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Interactions of Zooplankton, *Mysis relicta*, and Kokanees in Lake Granby, Colorado

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Abstract.—In studies of zooplankton and kokanees *Oncorhynchus nerka* in Lake Granby, Colorado, conducted from 1981 to 1983, we investigated the suspected role of introduced *Mysis relicta* in the decline of the kokanee sport fishery and egg take. *Mysis relicta* entered surface waters at night and preyed on zooplankton, except when summer temperatures above 14°C excluded it from the epilimnion and created a temporary refuge for cladocerans. We attributed the disappearance of hypolimnetic *Daphnia longiremis* to predation by mysids, and the virtual elimination of *Daphnia pulex* (once the preferred item in the kokanee diet) to the effects of intense selective predation by abundant *M. relicta* and to kokanee overstocking. *Daphnia galeata mendotae*, historically the most abundant daphnid, has replaced *D. pulex* as the principal item in the kokanee diet. Premysid populations of *Daphnia* spp. appeared by late May and peaked by late July, whereas postmysid populations appeared in late June and peaked in late August or early September. *Mysis relicta* appeared more frequently in stomachs of large kokanees (≥200 mm in total length) and sometimes contributed substantially to the biomass of the kokanee diet. However, actual numbers of mysids and their frequency of occurrence in individual kokanee stomachs remained low. The disappearance or persistence of *Daphnia* spp. in other Colorado waters containing mysids appears to be explained by thermal conditions. It is clear that the introduced *M. relicta* has not adequately substituted for the diminished daphnid populations that were used heavily by planktivorous fishes.

Mysis relicta has been introduced in many western lakes and reservoirs (Gosho 1975), including 50 in Colorado (Martinez and Bergersen 1989), to enhance forage bases for coldwater fish. Its establishment in Kootenay Lake, British Columbia (Sparrow et al. 1964), and the subsequent increased growth of kokanees *Oncorhynchus nerka* (Northcote 1972a, 1972b), provided impetus for further mysid introductions to benefit kokanee (Rieman and Falter 1981; Leathe and Graham 1982; Brown 1984).

Unfortunately, kokanees have not responded as positively in other lakes where *M. relicta* has been established as they did in Kootenay Lake. The deleterious effects of introduced mysids on daphnid populations have caused kokanee population declines in Lake Tahoe, California–Nevada (Morgan et al. 1978), Pend Oreille Lake, Idaho (Rieman and Falter 1981), and Whitefish Lake, Montana (G. Anderson and D. Domrose, Montana Department of Fish, Wildlife, and Parks, unpublished), and poor kokanee growth in Dillon Reservoir, Colorado (Nelson 1981).

Kokanees in Lake Granby, Colorado, have supported a major sport fishery and served as the source of several million eggs annually. In the late 1970s, the numbers of kokanees harvested and eggs collected declined considerably (Table 1). Sealing and Bennett (1980) attributed the declines to predation by lake trout *Salvelinus namaycush*, reservoir drawdown that reduced survival of kokanee fry, overstocking of kokanees, and the negative effect of introduced mysids on daphnid populations.

The loss of all *Daphnia* spp. in Lake Granby would be detrimental to the kokanee sport fishery and to the statewide stocking program dependent on the lake's kokanees for eggs (Nelson 1981). The objective of this study was to determine the interactions of zooplankton, *M. relicta*, and kokanees in Lake Granby.

Study Area

Lake Granby is 160 km northwest of Denver near the headwaters of the Colorado River (Figure 1). Constructed in 1949, the impoundment is a major source of irrigation water for northeastern Colorado via transmountain water diversion. It has a surface area of 2,938 hectares, a depth of 61 m, a mean depth of 22.6 m, and 64.4 km of

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TABLE 1.—Summary of Lake Granby kokanee fishery statistics, 1975–1987 (Sealing and Bennett 1980; Martinez and Wiltzius 1991).

Year	Total fishing hours[a] (thousands)	Kokanee: Number stocked[b] (millions)	Kokanee: Boat harvest[c] (thousands)	Kokanee: Spawning run[d] (thousands)	Kokanee: Egg take[e] (millions)	Kokanee: Mean total length of spawners (mm)
1975	228	1.4	69	88	10.1	330
1976	171	1.3	45	29	1.9	378
1977	131	1.8	43	30	5.5	399
1978	151	1.7	23	11	2.4	394
1979	130	1.2	21	32	4.6	356
1980		1.3		33	6.8	295
1981	126	1.1	16	104	16.4	312
1982	141	1.0	39	134	12.3	306
1983	141	1.0	44	154	10.2	304
1984	135	1.0	24	149	13.0	295
1985	137	0.9	16	80	6.8	269
1986	99	0.5	5	37	4.0	274
1987	75	0.5	3	39	6.1	287

[a]Includes effort expended by both boat and shore anglers.
[b]All stocked kokanee were fry until 1981. Larger sizes have been stocked experimentally in recent years.
[c]Includes all fish species; however, boat anglers caught kokanees primarily.
[d]Number of mature kokanees estimated to ascend the Colorado River.
[e]Numbers of kokanee eggs artificially stripped and fertilized at the Colorado River spawn-taking site.

shoreline at maximum elevation of 2,524 m above mean sea level. It is subject to wide surface-level fluctuation and can be drawn down as much as 28.7 m (Timm and Seeley 1970). In past investigations, the reservoir has been classified as oligotrophic (PHS 1963), oligomesotrophic (Timm and Seeley 1970), mesoeutrophic (USEPA 1977), and mesotrophic (Nelson 1982).

Mysis relicta, which was introduced in Lake Granby in 1971 (Finnell 1977), developed a relatively dense population by 1978 (Nelson 1981). Five fish species in addition to kokanee are abundant in Lake Granby: rainbow trout *Oncorhynchus mykiss*, brown trout *Salmo trutta*, lake trout, longnose sucker *Catostomus catostomus*, and white sucker *Catostomus commersoni*. Less common species are cutthroat trout *Oncorhynchus clarki*, brook trout *Salvelinus fontinalis*, johnny darter *Etheostoma nigrum*, and mottled sculpin *Cottus bairdi*.

Methods

Crustacean zooplankton was sampled in the entire water column at a single deep station and down to 10 m at several shallow stations (Figure 1). Midday samples were collected at monthly intervals from June to December. In 1983, samples were collected only once (deep station on 27 August) to confirm findings of the previous years. From June to October 1982, diel samples (midday, dusk, darkness, and dawn) were collected at the deep station to monitor vertical movements of zooplankton.

Quantitative collections of zooplankton were made with an opening–closing Clarke–Bumpus metered plankton sampler (0.12-mm-aperture netting) towed obliquely through the water column in nonoverlapping strata of 5, 10, and 20 m. While being towed, the sampler was opened at the stratum upper limit, lowered to the stratum lower limit, and then closed during retrieval at the stratum upper limit. Qualitative collections also were made through the ice at the deep station in January, March, and April 1982 by drawing a Wisconsin plankton net (0.12-mm-aperture netting) upward through the entire water column.

We periodically monitored the contribution of daphnids to Lake Granby from surrounding impoundments from June to December 1982 by collecting samples with a Clarke–Bumpus sampler held in the current of major inlets near their confluences with the reservoir.

Diel vertical distributions of *M. relicta* and kokanees were recorded with an echo sounder in 1982. Soundings were taken concurrently with our diel zooplankton sampling at the deep station from June to September.

The relative abundance of *M. relicta* in shallow water (3–7 m) was determined at monthly intervals from June to December 1982. Midday samples were collected at stations 1–6 (Figure 1) with

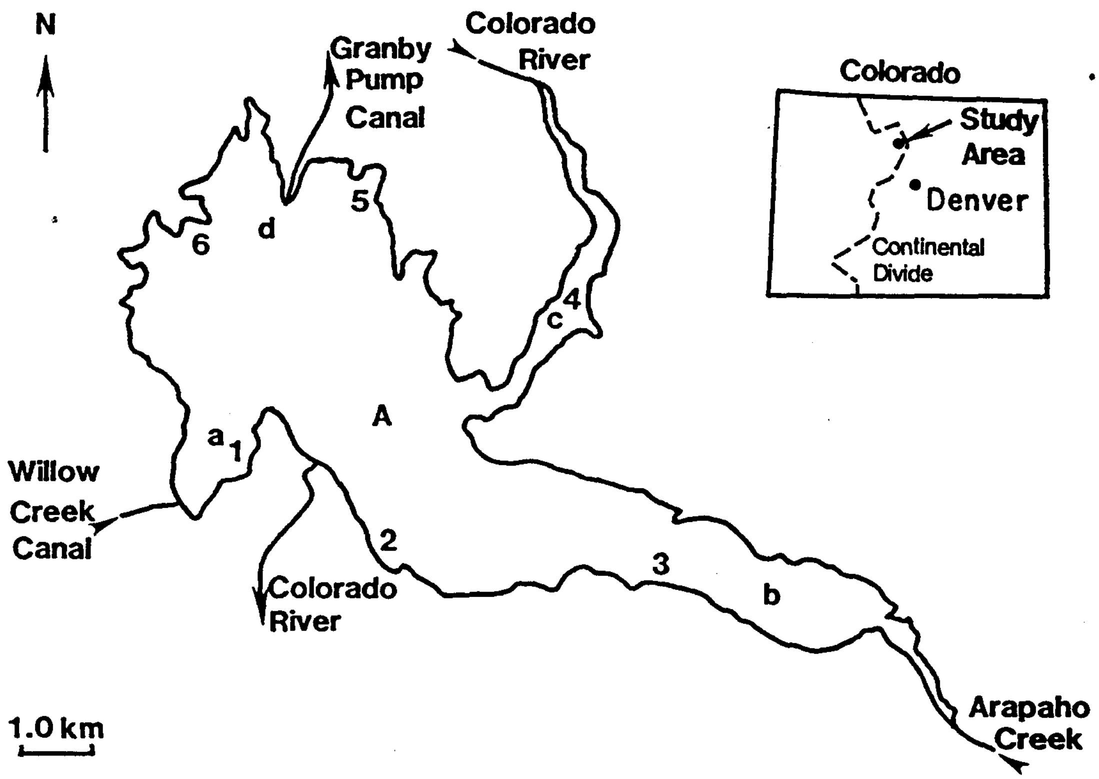

FIGURE 1.—Lake Granby, Colorado, showing sampling stations. Stations A (deep) and a, b, c, and d (shallow) are sampling sites for crustacean zooplankton; stations 1–6 are shallow-water sites used for epibenthic trawling for *Mysis relicta*. Broken line in inset denotes Continental Divide.

an epibenthic trawl fitted with 0.71-mm-aperture netting (Gregg 1976).

Kokanees were captured with a large midwater trawl (mouth 6-m square) towed just after dark in June, August, and October 1982 and in July, August, and October 1983, at depths of 10–20 m (Martinez and Wiltzius 1991). More than 1,400 stomachs were collected for food analyses. Gill nets were occasionally set overnight to collect kokanees in 1981 ($N = 63$) and 1982 ($N = 119$) for cursory examination of stomach contents to compare with other food data.

Water temperature and dissolved oxygen were measured on zooplankton sampling dates at the deep station in 1981 and 1982. Dissolved oxygen in water samples taken at 0, 5, 10, 20, 30, 40, and 50 m was measured by the Winkler method.

Mysids were removed from Clarke–Bumpus samples before the crustacean zooplankton was counted. Total counts of all species in three 1-mL aliquots were made in a Sedgwick–Rafter counting chamber. Copepod nauplii were not counted. In random subsamples, mysids were measured to the nearest 1.0 mm and zooplankters to the nearest 0.01 mm.

The consumption of zooplankton by mysids was studied by examining pooled stomach contents of 20–60 adult *M. relicta* each month from June to December 1982. Three to five stomachs were teased open into a Palmer–Maloney counting cell and all zooplankters were identified and counted. Ingested rotifers appeared to remain intact; cladocerans and copepods were identified by specific structures; *Bosmina longirostris* by the antennules, *Daphnia galeata mendotae* by the postabdominal claw, and *Diacyclops bicuspidatus thomasi*[2] by the urosome.

Mysids in kokanee stomachs were picked out and counted. Intact mysids were measured to the nearest 1.0 mm. An average length of ingested mysids was determined for estimating dry weight from a length–weight equation established for *M.*

[2]Called *Cyclops bicuspidatus thomasi* by other authors.

relicta in Lake Tahoe by Morgan (1979). After the mysids were removed, the remaining stomach contents were pooled, by date, for kokanees in 10-mm-length categories. The number of zooplankters in a pool was estimated by counting all individuals in three 1-mL aliquots in a Sedgwick–Rafter chamber. Average lengths of zooplankters were used to calculate wet weights from established length–weight equations (Edmondson 1971). Dry weight was estimated by multiplying wet weights by 0.1 (Rieman and Bowler 1980). Once the numbers and dry weights of zooplankters were estimated, stomach contents with large numbers of insects were filtered and dried at 60°C for 12 h. After these materials were weighed, the calculated zooplankton dry weight in the dilution was subtracted from the dried sample weight to estimate the dry weight of insects in the pooled samples.

Abundance and Distribution of Zooplankton, *Mysis relicta*, and Kokanees

Daphnid Population Changes

Studies conducted by Finnell and Reed (1969) and Nelson (1971) focused on three daphnids eaten by fish: *Daphnia longiremis*, *D. pulex*, and *D. g. mendotae*. Finnell and Reed reported that the daphnid population, in order of abundance, was composed of *D. g. mendotae*, *D. pulex*, and *D. longiremis*. Finnell and Reed (1969) and Nelson (1971) showed that *D. longiremis* was most abundant below 10 m, *D. pulex* was concentrated above 9–10 m, and *D. g. mendotae* was concentrated above 10 m. Maximum densities (number per liter) reported by Nelson (1971) from 1963 to 1965 were 18.4 for *D. g. mendotae*, 16.7 for *D. longiremis*, and 3.9 for *D. pulex*.

The composition of the Lake Granby daphnid community changed after the introduction of *M. relicta*. *Daphnia longiremis*, which formerly appeared in the kokanee diet (Finnell and Reed 1969), was not seen during the current study. Nelson (1971) suggested that predation on this species may have been slight because it was small (0.48–1.26 mm long; modal peaks at 0.61 and 0.81 mm) and concentrated in deep water. Although *D. pulex* was extremely rare during our study, it was once the species most heavily used by kokanees, composing 85% of all organisms ingested in 1965 and 92% in 1966 (Finnell and Reed 1969).

Seasonal Zooplankton Densities

Daphnia g. mendotae and *Bosmina longirostris* essentially composed the cladoceran community during our study. Both appeared in small numbers by late June. Although bosminids outnumbered daphnids in July in 1981 and 1982, daphnids surpassed bosminids for the rest of the year (Table 2). *Daphnia g. mendotae* flourished in all years of our study and its density peaked from late August to early September (Martinez 1986). *Daphnia pulex*, which appeared in October and November 1981 and in October and December 1982, never exceeded a mean density of 0.1/L (Martinez 1986). L. M. Finnell (Colorado Division of Wildlife, unpublished report) reported small numbers of cladocerans and copepods in Lake Granby in May and indicated that zooplankton concentrations in the upper strata peaked by late June or early July. He noted peak cladoceran numbers in July or August. Nelson (1971) suggested that densities of daphnids were greatest from late July to early August. Apparently, the seasonal abundance of daphnids in Lake Granby shifted after the establishment of mysids, as was reported for cladocerans in Pend Oreille Lake by Rieman and Bowler (1980), Rieman and Falter (1981), and Bowles et al. (1986). These investigators also reported seasonal shifts in abundance of *B. longirostris*. Unfortunately, no similar comparisons can be made for Lake Granby because historical data on bosminid abundance are lacking. The highest daphnid density seen during our study, in November 1982 (Table 2), may or may not have reflected typical population dynamics of *D. g. mendotae* in Lake Granby; however, it showed that substantial numbers of daphnids persisted in the presence of an established mysid population.

The cyclopoid copepod *Diacyclops bicuspidatus thomasi* was the most abundant crustacean zooplankter seen throughout our study (excluding nauplii), and was present in all collections (Table 2). It was virtually the only crustacean zooplankter in samples collected through the ice (Martinez 1986). The calanoid copepod *Diaptomus nudus*, rare throughout our study, appeared to be best represented from October to December (Martinez 1986).

Temporal and Spatial Distribution

Generally, all species of zooplankton were most abundant at depths above 10 m. Typically, *Daphnia g. mendotae* was concentrated above 10 m with peak densities above 5 m. Nelson (1971) found this species concentrated above 10–13 m in other Colorado lakes and reservoirs. The greatest density of *D. g. mendotae* observed in the main lake during our study exceeded 60/L at 0–5 m at

TABLE 2.—Mean midday densities of dominant crustacean zooplankton above 10 m in Lake Granby, 1981 and 1982.

		Density (number/L) of				
Date	Number of samples	*Bosmina longirostris*	*Daphnia galeata mendotae*	*Daphnia pulex*	*Diacyclops bicuspidatus thomasi*	*Diaptomus nudus*
1981						
Jun 18	2	<0.1	<0.1		34.8	
Jul 7	2	29.5	0.8		70.7	<0.1
Aug 23	7	14.4	38.0		31.5	<0.1
Sep 6	7	10.6	31.7		24.4	<0.1
Sep 26	7	5.4	17.3		12.1	<0.1
Oct 18	7	1.9	6.4	<0.1	11.0	0.1
Nov 21	7	3.0	18.3	<0.1	68.5	0.4
Dec 20	5	0.5	3.6		50.4	<0.1
1982						
Jun 1–2	12	<0.1	<0.1		3.5	
Jun 28–29	12	1.2	<0.1		9.7	<0.1
Jul 27–28	12	16.4	3.1		23.2	<0.1
Sep 3–4	12	4.3	27.7		29.3	<0.1
Oct 10–11	12	1.8	14.1	<0.1	19.0	0.3
Nov 14	12	6.0	64.9	<0.1	38.5	0.6
Dec 4	8	1.1	9.9	<0.1	46.6	0.1

the deep station in November 1982. *Daphnia pulex*, when present, showed no distinct distribution pattern; however, Finnell and Reed (1969) and Nelson (1971) found this species occasionally more abundant at depths of 5–20 m than at 0–5 m. *Diacyclops b. thomasi* occurred in all strata and was the most abundant crustacean below 10 m. *Diaptomus nudus*, which rarely exceeded a density of 0.2/L, was most abundant above 20 m (Martinez 1986).

Diel-stratified sampling in 1982 did not clearly demonstrate vertical migrations by zooplankton. Although densities within the same stratum differed among the four diel sampling periods (daylight, dusk, darkness, and dawn), the strata may not have been narrow enough to define vertical movements (Martinez 1986). Finnell and Reed (1969) did not observe diel vertical distribution trends in Lake Granby daphnids. In nearby Grand Lake, Pennak (1944) found no vertical migrations of *Diacyclops b. thomasi* and only moderate diel vertical movement (5.8 m) of *Daphnia longispina*.

Diel movements of *M. relicta* were clearly evident. Changes in mysid densities in the water column were closely correlated with echograms of mysid distributions (Martinez 1986). Typically, mysids were near the bottom or in deep water during daylight and migrated upward at night. At dawn, they returned to deep water. These downward migrations were rapid. Echograms indicated that the *M. relicta* population, pelagic at 10–20 m before dawn, descended to 40–50 m within 15–20 min. The upward migration at dusk appeared to be slower, requiring 30–40 min regardless of the vertical distance. These rates were similar to those reported by Rybock (1978) for ascents (48 m/h) and descents (100 m/h) of *M. relicta* in Lake Tahoe.

Finnell and Reed (1969) reported that kokanees in Lake Granby occupied the upper 9 m by day and migrated downward at night, when they concentrated between 9 and 18 m. Observations of kokanee movements during our study differed slightly. Echograms showed that kokanees were primarily above 10 m by day but occurred down to 20 m. They began descending at dusk, were concentrated between 10 and 20 m at night, and returned into surface waters at dawn (Figure 2).

Crustacean zooplankton appeared to be the organisms least affected by seasonal changes in limnological conditions. However, water circulation during the fall turnover distributed zooplankters (usually concentrated in the upper 10 m) throughout the water column.

The vertical extent of the diel mysid migration appeared to be restricted by temperature. *Mysis relicta* occurs in cold water, down to −2°C (Holmquist 1963), and has a strong preference for waters less than 14°C (Morgan 1979; Pennak 1989). It can withstand temperatures up to 20°C only through very gradual acclimation (Holmquist 1959; Smith 1970; DeGraeve and Reynolds 1975). Although *M. relicta* can endure high temperatures for short periods, DeGraeve and Reynolds (1975) demonstrated that mortality increased rapidly at temperatures above 13°C.

Mysids in Lake Granby did not enter surface waters when thermal stratification developed and

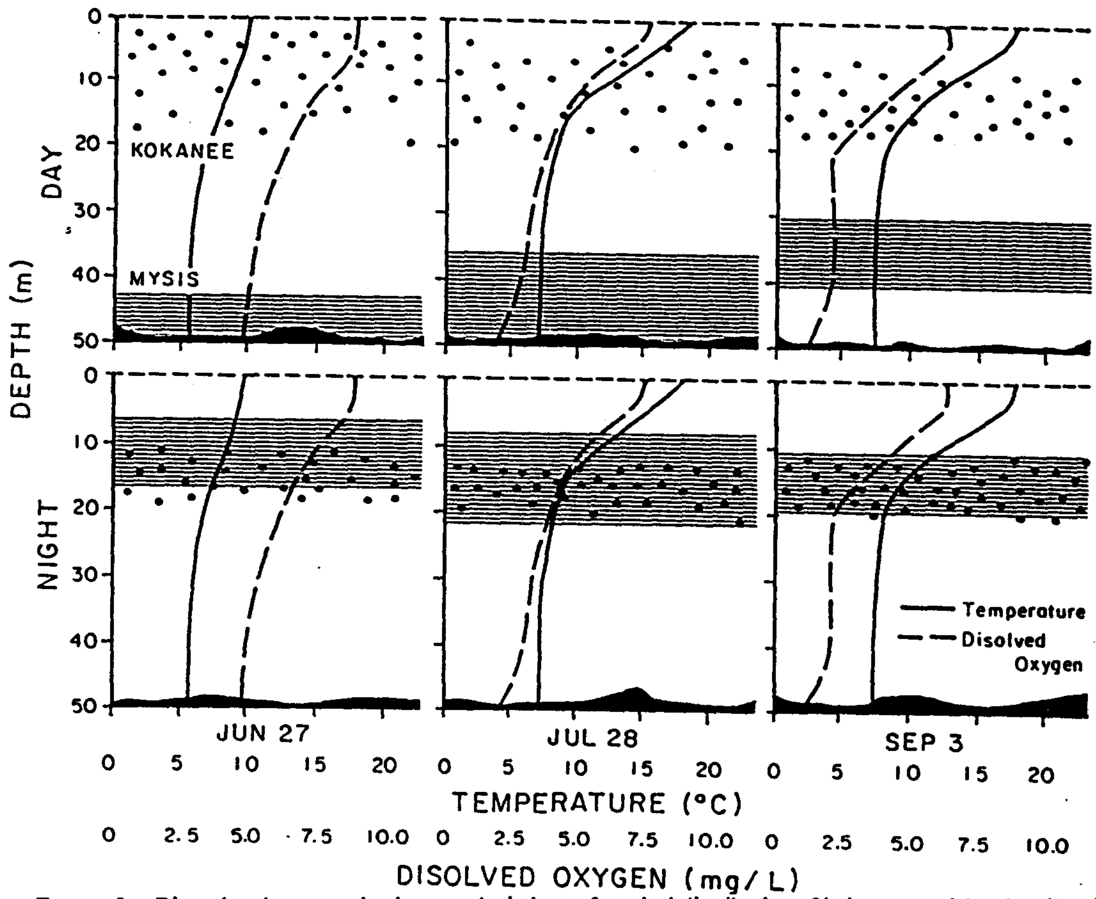

FIGURE 2.—Diurnal and nocturnal echogram depictions of vertical distribution of kokanees and *Mysis relicta* in Lake Granby at station A on 27 June, 28 July, and 3 September 1982. Solid line shows temperature profile; dotted line shows dissolved oxygen profile.

epilimnetic temperatures exceeded 14°C (Figure 3). As the epilimnion thickness increased, the upward limit of the vertical migration of *M. relicta* progressed downward. Beeton (1960) demonstrated not only that light was the most important factor governing timing of these vertical migrations, but that high epilimnetic temperatures were important in limiting vertical distribution. When thermal stratification was pronounced in Lake Granby during late July to mid-September, mysids were effectively excluded from the upper 10–11 m of the reservoir. It appeared that most of the population did not enter the upper water column where temperatures exceeded 14°C. Similarly, Rieman and Falter (1981) found that *M. relicta* in Pend Oreille Lake was seasonally isolated from the upper 10 m of the water column in August and September by increasing thermal stratification.

Mysis relicta also requires well-oxygenated water and can tolerate conditions of less than 2 mg/L for only short periods (Juday and Birge 1927; Brownell 1970; Sandeman and Lasenby 1980). Despite its ability to reduce oxygen consumption as ambient temperatures and oxygen concentrations decrease, it remains intolerant of oxygen below 2–3 mg/L (Sandeman and Lasenby 1980).

Declining dissolved oxygen in Lake Granby during late summer and fall was correlated with both vertical and horizontal movements of the mysid population. Hypolimnetic oxygen depletion began soon after the spring turnover. By late August or early September, dissolved oxygen below 40 m fell to less than 2 mg/L and the entire mysid population was suspended off the bottom (Figure 2). This avoidance of hypoxic conditions by mysids was evident in stratified Clarke–Bumpus net collections and in echograms (Martinez 1986). By October, dissolved oxygen concentrations at depths greater than 20 m fell below 2 mg/L

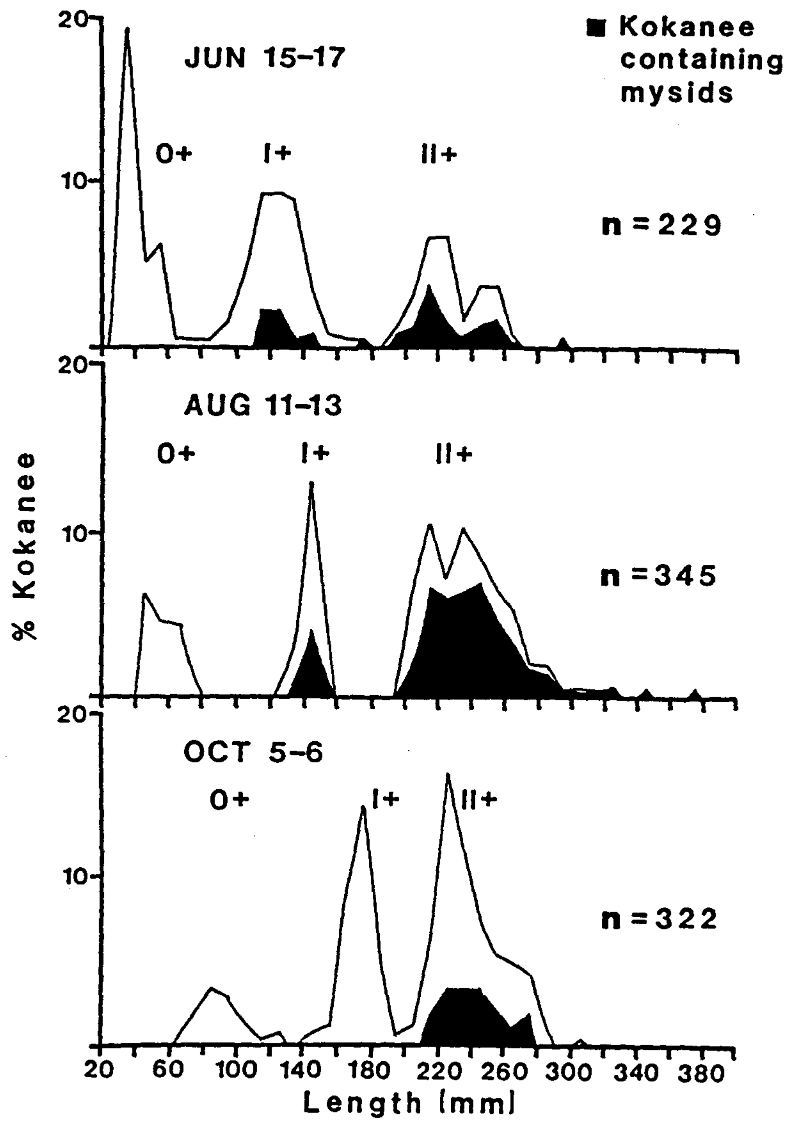

FIGURE 3.—Kokanee length-frequencies and occurrences of *Mysis relicta* in kokanee stomachs in Lake Granby, 1982.

(Martinez 1986). Instead of suspending in the water column above 20 m, most of the mysid population moved horizontally in the reservoir. They were scarce or absent in stratified zooplankton samples (Martinez 1986), absent in pelagic echogram records, and very abundant in epibenthic trawl collections taken in water 3–7 m deep (Table 3). Horizontal migrations of mysids from deep to shallow water in response to low dissolved oxygen in deeper portions of lakes have been documented by other investigators (Tattersal and Tattersal 1951; Holmquist 1959; Lasenby 1971; Morgan and Threlkeld 1982). In Lake Granby, *M. relicta* reappeared in open-water zooplankton samples below 20 m by late November, after fall turnover had replenished dissolved oxygen in deeper waters (Martinez 1986). Lasenby (1971) reported similar timing for the return of mysids to the depths of Stony Lake, Ontario, after the fall turnover. The abundance of *M. relicta* in inshore areas appeared to diminish as ice formation began in December (Table 3).

The persistence of large numbers of mysids in shallow water at station 1 (Table 3) may be

TABLE 3.—Occurrence of *Mysis relicta* in shallow water (3–7 m) in Lake Granby in 1982. A = abundant; P = present; 0 = absent. Stations are shown in Figure 1.

	Station					
Date	1	2	3	4	5	6
Jun 1	A	A	P	A	P	A
Jun 27	A	0	0	P	0	0
Jul 27	0	0	0	0	0	0
Sep 3	A	0	0	0	0	0
Oct 10	A	A	A	A	A	A
Nov 14	P	A	A	A	A	A
Dec 4	P	P	P	Ice	P	P

explained by age composition. Station 1 was in a large, relatively shallow part of the reservoir (Figure 1). All mysids collected in epibenthic trawls in this area during summer were young of the year. The summer occurrence of predominantly juvenile mysids in deeper water near station 1 was also noted by W. C. Nelson (Colorado Division of Wildlife, personal communication). Morgan and Threlkeld (1982) described horizontal migrations of newly hatched juvenile mysids into shallow water during summer in Lake Tahoe and nearby lakes. Juvenile mysids appeared less sensitive to light and temperature (Gosho 1975), which would explain their tolerance of summer conditions in shallower waters.

Water temperatures also appeared to influence the vertical distribution of kokanees. Generally, kokanees migrated to the lake surface during the day and to deeper waters at night (Finnell and Reed 1969). From late July to early September, when surface water temperatures were highest, kokanees did not appear to enter the upper few meters of water in the reservoir during daylight (Figure 2). Water temperatures at 0–3 m often exceeded 18°C during this period. This observation of kokanees avoiding near-surface waters was consistent with Brett's (1971) finding that the natural occurrence of the anadramous, conspecific sockeye salmon is limited to temperatures at or below 18°C, despite its ability to tolerate 24°C. Similarly, Finnell and Reed (1969) found kokanees in Lake Granby to be most abundant at depths of 4.5–13.5 m during the day from late July to mid-September. Because kokanees lived in the upper 20 m of the reservoir, oxygen depletion probably had no direct effect on their distribution.

Trophic Relations of Zooplankton, *Mysis relicta*, and Kokanees

Zooplankton in Mysid Diet

In June and July, rotifers (primarily *Kellicottia longispina* and a few *Keratella cochlearis*) composed the bulk of the zooplankters in the mysid diet (Table 4). The large rotifer *Asplanchna* sp., which appeared to be abundant in spring and early summer, was not detected in mysid guts. Either it was not eaten or we failed to recognize its parts among other zooplankton fragments. Rybock (1978) found positive selection for *K. longispina* by *M. relicta* in Lake Tahoe; however, Cooper and Goldman (1980) and Langeland (1981) showed that mysids fed on larger prey when available. As

TABLE 4.—Numbers and percentages (in parentheses) of zooplankton prey in pooled stomach contents of *Mysis relicta* (10–18 mm long) collected in Lake Granby, 1982.

	Date and sample size							
Prey type	Jun 1[a] $N = 49$	Jun 27[a] $N = 46$	Jul 27[a] $N = 62$	Aug 11[b] $N = 35$	Sep 3[a] $N = 28$	Oct 11[b] $N = 25$	Nov 14[b] $N = 30$	Dec 4[c] $N = 20$
Bosmina longirostris		2 (0.5)	143 (23.7)	238 (52.8)	37 (60.7)	12 (21.8)	15 (26.9)	4 (16.0)
Daphnia galeata mendotae				58 (12.9)	21 (34.4)	37 (67.2)	9 (16.0)	5 (20.0)
Diacyclops bicuspidatus thomasi			27 (4.5)	6 (1.3)		3 (5.5)		
Kellicottia longispina	345 (98.0)	334 (90.8)	424 (70.3)	149 (33.0)	3 (4.9)	3 (5.5)	32 (57.1)	16 (64.0)
Keratella cochlearis	7 (2.0)	32 (8.7)	9 (1.5)					

[a]*Mysis relicta* from Clarke–Bumpus collections.
[b]*Mysis relicta* from epibenthic trawl collections.
[c]*Mysis relicta* from Clarke–Bumpus and epibenthic trawl collections combined.

TABLE 5.—Frequency of occurrence of food items in stomachs of kokanees collected at night with a midwater trawl in Lake Granby, 1982 and 1983.

Date	Number of kokanees captured	Number of stomachs examined	Number (%) of food items: Crustacean zooplankton[a]	Insects[b]	*Mysis relicta*	Number (%) of empty stomachs
1982						
Jun 15–17	249	229	201 (87.8)	88 (38.4)	42 (18.3)	4 (1.7)
Aug 11–13	353	345	343 (99.4)	50 (14.5)	172 (49.9)	0
Oct 5–6	326	322	294 (91.4)	0	52 (17.7)	4 (1.2)
1983						
Jul 11–12	276	273	264 (96.7)	250 (91.6)	12 (4.4)	2 (0.7)
Aug 23–24	354	353	351 (99.4)	17 (4.8)	84 (23.8)	1 (0.2)
Oct 13	72	71	62 (87.3)	8 (11.3)	17 (23.9)	5 (7.0)

[a]Includes *Bosmina longirostris*, *Daphnia galeata mendotae*, *Daphnia pulex*, *Diacyclops bicuspidatus thomasi*, and *Diaptomus nudus*; however, not all species were consumed on all dates.
[b]Includes chironomids (pupae and adults) and hypmenopterans (ants).

cladoceran abundance and their consumption by mysids increased in August, fewer rotifers were eaten. Although rotifer densities were not determined, rotifers appeared to be relatively abundant throughout the open-water season. As cladoceran numbers diminished in late fall, *K. longispina* again became prevalent in the mysid diet (Table 4).

Daphnia spp. and *Bosmina* spp. are preferred prey of *M. relicta* (Lasenby and Langford 1973; Langeland 1981; Lasenby and Fürst 1981), but daphnids are preferred over other zooplankters (Grossnickle 1978; Cooper and Goldman 1980). *Bosmina longirostris*, appearing before *Daphnia g. mendotae* in early summer in Lake Granby, also appeared earlier in mysid stomachs and continued to be eaten in relatively large numbers for the rest of the year (Table 4). Even after July, when daphnids were more numerous at all depths, mysids in Lake Granby appeared to select *B. longirostris* as preferred prey. *Daphnia g. mendotae* was abundant and was eaten by mysids in August and September, but it did not compose the highest percentage of ingested zooplankters until October. Although *B. longirostris* and *D. g. mendotae* were most abundant above 10 m, both occurred in deeper water and were available to *M. relicta* even during summer when it was isolated from surface waters.

Despite its abundance and occurrence at all depths, few *Diacyclops bicuspidatus thomasi* appeared in mysid stomachs (Table 4). Lasenby (1971) found that mysids in Stony Lake also fed almost exclusively on cladocerans in summer, even in the presence of abundant copepods. Lasenby and Fürst (1981) suggested that mysids eventually would feed on copepods if cladoceran numbers remained low. *Diaptomus nudus* was not found in mysid guts, perhaps because of its scarcity, although mysids elsewhere have shown low (Grossnickle 1978) to negative (Rybock 1978) selection for *Diaptomus* spp.

Kokanee Food Habits

Kokanees in Lake Granby fed on crustacean zooplankton and insects (chironomid pupae and larvae and ants). Only a few rotifers and a single small kokanee were seen in kokanee stomachs. Crustacean zooplankton (cladocerans and copepods) appeared in 87–99% of the kokanee stomachs examined during all sampling periods (Table 5). The frequency of insect occurrence in kokanee stomachs ranged widely among the six sampling dates—from 0 to almost 92%. *Mysis relicta* occurred in 4–50% of the kokanees. The incidence of empty stomachs was low, ranging from 0 in July 1982 to 7% in October 1983.

The use of *Bosmina longirostris*, *Diacyclops bicuspidatus thomasi*, and insects by kokanees in Lake Granby was greatest in spring and early summer. Relatively few *B. longirostris* appeared in kokanee stomachs and (partly because of their small size) they contributed little to the biomass of the kokanees' diet (Table 6). Although *D. b. thomasi* was eaten by kokanees during all sampling periods, it contributed most to the diet biomass early in the year (Table 6). In Lake Chelan, Washington, Brown (1984) reported heavy, selective use of *Bosmina* spp. by kokanees. In Pend Oreille Lake, *Bosmina* spp. was an important kokanee food during spring and early summer, but it was little used when cyclopoids were extremely abundant (Rieman and Bowler 1980). Finnell (unpublished) reported heavy consumption of copepods and light use of aquatic and terrestrial insects by Lake Granby

TABLE 6.—Numbers and dry weight (mg) of food items in pooled stomach contents of age-0, age-1, and age-2 kokanees collected at night with a midwater trawl in Lake Granby, 1982 and 1983. *N* is the number of stomachs with food.

Date	Food item[a]	Age 0		Age 1		Age 2	
		Number	Weight	Number	Weight	Number	Weight
1982							
Jun 15–17		(*N* = 75)		(*N* = 85)		(*N* = 65)	
	Bosmina			4,718	12	605	2
	Diacyclops	5,998	33	69,873	384	31,241	172
	Insects	22	105	94	448	628	2,995
	Mysis			32	191	265	1,586
Aug 11–13		(*N* = 58)		(*N* = 70)		(*N* = 217)	
	Daphnia	12,518	89	191,034	1,356	449,048	3,188
	Bosmina	133	1	80	1	132	1
	Diacyclops	1,051	5	3,720	16	8,381	37
	Insects	29	138	14	67	233	1,111
	Mysis			39	262	1,134	7,613
Oct 5–6		(*N* = 33)		(*N* = 99)		(*N* = 186)	
	Daphnia	24,526	267	117,244	1,278	538,897	5,874
	Diacyclops	327	2	3,113	17	3,750	21
	Mysis					1,865	11,827
1983							
Jul 11–12		(*N* = 21)		(*N* = 15)		(*N* = 235)	
	Daphnia	120	1	300	2	2,523	18
	Bosmina	188	1	1,460	3	2,707	6
	Diacyclops	2,710	15	8,423	46	135,253	730
	Insects	33	145	437	1,926	1,205	5,311
	Mysis					47	298
Aug 23–24		(*N* = 37)		(*N* = 65)		(*N* = 250)	
	Daphnia	11,795	109	145,810	1,341	640,880	5,896
	Diacyclops	40	1	1,420	7	3,030	15
	Insects	7	31	3	13	27	119
	Mysis			14	89	227	1,440
Oct 13		(*N* = 5)		(*N* = 18)		(*N* = 43)	
	Daphnia	160	2	3,598	37	2,615	27
	Diacyclops	200	1	130	1	215	1
	Diaptomus			1,230	26	1,860	39
	Insects	5	22	8	35		
	Mysis	4	25			43	273

[a]Insects include chironomids (pupae and adults) and hypmenopterans (ants).

kokanees in early spring. In contrast, during the earliest sampling periods in 1982 and 1983, insects composed the bulk of the biomass ingested by kokanees of all ages (Table 6). Because of the comparatively large size of insects, relatively few made up a large percentage of the diet biomass.

Daphnia g. mendotae was the most used food of kokanees of all sizes after July, usually outnumbering all other organisms combined. Information on diet obtained from kokanees captured in gill nets also showed this (Martinez 1986). Clearly, the species composition of the kokanee diet has changed since Finnell and Reed (1969) reported that *D. pulex* was the most heavily used and preferred food of Lake Granby kokanees in the 1960s. Kokanee preference for daphnids is well documented (Rieman and Bowler 1980; Leathe and Graham 1982; Vinyard et al. 1982). As one of the larger crustacean zooplankters in the reservoir, *D. g. mendotae* also contributed significantly to the kokanees' diet biomass (Table 6).

The limited use of *Daphnia pulex* and *Diaptomus nudus*, the largest limnetic entomostracans, was probably due to their scarcity. *Diaptomus nudus* was absent from all kokanee stomachs examined except in October 1983, when it appeared in the stomachs of 1- and 2-year-old kokanees (Table 6). Large numbers of *Daphnia pulex* were found in the stomachs of 12 kokanees collected in a gill net on December 4, 1982. The net was set in the vicinity of zooplankton sampling station A (Figure 1). Zooplankton samples collected nearby at station A on the same day contained high densities of *Daphnia g. mendotae* and very few *Daphnia pulex*. These observations corroborate the strong selection for *Daphnia* *pulex* by kokanees in Lake Granby reported by Finnell and Reed (1969), even when the density of this daphnid is very low.

Use of Mysids by Kokanees

Although other food items were seasonally important to kokanees, there was no distinct peak in use of mysids. They appeared in nearly 50% of the kokanee stomachs examined in August 1982 (Table 6), and some stomachs contained mysids almost exclusively, but overall, few kokanees fed on them. Only 29% ($N = 896$) of the stomachs examined contained mysids in 1982 and 16% ($N = 697$) in 1983. Rieman and Bowler (1980) found *M. relicta* in 19–23% of the kokanee stomachs examined in Pend Oreille Lake in 1977–1978.

Rieman and Bowler (1980) reasoned that the contribution of mysids to the kokanee diet was less than such percentages indicated. *Mysis relicta* typically is not available to kokanees during the day (when kokanees often feed). If stomachs for food analysis came from kokanees collected just after dusk, the samples would tend to overrepresent the actual contribution of mysids to the daily kokanee ration (Rieman and Bowler 1980). Because kokanees in Lake Granby feed diurnally (Finnell and Reed 1969) and the stomachs examined in this study were from kokanees collected just after dusk, the same bias probably applies. In the gut samples, *M. relicta* appeared to be the last item ingested, which further supports this contention.

As with insects, mysids (because they are large) contributed substantially to the biomass of the kokanee diet, even when comparatively few were ingested. Overall, however, the numbers of ingested mysids were low. Individual kokanees contained up to 176 mysids, but most contained only 1–5 (Martinez 1986). There appeared to be a trend in Lake Granby toward higher mysid use by larger (≥200 mm) kokanees (Figures 3 and 4). This trend was reported also for kokanees in Lake Tahoe (Morgan et al. 1978) and Pend Oreille Lake (Rieman and Bowler 1980). The smallest kokanee to contain mysids during this study was 87 mm long. Rieman and Bowler (1980) reported *M. relicta* in kokanees as short as 40–45 mm.

Interactions of Daphnids, Mysids, and Kokanees

Daphnids versus Mysids

The disappearance of *Daphnia longiremis* in Lake Granby probably was caused by mysid predation. Because this cladoceran occurred in the hypolimnion (Finnell and Reed 1969), it was available to *M. relicta* as prey. Threlkeld et al. (1980) and Morgan et al. (1981) suggested that cladoceran species inhabiting deep water in lakes typically disappear after mysids are introduced.

Because daphnids were concentrated above 10 m, they were spatially separated from *M. relicta* for nearly 2 months (late July to mid-September). This seasonal exclusion of mysids from surface waters provided a thermal sanctuary for daphnids. Threlkeld et al. (1980) and Morgan et al. (1981) stressed the importance of thermal refugia in the coexistence of daphnids and mysids, and they proposed such refugia as the principal mechanism that allows cladocerans to persist in lakes containing natural mysid populations.

Temporal shifts in the development of daphnid populations have been attributed to intense selective predation by mysids (Rieman and Falter 1981). A similar pattern was evident in Lake Granby in the spring when mysids inhabited the entire water column during their vertical migration and, in the upper strata, preyed selectively on daphnids at night, severely depressing numbers of daphnids and inhibiting population development. As the thermal refuge developed in the summer, the daphnid population recovered rapidly and attained premysid densities, despite the presence of fewer species (Figure 5).

The importance of a thermal refuge in limiting mysid predation on epilimnetic daphnids is further supported by the scarcity of *Daphnia* spp. in Grand Lake, Dillon Reservoir, and Lower Twin Lake (Table 7). These waters formerly contained thriving populations of daphnids and also supported kokanee fisheries. Because *Daphnia* spp. became scarce after *M. relicta* was established, these lakes are no longer managed for kokanees. The stocking of juvenile rainbow trout has been discontinued in Dillon Reservoir because the trout was suspected of competing with stunted kokanees for extremely limited cladoceran forage (Stuber et al. 1985)—a situation apparently aggravated by a dense mysid population.

Thermal conditions appear to be the most important factor in the coexistence of daphnids and introduced mysids. In Colorado waters, where low epilimnetic temperatures allow *M. relicta* to enter surface waters almost year-round, daphnids can be expected to become scarce (Nesler 1986). Although surface temperatures exceed 14°C in Grand and Lower Twin lakes (Table 7), subsurface water temperatures are lower, and the short-

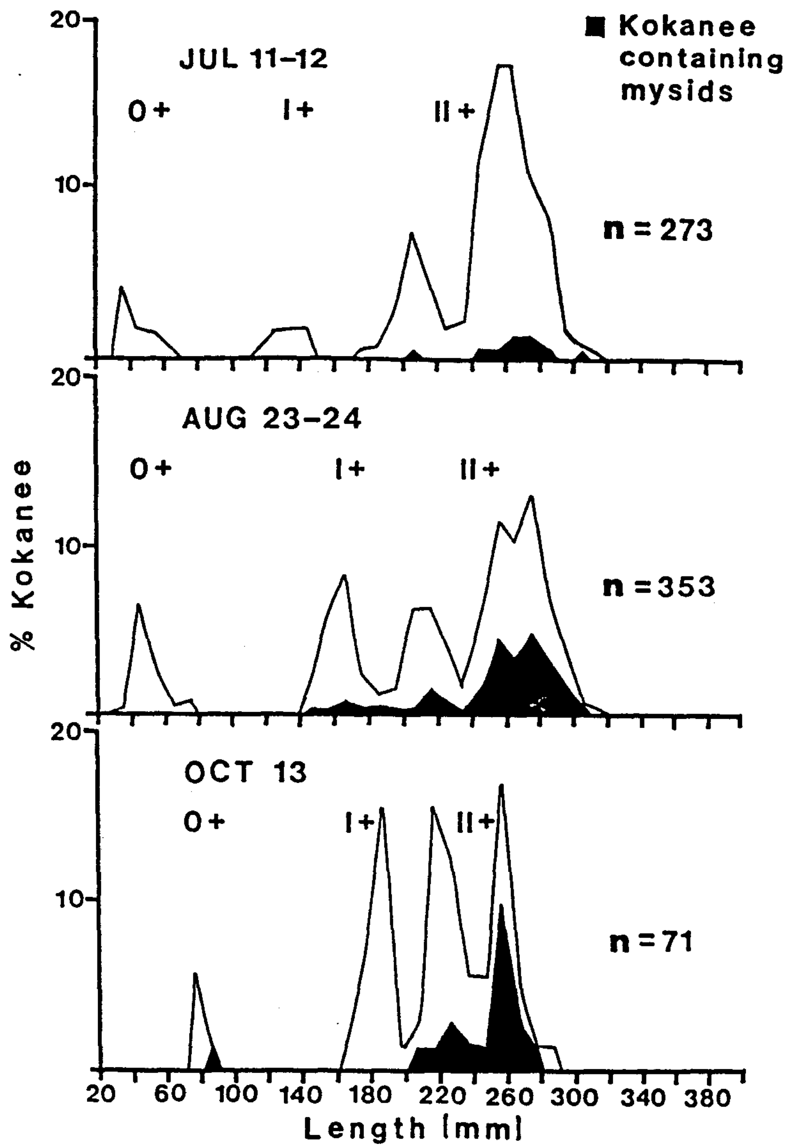

FIGURE 4.—Kokanee length-frequencies and occurrences of *Mysis relicta* in kokanee stomachs in Lake Granby, 1983.

ness of the warmwater period apparently does not exclude mysids long enough to allow daphnid populations to develop. In Lake Granby, where mysids are excluded from surface waters for nearly 2 months, daphnids persist.

The small numbers of *M. relicta* in Green Mountain Reservoir suggest that thermal regimes also may be important in establishing dense mysid populations. Green Mountain Reservoir does not stratify pronouncedly in summer (Table 7); instead, because of the reservoir's low retention time, water temperatures decrease gradually from top to bottom (Nelson 1981). Such thermal conditions apparently are not conducive to proliferation of *M. relicta*, because most of the reservoir exceeds 14°C during summer. Nelson (1981) suggested that inflow–outflow conditions in Green Mountain Reservoir did not favor development of a mysid population. This appears to have held true in the 15 years following the *M. relicta* introduction in the reservoir, where it is now rare to absent and daphnids remain abundant (Table 7).

Daphnia g. mendotae remained the dominant

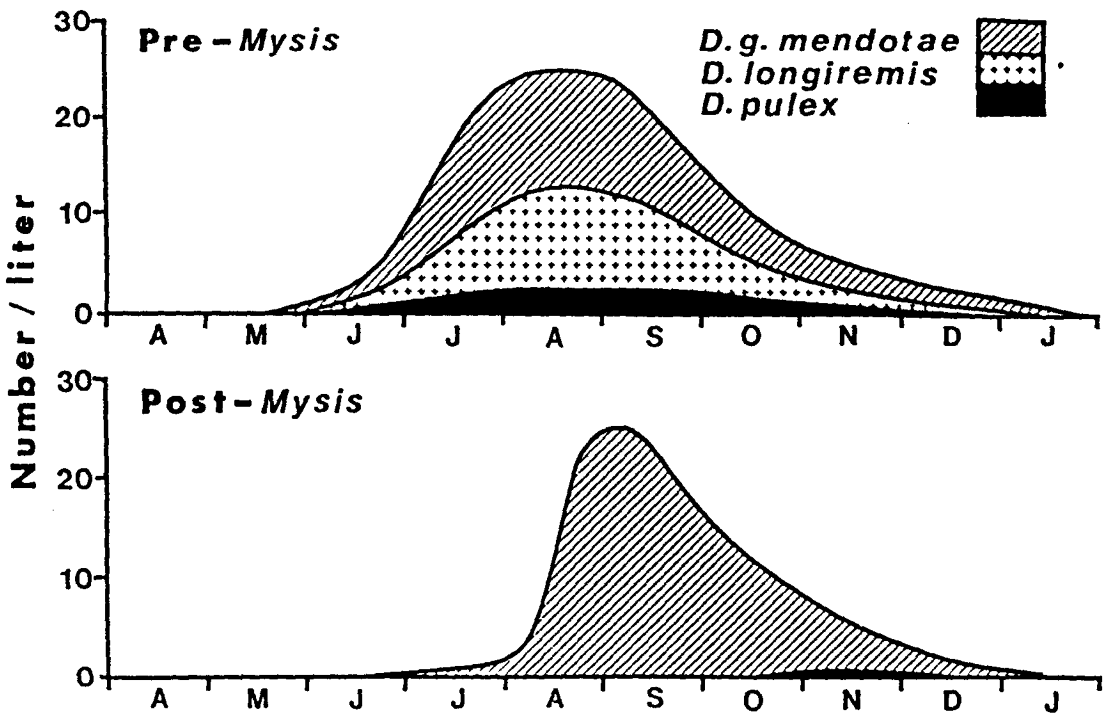

FIGURE 5.—Trends in composition and abundance for three species of *Daphnia* before and after the establishment of *Mysis relicta* in Lake Granby.

cladoceran in Lake Granby after mysids fed on the daphnid population. Rieman and Falter (1981) wrote that it replaced *D. thorata* as the dominant daphnid after *M. relicta* became established in Kootenay and Pend Oreille lakes. These investigators suggested that the helmet spikes of *D. g. mendotae* gave it a survival advantage over round-helmeted *D. thorata*. Because *M. relicta* must seize and manipulate larger prey for ingestion (Cooper and Goldman 1980), the helmet spikes might foil mysid attacks by impeding such manipulation. This feature alone, which can develop in several *Daphnia* species including *D. longiremis* (Zaret 1980), is not sufficient to avert mysid predation—as evidenced by the disappearance of the spike-forming species in several Colorado lakes. It may, however, preserve greater numbers of *D. g. mendotae*, whose populations can rebound more quickly once mysid predation is curbed by thermal stratification.

Typically, *D. pulex* was concentrated above 10 m in Lake Granby (Finnell and Reed 1969; Nelson

TABLE 7.—Comparison of *Mysis relicta* introduction dates and current status, mean August temperature profiles, and current status of daphnid populations in five Colorado lakes.

Species and variable	Lake Granby	Grand Lake	Green Mountain Reservoir	Dillon Reservoir	Lower Twin Lake
Mysis relicta					
Year introduced	1971	1969	1974	1970	1962
Status 1983[a]	A	A	RA	A	A
Water temperature (°C)[b]					
Surface	18	15	16	14	16
10-m depth	15	10	16	13	13
20-m depth	9	7	14	8	8
40-m depth	8	5	12	6	
Daphnia spp.					
Status 1983[a]	A	RA	A	RA	RA

[a]A = abundant; RA = rare to absent.
[b]Temperature data for all lakes except Lower Twin Lake are from Nelson (1981).

1971) and should have received the same sanctuary in warm surface waters enjoyed by *D. g. mendotae*. That it did not indicates selective fish predation was responsible for the suppression of *D. pulex* numbers.

Daphnids versus Kokanees

The virtual elimination of *D. pulex* in Lake Granby probably was among the chief causes of the kokanee fishery's decline. Ironically, the scarcity of *D. pulex* in 1981–1983 apparently resulted from intense kokanee predation that followed kokanee overstocking. Despite its addition to the reservoir from surrounding impoundments (Martinez 1986), *D. pulex* has been unable to recolonize the reservoir.

Suppression of particular daphnid species, however, depends not only on selective removal of larger members of the population, but on whether the fish consume both mature and immature forms (Galbraith 1967). If fish feed primarily on mature daphnids, adequate numbers of reproducing females usually survive to sustain the population; this tends not to be the case if fish consume immature as well as mature daphnids (Galbraith 1967). Obviously, size at maturity becomes an important factor in the capacity of different daphnid species to withstand fish predation. *Daphnia g. mendotae* typically matures at about 1 mm and *D. pulex* at 2 mm (Zaret 1980). In Lake Granby, kokanees preyed primarily on *D. g. mendotae* longer than 1 mm, whereas most of the *D. pulex* in kokanee stomachs were shorter than 2 mm (Martinez 1986). Consistent with Galbraith's (1967) findings, *D. pulex* appeared unable to sustain a viable population when faced with intense predation by kokanees.

This suppression of *D. pulex* implies that the rate of kokanee predation on limnetic daphnids has increased since the kokanee harvest and egg take went into decline in the late 1970s. At that time, larger kokanees appeared in fishermen's creels and in spawning runs. In the early 1980s, the Lake Granby kokanee fishery was characterized by low harvest of small kokanees and record numbers of smaller and older spawners (Table 1). Brown (1984) reported a negative relation between mean size of kokanees and angler catch rate. This negative relation seemingly developed in Lake Granby (Martinez and Wiltzius 1991). The reduced catch rate and harvest meant that thousands of kokanees were not removed by fishermen and remained in the lake. These trends toward smaller kokanees, lower harvests, and numerous spawners led to stunting due to overstocking (Martinez and Wiltzius 1991). Stunting undoubtedly increased intraspecific competition between all age-classes of kokanees that rely on the same pelagic foods. It seems reasonable to presume that this competition intensified predation on all available prey, particularly on preferred items.

Daphnia g. mendotae may have an additional survival advantage over *D. pulex* because of its extreme transparency, which conceivably protects it from sight-feeding kokanees. Transparency in zooplankton is believed to be an effective adaptation against sight-feeding predators (Kerfoot 1980). Nelson (1971) suggested that *D. g. mendotae* may have been protected from fish predation by its ability to produce small, helmeted morphs during summer. Both helmeted and unhelmeted forms occurred in Lake Granby during our study. Possibly transparency and smaller morphs both contributed to the persistence of *D. g. mendotae* by making detection by kokanees more difficult.

Mysids versus Kokanees

It appears that the decline of the Lake Granby kokanee fishery can be attributed to changes in the daphnid populations resulting from the joint effects of intense selective predation by introduced mysids and overabundant kokanees, particularly kokanees. Although thermal conditions allow daphnids to persist in the reservoir, the temporal shift of the daphnid population may effectively shorten the season of optimum kokanee growth. Kokanees now appear to grow only during a 2-month period from late August to late October (W. J. Wiltzius, Colorado Division of Wildlife, personal communication).

Because kokanee growth is strongly density dependent (Goodlad et al. 1974; Leathe 1984), stunting of the kokanee population before *Mysis* became established could have been easily corrected by a reduction in stocking rate. However, the postmysid situation may be more complex. It does not appear that the inclusion of other zooplankton, insects, or even *M. relicta* in the kokanee diet has adequately compensated for the diminished daphnid forage. The reduction in annual growth may mean that the reservoir can no longer support the kokanee density that produced exceptional kokanee fishing (Table 1).

Martinez and Wiltzius (1991) noted an increased frequency of occurrence of *M. relicta* in Lake Granby kokanees and rainbow trout in September 1981. Because hypolimnetic oxygen became depleted by August (Martinez 1986), many mysids may have been trapped between hypoxic conditions in deeper waters and high temperatures in the epilimnion, which could have increased their availability to the fish.

Despite the trend toward higher use of mysids by larger kokanees, the consumption of *M. relicta* in populations containing more large kokanees would probably remain low. Simply put, *M. relicta* typically is available to kokanees only at night when the fish cease feeding (Finnell and Reed 1969; Doble and Eggers 1978). *Mysis relicta* has not enhanced kokanee growth in Lake Granby and probably will not benefit kokanees in other Colorado lakes where it has become established.

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