Effects of Rotenone on Zooplankton Communities and a Study of their Recovery Patterns in Two Mountain Lakes in Alberta[1]

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ANDERSON, R. S. 1970. Effects of rotenone on zooplankton communities and a study of their recovery patterns in two mountain lakes in Alberta. J. Fish. Res. Bd. Canada 27: 1335–1356.

The devastation and recovery of the zooplankton communities were studied in conjunction with the application of rotenone to two mountain lakes in Jasper National Park. Crustacean plankters were absent for about 6 months after treatment, but rotifers and net phytoplankton were never completely absent. All crustacean species except one reached prerotenone abundance in about 3 years, probably the minimum time for recovery in these lakes.

The speed of recovery is likely related to fecundity, time of reproduction, and the presence of resistant stages. *Diaptomus sicilis* had not reached reproductive maturity when rotenone was applied, and it was the last species to recover to its original numbers.

Some species not found in samples before application were found in small numbers afterwards, probably due in part to movement from the littoral into the limnetic zone. In both lakes, blooms of small cladocerans after treatment were soon supplanted by increases in large cladoceran numbers. Most variations in composition and abundance after rotenone were likely due to changes in competition and predation pressures rather than to changes in environmental factors or to direct effects of rotenone.

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Le dépeuplement en zooplancton de deux lacs de montagne du Parc national de Jasper, consécutif à l'application de la roténone, ainsi que le repeuplement qui l'a suivi ont été étudiés pendant une période de 3 ans. Pendant les 6 premiers mois suivant le traitement, aucun crustacé n'a été trouvé; par contre, les rotifères et le phytoplancton n'ont jamais complètement disparu. Trois ans après, toutes les espèces de crustacés sauf une avaient retrouvé l'abondance qui les caractérisait avant le traitement. Il semble que 3 ans soient le temps minimum de retour au peuplement normal dans ces lacs.

La vitesse du repeuplement dépend probablement, pour chaque espèce, de la fertilité, de la phase du cycle reproducteur et de la présence de formes résistantes au moment du traitement. *Diaptomus sicilis*, dont les individus n'avaient pas encore atteint la maturité sexuelle quand la roténone fut appliqué, n'a retrouvé que plus lentement son abondance d'avant le traitement.

Quelques espèces qui n'avaient pas été trouvées avant, l'ont été, en petites quantités, après le traitement; ceci pourrait être dû à leur émigration de la zone littorale à la zone pélagique, la compétition étant devenue minime dans celle-ci. Dans les deux lacs, peu après le traitement, des proliférations rapides de petits cladocères furent remplacées par

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l'augmentation des nombres de grands cladocères. La plupart des variations de composition et d'abondance planctonique qui ont suivi le traitement semblent avoir été dues plus à des changements de l'intensité de la compétition et de la prédation qu'à des changements du milieu ambiant ou qu'à l'action directe de la roténone.

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INTRODUCTION

ROTENONE has been used as a fish toxicant in sport-fisheries operations in North America for over 30 years (Kiser et al., 1963; Solman, 1950). Most of the earlier published accounts of rotenone applications in aquatic environments were concerned with methods or the effectiveness of rotenone as an eradicator of undesirable fish species (Bowers, 1955; Hayes and Livingstone, 1955; Hooper, 1955; Smith, 1940). More recently, investigations have been carried out on the effects of rotenone on other components of the aquatic community and on the physiological effect of rotenone on individual organisms.

Several field studies have dealt with the initial effects of rotenone on stream insects or on benthic fauna in lakes (Almquist, 1959; Cushing and Olive, 1957) and on lake and pond zooplankton (Kiser et al., 1963), but fewer studies have focused on the long-term effects and recovery patterns of these groups at generic or specific levels (Binns, 1967; Cook and Moore, 1969; Hrbáček and Novotná-Dvořáková, 1965). Investigations of the physiological effects of rotenone on fishes (Öberg, 1965) and certain invertebrates (Claffey and Ruck, 1967) and some other laboratory studies (e.g., Nishiuchi and Hashimoto, 1967) indicate that fish and invertebrates are not affected by rotenone in the same way or to the same extent.

In waters treated with rotenone, invertebrates may have a lower tolerance to rotenone than fish (Sanders and Cope, 1966), and at least one critic of the use of rotenone has suggested that it may eliminate nontarget organisms more effectively than target organisms (Hubbs, 1964). However, complete recovery of the invertebrate community after rotenone treatment is possible, at least in theory, because most aquatic invertebrates have highly resistant eggs or resting stages, can escape the rotenone by retreating into the bottom sediments, or have high passive dispersal potentials.

The present investigation of the long-term effects of rotenone on zooplankton communities was undertaken in conjunction with a fisheries management project in which rotenone was used to eradicate undesirable coarse fish species from two mountain lakes. Concomitant investigations of physical and chemical limnology were carried out so that factors other than fish and the effects of rotenone could be considered in the event that marked changes occurred in the zooplankton communities. It was not feasible to conduct extensive winter or vertical distribution studies at the time of the main project, nor was it possible to make extensive collections prior to rotenone application.

THE STUDY AREA

Patricia Lake is about 3 km north and Celestine Lake about 35 km north of the Jasper townsite in Jasper National Park, Alberta. Patricia Lake is one

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and Beacon Lake (45 m). Celestine L
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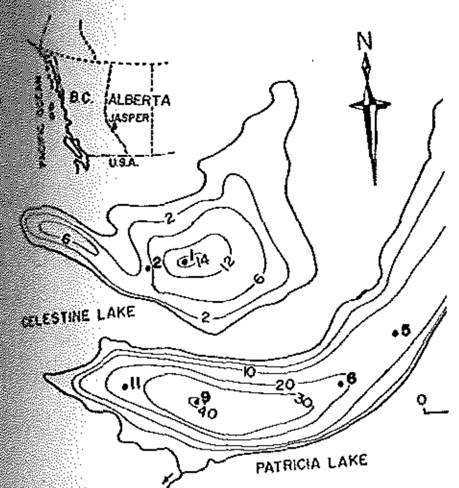

TABLE 1. Geographic and
and Celestine lakes, Ja

Map grid reference
Elevation (*m*)
Area (*ha*)
Max depth (*m*)
Mean depth (*m*)
Volume (m^3)

Both lakes are located in th(
Celestine Lake is near the upper
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of 3 m is coarse gravel and most of
In both lakes, scattered patches (
in shallow water.

of the deepest lakes in Jasper National Park, exceeded by Maligne Lake (95 m) and Beacon Lake (45 m). Celestine Lake is near the mode for lakes 4–40 ha in area in Banff and Jasper national parks (Anderson, 1970a, and unpublished data). Proportionately more of Celestine Lake than Patricia Lake is less than 3 m deep (Fig. 1). Some basic data for the two lakes are summarized in Table 1.

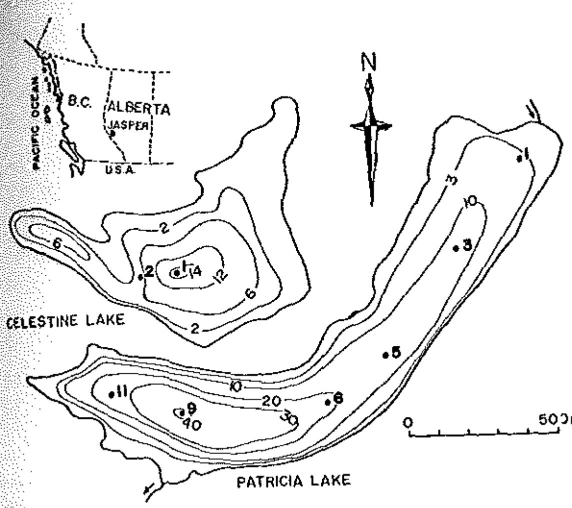


FIG. 1. Bathymetric maps for Patricia and Celestine lakes, Jasper National Park. All depths are in metres; main sampling stations are in bold print.

TABLE 1. Geographic and morphometric data for Patricia and Celestine lakes, Jasper National Park, Alberta.

	Patricia	Celestine
Map grid reference	259618/MJ	301934/MJ
Elevation (*m*)	1180	1260
Area (*ha*)	69	39
Max depth (*m*)	42	14
Mean depth (*m*)	12	4
Volume (m^3)	8.39×10^6	1.54×10^6

Both lakes are located in the montane forest zone (Rowe, 1959), but Celestine Lake is near the upper altitudinal limit of this zone. Both lakes are sheltered from strong winds by the surrounding forests, although Patricia Lake, because its long axis is in line with prevailing winds in the valley, is subject to more wind action than Celestine Lake.

Most of the lake bottom at Celestine is flocculent organic sediment with marly patches in the shallows. In Patricia, about half the bottom to a depth of 3 m is coarse gravel and most of the remainder is flocculent organic material. In both lakes, scattered patches of *Chara* sp. and other rooted plants occur in shallow water.

The fish species present in the lakes before the application of rotenone were: Patricia Lake (1966) — *Hybopsis plumbea* (Agassiz), *Prosopium williamsoni* (Girard), *Catastomus catastomus* (Forster), *Salvelinus fontinalis* (Mitchill), *Salvelinus namaycush* (Walbaum), *Salmo gairdneri* Richardson; Celestine Lake (1967) — *H. plumbea* (Agassiz), *S. gairdneri* Richardson. Patricia Lake was restocked with *S. fontinalis* and *S. gairdneri* in 1967 and Celestine Lake with *S. gairdneri* in 1968. Because no natural reproduction occurs in the lakes these species have to be maintained in the lakes by stocking hatchery-reared fish.

Analyses of stomach contents of *S. gairdneri* (both lakes) and *S. fontinalis* and *S. namaycush* (Patricia Lake) indicated that the main food organism prior to rotenone treatment was *Gammarus lacustris*, and that chironomid, caddisfly, and damselfly larvae, mollusks, and some fish were also frequently eaten. *Gammarus lacustris* was comparatively more common in stomach contents of fish restocked after the rotenone treatment. There was no evidence that the above three fish species fed on zooplankton. Stomach analyses were not done for *H. plumbea*.

No detailed limnological investigations have been carried out in either lake, although one or both lakes have been included in some survey studies (Bajkov, 1927, 1929; Bere, 1929; Rawson, MS, 1940; Reed, MS, 1959).

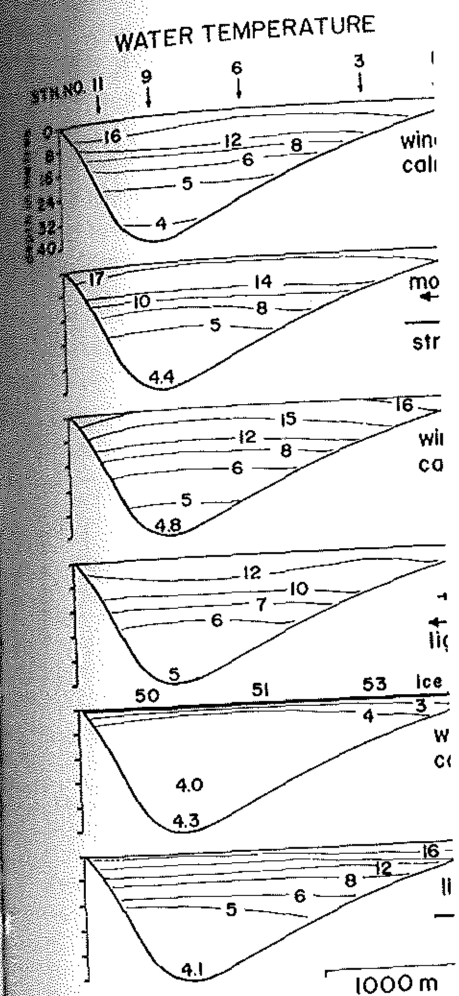
METHODS

Most zooplankton sampling was done with a Wisconsin-style plankton net (no. 20 bolting silk; mouth area 450 cm²; net length 80 cm) weighted at the bottom so that the mouth was directed upwards during descent. The extra weight made it possible to ascertain that the bucket had reached bottom, after which the line was lowered an additional 0.5 m. The net was hauled vertically at a constant speed of 0.5 m/sec. Quantitative samples for determining vertical distribution and plankton net efficiency were made with a plastic-bag sampler (Anderson, 1967). The physical and chemical methods used were described elsewhere (Anderson, 1970a). Both stereo- and compound microscopes were used in counting and identifying zooplankters. Identifications and nomenclature are according to Edmondson (1959) and Bailey et al. (1960).

Quantities of derris root powder (5% rotenone) equivalent to 0.75 ppm for each lake were distributed by boat over the lake surfaces. The operation was completed on Patricia Lake between 7:00 AM and 6:00 PM, September 7, 1966, and on Celestine Lake between 9:30 AM and 1:30 PM, September 26, 1967. The powder was applied at 0.75 ppm rather than the frequently recommended 0.50 ppm (Hooper, 1955) because of calm weather conditions and comparatively high hypolimnetic oxygen concentrations in both lakes. In Celestine Lake, derris powder was applied from shore to shallow regions marked by emergent vegetation. Eradication of fish from both lakes was believed complete. Checks were carried out by means of live fish in cages at various depths, sets of gillnets, and visual observations by scuba divers.

PHYSICAL AND CHEMICAL LIMNOLOGY

Measurements of temperature and dissolved oxygen made at five or six stations on Patricia Lake, 1966–67, indicated a consistently horizontal thermocline near the 12-m depth from June until October. During this time, the isopleth for 90% saturation was usually near 16 m (Fig. 2). Because moderate or strong winds rarely blow consistently from one direction for as much as 10 or 12 hr on Patricia Lake, it is unlikely that wedge-shaped thermoclines



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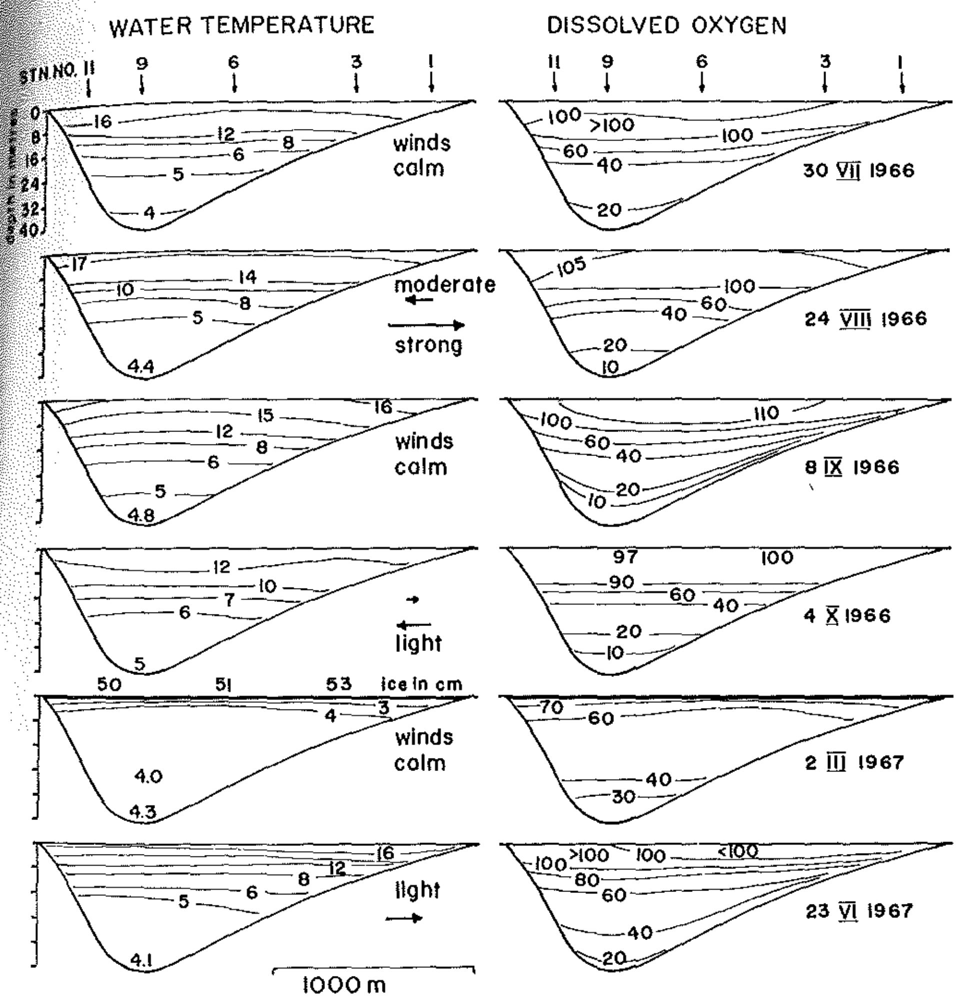

FIG. 2. Horizontal distribution of temperature (C) and oxygen (percent saturation) for Patricia Lake on selected dates, 1966–67.

ever develop to the extent described by Mortimer (1961) for Windermere Lake. Prevailing winds blow from the deep to the shallow end of Patricia Lake and, because of the basin shape, surface waters blown to the shallow end probably circulate to the northwest rather than downward. Mixing of surface waters to a depth of 6–8 m during the summer was indicated by the temperature profiles (Fig. 2, 3).

The isotherm patterns for Patricia Lake were strikingly similar for the open-water seasons from 1966 to 1969 (Fig. 3). Maximum surface temperatures varied less than 1 degree C in the 4 years, although precipitation and winds were much higher and air temperatures generally lower in 1966 and 1968 than in 1967 and 1969 (unpublished data). Although maximum oxygen con-

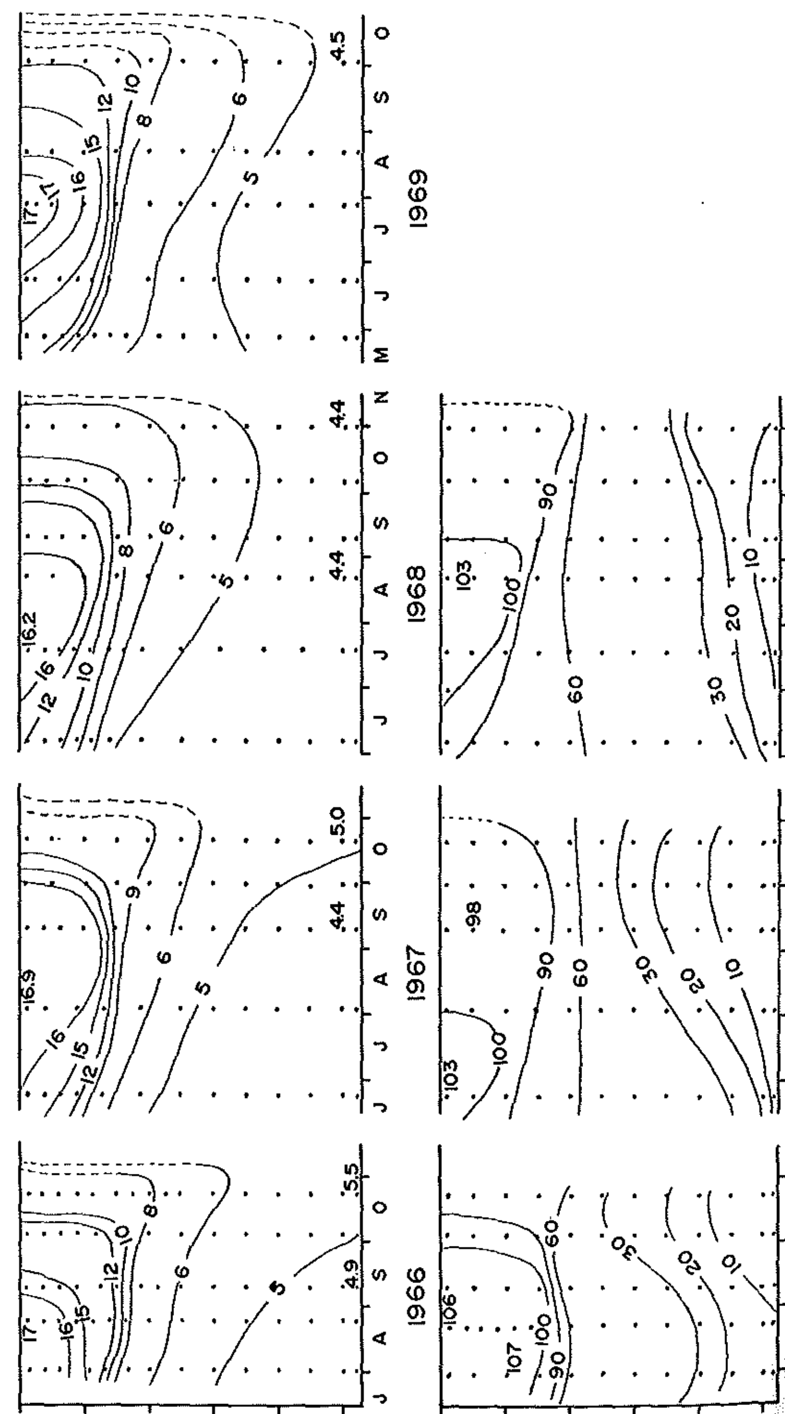

FIG. 3. Temperature (C) (upper) and percentage saturation oxygen (lower) isopleths for Patricia Lake (station 9) in ice-free periods, 1966–69.

centrations differed, the patterns of the oxygen isopleths were similar in 1966, 1967, and 1968.

Maximum surface temperatures for Celestine Lake varied even less than those for Patricia Lake, but the isopleths for temperature and dissolved oxygen differed more from year to year than those in Patricia Lake. The smaller variation in Patricia Lake is undoubtedly due to the fact that the larger lake has a volume over five times that of the smaller lake, and a surface area less than twice that of the smaller (Table 1). The isopleths for Celestine Lake also suggest that mixing due to wind probably extends to 6 or 8 m (Fig. 4).

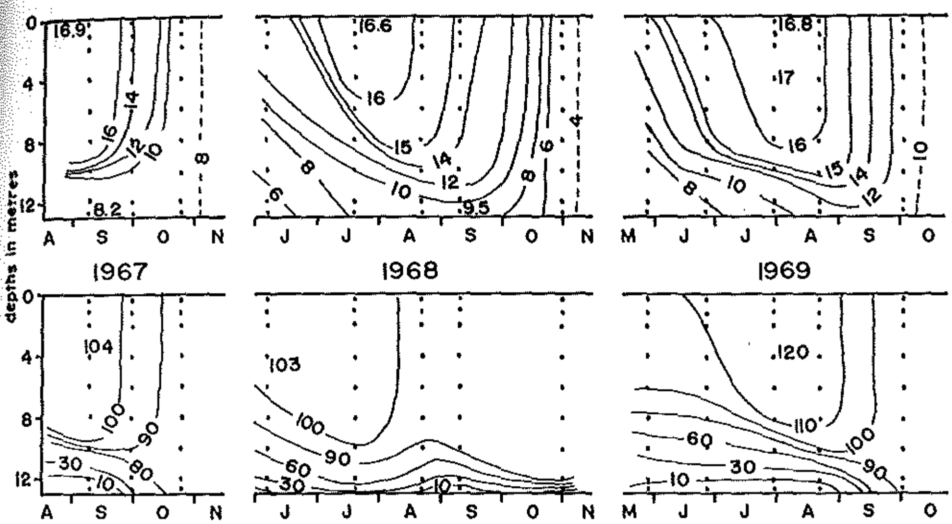

FIG. 4. Temperature (C) (upper) and percentage saturation oxygen (lower) isopleths for Celestine Lake (station 1) in ice-free periods, 1967–69.

Vernal circulation in most years probably does not occur in either lake and autumnal circulation in some years may be incomplete in Patricia Lake (see Fig. 3, 4). Such circumstances can be expected in "continental dimictic" lakes (Löffler, 1968) where hypolimnetic temperatures of 4 C prevail during the winter (Einsele, 1941; Anderson, 1970a). Autumnal homeothermy develops slowly in Patricia Lake and is short-lived before ice formation. In Celestine Lake, homeothermy usually occurs in September and persists for 2 months or more until freezeup.

Water analyses over 4 years indicated that the aquatic environment of Patricia Lake was fairly stable. Consistently higher salinities and lower *p*H levels occurred below 25 m than at the surface throughout the sampling period. Yearly seasonal variations were small in water analyses of comparable time and depth. A slight dilution of surface waters was evident during 1966 and 1968 in Patricia Lake.

Concentrations of all constituents were higher in Celestine Lake in 1967 and 1969 than in 1968, undoubtedly a reflection of the warm, dry weather in 1967 and 1969 when much of the forest in Jasper National Park was closed to the public due to extreme fire hazard. Concentrations of constituents and *p*H readings were very similar in samples from 2 and 12 m from September until November in 1968 and 1969. The more thorough circulation of Celestine Lake is indicated by the mean, maximum, and minimum values of the chemical analyses for the two lakes (Table 2).

PLANKTON NET EFFICIENCY

To determine a factor for estimating actual zooplankton numbers from plankton net catches, total counts were made on the contents of vertical plankton net hauls and on the contents of series of quantitative samples taken at the same time. Curves were plotted from series of vertical samples and total numbers present were estimated by planimetry. The results of one such series are plotted in Fig. 5. A mean efficiency of 21.5% (range 14–28%; standard deviation 4.4%) was determined earlier in the same manner (Anderson, 1967, MS, 1968). Efficiencies as high as 40% were found if the net was hauled vertically at a rate of 2 m/sec (unpublished data), so care was taken to maintain a constant rate of 0.5 m/sec on all vertical hauls. Clogging lowered plankton net efficiency (mean 17%) during May and June, because phytoplankton was more abundant then than in July and later (see also Ward, 1957).

The low filtration efficiency was in line with the general expectations summarized by Tranter and Smith (1968) for nets of similar design. Undoubtedly, the main factors contributing to poor performance were the slow towing speed, a comparatively low open-area ratio of approximately 1.4, and the net design. A factor of 6 was used for converting May and June plankton net catches and a factor of 5 was used for the rest of the year.

INITIAL EFFECTS OF ROTENONE

The immediate effect of rotenone on the crustacean zooplankton was catastrophic. Within 24 hr, total numbers of these crustaceans were less than 5% of prerotenone levels, and no crustaceans were present in net samples 1 month after the operation. Small numbers of *Cyclops vernalis* were found in samples from Patricia Lake 6 months after rotenone and 30% of species present before rotenone had reappeared the following June. A few *Daphnia pulex* occurred in samples from Celestine Lake 9 months after rotenone and about 40% of prerotenone species had reappeared by the following July.

Although the total number of rotifers was down considerably and most species disappeared immediately after rotenone, *Kellicottia longispina* and *Keratella cochlearis* were not greatly affected. By June or July of the year following rotenone application, all species of rotifers were back in approximately prerotenone numbers. The appearance of small numbers of some additional species may have been due to the examination of greater numbers of samples or to normal seasonal variations. In Celestine Lake, moderate numbers of *Asplanchna priodonta* the year after rotenone, a decline in the second year, and the apparent absence before rotenone indicate that competition

TABLE 2. Mean, maximum, and minimum values for laboratory water analyses for Patricia and Celestine lakes (values are ppm except *p*H[a]).

	Patricia Lake 1966–69						Celestine Lake 1967–69					
	Above 10 m ($n=12$)			Below 25 m ($n=9$)			Above 5 m ($n=5$)			Below 12 m ($n=2$)		
	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min	$\bar{x}$	Max	Min
Calcium	30.76	34.0	22.6	31.90	37.0	24.8	25.4	28.7	23.0	26.35	29.7	23.0
Magnesium	52.86	55.0	51.1	55.26	58.9	52.9	18.4	19.3	18.1	18.6	19.3	17.9
Iron (dissolved)	–	0.02	<0.01	–	0.02	<0.01	–	0.01	<0.01	–	0.03	<0.01
Aluminum	–	0.29	0.16	–	0.44	0.18	–	–	–	–	–	–
Manganese (dissolved)	–	<0.006	0.000	–	0.010	0.000	–	<0.006	<0.001	–	<0.006	<0.001
Sodium	21.45	22.7	20.4	22.15	24.0	21.6	1.74	2.2	1.4	1.75	1.9	1.6
Potassium	4.54	5.0	4.0	4.80	5.1	4.5	2.28	2.6	2.1	2.55	2.7	2.4
Bicarbonate	279.50	300	258	304.33	312	300	167.4	178	157	175	178	172
Sulfate	98.61	101.0	96.1	103.22	102.0	102.0	2.94	3.6	2.4	3.45	4.1	2.8
Chloride	1.38	1.7	0.8	1.47	1.8	0.8	0.46	0.8	0.2	0.65	0.7	0.6
Fluoride	0.15	0.20	0.12	0.16	0.20	0.13	0.12	0.14	0.10	0.11	0.11	0.11
Silica	3.15	4.2	2.0	5.16	6.7	3.7	2.26	3.0	1.9	2.5	3.1	1.9
Copper	–	0.010	0.000	–	0.019	0.000	–	0.0007	<0.001	–	<0.002	<0.001
Zinc	0.006	0.020	0.000	0.008	0.025	0.000	–	0.007	<0.001	–	0.004	<0.001
Lead	–	<0.010	<0.003	–	<0.010	<0.003	–	<0.010	<0.005	–	<0.010	<0.005
Ammonia	–	–	–	–	–	–	0.12	0.2	0.1	0.15	0.2	0.1
Total phosphate	0.02	0.04	<0.01	0.06	0.23	0.02	0.014	0.02	<0.01	–	0.02	<0.01
Nitrate	–	1.0	<0.01	–	1.5	<0.01	–	0.10	<0.1	–	0.13	<0.1
Sum constituents	358	369	340	375	379	370	137.8	146	131	142	147	137
*p*H	8.6(20)	8.8	8.2	8.0(13)	8.3	7.7	8.5(9)	8.7	8.4	8.2(5)	8.4<	7.8

[a]*p*H values are field values, number of analyses in parentheses.

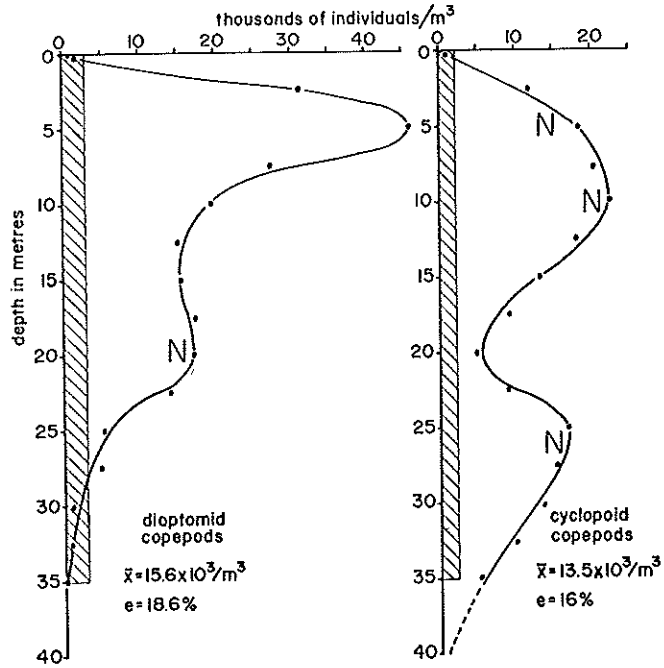

FIG. 5. Vertical distribution of dominant zooplankters, Patricia Lake, May 27, 1969. Hatched area represents plankton net haul. Mean number per m³ ($\bar{x}$) determined by planimetry; N indicates greatest abundance of nauplii; e = calculated net efficiency.

with, or predation on, this species was minimal in 1968. Some reports indicate that rotifers are virtually eradicated by rotenone (Almquist, 1959) and others suggest inconsistent effects (Kiser et al., 1963). The following table summarizes rotifers present in the two lakes before and after rotenone:

	Patricia L.		Celestine L.	
	Before	After	Before	After
Polyarthris vulgaris	×	×	×	×
Filinia longiseta	×	×		
Kellicottia longispina	×	×	×	×
Keratella cochlearis	×	×	×	×
Keratella quadrata	×	×		×
Synchaeta oblonga		×	×	×
Asplanchna priodonta		×		×
Brachionus (? *plicatilis*)		×	×	×
Lepadella (? *ovalis*)				×
Conochiloides (? *dossuarius*)			×	×
? *Cephalodella* sp.				×
? *Gastropus* sp.				×
? *Sinantherina* sp.				×
? *Epiphanes* sp.		×		

Phytoplankton abundance and species composition were almost unaffected by the rotenone. Compared with subsequent years and prerotenone abundance, there was a small phytoplankton bloom shortly after treatment. *Ceratium hirudinella* was very abundant in Patricia Lake 1 month after rotenone, but was not found in Celestine Lake after rotenone. *Ceratium hirudinella* was absent from Celestine Lake in autumn the following 2 years but was present in Patricia Lake each autumn. In some studies (Kiser et al., 1963) dinoflagellates disappeared for a year after rotenone. The only other marked phytoplankton change was a moderate *Volvox* sp. bloom in Celestine Lake in June 1968. Binns (1967) has suggested that enrichment from the decomposition of zooplankton may cause such blooms. However, water analyses for both lakes showed that phosphate and nitrate decreased slightly after rotenone.

The first benthic invertebrates to show high mortality were the leeches (Patricia Lake) and the snails (Celestine Lake). Comparative collections were not made, but both groups were fairly abundant 2 years after treatment. In contrast with the total mortality of amphipods reported after toxaphene treatment, mortality of *Gammarus lacustris* was not noted in these lakes (Stringer and McMynn, 1958; J. C. Ward, unpublished data). In fact, their numbers in PatriciaLake apparently increased soon after treatment. *Hydra* spp. numbers were not noted at the time of rotenone application, but were estimated as high as 1000/m^2 along the stony shore of Patricia Lake in 1968 and 1969. Benthic oligochaetes and dipteran larvae appeared to be unaffected by rotenone. These observations concur with the general findings of Almquist (1959), Cushing and Olive (1957), and Kiser et al. (1963). Damselfly and caddisfly larvae were present in moderate numbers the year after application, and mortality from rotenone was possibly no higher than it would have been from fish predation (see Claffey and Ruck, 1967).

RECOVERY OF THE PLANKTON COMMUNITY

Plankton Composition

A comparison of samples taken before and after rotenone in both lakes indicates that the zooplankton community did not change a great deal (Table 3). The table includes the only available lists of species previously reported for the lakes, but direct comparisons are not especially valid. Bajkov's (1929) list for Patricia Lake is probably inaccurate (M. S. Wilson, personal communication) and Reed's (MS, 1959) lists, compiled from samples collected by D. S. Rawson mainly during July and August in the 1930's, are undoubtedly incomplete.

Of the six main crustacean zooplankters (>1% of most abundant species) present in Patricia Lake before rotenone in 1966, two were copepods and four were cladocerans. Three cladocerans reached nearly the same densities in 1967; two cladocerans and one copepod returned to prerotenone densities in 1968, *Ceriodaphnia* spp. having been supplanted by *Cyclops bicuspidatus thomasi*. All six of the main prerotenone species returned to their 1966 densities

TABLE 3. Limnetic species (except rotifers) in Patricia and Celestine lakes.

Species	Patricia				Celestine		
	Bajkov (1929)	Reed (MS, 1959)	Before rotenone 1966	After rotenone	Reed (MS, 1959)	Before rotenone 1967	After rotenone
Diaptomus sicilis Forbes	×	×	×	×			×
Diaptomus tyrrelli Poppe	×						
Diaptomus leptopus Forbes					×		
Cyclops bicuspidatus thomasi Forbes	×	×	×	×			
Cyclops vernalis Fischer			×	×		×	×
Cyclops bicolor Sars	×						
Cyclops fimbriatus Fish.[a]	×						
Eucyclops agilis (Koch)		×	×	×			
Macrocyclops albidus (Jurine)			×	×			×
Leptodora kindtii (Focke)				×			
Polyphemus pediculus (Linné)	×			×		×	×
Diaphanosoma brachyurum (Liéven)	×						×
Diaphanosoma leuchtenbergianum Fischer	×		×	×			
Daphnia pulex Leydig emend. Richard		×	×	×		×	×
Daphnia pulex de Geer[a]	×						
Daphnia pulex v. *obtusa* Kütz[a]	×						
Daphnia longispina (O.F.M.)[a]	×						
Daphnia galeata Sars *mendotae* Birge				×		×	
Daphnia schødleri Sars					×		
Simocephalus vetulus Schødler							×
Scapholeberis kingi Sars							×
Ceriodaphnia lacustris Birge			×	×		×	×
Ceriodaphnia quadrangula (Müller)		×	×	×			
Ceriodaphnia reticulata (Jurine)	×						
Bosmina coregoni Baird		×	?	?			
Bosmina longirostris (Müller)			×	×		×	×
Eurycercus lamellatus (Müller)				×			
Acroperus harpae Baird							×
Leydigia quadrangularis (Leydig)				×			
Alona guttata Sars				×		×	×
Alona affinis (Leydig)				×			×
Alona rectangula Sars				×			×
Alonella nana (Baird)				×		×	×
Chydorus sphaericus (Müller)		×	×	×	×		
Gammarus lacustris lacustris Sars			×	×			
Hyalella azteca (Saussure)							×
Chaoborus flavicans (Meigen)						×	×

[a]Probable errors in identification or terminology.

by 1969 (Fig. 6). One previously scarce cyclopoid, *Cyclops vernalis*, was the first crustacean zooplankter to reappear; it attained moderate abundance in 1967, but declined continually during 1968 and 1969. *Bosmina longirostris*

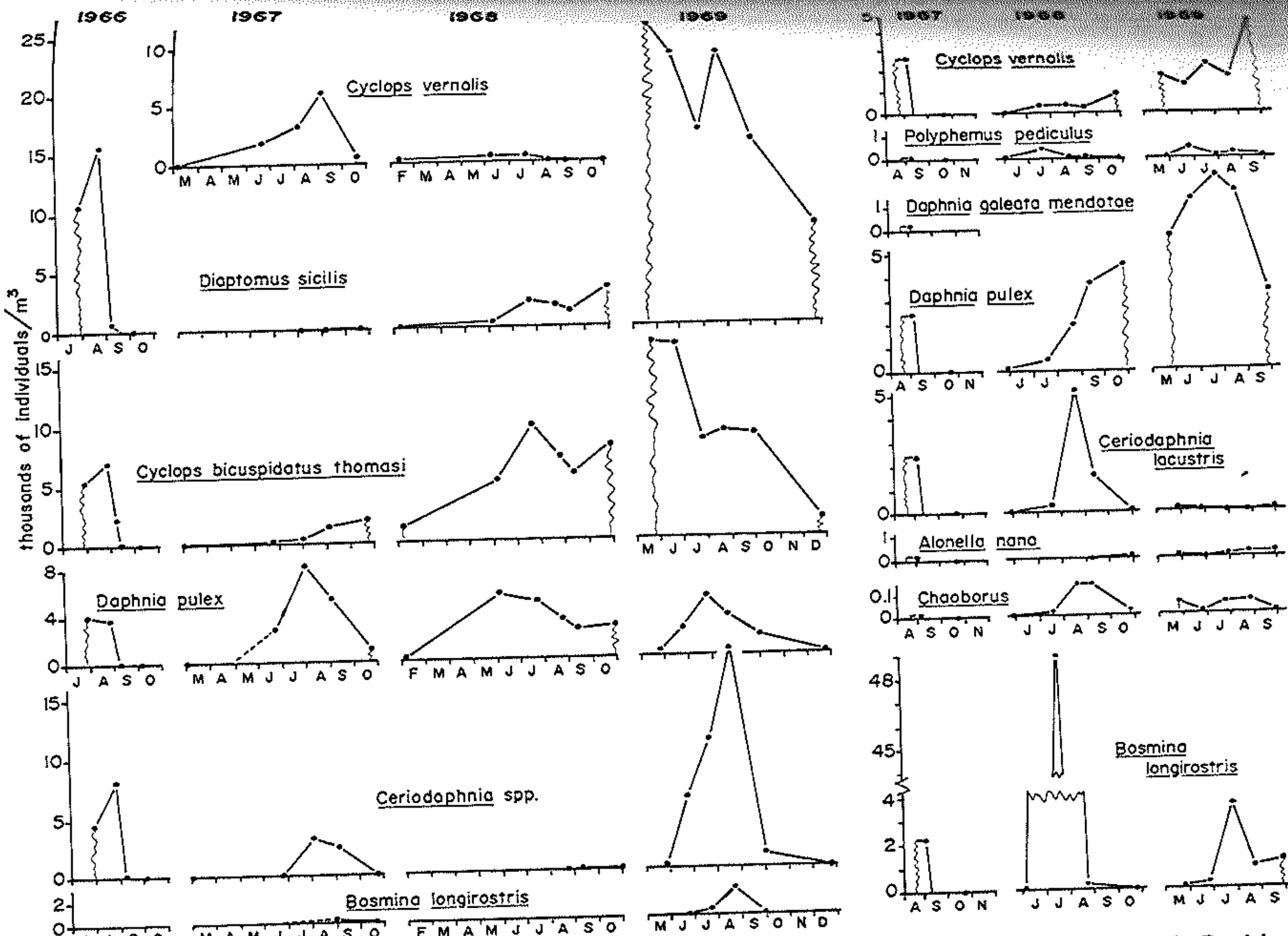

FIG. 6. Seasonal distribution of main zooplankters in Patricia (*left*) and Celestine (*right*) lakes. Mean abundance in Patricia determined by combining five or more total vertical hauls from five or six stations. Mean abundance in Celestine determined by combining four or more vertical hauls from two stations.

and *Polyphemus pediculus* were much more abundant in 1967 and 1969 than in 1966. A few *Leptodora kindtii* were collected the 1st year after rotenone, and a few *Daphnia galeata mendotae* appeared in 1969 (perhaps the *Daphnia longispina* in Table 3). The less abundant cyclopoid species reached prerotenone numbers the 2nd and 3rd years after treatment. Nine cladocerans not found in 1966 (Table 3) occurred in subsequent years in very small numbers. Bajkov (1929) reported *Diaptomus tyrrelli* in Patricia Lake, but none was found in this study. A possible earlier misidentification may have been related to the distinct size bimodality exhibited by *Diaptomus sicilis* in this lake.

Of six main prerotenone crustacean zooplankters in Celestine Lake, five were cladocerans and one was a copepod. Two cladocerans and the copepod had recovered to approximately prerotenone densities in 1968 and one cladoceran, *B. longirostris*, reached numbers greatly exceeding 1966 levels; four of the original six main species, the copepod and three cladocerans (one different from 1968), were close to prerotenone densities by 1969 (Fig. 6). Five cladocerans and two copepods not found in 1967 appeared in subsequent years (*Macrocyclops albidus* and *Acroperus harpae* in 1968 and the others in 1969). Both *D. leptopus* and *D. sicilis*, occasionally very abundant, were reported in some years and not in others (Reed, MS, 1959; other unpublished data). *Daphnia galeata mendotae* was not found after 1967. *Chaoborus flavicans* larvae began to reappear in July 1968, and by August greatly exceeded 1967 numbers. In 1969, chaoborids were near prerotenone numbers. In 1967 and 1969, all limnetic larvae collected were in the lower 5 m of the lake, whereas in 1968, they were present at all depths, even at midday. Similarly, it was notable that the common daytime occurrence of *Gammarus lacustris* and *Hyalella azteca* in limnetic samples from the two lakes was restricted to the fish-free period.

Ceriodaphnia spp., among the first zooplankters to occur abundantly in both lakes, were very scarce in both lakes the 2nd year after treatment. *Bosmina longirostris* (in Celestine Lake) exhibited the most extreme increase of any cladocerans and counts reached nearly 25 times "normal" the 1st year.

Plankton Distribution

To estimate the uniformity of zooplankton distribution in the epilimnion of Patricia Lake, series of 14-m vertical hauls were taken at three or four stations and multiple hauls were taken from the same depth near a single station. Most sets of samples indicated that distribution was fairly uniform above the thermocline and counts generally differed from the mean by less than 25% (Table 4). Differences were remarkably small, even shortly after rotenone application. Some sets of samples produced large differences for one species (e.g., *D. sicilis*, July 1966) indicating that the nearness of the lake bottom influences horizontal distribution at certain times.

Although no study of horizontal distribution was undertaken in Celestine Lake, greater variations than occur in Patricia Lake could be expected because of differences in species composition and basin morphometry, and more variable

TABLE 4. Numbers of zooplankters in series of vertical net hauls to a constant depth.

	July 30, 1966				Sept. 8, 1966					Dec. 22, 1969					
	14 m				14 m					13 m			22 m		
Station:	5	7	9	11	3	6	9	9	11	3	3	3	6	6	6
Diaptomus sicilis	1219	1003	882	649	225	111	24	23	37	315	203	306	2064	1923	1853
Cyclops bicuspidatus thomasi	348	356	429	440	108	358	420	440	310	90	46	73	472	335	325
Daphnia pulex	396	630	576	495	0	1	1	2	1	3	2	6	57	50	52
Daphnia galeata	–	–	–	–	–	–	–	–	–	0	0	0	0	1	1
Ceriodaphnia spp.	279	432	270	261	7	36	8	10	1	–	–	–	–	–	–
Leydigia quadrangularis	–	–	–	–	–	–	–	–	–	1	8	2	3	2	3

physical and chemical conditions. Studies on other lakes indicate greater variation in zooplankton abundance from station to station than occurred in Patricia Lake, and horizontal distribution is unlikely to be the same for one species or similar species in different lakes (Barthelmes, 1960; Bittel et al., 1965; Langford and Jermolajev, 1966; Nauwerck, 1963; Patalas, 1969; Schroeder and Schroeder, 1964; Ward, 1957).

At certain times of the year, some species were most abundant and uniformly distributed in the hypolimnion: *D. sicilis* in July and August; *Ceriodaphnia* spp. in August; *Daphnia pulex* in June and July; *B. longirostris* in August. In September and October, as the lake approached homeothermy, *D. sicilis*, *C. b. thomasi*, and the remains of most cladoceran populations were fairly evenly distributed at all depths and stations. Certain species showed seasonal differences in distributional patterns: *C. b. thomasi* and *Ceriodaphnia* spp. were abundant first at moderate depths, then in deep water, and then became uniformly distributed in autumn; *D. sicilis* was abundant first in shallow water, was evenly distributed in June and in autumn, and was abundant in deep water during July and August; *D. pulex* remained in deep water until August and then was uniformly distributed until becoming concentrated in the shallow water in autumn (Fig. 7).

In general, the species most abundant in inshore samples from both lakes were nearly the same as those most abundant in the epilimnion at the same time. Of the inshore exceptions (*Polyphemus pediculus* in both lakes; *Chydorus sphaericus*, *Eucyclops agilis*, and *Macrocyclops albidus* in Patricia; *Scapholeberis kingi* and *Alona* spp. in Celestine) only *S. kingi* was especially abundant. Some common limnetic species (*B. longirostris*, *Ceriodaphnia lacustris*, *Diaphanosoma leuchtenbergianum*, and, at times, *D. pulex*) were less numerous in inshore samples.

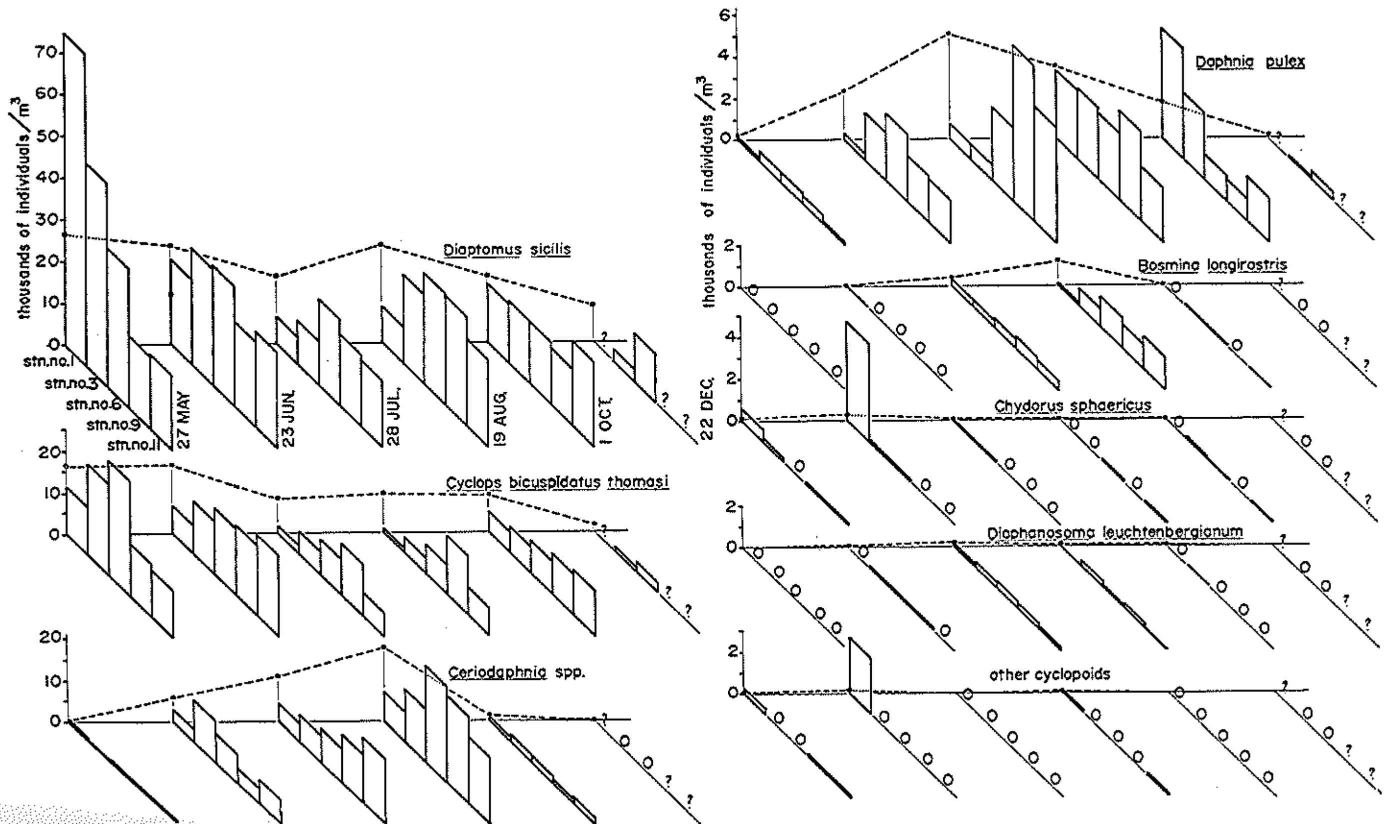

FIG. 7. Distribution of zooplankton at each of five stations in Patricia Lake, 1969. Each bar represents mean numbers per m^3 throughout water column at each station. Broken-line graphs are mean values for total lake distribution (from Fig. 6).

Studies in Patricia Lake indicated that variations in vertical distribution of copepods were related to age (Fig. 5). In May, early nauplii of *D. sicilis* were most abundant near the 20-m depth, whereas advanced nauplii and copepodids were more abundant in the upper 10 m. Most eggs may have hatched from the bottom between 10 and 25 m. Cyclopoid nauplii were most abundant at and below 24 m as well as near the surface, but it was not known whether the nauplii were of the same species. *Cyclops vernalis*, for example, seems to be restricted to the deeper water of some of the lakes, possibly as a result of competition (unpublished data).

Reed (MS, 1959) indicated the presence of *D. pulex* in Patricia and *D. schødleri* in Celestine Lake. The examination of current material indicated morphological variability in the daphnids from both lakes, but produced no evidence that the daphnids in the two lakes were different species. Larger females in both lakes were most abundant in deeper water, had short shell spines, and were definitely *D. pulex*, whereas smaller females collected in the upper 5 or 10 m of both lakes had longer shell spines and were more *schødleri*-like. However, the most extreme long-spined individuals were at best intermediate between *D. pulex* and *D. schødleri* and it was concluded that all were *D. pulex* (cf. Brooks, 1957).

PREDATION AND COMPETITION

In August and September 1967, *Daphnia pulex* was virtually absent from the upper 5 m of Celestine Lake, although the smaller *Daphnia galeata mendotae* was fairly abundant there. In 1968, *D. pulex* was abundant at all depths in this lake and *D. g. mendotae* was absent. Similarly in Patricia Lake, *D. pulex* was much more abundant in surface waters the year after rotenone treatment. This raises the possibility that predation on *D. pulex* by *Hybopsis plumbea* (and possibly trout as well) was quite intense before rotenone and that *D. g. mendotae* was competitively excluded from the epilimnion after rotenone by the larger *D. pulex*.

The large increases in numbers of *Ceriodaphnia* spp. and *B. longirostris* that occurred in both lakes in the season following rotenone treatment were probably due to a combination of reduced competition (*D. pulex* was slower to reappear) and little predation at this time by *Cyclops vernalis*, *C. b. thomasi*, and *Chaoborus flavicans* in the respective lakes (Fig. 6). A close inverse relation between numbers of large cladocerans and small cladocerans has been noted frequently (Brooks, 1969; Brooks and Dodson, 1965; Hrbáček et al., 1961; Hrbáček and Novotná-Dvořáková, 1965; Kiser et al., 1963). A residuum of ephippial eggs and comparatively high fecundities are undoubtedly factors contributing to the quick recovery of small cladocerans whose numbers have been found to vary greatly from year to year (e.g., Kowalxzyk, 1964).

Maximum monthly predation rates of about five prey animals per predator have been determined for *C. b. thomasi* (Anderson, 1970b). If half the *C. b. thomasi* in Patricia Lake were considered to be copepodids IV–VI, then decreases from maximum numbers for *Bosmina longirostris*, *Ceriodaphnia* spp., and *Diaptomus sicilis* in 1969 could be accounted for by cyclopoid predation. The much smaller declines in the prey species in 1968 are in accordance with smaller predator numbers, especially before July (Fig. 6).

The possible role of predaceous zooplankters in Celestine Lake is less clear. *Cyclops vernalis* can consume up to six prey per day (Anderson, 1970b), and drops in the numbers of small cladocerans in 1968 could be partly accounted for by predation (Fig. 6). However, the numerical increase in *C. vernalis* followed the decline in numbers of *B. longirostris*, so that the decline may have been the result of competition from *D. pulex* and predation by *Chaoborus flavicans*. A high rate of recruitment was indicated by the graphs for *B. longirostris* and *Ceriodaphnia* spp. in 1968, and the presence of only small numbers of those species in 1969 suggests the likelihood of intense cropping by *C. vernalis*. However, it is unlikely that recruitment in these prey species is sufficient to satisfy the food requirements of *C. vernalis*. Other possible sources of food for cyclopoids are rotifers, algae, chironomid larvae, and *P. pediculus*. Cannibalism and actual predation rates lower than those found experimentally may also be important factors (Fryer, 1957; McQueen, 1969; Monakov, 1959; Saunders, 1969). *Chaoborus flavicans*, known to prey on entomostraca (Coker, 1954), may be responsible for limiting numbers of *C. vernalis* and for reducing standing stocks of certain cladocerans.

ZOOPLANKTON SUCCESSION

In the two Jasper lakes, the plankton groups least affected by rotenone were the first to return to their prerotenone numerical and species abundance (i.e., phytoplankters first and rotifers second). A similar early succession was noted in some Czechoslovakian ponds (Hrbáček and Novotná-Dvořáková, 1965). In the Jasper lakes large cladocerans exceeded prerotenone numbers during the summer after treatment. Similar increases have been observed in some other studies (Hrbáček and Novotná-Dvořáková, 1965; Kiser et al., 1963). The numerical surge of large cladocerans was preceded in Celestine Lake by a short-lived increase in numbers of small cladocerans, and in Patricia Lake by a marked increase in numbers of *Cyclops vernalis*. Successional development of the plankton species after rotenone treatment probably depends on fecundity, the susceptibility of the species to the poison, and the ability to produce resistant eggs or to encyst. Rotenone will be more devastating to species not having reached their annual reproductive peak. In Patricia Lake, for example, reproductive maxima for most cladoceran species were in July and August, whereas the maximum for *Diaptomus sicilis* was in November and December.

The postrotenone appearance of species apparently new to the limnetic zone of a lake may be due to closer and more numerous examinations of samples (Dussart, 1956) or to the movement of littoral species into the limnetic zone after rotenone treatment (Kiser et al., 1963). *Scapholeberis kingi* was abundant in the littoral zone and common in the limnetic zone of Celestine Lake in 1969 but not in the previous 2 years. This occurrence was probably due at least in part to the eradication of *Hybopsis plumbea*. The usually very scarce *Acroperus harpae* became abundant in a small aquarium of water and shoreline rocks from Patricia Lake, indicating that reduced competition and changes in the physical and chemical environment are possibly the main reasons for numerical surges in species that are usually rare.

GENERAL DISCUSSION

The application of rotenone to Patricia and Celestine lakes affected the phytoplankton very little and suppressed the rotifers only temporarily. Some species began to reappear within 6 months of the initial devastation of crustacean zooplankton and most had reappeared after 10 months, many in numbers much higher than before treatment. One Celestine Lake species, *Daphnia galeata mendotae*, failed to reappear in posttreatment samples, although single or immature specimens could have remained undetected among large numbers of immature *Daphnia pulex*. In general, the adverse side effects of a single application of rotenone to a lake are likely to be minimal, especially in comparison with the detrimental effects of certain other fish-eradicating toxicants, such as toxaphene or copper sulfate.

In these two lakes, 3 years appeared to be the minimum time required for the zooplankton to recover to prerotenone levels of species diversity and abundance. Because marked fluctuations in the numbers of certain species are known to occur in small lakes and ponds from year to year, some of the fluctuations in the present study appear to have been only indirectly related to the rotenone treatment. The small changes that occurred in the zooplankton of the lakes is evidence of the innate stability of the communities, a stability that is likely to increase with the size of the water body (D'Ancona, 1955; Elgmork, 1964).

There is a need for studies of the feeding habits of lake chub (*Hybopsis plumbea*) in mountain lakes and for investigations of the relations between *Chaoborus* and certain zooplankton species. The relation between the presence or absence of fish and the limnetic occurrence of *Chaoborus* and *Gammarus* also warrants detailed investigation.

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