, several factors created a favorable environment for lake trout: high reservoir volume increased the environment available to lake trout and facilitated their reproduction (Martinez and Wiltzius 1991); *M. relicta* was probably peaking in density, which contributed to lake trout recruitment (Griest 1976); overabundant, small kokanees provided abundant prey; and protected-slot regulations for lake trout (508–812 mm in 1988–1989 and 558–864 mm in 1990–1992, both with a one-fish limit) were implemented. Martinez and Wiltzius (1991) recommended reduced kokanee stocking rates (which commenced in 1986) to alleviate kokanee overpopulation, enhance the kokanee fishery, and ensure sufficient egg numbers. However, enhanced lake trout management was not part of this recommendation. These reduced kokanee stocking rates, in concert with the intensive lake trout management, minimize the likelihood that the kokanee harvest will return to the high levels observed in 1975–1984.

Even increased stocking may not be sufficient to maintain or recover kokanees if low kokanee recruitment during periods of delayed *Daphnia* population development fails to saturate piscivores (Bowles et al. 1991). Lake trout stocking in Lake Granby was halted in 1992 (at least temporarily), and the protected slot was shifted to 660–915 mm (with a two-fish limit) to reduce the reservoir's lake trout population. Managing the kokanee population for a summer fishery and an egg source would probably best be served by the 1985–1987 lake trout minimum length limit of 508 mm that protected the mysid-consuming component of the population and encouraged harvest of the more piscivorous component. However, a 508-mm minimum length limit may reduce the number of trophy lake trout, which are highly valued by some anglers and attract both media and management attention. Despite flexibility in Lake Granby kokanee stocking rates, optimizing kokanee management to meet three conflicting demands—summer harvest, a substantial spawning run, and an ample lake trout prey base—appears far more complex than strictly managing for the summer kokanee fishery and egg supply.

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