

Gammarus and Chaoborus predation

**by R. Stewart Anderson
and Linda G. Raasveldt**



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Gammarus predation
and the possible
effects of **Gammarus**
and **Chaoborus**
feeding on the
zooplankton composition
in some small lakes
and ponds in
western Canada

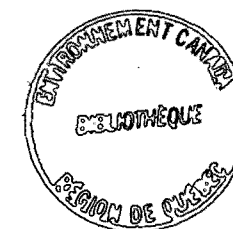
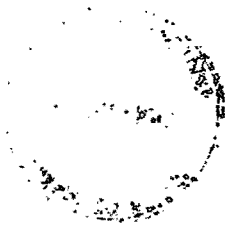
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Abstract

In the lakes and in laboratory experiments *Gammarus lacustris lacustris* adults captured and ate several invertebrate species with which these amphipods commonly co-occur. In the laboratory, they also readily ate species with which they do not co-occur in the waters studied. Experimental evidence and data from 52 aquatic communities suggest that *Gammarus* predation may be an important reason why *Gammarus* seldom, if ever, co-occurs with anostracans, and why co-occurrences of *G. l. lacustris* and *Chaoborus* spp. were rare in the waters investigated. The relative abundance of these two genera and their diurnal limnetic occurrence in fish-free lakes greatly influenced the abundance of certain aquatic invertebrates and the species composition of the invertebrate communities.

Résumé

Des études effectuées dans des lacs et dans le laboratoire ont démontré que les adultes *Gammarus lacustris lacustris* capturaient et mangeaient plusieurs espèces d'invertébrés avec lesquelles les amphipodes coexistent généralement. Ils mangeaient aussi avec empressement des espèces avec lesquelles ils ne coexistent pas dans les eaux étudiées. D'après des observations sur 52 communautés aquatiques, on déduit que le caractère prédateur du *Gammarus* peut expliquer pourquoi cet amphipode coexiste rarement, pour ne pas dire jamais, avec des anostracés, et pourquoi son association avec les espèces de *Chaoborus* est très rare dans les eaux étudiées. Le nombre de certains invertébrés aquatiques et la composition de leur communautés étaient largement influencés par le caractère prédateur des *Gammarus* et *Chaoborus*, aussi bien que par leur abondance et leur présence diurne dans ces lacs sans poissons.

Introduction

Mean population densities of 1000 *Gammarus lacustris lacustris* Sars per square metre were determined for Linnet Lake, a small mountain lake in Waterton Lakes National Park, Alberta (Anderson, Donald, and Krochak, 1972) and isolated densities as high as 70,000 m⁻² have been assessed (J. Whitaker, pers. comm.) in some small lakes in Manitoba where experimental trout-farming investigations are underway (Johnson, Lawler, and Sunde, 1970). Considering the biomass and numerical prominence of *Gammarus* spp. in these and other waters of the world and the importance of these amphipods in food webs of the aquatic communities, few studies have been made of the food and feeding habits of *Gammarus*.

In many laboratory studies of *Gammarus* spp., either a plant or detritus diet has been prescribed (Arthur and Leonard, 1970; Culver, 1970, 1971; Kendeigh, 1961; Macan, 1963; Schmitz, 1967; Smith, 1973; Suomalainen, 1958), or, assuming the animals to be "mixed feeders", this diet has been supplemented with chopped earthworm, canned dog food, or similar animal material (Steele and Steele, 1970; Clemens, 1950). Field observations, gut-content analyses, and general studies have led to similar assumptions regarding *Gammarus* spp. diets (Barnes, 1963; Ermolaeva, 1962; Hynes, 1954; Grimås, 1961, 1964; Greze, 1968; Menon, 1969; Pennak, 1953). Using serological techniques, Davies (1967, 1969) found no evidence of predation by *Gammarus pulex* Linnaeus on triclads, but other studies and observations provide indications that predation may be an important feeding method for *G. pulex* and possibly other gammarid species (Biette, 1969; Bjarnov, 1972; Deksbakh and Sokolova, 1965; several studies cited by Hynes, 1954; Jenkins, cited by Davies, 1967; Minckley and Cole, 1963). Several authors (Schmitz, 1967; Sexton, 1924; Steele and Steele, 1969) have

reported cannibalism among *Gammarus* spp. Enequist (1949) noted that the marine gammarid, *G. locusta*, was a scavenger, but also caught and ate small, living animals. Clemens (1950) found that *G. fasciatus* Say would eat up to 52 *Daphnia magna* Straus neonates per day, but he is the only author reporting on experimental studies of *Gammarus* predation in detail.

We were interested in the possible role of *G. l. lacustris* as an important predator in certain small lakes and ponds on the Alberta prairies and in mountain lakes and ponds in western Alberta and eastern British Columbia. We had observed attacks by *G. l. lacustris* on other crustaceans and insect larvae in these waters and became interested in the ecological significance of the nektoplanktonic behaviour of *G. l. lacustris* in certain lakes and ponds (for discussion, see also Hutchinson, 1967). We saw *G. l. lacustris* attacking and eating copepods in some shallow prairie lakes near Keoma, Alberta, and observed the same species catching and consuming *Clinotanypus* sp. larvae in Linnet Lake, Waterton Lakes National Park, Alberta. Furthermore, we noted that many freshly captured *G. l. lacustris* from Lily Pond, Jasper National Park, Alberta, had ingested one-half to seven-eighths of entire *Chaoborus americanus* (Joh.) *sonjai* (Saether) instar IV larvae, a phenomenon also observed by R. Walsh (pers. comm.) in some shallow lakes near Edmonton, Alberta. We observed *G. l. lacustris* swimming at the surface in open water (up to 15 m deep) at midday in several lakes, all of which were free of fish and most of which are oligotrophic mountain lakes having few or no macrophytes and little organic detritus in the sediments. We also observed *Chaoborus* spp. fourth instar larvae, usually considered to be benthic by day and planktonic by night, swimming limnetically in certain lakes under similar conditions. It was plausible that both *Gammarus* and *Chaoborus* had become

Methods

limnetic in order to capitalize on the only abundant food, the zooplankton. It also seemed plausible that such feeding might have an important effect on the composition of the plankton communities of these waters, especially the oligotrophic mountain lakes and ponds which characteristically have rather simple communities (Anderson, 1971).

We conducted some experimental laboratory studies of predatory feeding and food preferences of *G. l. lacustris*, *C. americanus*, and some copepod species and examined the community compositions of 52 lakes and ponds to assess the possible effects of feeding by these predators on the presence or abundance of potential zooplankton prey species in the lakes and ponds.

1. Field collections

We sampled zooplankton with a conical towing net of bolting silk (aperture approximately 76 μ) which we hauled vertically from near bottom to the surface in the deepest part of each lake or pond. We collected additional samples near shore and in some of the shallower ponds, either with a dip net or by towing a plankton net horizontally. The procedures used to calculate densities are described elsewhere (Anderson, 1970a). We collected benthic samples with an Ekman dredge (15 x 15 cm) and frequently with a small trawl (30 cm wide); in some shallow ponds, we obtained adequate benthic samples using a dip net. We brought back live samples to the laboratory in 10-l containers and maintained the samples at temperatures close to or slightly lower than the temperatures of the waters from which they came. Physical and chemical methods used are described elsewhere (Anderson, 1970b).

2. Laboratory experiments and identifications

We conducted three groups of feeding experiments with amphipods: over 6-h, 8-day, and 16-day periods. Prey and prey:predator ratios varied within each group of experiments and sometimes changed when prey were replenished, hourly in the 6-h experiments and daily in the 8- and 16-day experiments, during the course of a set of experiments. Individual adults were kept and fed in jars containing 100 ml of water. We maintained the group of 6-h experiments, which we checked hourly, at room temperature (approximately 20 C) and the 8- and 16-day experiments, checked daily, at 14 C. In the *Chaoborus* experiments, we kept individual instar IV larvae at 8 C in jars containing 65 ml of water and counted and replenished prey at 2-day intervals. For both amphipod and *Chaoborus* experiments, we brought in fresh prey animals from the

Results

1. Species used in experiments

Table 1 gives the species of animals used in the experiments and their sources. Table 7, which is discussed elsewhere, gives the detailed locations for all lakes and ponds, except Moab (11U/MJ 355347) and Herbert (11U/NH 542010) lakes.

2. Laboratory experiments

2.1. Gammarus

The initial purpose of the *G. l. lacustris* feeding experiments was to determine whether the amphipods would prey readily on certain other species with which they were known to occur. Anostracans were also included to see if they were acceptable prey. Although we counted the number of prey eaten, we cannot accept these as maximum numbers under the conditions of the experiments, because in many cases all

Table 1
Species of animals used in experiments and their sources

Species	Lake or pond	Location ^a
<i>Gammarus lacustris lacustris</i> Sars	Linnet Lake	WLNP
<i>Hyalella azteca</i> (Saussure)	Patricia Lake	JNP
<i>Eubrachyptus intricatus</i> Hartland-Rowe	Teardrop Pond	CFR
<i>Branchinecta paludosa</i> (O.F. Müller)	Plateau Pond	CFR
<i>Diaptomus shoshone</i> Forbes	Teardrop Pond	CFR
<i>Diaptomus arcticus</i> Marsh	Buffalo Paddock	WLNP
<i>Diaptomus nevadensis</i> Light	Thurston's Pond	prairie
<i>Diaptomus victoriaensis</i> Reed	Plateau Pond	CFR
<i>Diaptomus leptopus</i> Forbes	Linnet Lake	WLNP
	Moab Lake	JNP
<i>Diaptomus forbesi</i> Light	Buffalo Paddock	WLNP
<i>Diaptomus sicilis</i> Forbes	Herbert Lake	BNP
	Patricia Lake	JNP
	Thurston's Pond	prairie
<i>Daphnia pulex</i> Leydig emend. Richard	Patricia Lake	JNP
<i>Daphnia rosea</i> Sars emend. Richard	Herbert Lake	BNP
<i>Daphnia pulicaria</i> Forbes	Buffalo Paddock	WLNP
	Linnet Lake	WLNP
	Thurston's Pond	prairie
<i>Cyclops bicuspidatus thomasi</i> Forbes	Linnet Lake	WLNP
<i>Chaoborus americanus</i> (Johannsen)	Herbert Lake	BNP
var. <i>sonjai</i> (Saether)		
<i>Clinotanytus</i> sp. larvae	Linnet Lake	WLNP
<i>Helobdella stagnalis</i> (Linnaeus)	Linnet Lake	WLNP

^aWLNP, Waterton Lakes National Park; JNP, Jasper National Park; BNP, Banff National Park; CFR, Crowsnest Forest Reserve.

Table 2
Results of 16-day *Gammarus* feeding experiments at 14 C, days 1-8 (\bar{X} , mean; SEM, standard error of the mean)

Set	Prey	Prey: pred.	No. expts.	Days from beginning of experiments ^a							
				1		2		3		4	
				\bar{X}^b	SEM	\bar{X}	SEM	\bar{X}	SEM	\bar{X}	SEM
A	<i>D. leptocephalus</i>	10:1	6	3.0	(0.73)	4.0	(1.03)	3.0	(2.83)	1.8	(2.23)
B	<i>Daphnia</i> spp.	10:1	5	9.4 ^c	(0.89)	9.2 ^c	(1.10)	8.2 ^c	(2.49)	8.8	(1.64)
D ₁	<i>D. leptocephalus</i>	5 } :1	4	1.0	(1.41)	1.0	(0.81)	0.3	(0.5)	0.3	(0.5)
	<i>Daphnia</i> spp.	5 }		4.8 ^c	(0.5)	4.8 ^c	(0.5)	4.3	(0.3)	4.5 ^c	(1.0)
D ₂	<i>Clinotanytus</i> sp. larvae	3:1	2	0.8	—	2.0	—	2.5	—	2.0	—
E ₁	<i>D. arcticus</i>	2:1	4	0.8	(0.5)	0.5	(0.57)	1.3	(0.5)	1.3	(0.5)
E ₂	<i>D. forbesi</i>	5:1	3	—	—	2.3	(1.53)	2.7	(1.52)	2.3	(0.58)
E ₃	<i>H. stagnalis</i>	1:1	1	0	—	0	—	0	—	0	—

^a Prey renewed to starting ratio at each counting.
^b Prey eaten predator⁻¹ day⁻¹.
^c All prey eaten in over half the experiments.

Table 3
Results of 16-day *Gammarus* feeding experiments at 14 C, days 9-16 (\bar{X} , mean; SEM, standard error of the mean)

Set	Prey	Prey: pred.	No. expts.	Days from beginning of experiments ^a							
				9		10		12		14	
				\bar{X}^b	SEM	\bar{X}	SEM	\bar{X}	SEM	\bar{X}	SEM
A	<i>D. leptocephalus</i>	10:1	5	3.1	(3.25)	2.6	(2.19)	2.0	(1.05)	2.9	(0.81)
B	<i>Daphnia</i> spp.	10:1	5	9.4	(0.89)	9.6 ^c	(0.89)	5.0 ^d	(0)	5.0 ^d	(0)
D	<i>D. leptocephalus</i>	5 } :1	6	1.2	(1.33)	0.5	(0.84)	1.3	(0.42)	1.8	(0.52)
	<i>Daphnia</i> spp.	5 }		4.8 ^c	(0.42)	4.2	(0.97)	2.3 ^c	(0.26)	2.5 ^d	(0)
E ₁	<i>Daphnia</i> spp.	10:1	4	10.0 ^d	(0)	9.5 ^b	(1.0)	5.0 ^d	(0)	4.6 ^c	(0.52)
E ₂	<i>D. forbesi</i>	2 } :1	4	1.3 ^c	(0.95)	0.3	(0.50)	0.4	(0.24)	0.9 ^c	(0.24)
	<i>D. nudus</i>	3 }		1.0	(0)	1.0	(0.81)	0.6	(0.24)	0.5	(0.71)
E ₃	<i>D. shoshone</i>	5:1	—	—	—	—	—	—	—	—	—

^a Prey renewed to starting ratio at each counting.
^b Prey eaten predator⁻¹ day⁻¹.
^c All prey eaten in over half the experiments.
^d All prey eaten.

Table 4
Results of 6-h *Gammarus* feeding experiments at room temperature, 20 C; (checked hourly; \bar{X} , mean; SEM, standard error of the mean)

Set	Prey	Prey: pred.	No. expts.	Hours from beginning of experiments ^a							
				1		2		3		4	
				\bar{X}^b	SEM	\bar{X}	SEM	\bar{X}	SEM	\bar{X}	SEM
BE ₁	<i>Daphnia</i> spp.	10:1	8	6.8	(3.16)	3.5	(2.14)	3.8	(2.64)	2.1	(2.07)
DF ₁	<i>D. shoshone</i>	5:1	5	1.2	(1.31)	0.8	(1.31)	0.4	(0.55)	1.4	(0.89)
DF ₂	<i>D. shoshone</i>	10:1	—	—	—	—	—	—	—	—	—

^a Prey renewed to starting ratio at each counting.
^b Prey eaten predator⁻¹ day⁻¹.

Table 5
Results of 8-day *Gammarus* feeding experiments at 14 C (\bar{X} , mean; SEM, standard error of the mean)

Set	Prey	Prey: pred.	No. expts.	Days from beginning of experiments ^a					
				1		3		8	
				\bar{X}^b	SEM	\bar{X}	SEM	\bar{X}^b	
X	<i>E. intricatus</i>	1 } :1	8	1.0 ^d	—	0.5 ^d	—	All eaten	
	<i>D. shoshone</i>	3 }		1.1	(1.36)	1.0	(0.25)	1 left in each of 4 only	
Y	<i>H. stagnalis</i>	1:1	10	0	—	0	—	Leeches eaten in 4 expts.	
Z	<i>B. paludosa</i>	1 } :1	8	0.7 ^c	—	0.4 ^c	—	All prey eaten	
	<i>D. shoshone</i>	2 }		1.5 ^c	—	0.8 ^c	—	All prey eaten	
	<i>D. victorianaensis</i>	2 }		1.5 ^c	—	0.8 ^c	—	1 prey left in 1 expt.	

^a Prey renewed to starting ratio at each counting.
^b Prey eaten predator⁻¹ day⁻¹.
^c All prey eaten in over half the experiments.
^d All prey eaten.

prey animals were eaten and probably more might have been consumed had they been available. In many cases, we offered predators two or three prey species at once to determine whether there were food preferences.

In most experiments, the number of prey eaten per day remained fairly constant throughout the duration of the experiments. Tables 2 and 3 show that adult *Daphnia* were eaten in larger numbers than were adult *Diaptomus* and that, when we offered the two prey species together, more *Daphnia* were eaten. Fewer of the large species of *Diaptomus* prey (*D. arcticus*) were eaten than mid-sized (*D. leptocephalus* or *D. forbesi*), but *D. arcticus* seemed able to avoid capture by *G. l. lacustris* better than the smaller species could. In the 6-h experiments (Table 4) in which we counted numbers hourly, the results were similar in that more *Daphnia* were eaten than *Diaptomus*; however, total numbers eaten per day were higher and there was a decline with time in the numbers eaten throughout the day. Because we replenished prey to original densities at each count, the mean prey density throughout the day was higher than in the other experiments, and this could be the reason for greater consumption per day or fraction thereof.

In experiments in which we used anostracans as prey (Table 5), gammarids attacked the fairy shrimp voraciously and immediately. In many cases, about one-fourth to one-third of each prey animal remained uneaten. Only after feeding on the anostracans did *G. l. lacustris* capture and eat copepods.

In experiments in which we offered leeches, the gammarids frequently attempted to grasp them in the first few days, but ate some only after about a week. In two cases, the leeches moved actively as they were being eaten, indicating that they were alive when captured.

The *Clinotanytus* sp. larvae offered in two experiments (Table 2) were readily eaten.

Most of the *G. l. lacustris* used in these experiments were alive and active in the aquaria at 14 C 2 months after the experiments. To the more vigorous of these, we offered *Chaoborus americanus* instar IV larvae and the *G. l. lacustris* ate an average of one *C. americanus* every 3 days. On several occasions, when first fed, the predators captured and swallowed up to three-fourths of an individual larva in 30 seconds.

In the laboratory, we offered bits of leaf or algae, live *Daphnia*, and live *Diaptomus* in quick succession to individual *G. l. lacustris* that

had been starved for 2 or 3 days. Each gammarid immediately grasped the first particle offered and began to eat it. They also quickly grasped the second and third items offered and, for a time, carried all three around. In all cases, gammarids rejected plant matter in favour of the live animal prey, with *Daphnia* seemingly preferred over *Diaptomus* in these experiments, although we did not accumulate quantitative data.

We maintained several *Hyaella azteca* (Saussure) individually under the same conditions as *G. l. lacustris* and gave them the same prey species as *G. l. lacustris*. However there was no evidence of predatory feeding by *H. azteca*.

2.2. Chaoborus

The *Chaoborus* feeding experiments are still going on, but Table 6 gives some results. These experiments showed a fairly consistent predation rate throughout. Adjusting for the greater number of cyclopoids available in the first set of experiments, *Diaptomus sicilis* Forbes (rostrum-ramus = R-R = 1.0-1.2 mm) was preferred to *Cyclops bicuspidatus thomasi* Forbes (R-R = 0.9-1.2 mm) at a ratio greater than 3:2 ($p < 0.05$), and *D. sicilis* was preferred to *Daphnia* spp. at a

ratio of about 2:1 ($p < 0.05$), except in the case of very small *Daphnia rosea* Sars emend. Richard, for which the ratio was only 5:4. These experiments strongly indicated that feeding rates were higher when the density of preferred prey was higher, but we have not yet been able to verify this significantly. We also cannot rule out the possibility that, in these experiments, the cyclopoids ate an occasional diaptomid, even though frequent observations provided no evidence that this was occurring.

We ran two additional experiments for 24 days and, as above, counted every 2 days. In each, we kept one *C. americanus* with one large *Daphnia pulicaria* Forbes (H + V = 2.5 mm) and one *Diaptomus nevadensis* Light (R-R = 3.0 mm; Anderson, 1970c). One *C. americanus* ate four *Daphnia* and another ate six, but the *D. nevadensis* were still alive and active after 24 days. In two sets of control experiments with no *Chaoborus*, *D. nevadensis* did not prey on the large daphnids, although the copepod did eat small daphnids.

2.3. Copepods

Ten experimental vials, each containing two adult *Diaptomus leptopus* Forbes and five *D. b. thomasi*, were maintained for 18 days and checked at least every second day (material from Linnet Lake, 1972). We also set up ten control experiments, five with two diaptomids only and five with five cyclopoids only, to test for cannibalism. Of the first ten experiments, six showed no predation; three showed predation of one cyclopoid; and one, predation of two cyclopoids. No diaptomids were eaten. Although we cannot rule out the possibility of cannibalism by the cyclopoids, there was no evidence of cannibalism in the ten control experiments.

To test for cannibalism by *D. leptopus* adults on their own nauplii, we set up 14 experimental vials, each containing two adults and several

naupliar instars IV-VI (material from Moab Lake, 1970). We ran these experiments for 2 weeks. In each experiment, the copepods produced at least one clutch of eggs which hatched during the course of the experiments. The adult *D. leptopus* ate an average of one nauplius IV-VI per day in the 2 weeks, and consumed all newly hatched nauplii (instar I) soon after hatching (an estimated 18 to 36 nauplii I per vial over the 2-week period).

In other observational experiments in which we gathered no quantitative data, both *D. leptopus* and *C. b. thomasi* ate both their own nauplii and those of the other species. However, we obtained no evidence that the adults of one species would prey on adults of the other.

3. The study area

Figure 1 shows the general locations of the lakes and ponds included in this study. Table 7 includes detailed grid references for all of the lakes used in the experiments except Moab and Herbert lakes (see Results, section 1). We studied Celestine Lake, Jasper National Park (Anderson, 1970a) and Linnet Lake, Waterton Lakes National Park, in more detail than the other lakes and a summary of some July data for these two lakes follows:

Lake	Military grid ref.	Elevation (m)	Area (ha)	Max depth (m)	TDS	pH
Linnet	12U/TK 878382	1280	3	4.7	104	8.3
Celestine	11U/MJ 301934	1260	39	14.0	138	8.5

4. Lake communities — man-induced changes

Some of the changes in the invertebrate communities of Linnet and Celestine lakes appear to be directly related to large-scale manipulations. Both of these lakes have been frequently stocked with hatchery-reared trout, and both have been

treated with rotenone (Celestine, once; Linnet, twice). Anderson (1970a) summarized the effects of rotenone on the plankton of Celestine Lake but some of his data with additional data relative to fish stocking and benthic fauna are reconsidered here.

No data are available concerning the effects of rotenone applied to Linnet Lake in 1950 and 1966, but some early notes on the nature of the community (Rawson, 1938) and some indications of the effects of recent fish stocking are summarized below.

Rawson indicated that, in the fall of 1936, fathead minnows (*Pimephales promelas* Rafinesque), common suckers (*Catostomus commersoni* (Lacépède)), and salamanders (*Ambystoma tigrinum* Cary) were abundant in Linnet Lake. There were few *G. l. lacustris* and zooplankton generally was sparse and consisted only of very small species (not listed). Fingerling cutthroat trout (*Salmo clarki* Richardson) were stocked in the lake for the first time in 1936, but they winter-killed that winter. The lake has been restocked many times since then and, although there has been survival some years, winterkill has been common. Twice, as noted above, the coarse fish species were eliminated with rotenone and few, if any, are thought to live in the lake now. *Salvelinus* and *Salmo* spp. do not reproduce successfully in the lake. The zooplankton and benthic communities were sampled twice each summer during 1970, 1971 and 1972, and four times during 1973. cursory examinations were made in the winter of 1970-71 (E.K. Goble, pers. comm.). Figure 2 gives the results of these investigations and a brief survey of fish stocking from 1967 to 1972. There was no stocking in 1973. From general observations and other studies in the general area (Anderson et al., 1972), we know that the population of *Daphnia pulicaria* in the lake drops almost to zero during winter, whereas the *G. l. lacustris*, *Diaptomus*

Table 6
Summary of 2-day preferential feeding experiments at 14 C for *Chaoborus americanus* fed on *Daphnia* spp., *Cyclops bicuspidatus thomasi*, and *Diaptomus sicilis*

No. 2-day expts.	No. predators per expt.	No. prey per expt.	Total prey eaten	Mean no. prey animals eaten per predator per day
(Cycl./Diapt.)				
48	1	6:3	45:45	0.94
128	1	5:5	128:194	1.26
(Daphnia/Diapt.) ^b				
36	1	3:3	27:57	1.17
16	1	5:5	20:29	1.53
(lg.-Daph./sm.-Daph./Diapt.) ^a				
41	1	2:2:2	20:33:40	1.13

^aLarge *Daphnia* = *D. pulicaria* or *D. rosea*; small *Daphnia* = *D. rosea*.

^b*Daphnia* spp. approximately same biomass as *Diaptomus sicilis* used.

Table 7
Summary of the invertebrate communities by population category^a for 50 lakes and ponds in Alberta and British Columbia (F, fish; S, simple; D, diverse)

		Community type										Elevation (m)	Surface area (ha)	Max. depth (m)	pH	Dissolved solids (ppm)	Military grid ref.	
		Gammarus L. lacustris ^b	Chaoborus spp. ^{b,c}	Anostraca	Large-Diaptomus spp. ^d	Daphnia spp. ^e	Small-Cladocera	Cyclopoida ^f	Small-Diaptomus spp. ^g	Hydrella azteca ^h	Rooted macrophytes	Aquatic habitat						
Storm (K37)	I	2	0	0	2	1	0	0	0	0	S	2241	6.0	16.0	54	8.7	11U/NG686741	
Phalarope (J74)	I	1	0	0	1	0	0	0	2	0	0	S	2220	1.5	6.0	—	—	11U/MJ704153
Crescent (B229)	I	2	0	0	2	2	0	0	0	1	S	2204	4.0	5.5	98	8.5	11U/NH928057	
Outer Rink (J441)	I	1	0	0	2	2	0	1	0	0	0	S	2027	9.5	18.0	38	7.6	11U/LG936646
Up. Cairn (J253)	I	1	0	0	2	2	0	1	3	0	0	S	2180	20.0	27.0	122	8.4	11U/MJ894393
Rae Tarn (Alta.)	I	2	0	0	0	2	2	2	1-2	0	1	S	2180	3.3	3.5	117	8.7	11U/PG434133
Medicine Tent 1 (J254)	I	1-2	0	0	2	1	0	1	3	0	0	S	2138	45.0	34.0	134	8.4	11U/MJ891408
West Altrude (B85)	I	2	0	0	0	3	1	2	3	0 ^{g?}	1	S	1628	3.0	6.1	150	8.5	11U/NG667757
Kesler (W51)	I	2	0	0	1	1-2	3	3	3	2 ^{g?}	3	D	1503	10.0	2.0	105	8.2	12U/TK860518
Buffalo Paddock (W46)	I	2-3	0	0	1	1-2	1-2	2	3	2-3	2	D	1351	5.0	1.0	132	8.5	12U/TK904454
Indian Springs (W47)	I	2	0	0	1	1	2	2	3	3 ^{g?}	2	D	1351	2.5	2.0	148	8.8	12U/TK904459
Edna (J505)	I	2	0	0	0	2-3	3	3	2	0 ^{g?}	1	S	1000	25.0	2.0	285	8.2	11U/MJ305808
Bear Lake (Alta.) ⁱ	II	2	2	0	2	3	0	2	0	1	3	D	1800	2.0	4.0	30	7.3	11U/PF834658
Herbert Pond (B183) ⁱ	II	2	2	0	0	3	1	2	2	0	2	D	1615	0.3	1.5	127	8.1	11U/NG541007
Herbert Lake (B182)	II	1-2	1	0	0	2	1	2	3	2-3 ^g	1	D	1615	5.7	13.3	155	8.1	11U/NG542010
Island Lake (B165) ⁱ	II	2	2	0	0	3	0	3	2	0	1	D	1573	12.5	5.0	118	8.5	11U/NG618935
unn. pond (W31)	II	2-3	3	0	1	1	1-2	3	0	3	3	D	1524	2.0	3.0	191	8.2	12U/TK997380
Lily pond (J421)	II	2	3	0	2	2	2	3	0	1	3	D	1323	0.8	4.0	63	8.0	11U/MJ174592
Tekarra (J392)	II	2	2	0	2-3	3	0	2	0	0	3	D	1098	0.2	1.5	—	—	11U/MJ292558
Cold Sulfur (J506)	II	2	3	0	0	1-3	0	1-3	2	0	2	D	1006	0.4	1.5	372	8.4	11U/MJ273773
Thurston's pond (T2)	II	3	0-1	0	3	2-3	0	1	3	0	3	D	925	5.0	1.5	1200	9.2	12U/UM358759
Opabin pond 3 (Y13)	III	0	3	0	0	0	1	3	0	0	0	S	2232	0.3	1.5	10	8.1	11U/NG474881
Opabin pond 4 (Y11)	III	0	3	0	0	0	3*	3	0	0	0	S	2232	0.3	1.4	10	8.1	11U/NG473883
E. Henry pond (J481B)	III	0	2-3	0	0	0	0-1	2	0	0	0	S	2105	3.5	4.5	—	—	11U/LJ150658
Moren 1 (J471)	III	0	2	0	0	0	3*	2	0	0	0	S	2073	3.0	10.0	3	7.7	11U/LJ964747
Summit Lake (W9)	III	0	2	0	0	1	2-3*	0	0	0	0	S	1931	1.8	2.0	4	7.0	11U/QF177324
Nutcracker (Alta.)	III	0	3	0	0	2	3	2	3	0	0	S	1881	0.5	0.8	27	7.3	11U/PF858626
Tadpole pond (Alta.)	III	0	2	2	0	3	0	1	2	0	0	S	1793	<0.1	0.5	13	7.8	11U/PF833657
Rink Lake (J444)	III	0	2	0	0	0	3*	1	0	0 ^{g?}	0	S	1793	15.0	6.0	13	7.4	11U/LJ932624
Mariou Lake (G10) ⁱ	III	0	2	0	0	3	1	1	0	0	3	D	1723	0.5	6.0	3	6.0	11U/MG646787
Little Herbert (B184)	III	0	1	0	0	3	1	3	3	1 ^{g*}	1	D	1577	0.3	8.2	175	8.2	11U/NH546001
uuu. pond (W60)	III	0	1	2	2	3	0-2	3	3	0	2	D	1293	0.2	1.0	134	7.4	12U/TK891390
Kootenay pond (K18)	III	0	1-2	0	2	2	1-3	1-2	0	0 ^{g*}	2	S	1213	3.0	7.5	237	8.1	11U/NG675381
Leach pond 2 (J292)	III	0	2	0	1-2	3	2	3	2-3	0	1	S	1200	1.0	1.0	134	8.4	11U/MJ398360
Nixon pond (K6) ⁱ	III	0	2	0	2	3	1	1	0	0	1	S	1183	2.5	1.0	117	8.8	11U/NG754211
Palisades (J800)	III	0	2	0	1-2	3	3	1-2	3	0	2	D	1027	0.4	1.0	143	8.8	11U/MJ295685
Little Bighorn (B500)	IV	0	0	3	3	2	0	0	0	0	0	S	2420	0.8	8.0	163	8.3	11U/NH937001
Dolomite pond (B290)	IV	0	0	3	2	0	2	0	0	0	0	S	2385	1.0	3.0	87	8.5	11U/NH427269
Branchinecta (J76)	IV	0	0	1	1	1	0	0	1	0	0	S	2270	0.5	2.5	—	—	11U/MJ709148
Brachiopod (B200)	IV	0	0	0	2	0	1	0	3	0	0	S	2270	1.2	3.0	65	7.8	11U/HH677034
Plateau pond (Alta.)	IV	0	0	2-3	2	2	0	1	3	0	0	S	2180	0.5	5.0	86	7.8	11U/PF778671

Table 7, cont.
Summary of the invertebrate communities by population category^a for 50 lakes and ponds in Alberta and British Columbia (F, fish; S, simple; D, diverse)

	Community type	Gammarus L. lacustris ^b	Chaoborus spp. ^{b,c}	Anostraca	Large-Diaptomus spp. ^d	Daphnia spp. ^e	Small Cyclopoida ^f	Small-Diaptomus spp. ^g	Hydrella azteca ^h	Rooted macrophytes	Aquatic habitat	Elevation (m)	Surface area (ha)	Max. depth (m)	Dissolved solids (ppm)	pH	Military grid ref.	
O'Beirne 1 (J453)	IV	0	0	0	2	2	0	1-2	0	0	0	S	2133	4.7	24.0	9	7.4	11U/LJ922647
Teardrop pond (Alta.)	IV	0	0	1-3	3	1	3	0	3	0	3	D	2030	0.4	1.5	41	9.8	11U/PF823630
O'Beirne 2 (J448)	IV	0	0	1-2	2	1	2*	1	0	0	0	S	2027	8.5	33.0	7	7.4	11U/LJ923626
O'Beirne 5 (J452)	IV	0	0	1-2	2	1	3*	0	0	0	0	S	2000	6.4	33.0	12	7.7	11U/LJ922617
North Summit (J373) ⁱ	IV	0	0	2	2-3	1	0	1	3	0	0	S	1540	12.0	3.0	106	8.3	11U/MJ486606
South Summit (J372) ⁱ	IV	0	0	0	2	2	1-2	1	3	0	1	D	1540	14.0	3.0	118	8.3	11U/MJ493598
Church's pond (Alta.)	IV	0	0	2	2	3	3	3	2	0	3	D	1241	<0.1	0.6	560	9.0	11U/PC909726
Thurston's pond (T1)	IV	0	0	0	2	2	3	2	3	0	3	D	925	0.5	1.5	302	8.7	12U/UM369758
Keoma lake (K1)	IV	0	0	3	3	3	0	0	3	0	0	S	944	38.0	1.0	6200	9.6	12U/UM302763

^a Scale of relative abundance (approximately by order of magnitude): 0 = absent, possibly very rare; 1 = few; 2 = fairly numerous; 3 = abundant to extremely abundant. (Mean July–August abundance).

^b In fish-free lakes, *Gammarus* and *Chaoborus* frequently observed in epilimnion at midday.

^c Includes *Chaoborus americanus*, *C. nyblaei*, *C. brunskilli*, *C. flavicans*.

^d Includes species of *Hesperodiaptomus* and *Aglaodiaptomus*.

^e Includes *Daphnia pulex*, *D. pulicaria*, *D. schoedleri*, *D. middendorffiana*, *D. rosea*, *D. similis*.

^f Includes species of *Chydorus*, *Bosmina*, *Alonella*, *Alona*, *Ceriodaphnia*, *Polyphemus*, and *Holopedium*. x = dominated by *Holopedium gibberum*.

^g Includes *Acanthocyclops vernalis*, *Cyclops bicuspidatus thomasi*, *Diacyclops navus*, *Orthocyclops modestus*.

^h Includes species of *Leptodiaptomus*, *Acanthodiaptomus*, *Onychodiaptomus*, and *Arctodiaptomus*.

ⁱ Indicated lakes stocked with "trout" more than 10 years ago; fish survival seldom more than 1 year; no fish reported in past 10 years. Numbers in parentheses refer to National Parks Master Map numbering system.

^j F? = slight doubt regarding status and/or abundance of fish; no fish stocked for 2 years prior to this study; presence of fish in Rink Lake never substantiated. F* = probably no overwintering; stocked annually. F = substantial fish population.

leptopus, and *C. b. thomasi* populations are usually present throughout the year. The winter-kill of fish in 1970–71 may have contributed to the increase in the *Gammarus* population in the following summer, at which time *D. leptopus* was absent, *D. pulicaria* lower than in the other two years, and *C. b. thomasi* somewhat higher than in the other two years, especially in late summer when *D. leptopus* adults are usually abundant, if present. Although there was one late spring stocking of brook trout (*Salvelinus fontinalis* (Mitchill)) in 1971, they were only 10-cm fish, whereas the later stockings were of 15-, 18-, and 30-cm brook trout and rainbow trout (*Salmo gairdneri* Richardson). Mr. J. Whitaker (pers. comm.) has indicated that 8- to 10-cm rainbow trout stocked in the experimental lakes in Manitoba (see Introduction) do not feed at first on

Gammarus, allowing the amphipods time to produce their broods. The continuous increase in *Gammarus* abundance during the summer of 1971 in Linnet Lake suggests that the 10-cm fish may not have preyed significantly on *Gammarus* in this lake either.

Only 2-year-old fish were stocked in Linnet Lake in 1972, and fishing pressure was rather heavy early in the season (E.K. Goble, pers. comm.). Although the number of fish in the lake in 1972 may have been smaller than in other years because of a partial winterkill the previous winter and because of the smaller number of fish stocked in 1972 (Fig. 2), the fish present were larger. This was likely the reason why *Gammarus* numbers remained low in 1972. Because of fishing pressure and no stocking in 1973, however, fish numbers apparently have been greatly

Figure 1
Map of the study area showing the National Parks and the location of some of the lakes

Figure 1

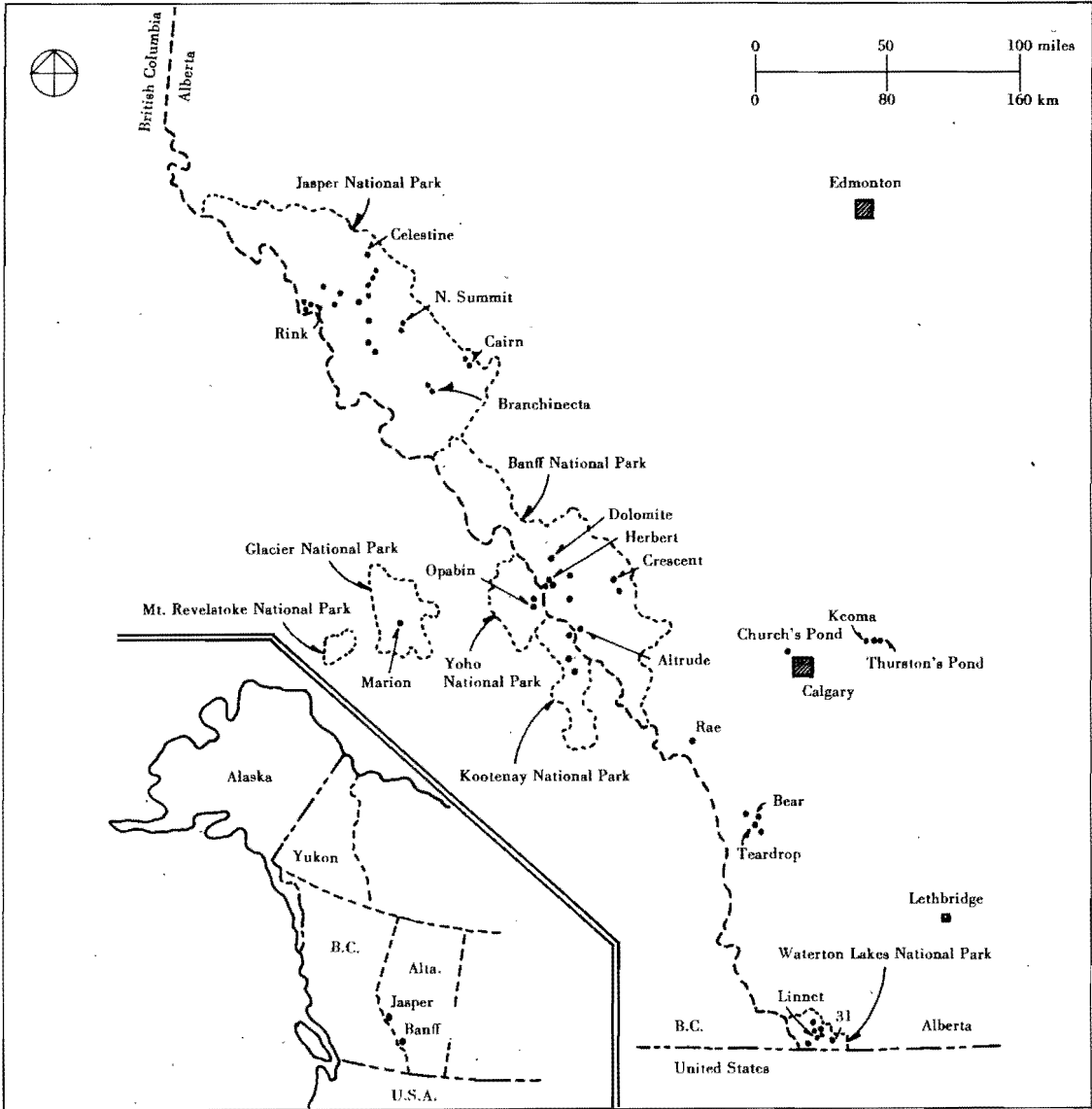
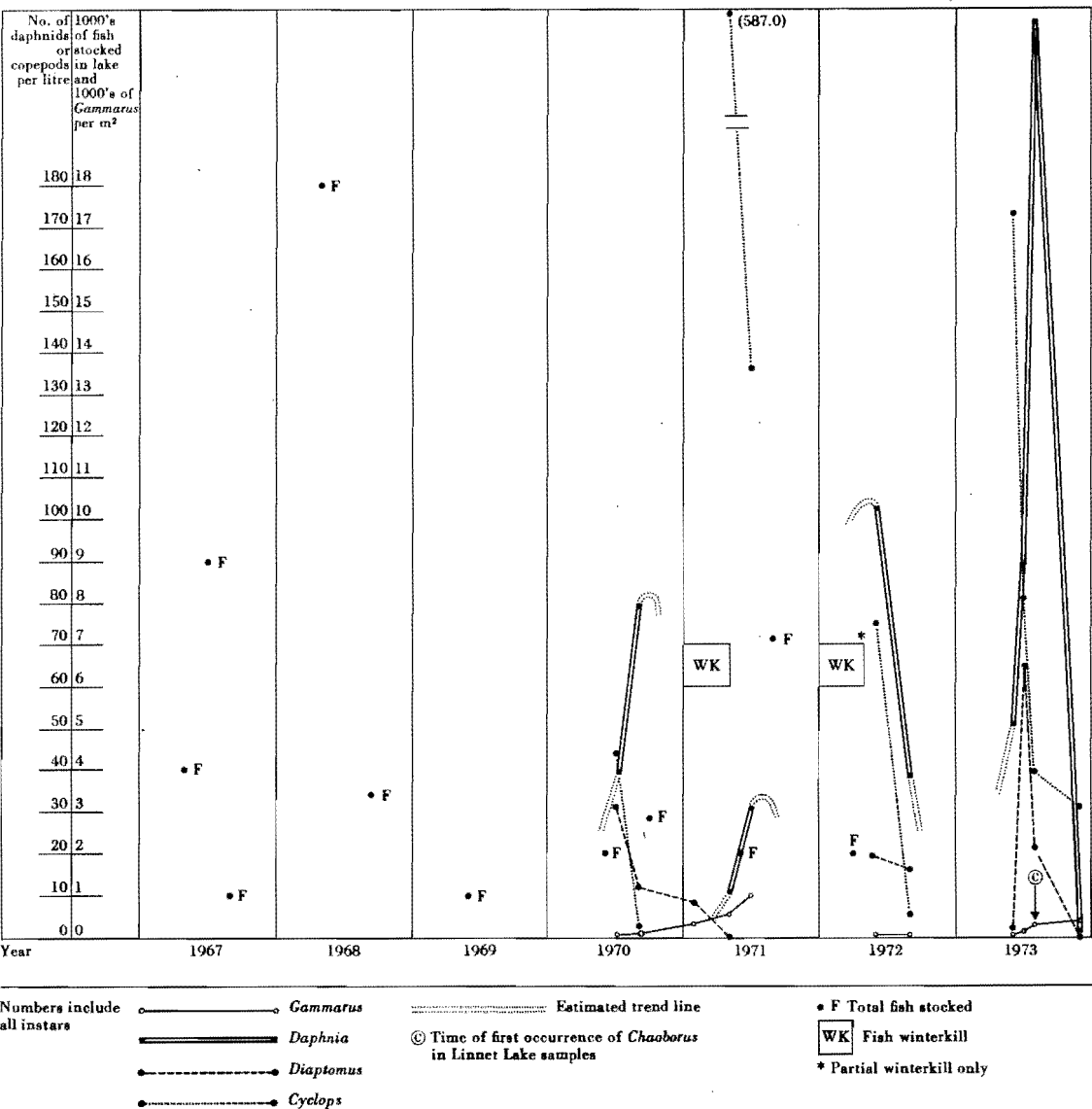


Figure 2
Summary of the changes in the dominant components of the aquatic community, Linnet Lake, Waterton Lakes National Park

Figure 2



reduced. Early indications are that *Gammarus* numbers have begun to recover, that *Diaptomus* and *Daphnia* numbers were unusually high in 1973, and that *Cyclops* numbers did not drop as much as might have been expected seasonally according to the 1970 and 1972 data. High *Cyclops* numbers have tended to occur with relatively high *Gammarus* numbers and lower or declining *Diaptomus* numbers, although the trend occurred later in the season in 1973 than in 1971. Whether the dramatic decline in *Daphnia* numbers in 1973 was due to increased numbers of *Gammarus* or to seasonal changes will not become certain until sampling is done in 1974.

Following the application of rotenone to Celestine Lake in 1967 (Fig. 3), no zooplankton was collected in the limnetic zone for several months. Although the numbers of *G. l. lacustris* in Celestine Lake were estimated only, it was known that the rotenone had little effect on the amphipods in Patricia Lake the previous fall (Anderson, 1970a). In Celestine Lake, gammarids were seen swimming limnetically in the spring and early summer of 1968 and were taken in plankton samples, as was *Chaoborus flavicans* (Meigen). Both species became less abundant in the following years and gammarids were not caught or observed limnetically. It was interesting to note the reappearance of *D. leptopus* in Celestine Lake samples in 1972, a year when *G. l. lacustris* and *C. flavicans* numbers appeared to be at their lowest in the study period. The last reported occurrence of *D. leptopus* in this lake was by Reed (1959), who was working with samples collected by D.S. Rawson in the late 1930's and 1940's, although occasional immature diaptomids occurred in 1969 samples. Because of the relative isolation of Celestine Lake and the existence of potential refuges within the lake (e.g. isolated reedbeds and small bays along the shore), the reappearance of *D. leptopus* was

likely due to the resurgence of a small population residuum, rather than to the reinvasion from outside the lake. Figure 3 indicates that *Daphnia pulex* and *Cyclops vernalis* Fischer summer populations increased in abundance fairly regularly after 1968, except that cyclopoid numbers appeared to have dropped earlier than usual in the year with the resurgence of *Diaptomus leptopus*.

5. Survey of 50 lake and pond communities

Table 7 gives a summary of the communities of 50 representative small lakes and ponds in the general study area (Fig. 1). We have divided these communities into four groups: I — containing *Gammarus*, but not *Chaoborus*; II — containing both *Gammarus* and *Chaoborus*; III — with *Chaoborus* but not *Gammarus*; IV — neither *Gammarus* nor *Chaoborus*. There were no obvious reasons why these two genera were absent from group IV, even though some are temporary waters; Holsinger (1972) notes that gammarids inhabit both permanent and temporary waters. Some of the shallower waters in group III freeze to the bottom in winter or dry up in summer, indicating that at least some *Chaoborus* spp. are able to inhabit temporary waters, in contrast to the conclusions of Dodson (1970) and Sprules (1972).

Chaoborus was not present with *Gammarus* unless the lake habitat was diverse (i.e. usually abundant rooted or emergent macrophytes and the existence of true littoral and limnetic zones). Anostracans were never present with *Gammarus*. Large-*Diaptomus* species (see footnote, Table 7) were present in significantly lower actual numbers ($p < 0.05$) in groups I-III, but especially in group III, the *Chaoborus* lakes. Furthermore, in groups I and III, the numbers of large diaptomids present in the individual lakes and

Figure 3
Summary of the changes in the dominant components of the aquatic community, Celestine Lake, Jasper National Park

Figure 3

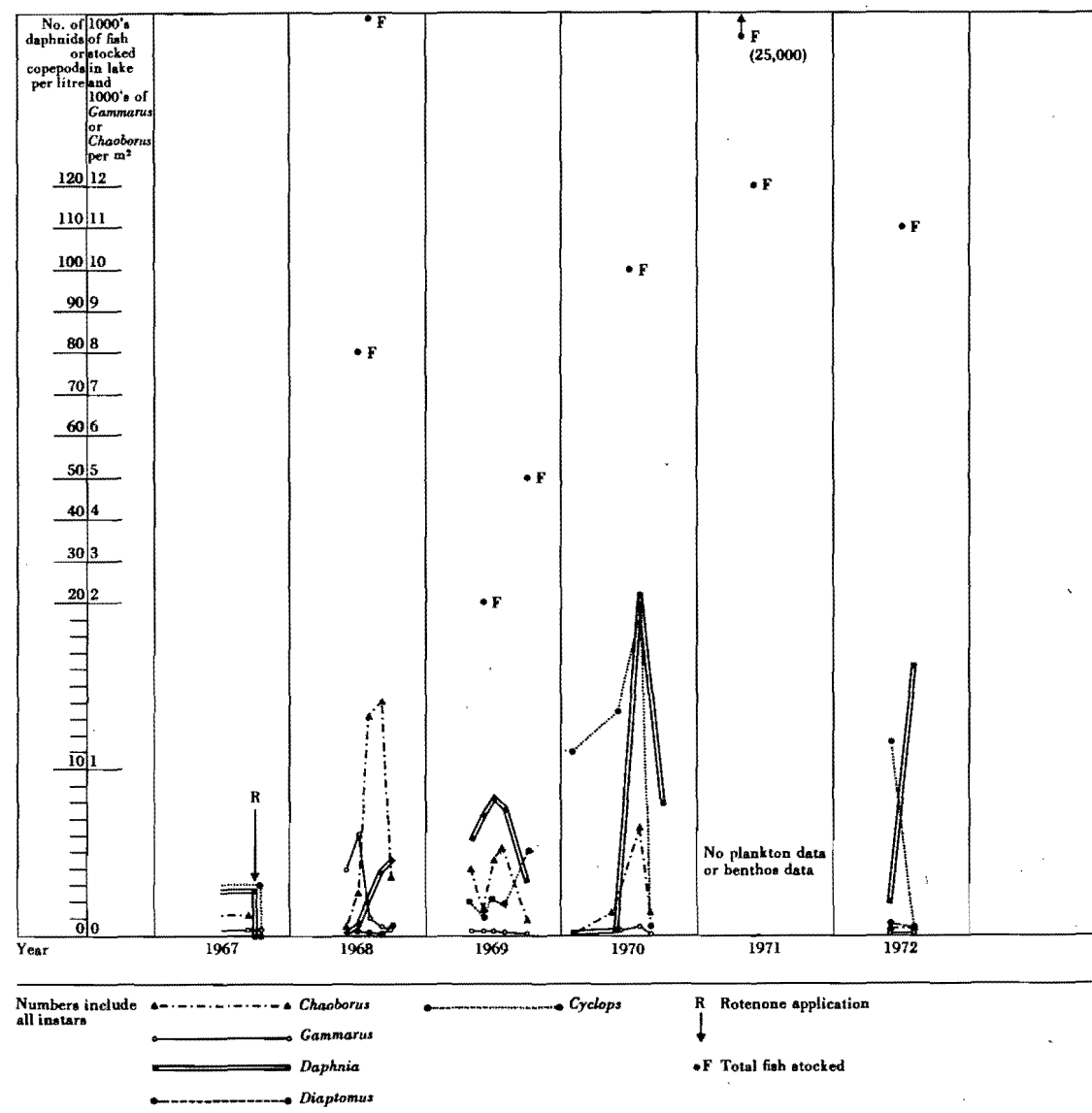
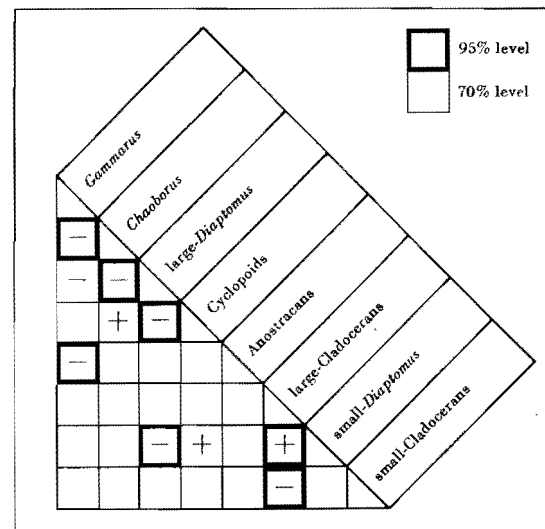


Figure 4
Summary of the significant correlations between components of the aquatic communities, based on abundance

Figure 4



Considering the communities of the 50 lakes and ponds as a group, and using the actual counts of animals, we calculated coefficients of correlation for the eight population categories considered in Table 7 and summarized the results in Figure 4. We accepted only seven of the 28 correlations calculated as significant ($p < 0.05$; six negative and one positive).

ponds were inversely proportional to the numbers of *Gammarus* or *Chaoborus* present.

Cyclopoid numbers were lowest in group IV for which numbers of large-*Diaptomus* were highest, and actual cyclopoid counts were highest in group III, for which large-*Diaptomus* species numbers were lowest. In groups I and II, cyclopoid densities were inversely proportional ($p < 0.05$) to large-*Diaptomus* species densities. Although there was a weak positive correlation ($p < 0.30$) between the population counts for small-*Diaptomus* species and cyclopoid species in the 50 communities, mean cyclopoid densities were higher in communities including *Chaoborus* spp. and mean densities of small-*Diaptomus* species were lower when *Chaoborus* spp. were present.

Although there was no clear trend in *Daphnia* abundance relative to community groups, their numbers tended to be higher in communities having more diverse habitats, as indicated by the abundance of macrophytes (Table 7). In group II, mean densities of small cladocerans were lowest, whereas mean densities of *Daphnia* spp. were highest. Mean densities for both groups of cladocerans were high in group III, although actual population counts in the two cladoceran groups were inversely correlated ($p < 0.05$). *Chaoborus* preferred copepods to daphnids as prey (Table 6), and the higher numbers of cladocerans were probably at least partly due to the lower levels of competition resulting from smaller numbers of copepods present in group III lakes.

Hyalella azteca were not abundant in any of the 50 lakes and ponds, but Table 7 indicates that they most likely occur in the type of waters suitable to *G. l. lacustris*, especially waters with diverse habitats (i.e. group II and lower-altitude group I).

Discussion and conclusions

There have been many reports on *Chaoborus* spp. predation and food preferences (Dodson, 1970; Parma, 1971; and Roth and Parma, 1970) and some on predatory feeding by certain cyclopoid and *Hesperodiaptomus* species (Anderson, 1970c; Fryer, 1957; McQueen, 1969). However, the possibility of cannibalism or predation by *Aglaodiaptomus* spp. on small zooplankters has not been reported; nor has much consideration been given to the possibility that predation by *Gammarus* could greatly affect the abundance and distribution of other aquatic invertebrates.

Our experiments and observations indicate that *G. l. lacustris* can eat a variety of aquatic invertebrates of the same size or smaller. In two lakes, fluctuations in the densities of certain zooplankton populations corresponded closely to variations in *G. l. lacustris* abundance, and indicated that the intensity of predation by the amphipod probably directly or indirectly affected the abundance of certain plankton species in the lakes. In a consideration of all lakes of the study, *Diaptomus leptopus* and other large diaptomid species were present at lower mean densities when either *G. l. lacustris* or *Chaoborus* spp. were present, and densities of these copepods were correlated inversely with *Gammarus* or *Chaoborus* densities, especially in groups I and III (Table 7). On the basis of both experimental and community-composition data, cyclopoid copepod numbers are likely to be significantly lower in the presence of abundant copepods of the subgenera *Hesperodiaptomus* and *Aglaodiaptomus*, probably because of competition or predation on early cyclopoid instars in the case of *Aglaodiaptomus*. *Hesperodiaptomus* spp. have been shown to prey readily on adults and all copepodid instars of the cyclopoid species with which they commonly co-occur in the study area (Anderson, 1970c).

Fairy shrimp other than *Artemia salina* (Linnaeus) are usually considered to be inhabi-

tants of temporary waters (Dexter, in Edmondson, 1959), but some of our collections indicated that these animals may live in a wider range of habitats. Although proof is lacking that they complete their life cycles in permanent lakes, we have collected fairy shrimp in three such lakes in the study area (two O'Beirne lakes, Table 7, and Lost Lake in Waterton Park, 11U/QE 083475). It is of interest that we collected them only from very near the bottom of the deepest part of these lakes. The basic data for the lakes listed in Table 7 suggest that fairy shrimp could conceivably inhabit some of the other waters listed in Table 7 but for the presence of *G. l. lacustris*.

That the population densities of *G. l. lacustris* were low when densities of fish were high (or dropped shortly after the stocking of fish) can be determined from the results in Figures 2 and 3. These data suggest that, although fish introduction may not have an immediate or permanent effect on populations of food organisms such as *G. l. lacustris*, continuous stocking of large numbers of fish could have a lasting effect. Numbers of fish stocked in two lakes (maximum 7,000 ha⁻¹ in Linnet Lake; maximum 1,000 ha⁻¹ in Celestine Lake) probably have kept the *G. l. lacustris* populations too small to be of value as a consistent food resource for the fish. Although the fish present in some lakes appear to eliminate *Hesperodiaptomus* spp. quickly (Anderson, 1972), fish and *Aglaodiaptomus* spp. often co-occur in the study area. The latter copepod subgenus is usually smaller than the former, and is apparently near the lower limit of the prey size upon which trout species can profitably feed.

Population densities of diaptomid copepods, especially large species, may be controlled by *Chaoborus* spp. (Table 7). In contrast to Sprules' (1972, p. 377) results, but in agreement with Dodson's (1970, p. 135) and Allan's (1973, p. 493) results concerning prey-size selection, our

experiments and observations indicated that intense predation by *Chaoborus* instar IV larvae on adults of large species of *Diaptomus* (e.g. *Aglaodiaptomus* and *Hesperodiaptomus*) was unlikely, although predation on adults of small species (e.g. *Leptodiaptomus*) was common. Because chaoborid larvae are present year-round in waters where they occur, they would be there to prey on the nauplii of the large copepod species which usually appear earlier than the small species in the waters of this study. Also, most of the large-species populations produce only one generation per year in these waters, whereas some of the small species produce two or more, except in the very high lakes. This may account for the relatively infrequent occurrence of *Chaoborus* spp. with large diaptomids such as *D. nevadensis*, *D. novemdecimus*, *D. arcticus*, and *D. shoshone*, the four species of the subgenus *Hesperodiaptomus* which occur in the lakes and ponds of the study area. The infrequent occurrence of fairy shrimps with *Chaoborus* spp. may have a similar explanation.

Sometimes the predominant predators of this study occurred in very simple communities where prey animals were few in number, especially in the more oligotrophic waters. Low densities or absence of certain species in these communities were undoubtedly due to the presence of these predators (*Chaoborus* spp., large *Diaptomus* spp., and *G. l. lacustris*), all of which are opportunistic feeders to a remarkable degree and are able to complete their life cycles on a plant or detritus diet (Anderson, 1970c; Parma, 1971; many *Gammarus* references cited previously). Because some of these predators are present year-round, there is little chance that potential prey species can increase in numbers unless an event of great impact alters the balance (e.g. introduction of fish or the application of rotenone: Figs. 2 and 3; also Anderson, 1970a). Because of higher

fecundity and shorter generation time for *Daphnia* spp., small cladocerans, cyclopoids, and some small *Diaptomus* spp., populations of these smaller species and *Daphnia* were characterized by large seasonal variations in population densities and the potential for rapid population growth after a large impact on the environment, regardless of community type.

In this study, most significant negative correlations (Fig. 4) involved species usually having only one generation per year (*Gammarus*, *Chaoborus*, large *Diaptomus* spp., anostracans) and indicated predator-prey relationships, although the negative correlation between large and small cladocerans probably reflected competition. The relationship between "small cladocerans" and other groups in this study may have been biased in groups III and IV by the inclusion of *Holopedium gibberum* Zaddach with the small cladocerans, even though the number of occurrences of *H. gibberum* was small. This species did not occur with *G. l. lacustris*, but was often abundant when *Chaoborus* populations were fairly dense (Table 7). It is possible that the large gelatinous case of *H. gibberum* inhibits predation by *Chaoborus* spp. but not by *G. l. lacustris*. Allan (1973) has noted selective predation by *Chaoborus* on *Daphnia* over *Holopedium*. The possibility of competition must also be considered. Allan (1973) indicates a competitive advantage by *Daphnia* over *Holopedium* but, in the present study, when *Holopedium* occurred it was usually abundant and *Daphnia* spp. were usually sparsely represented or absent.

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