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HORIZONTAL DISPERSION AND DENSITY OF LIMNETIC CRUSTACEANS IN FOUR SUB-ALPINE LAKES

A Thesis

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ABSTRACT

Limnetic crustaceans from four subalpine lakes in northeast Idaho were studied during the summers of 1966 and 1967. Four methods were used to take quantitative vertical plankton samples. These collections were used for comparison of lakes, comparison of sampling methods within lakes, and comparison of sample sizes.

The four lakes were similar in having a simple species composition and low density of limnetic crustaceans. For all samples Fisher's coefficient of dispersion $S^2/\overline{X}$ was computed and used as a measure of horizontal dispersion. Mean total crustacean density and dispersion appeared to approximate taxa density and dispersions. Data for all comparisons were based on the density and horizontal dispersion of mean total crustaceans.

The meadow lakes had higher densities of limnetic crustaceans than the headwall lakes, 1966 and 1967. There was an indication that a positive linear relationship existed between total crustacean density and coefficient of dispersion when sampled by different methods in each of the four lakes. Similarities of total crustacean density and dispersion estimates from different methods and sample sizes was attributed to the low density in limnetic regions. Reliability of data was possibly affected by small sample sizes and avoidance behavior of crustaceans to samplers.

INTRODUCTION

Quantitative investigations of zooplankton communities in mountain lakes are difficult because of inadequate sampling apparatus. This problem is the direct result of the logistics involved in the transportation and use of limited amounts of equipment in remote areas. Sampling is usually from a rubber raft with simple plankton traps, tow nets and water bottles (Rawson, 1953; Pennak, 1955; Reimers, et al 1955; Raleigh, 1957; Rabe, 1964; and Colborn, 1966). The shallow depths of these waters and the instability of rafts usually precludes the use of metered nets or other elaborate equipment for large volume sampling.

The limnetic crustaceans of four similar subalpine lakes were studied from July to September during the years 1966 and 1967. Four methods were used to sample crustacean plankton. Results are based on the comparison of density and dispersion of mean total crustaceans within and between lakes. This study describes difficulties encountered in analyzing zooplankton collected from extreme oligotrophic waters.

DESCRIPTION OF STUDY AREA

A. General

Silver, Gold, Tin, and Copper Lakes are located in the Five Lakes Butte Area of the Bitterroot Mountains (Clearwater National Forest) at elevations of 1751 meters to 1873 meters (Fig. 1). They are 38 miles southwest of Superior, Montana in Shoshone County, Idaho. Forest Development Road 338 passes within one and a half miles of the lakes which are accessible by trail. They are located within one-half mile of each other in an east-facing glacial valley that forms part of the headwaters of Meadow Creek. This drains into the North Fork of the Clearwater River.

The lakes are in the montane zone based on elevation, latitude, insolation, temperature, precipitation, geochemistry, and general topography (Pennak, 1963). Tin and Copper Lakes are apparently filling in more than the headwall lakes because they are fed by a larger drainage area. Silver and Gold Lakes appear to have changed little since time of formation.

B. Geology

The principle formation of the area is a highly metamorphosed rock that consists of a low-grade phyllite-siltite. It is part of the Upper Wallace Formation and is included in the Precambrian Belt Series. There is evidence of heavy faulting and possible intrusions of meta-

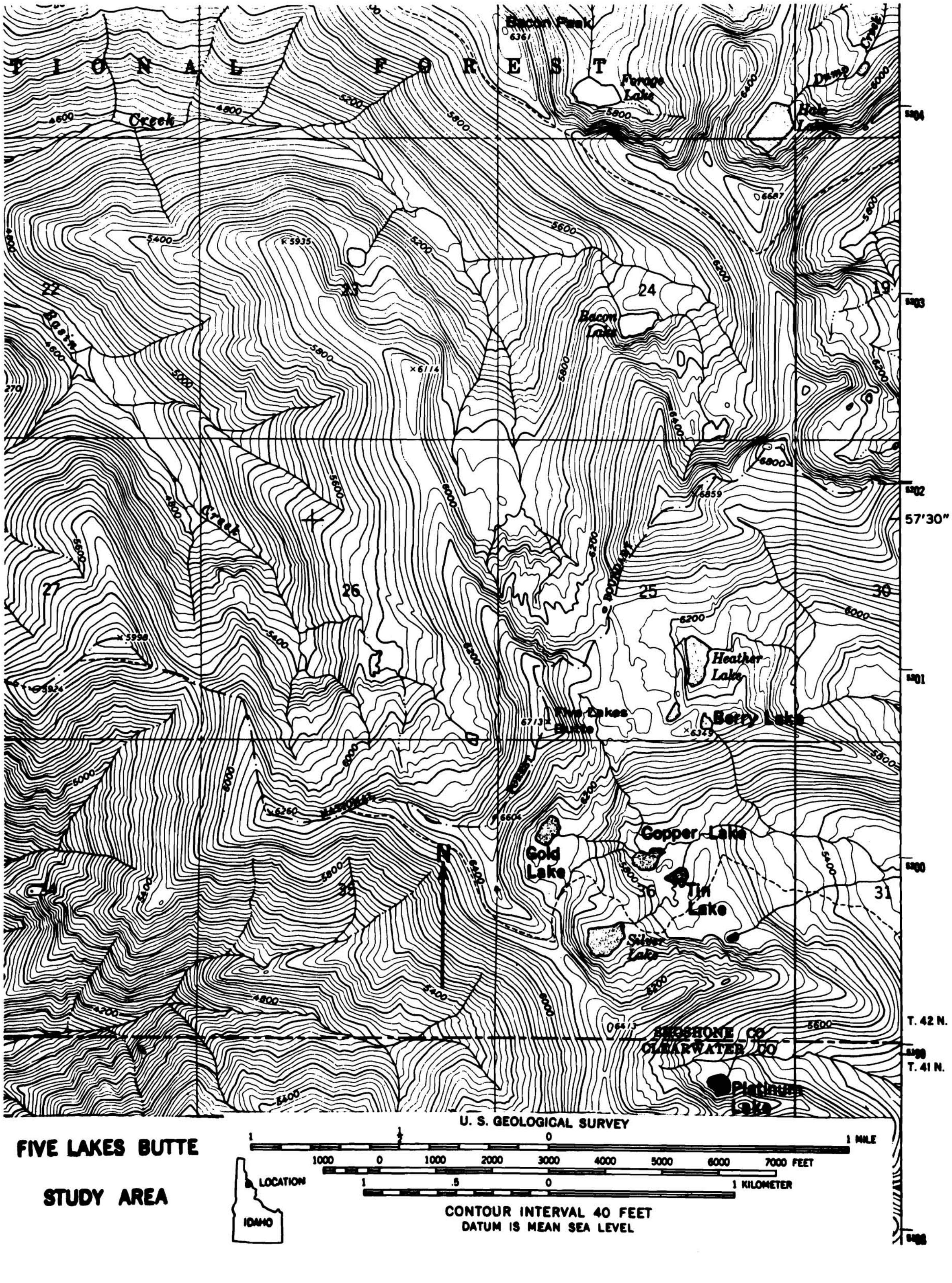


Figure 1. Topographic section of study area.

diabase. The Laramide Orogeny apparently had little effect on the geology of the area since the rock is essentially unchanged from its original condition, except for glacial modification during the Pleistocene Period (Greenwood, oral communication). The metamorphic rock of the area appears to be more inert to weathering than other igneous substrates commonly found in many high mountain lake drainages.

C. Morphometry and Hydrography

The lakes are located in cirque basins on a series of benches (Fig. 2-5). Tin and Copper Lakes are in meadows on the lowest bench (1751 meters) and are separated by a bedrock spur that extends up between Silver and Gold Lakes to the main headwall of the valley. Silver Lake is on the second bench (1800 meters) and south of the bedrock spur. Gold Lake is north on the third bench (1873 meters).

Maximum depths of Silver, Gold, Tin, and Copper Lakes in that order are 12.8, 3.7, 2.1, and 3.1 meters. Total areas are 3.5, 1.7, 1.0, and 1.6 hectares respectively. Other morphometric features are listed in Table 1.

D. Water Chemistry and Substrate

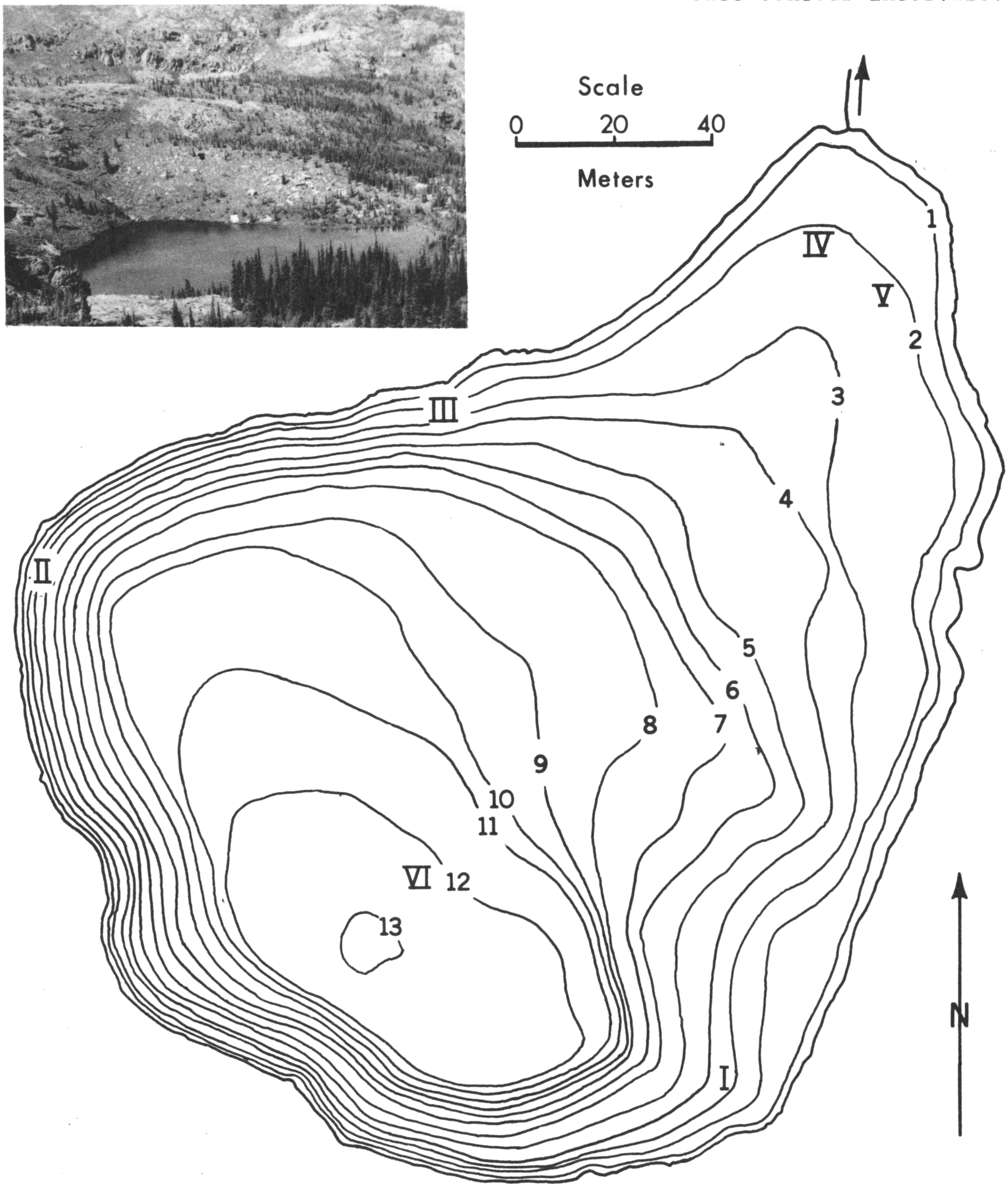
The chemical and physical characteristics of the lakes were remarkably similar for 1966 and 1967. The pH values ranged from 6.1 to 6.9. Methyl orange alkalinity was 2-5 mg/l. Dissolved oxygen

Hydrographic Map

SILVER LAKE

Contour Interval 1 Meter

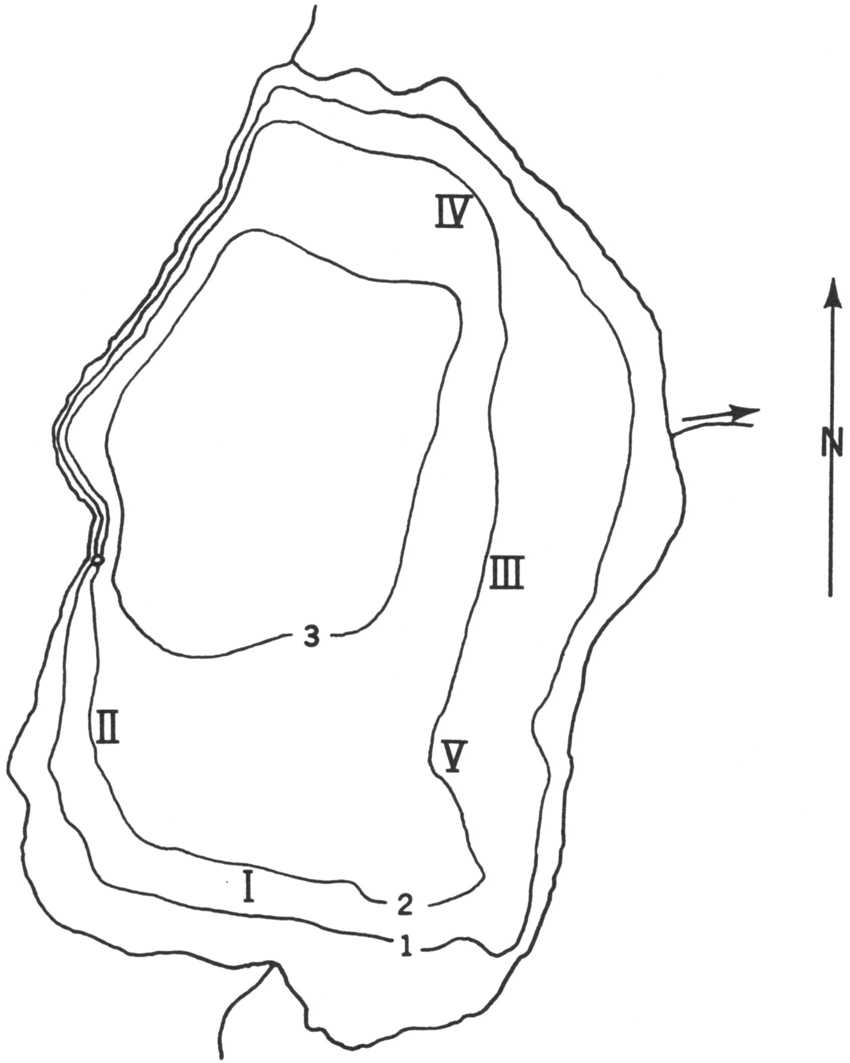
Figure 2. Hydrographic map of Silver Lake. Roman numerals indicate plankton stations. Arabic numbers indicate contour intervals.



Hydrographic Map

GOLD LAKE

Contour Interval 1 Meter



Scale

0 20 40

Meters

Figure 3. Hydrographic map of Gold Lake. Roman numerals indicate plankton stations. Arabic numbers indicate contour intervals.

Hydrographic Map

TIN LAKE

Contour Interval 1 Meter

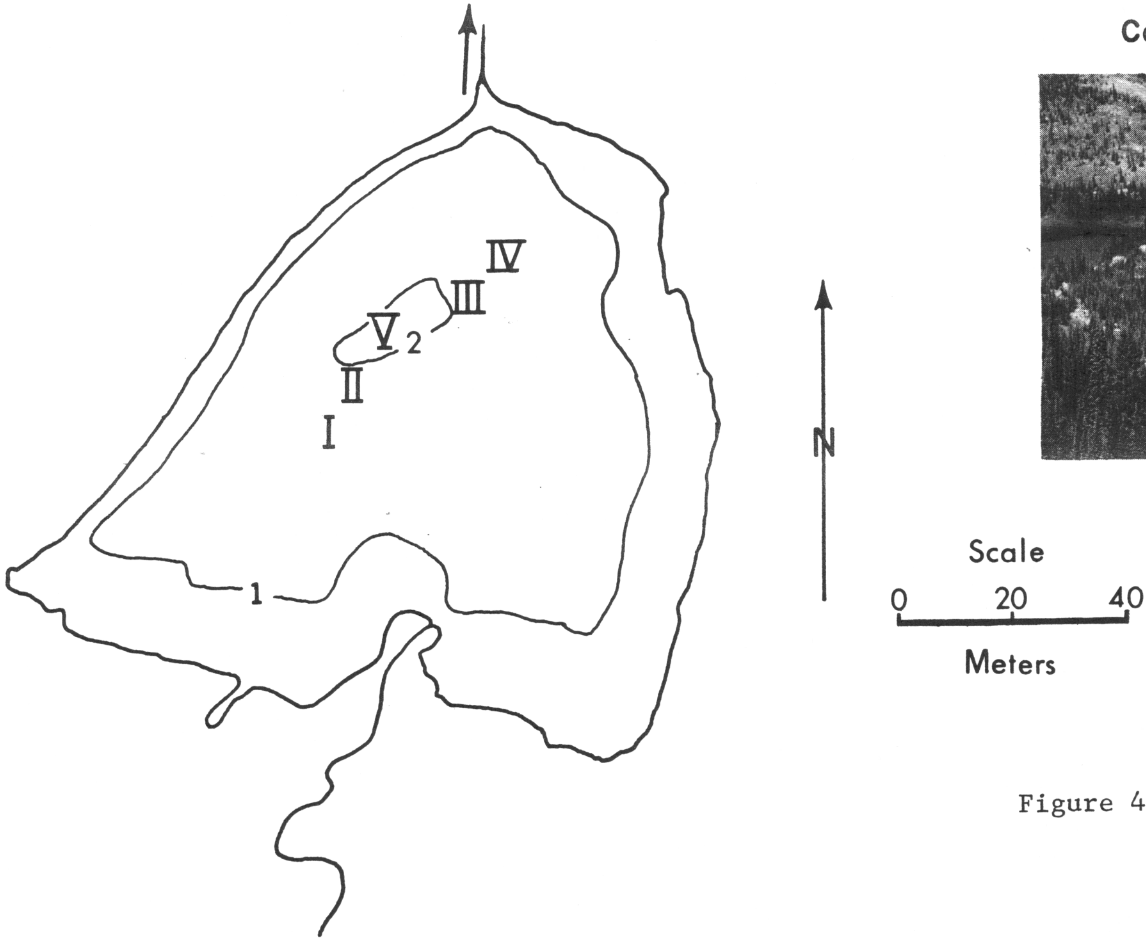


Figure 4. Hydrographic map of Tin Lake. Roman numerals indicate plankton stations. Arabic numbers indicate contour intervals.

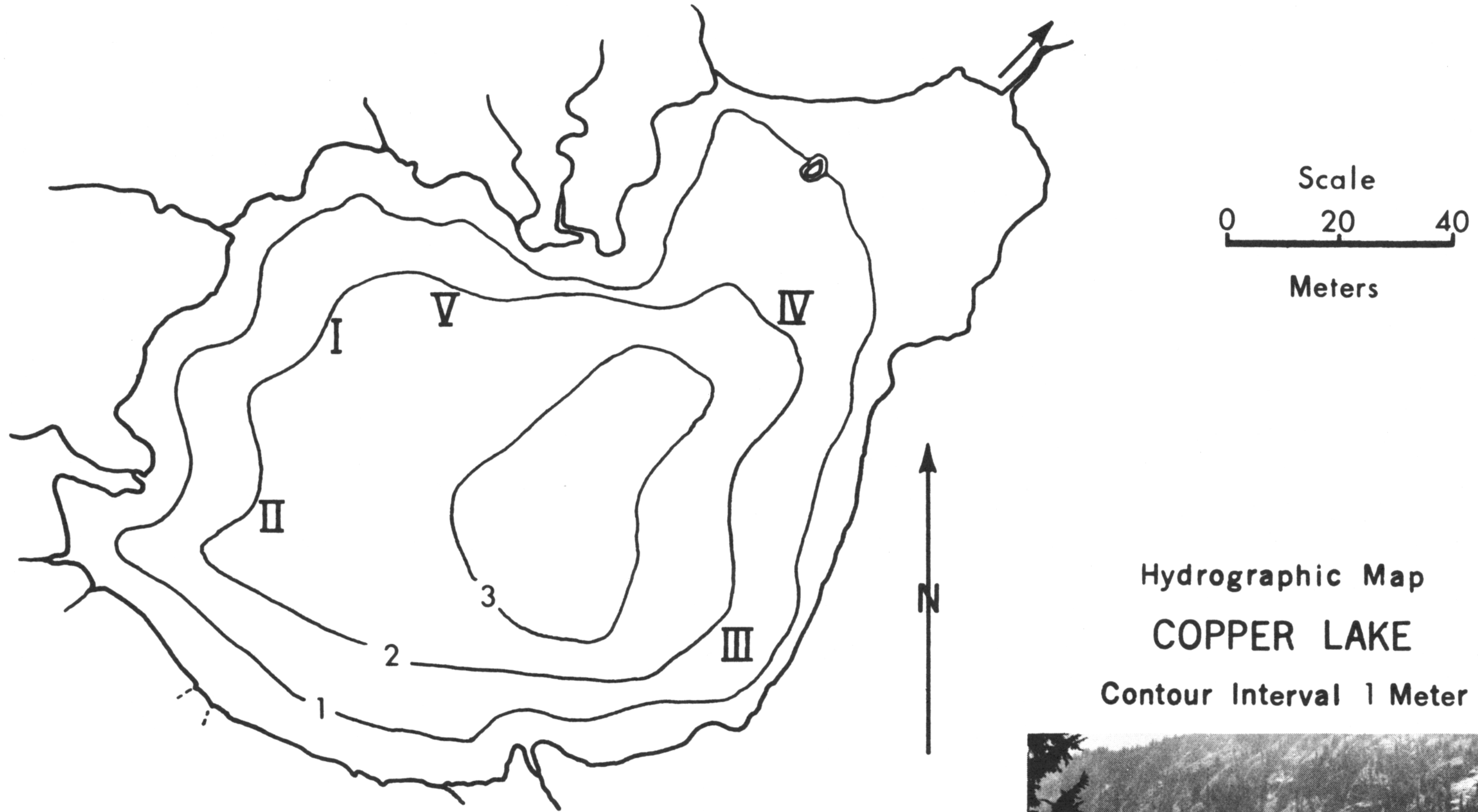


Figure 5. Hydrographic map of Copper Lake. Roman numerals indicate plankton stations. Arabic numbers indicate contour intervals.

Table 1. Morphometric features of Silver, Gold, Tin and Copper Lakes.

	Silver L.	Gold L.	Tin L.	Copper L.
Elevation				
Meters	1799.5	1872.7	1750.7	1750.7
Feet	5900.0	6140.0	5740.0	5740.0
Area				
Hectares	3.5	1.7	1.0	1.6
Acres	8.7	4.1	2.5	4.0
Volume				
Cubic Meters	212,066.5	33,827.8	11,485.0	25,251.5
Acre Feet	172.0	27.4	8.6	20.5
Maximum Depth				
Meters	12.8	3.7	2.1	3.1
Feet	42.0	12.0	7.0	10.0
Mean Depth				
Meters	6.0	2.0	1.1	1.6
Feet	19.9	6.7	3.5	5.1
Shoreline Length				
Meters	741.1	530.7	443.8	585.6
Feet	2430.0	1740.0	1455.0	1920.0
Shoreline Development	1.1	1.2	1.3	1.3
Mean Slope	16.7%	7.0%	4.8%	6.3%
Maximum Length				
Meters	256.2	185.7	146.4	190.8
Feet	840.0	609.0	480.0	652.5
Maximum Width				
Meters	205.8	118.9	118.9	118.9
Feet	675.0	390.0	390.0	390.0

concentrations were above saturation. Water transparencies indicated the bottoms visible at all times. Surface temperatures ranged from 16 C to 19 C.

The substrates varied from soft organic mud in the meadow lakes (Tin and Copper Lakes) to bedrock, talus, rubble, and gyttja in Silver and Gold Lakes. Soil samples from Tin and Copper Lakes had about 27% organic matter. Silver and Gold Lakes contained 16%. Single pH samples from Silver, Gold, Tin, and Copper Lakes were 5.0, 5.6, 5.8, and 6.1 respectively.

E. Vegetation

The four lakes are in the subalpine zone. The mountain hemlock, *Tsuga mertensiana* (Bong.) Carr., and subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. are the common conifers. Englemann spruce, *Picea engelmanii* (Parry) Engelm. and whitebark pine, *Pinus albicaulis* Engelm., are less abundant (Davis, 1952). The mountain hemlock of this area occurs where there is annual moisture above 49 inches to higher elevations with 70 inches per year (Habeck, 1967). The above mentioned species reflect the disturbance caused by the large 1910 fires.

The most common understory encountered are beargrass, *Xerophyllum tenax* (Pursh) Nutt., fool's huckleberry, *Menziesia ferruginea* Sm., true huckleberry, *Vaccinium membranaceum* Dougl. ex Hook., *Spiraea* sp., and rose heather, *Phyllodoce empetriformis* (Sw.) D. Don. The sedge, *Carex* sp., was commonly found in the meadows and along lake shores.

Aquatic plants were burr-reed, Sparganium angustifolium Michx. in the shallows, and the mosses, Sphagnium sp. and Fontinalis sp., on the shorelines. Bottom vegetation was the moss, Drapanocladus sp. and the quillwort, Isoetes sp. Algae commonly observed in the plankton samples were the Chlorophycean, Xanthidium sp. and the Dinophycean, Ceratium sp.

F. Aquatic Fauna

Aquatic invertebrates included the classes Rotifera, Pelecypoda, Oligochaeta, Crustacea, and Insecta (Table 2). Fish present were rainbow trout, Salmo gairdneri Richardson and cutthroat trout, Salmo clarki Richardson.

Table 2. Aquatic invertebrates of the Five Lakes Butte Area.

Class Rotifera
- *Conochilus* sp.
- *Polyarthra* sp.
- *Keratella* sp.
- *Trichotria* sp.

Class Pelecypoda
- *Pisidium* sp.

Class Oligochaeta

Class Crustacea
- Subclass Copepoda
  - *Diaptomus lintoni* S.A. Forbes 1893
  - *Cyclops* sp.
- Subclass Branchiopoda
  - *Daphnia rosea* Sars 1862 amend. Richard 1896
  - *Holopedium amazonicum* Stingelin 1904

Class Insecta
- Family Heptageniidae
- Family Baetidae
  - *Pseudocloeon* sp. Klapalek
- Family Libellulidae
  - *Leucorrhinia hudsonica* Selys 1850
- Family Aeshnidae
  - *Aeshna palmata* Hagen
- Family Coenagrionidae
  - *Enallagma boreale* Selys
  - *Ischnura cervula* Selys
- Family Nemouridae
  - *Nemoura* sp.
  - *Leuctra* sp.
- Family Perlodidae
  - *Isoperla* sp.
- Family Chloroperlidae
  - *Alloperla* sp.
- Family Gerridae
- Family Sialidae
- Family Rhyacophilidae
  - *Rhyacophilia* sp.
- Family Psychomyiidae
- Family Limnephilidae
- Family Dytiscidae

Table 2. (Continued) Aquatic invertebrates of the Five Lakes Butte Area.

Family Hydrophilidae
Family Tipulidae
Family Culicidae
Subfamily Culicinae
Subfamily Chaoborinae
Chaoborus sp.
Family Ceratopogonidae
Alluandomyia sp.
Family Simuliidae
Family Chironomidae
Family Rhagionidae

METHODS

A. Zooplankton

The four lakes were studied from July to September, 1966-1967. Each lake was sampled four times during the season. Quantitative vertical zooplankton collections were used for comparison of lakes, comparison of sampling methods within lakes, and comparison of sample sizes. Samples are represented by limnetic crustacean counts. The zooplankton sampling schedule is presented in Table 3.

The collections used for comparison of lakes in 1966 were taken by the Pennak sampler, a rubber tube used for vertical column samples. (Pennak, 1962).

The Pennak sampler and a Kemmerer water bottle were used for comparison of methods in 1966. In 1967 Van Doren water bottle samples were compared to the 1966 methods. Samples from water bottles were filtered through a Wisconsin net and plankton bucket (No. 20 mesh). Limnetic crustaceans were preserved in 3% formalin.

Zooplankton samples for comparison of sample sizes were collected in 1966 with the Kemmerer bottle. The Van Doren bottle and a metered tow net were used in 1967. The metered tow net was constructed with modifications from the Hardy plankton sampler (Miller, 1961). It consists of a plastic cylinder equipped with a flow meter, towing buckle and three stabilizing fins. Attached to the rear is a net and plankton bucket (No. 20 mesh).

Table 3. Zooplankton sampling schedule.

TREATMENT	METHOD	STATION NUMBER	STATION MAX. DEPTH (Meters)	DEPTH STRATA SAMPLED (Meters)	SAMPLE SIZE (Liters)	LAKE	YEAR
Comparison of Lakes	Pennak	1-4	2.5	0-2	10*	Four Study Lakes	1966
Comparison of Methods	Pennak	5(cp)	2.5	0-2	30*	Four Study Lakes	1966-1967
	Kemmerer	5(cp)	2.5	0-2	10**		
	Van Doren	5(cp)	2.5	0-2	30**		
Comparison of Sample Sizes	Kemmerer	6(cp)	12.0	0-10	45**	Silver	1966-1967
	Van Doren	6(cp)	12.0	0-10	180**	Silver	
	Metered Tow Net	6(cp)	12.0	0-10	820*x	Silver	

* Vertical column.
** Vertical series.
x Total of 10 vertical hauls.
(cp) Chemical and physical data collected with plankton samples.

The metered tow net was used to collect large volume samples. The volume of water filtered was calculated as the area of the sampling aperture times the height. The height was the distance the net was towed. The volume sampled could also be estimated from meter readings provided towing rates were constant. The meter was calibrated by towing the net over a known distance ten times. The ten readings were then averaged to obtain "revolutions per liter" value. Flow rates ranged from 90 to 102 revolutions per minute with 1.9 to 3.4 liters per revolutions respectively.

Zooplankton were identified using keys in Ward and Whipple (1959) and Pennak (1953). The estimate of each sample was based upon four enumerations. Each enumeration was in a separate mount of a 1 ml Sedgewick-Rafter counting cell under 60 X magnification of a compound microscope. Appropriate calculations were made to determine the number of individuals per liter (Welch, 1948). All values were normalized by a square root transformation of the form $\sqrt{X + 0.5}$ (Kutkuhn, 1958).

B. Aquatic Invertebrates

Benthos of the lakes were sampled with a 91.4 cm^2 Ekman Dredge. The samples were sieved on shore with Tyler screens, hand-picked with forceps and preserved in 70% alcohol. Aerial nets were used to obtain adult aquatic insects. Hand screens were used to work the shorelines, seepages, inlets and outlets of the four lakes. Aquatic insects were identified using keys in Usinger (1963).

C. Chemical and Physical

In 1966 water samples for chemical analysis were collected at the surface, midway, and two meters above the bottom with a two liter Kemmerer water bottle. Since chemical determinations in 1966 indicated similar results at different lakes and depths, water samples in 1967 were taken only at the surface. Water chemistry methods were as follows: dissolved oxygen using the unmodified Winkler method (Welch, 1948); total alkalinity as methyl orange alkalinity (Needham and Needham, 1952); and pH using a Hellige color comparator. Soil samples were taken at comparable sites in each lake with a 91.4 cm^2 Ekman Dredge. These were analyzed by personnel of the Agriculture Biochemistry Department, University of Idaho.

Water transparency was estimated with a Sechii disc. Temperatures were recorded at one foot intervals with an Allied Electronic Thermometer. Surface temperatures were taken with a mercury filled glass thermometer. Morphometric and hydrographic features were measured as described by Welch (1948).

RESULTS AND DISCUSSION

A. Zooplankton Composition and Density

The four lakes were similar in having a simple species structure and low density of zooplankton. These similarities are attributed to regulating and limiting factors of the environment. The waters are characterized by low nutrients and a short growing season. Primary production is apparently quite low in such oligotrophic lakes.

All zooplankton samples were considered as limnetic or collected in the open water. The littoral areas of the four lakes were almost devoid of macrophytes as compared with lowland lakes which may contain abundant rooted aquatics.

The principle zooplankton were represented by two copepods, *Diaptomus lintoni* and *Cyclops* sp., and two cladocerans, *Daphnia rosea* and *Holopedium amazonicum*. *Holopedium amazonicum* was only found in samples from Silver and Gold Lakes in 1966 and also in Copper Lake in 1967. Rotifers were represented by *Conochilus* sp. and *Polyarthra* sp.

Limnetic crustaceans were the only zooplankton with counts fitting the assumptions of the "F" test. The variation of rotifer counts was too large for use in the "F" test. Copepods were enumerated collectively as total copepodids and total copepodid nauplii, cladocerans as *Daphnia* and *Holopedium* and all crustaceans as total crustaceans. These counts for sampling dates and seasons were grouped and averaged.

Data for comparison of lakes are presented in original and transformed figures (Table 4). Most original counts were between zero and ten. Therefore, the square root transformation $\sqrt{X + 0.5}$ was applied to all data used for comparisons in an attempt to satisfy the assumption of normality. This permitted the use of the "F" test or analysis of variance.

Separate analyses of total copepodids, total copepodid nauplii, *Daphnia*, and *Holopedium* were impractical because of low density estimates. I assumed that by combining all crustaceans (total crustaceans) and therefore increasing counts within samples that data variances could be used in "F" tests. This assumption was justified by not assessing niche requirements of crustaceans. All data represented horizontal dispersions.

The transformed data of Table 4 are presented in Fig. 6. Crustacean composition and density remained about the same from July to September, 1966. Taxa means for all sampling dates (season) appear to represent those of each sampling date. Taxa counts for each sampling date were combined and averaged as mean total crustaceans. Taxa for all sampling dates (season) were combined and averaged as total crustaceans. It is then assumed that total crustaceans can be used as denisty estimates of taxa.

B. Comparison of Lakes

Horizontal dispersion of limnetic crustaceans in these lakes is thought to be uniform due to similar environmental conditions.

Table 4. Original and transformed* ($\sqrt{X + 0.5}$) data for mean number of taxa and total crustaceans per liter, 1966.

	SILVER LAKE		GOLD LAKE		TIN LAKE		COPPER LAKE	
		*		*		*		*
Daphnia	0.2	0.8	2.0	1.5	9.0	2.8	10.7	3.1
Holopedium	0.9	1.0	0.6	0.9	-	-	-	-
Total Copepodids	0.7	1.0	2.9	1.7	13.1	3.5	6.9	2.5
Total Copepodid Nauplii	2.3	1.6	16.2	2.7	5.7	1.9	3.5	1.8
Total Crustaceans	1.0	1.1	5.4	1.7	9.3	2.7	7.0	2.5

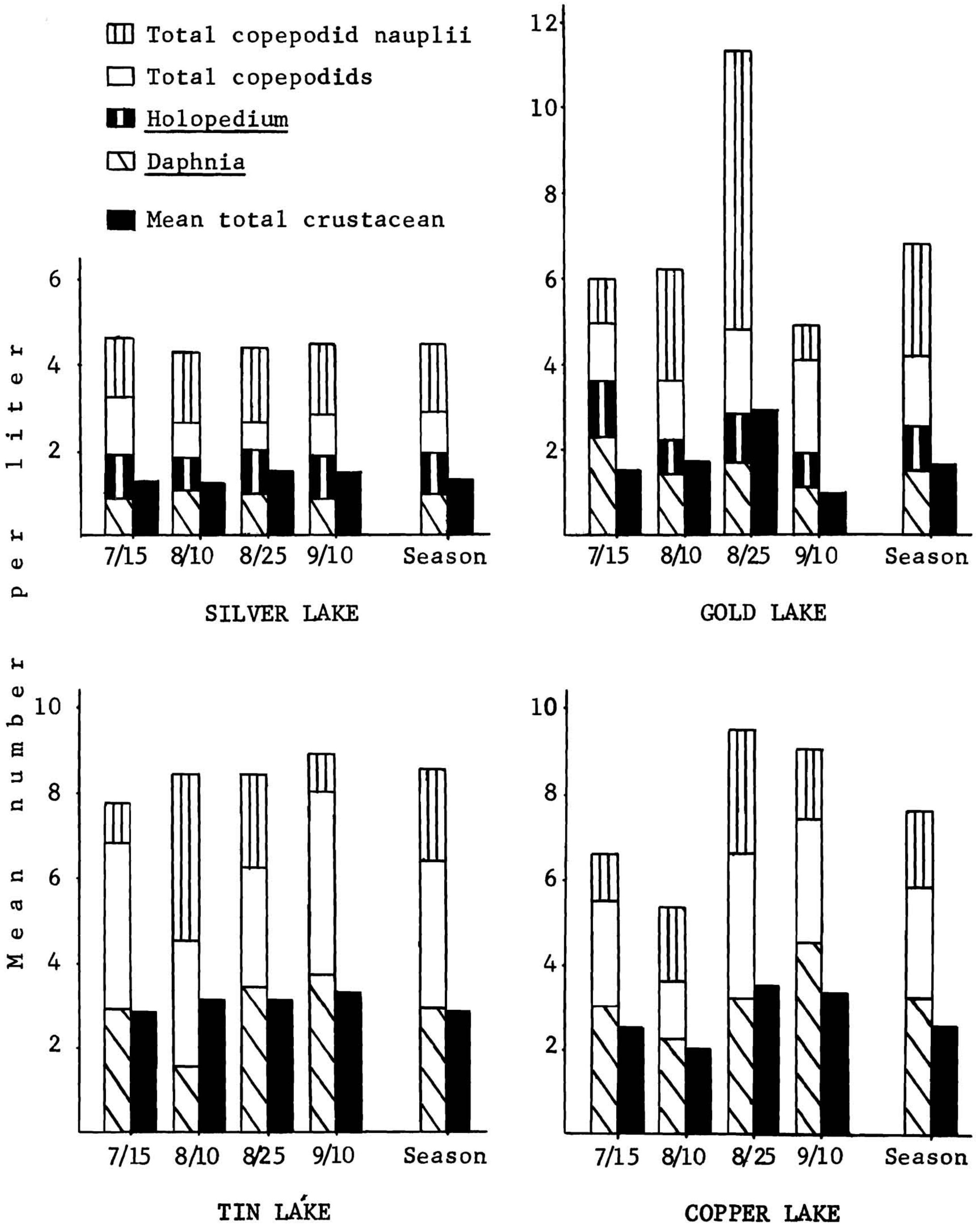


Figure 6. Comparison of lakes, 1966.

Ricker (1938) found that choosing a central station to represent the whole pelagic region is generally satisfactory since plankton are reasonably uniform over the entire offshore area. He stated that vertical net hauls have a random distribution in the horizontal plane.

Cassie (1962) relates that plankton can be distributed as a Poisson series which may be described by a single parameter, the mean $\bar{X}$. The Poisson model is only a special case of the general binomial model. Tests for Poisson are mainly tests for randomness. Plankton dispersions can be examined on the basis of the relationship between the variance and the mean. Comita and Comita (1957) showed that for uncrowded plankton populations this produces the following three types of distributions:

Infradispersed----------- $S^2 < \bar{X}$ (More evenly spaced than random)

Random------------------- $S^2 = \bar{X}$ (Poisson)

Superdispersed----------- $S^2 > \bar{X}$ (Grouped)

Fisher's coefficient of dispersion $S^2/\bar{X}$ is used to determine distributions. The deviations of $S^2/\bar{X}$ from one corresponds to the three types of dispersion. Less than one is equated with infradispersion, one is random, and greater than one is superdispersion. The significance of the deviation of $S^2/\bar{X}$ from one can be tested by the equation: $X^2 = (N-1)S^2/\bar{X}$, where N is the number of counts.

In this study horizontal distributions are calculated for Daphnia, Holopedium, total copepodids, total copepodid nauplii, and total crustaceans. An estimate of total crustacean dispersion is necessary to determine if they represent distribution of their components. If dispersions are similar, they may support the assumption of comparable mean densities.

The horizontal distributions of the comparison of lakes data (Fig. 6) are indicated in Table 5. All components and total crustaceans have high probabilities for infradispersion and low probabilities for superdispersion. All crustaceans were infradispersed except total copepodid nauplii in Gold and Tin Lakes. The superdispersion in Gold Lake was attributed to total copepodid nauplii density on August 25 (Fig. 6). This increase may have been due to counting errors caused by clumping during preservation or too rapid growth in one of the many developmental stages.

Total copepodid nauplii from Tin Lake were superdispersed with the highest density occurring on August 10. Abundance and subsequent maturation of these nauplii was indicated by total copepodid increase on August 25 and September 10. Comita and Comita (1957) found that nauplii can be superdispersed because developmental stages are of different sizes and coexist in microhabitats where competition for food is less. Infradispersion occurs when stages are considered separately or when there is a preference for similar grazing spaces.

In this study, frequent occurrence of infradispersion was due to the extreme low density of crustaceans and apparent sparse food supply. Crustaceans commonly forage on nannoplankton (Ruttner, 1963). These forms are not reported in any great abundance in high lakes (Rabe, 1964).

Table 5. Types of horizontal dispersion for mean number of taxa and total crustaceans per liter, 1966.
I = Infradispersion, R = Random, S = Superidspersion.

	d.f.	$\overline{X}$	S^2	$S^2/\overline{X}$	X^2	P	DISPERSION
Silver L.							
Daphnia	15	0.8	0.1	0.1	1.5	~.995	I
Holopedium	15	1.0	0.3	0.3	4.5	~.995	I
Total Copepodids	15	1.0	0.1	0.1	1.5	~.995	I
Total Copepodid Nauplii	15	1.6	0.4	0.3	4.5	~.995	I
Total Crustaceans	63	1.1	0.3	0.3	16.4	~.995	I
Gold L.							
Daphnia	15	1.5	0.4	0.3	4.5	~.995	I
Holopedium	15	0.9	0.2	0.3	4.5	~.995	I
Total Copepodids	15	1.7	0.5	0.3	4.5	~.995	I
Total Copepodid Nauplii	15	2.7	10.0	3.7	56.3	~.005	S
Total Crustaceans	63	1.7	3.1	1.8	114.7	~.005	S
Tin L.							
Daphnia	15	2.8	2.1	0.8	12.0	~.750	R> I
Total Copepodids	15	3.5	2.0	0.6	9.0	~.900	I
Total Copepodid Nauplii	15	1.9	2.7	1.4	21.0	~.200	S
Total Crustaceans	47	2.7	2.4	0.9	41.8	~.750	R> I
Copper L.							
Daphnia	15	3.1	1.5	0.5	7.5	~.750	I
Total Copepodids	15	2.5	1.0	0.4	6.0	~.975	I
Total Copepodid Nauplii	15	1.8	0.8	0.4	6.0	~.975	I
Total Crustaceans	47	2.5	1.1	0.4	20.2	~.995	I

It is then assumed that total crustaceans were infradispersed. Similarities of dispersions help justify analyses based on total crustacean densities.

Densities of mean total crustaceans for the 1966 season were compared by an analysis of variance (Table 6). Results indicate significant differences at the .05 and .01 probability levels. Highest standing crops were in Tin and Copper Lakes. This assumption was based on a multiple range test of means (Duncan, 1955). The standing crop in Gold Lake was greater than in Silver Lake. The small differences of lakes was in agreement with the dispersion estimates. The data show that there are no tendencies of organisms being exclusively random or superdispersed indicative of higher densities (Table 5).

The dispersion and densities of total crustaceans were also analyzed for variation between lakes and sampling dates. Horizontal dispersions are presented in Table 7; infradispersion was predominant. Superdispersion in Gold Lake on August 25 was caused by a high total copepodid nauplii count. This particular pulse made total copepodid nauplii appear superdispersed for the entire season (Table 5). The randomness of total crustaceans in Tin Lake on July 15 and September 10 was attributed to high counts of <u>Daphnia</u> and total copepodids.

The density of total crustaceans in each lake was tested for variations between sampling dates. Silver and Tin Lakes showed no significant difference for total crustaceans. Gold Lake showed a significant difference at the .05 probability level. The multiple

Table 6. Comparison of mean total crustaceans per liter in the four lakes, 1966.

A. Analysis of Variance

Source of Variation	d.f.	S.S.	M.S.	"F"
Among Lakes	3	93.8	31.3	18.1**
Within Lakes	220	381.1	1.7	
	223	474.9		

B. Duncan's Multiple Range Test

Silver L.	Gold L.	Tin L.	Copper L.
1.1	1.7	2.5	2.7

Table 7. Types of horizontal dispersion for sampling dates of lakes.* I = Infradispersion, R = Random, S = Superdispersion.

		SILVER LAKE	GOLD LAKE	TIN LAKE	COPPER LAKE
	d.f.	15	15	11	11
JULY 15	$\bar{x}$	1.1	1.4	2.7	2.4
	s^2	0.2	0.4	3.1	0.9
	$s^2/\bar{x}$	0.22	0.2	1.1	0.4
	x^2	3.0	3.0	16.5	6.0
	P	^.995	^.995	^.425	^.975
	DISPERSION	I	I	R	I
AUG. 10	$\bar{x}$	1.0	1.5	3.0	1.9
	s^2	0.2	1.0	1.7	1.0
	$s^2/\bar{x}$	0.2	0.7	0.6	0.5
	x^2	3.0	10.5	9.0	7.5
	P	^.995	^.825	^.850	^.950
	DISPERSION	I	R > I	I	I
AUG. 25	$\bar{x}$	1.1	2.7	3.0	3.4
	s^2	0.4	9.5	1.9	0.4
	$s^2/\bar{x}$	0.3	3.5	0.6	0.1
	x^2	4.5	5.2	9.0	1.5
	P	^.995	^.990	^.850	^.995
	DISPERSION	I	S	I	I
SEPT. 10	$\bar{x}$	1.3	1.2	3.2	3.2
	s^2	0.3	0.6	3.5	2.0
	$s^2/\bar{x}$	0.2	0.5	1.1	0.6
	x^2	3.0	7.5	16.5	9.0
	P	^.995	^.950	^.425	^.850
	DISPERSION	I	I	R	I

* Expressed as mean number of total crustaceans per liter.

range test indicated that total crustaceans density only varied on August 25 when total copepodid nauplii counts were high (Table 8). Copper Lake had a significant difference between dates at the .01 probability level. The multiple range test indicated that highest total crustacean density occurred on August 25 and September 10 (Table 8). An increase in Daphnia and total copepodids seemed to cause this increase (Fig. 6).

The density of total crustaceans for each sampling date was tested for variations between lakes. On any of the four dates, at least one of the lakes showed a significant difference in total crustacean density (.01 and .05 probability levels). This was confirmed by multiple range tests (Table 9). The tests support the estimate of highest densities of total crustaceans in Tin and Copper Lakes for 1966. Differences in density for each taxon explain variations of lakes (Fig. 6).

The comparison of lakes was based on densities (mean total crustaceans $\bar{X}$) and horizontal distributions (coefficient of dispersion $S^2/\bar{X}$) of limnetic crustaceans. Comita and Comita (1957) proposed that their data was randomly distributed when the population was low and superdispersed when the population was high. This was examined by plotting the population density against the coefficient of dispersion for all developmental stages of copepodids. Their results indicated that there may be a linear relationship between the population density and the coefficient of dispersion.

It appears that my data may have been likewise randomly distributed. Total crustaceans density was plotted against its coefficient

Table 8. Comparison of sampling dates for each lake, 1966.*

GOLD LAKE			
September 10	July 15	August 10	August 25
1.2	1.4	1.5	2.7

COPPER LAKE			
July 10	August 10	August 25	September 10
2.4	1.9	3.4	3.2

* Expressed as mean number of total crustaceans per liter.

Table 9. Comparison of lakes for each sampling date, 1966.*

JULY 15			
Silver L.	Gold L.	Copper L.	Tin L.
1.1	1.4	2.4	2.7

AUGUST 10			
Silver L.	Gold L.	Copper L.	Tin L.
1.0	1.5	1.9	3.0

AUGUST 25			
Silver L.	Gold L.	Copper L.	Tin L.
1.1	2.7	3.4	3.0

SEPTEMBER 10			
Silver L.	Gold L.	Copper L.	Tin L.
1.3	1.2	3.2	3.2

* Expressed as mean number of total crustaceans per liter.

of dispersion for the four lakes and there was an indication that a linear relationship existed. The correlation coefficient for $\bar{X}$ and $S^2/\bar{X}$ was found to be 0.6109, which was significantly different from zero at the .05 level, (Fig. 7).

C. Comparison of Methods

Three plankton collecting methods (Pennak, Kemmerer and Van Doren) were compared. Densities of total crustaceans appeared similar in each lake during 1966 and 1967. The highest densities of total crustaceans for the two years were in Tin and Copper Lakes (Fig. 8).

The types of horizontal dispersion of total crustaceans were considered for the three methods in the four lakes (Table 10). Silver and Gold Lakes were infradispersed supporting the low density estimates. Tin and Copper Lakes had essentially random distributions which indicated higher densities. Superdispersion in Tin Lake had low probabilities and were considered as random.

An "F" test for three methods in Tin and Copper Lakes indicated no significant difference at the .05 probability level. There was a significant difference at the .05 probability level for Silver and Gold Lakes. The multiple range test indicated similarity of methods except in Gold Lake (Table 11). Pennak's sampler exhibited higher counts for taxa, but the magnitude of the differences were not considered significant. Similar total crustaceans counts were collected by the three methods in each lake.

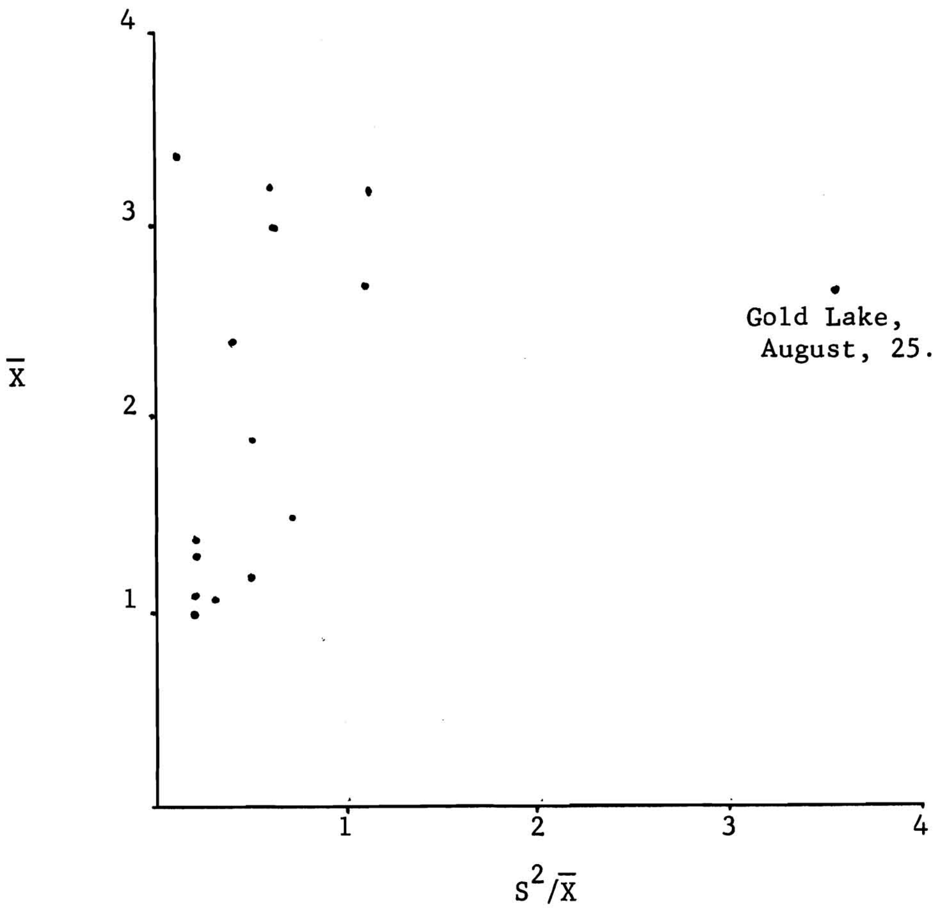


Fig. 7. Population densities plotted against Fisher's coefficient of dispersion for sampling dates of lakes. Expressed as mean number of total crustaceans per liter.

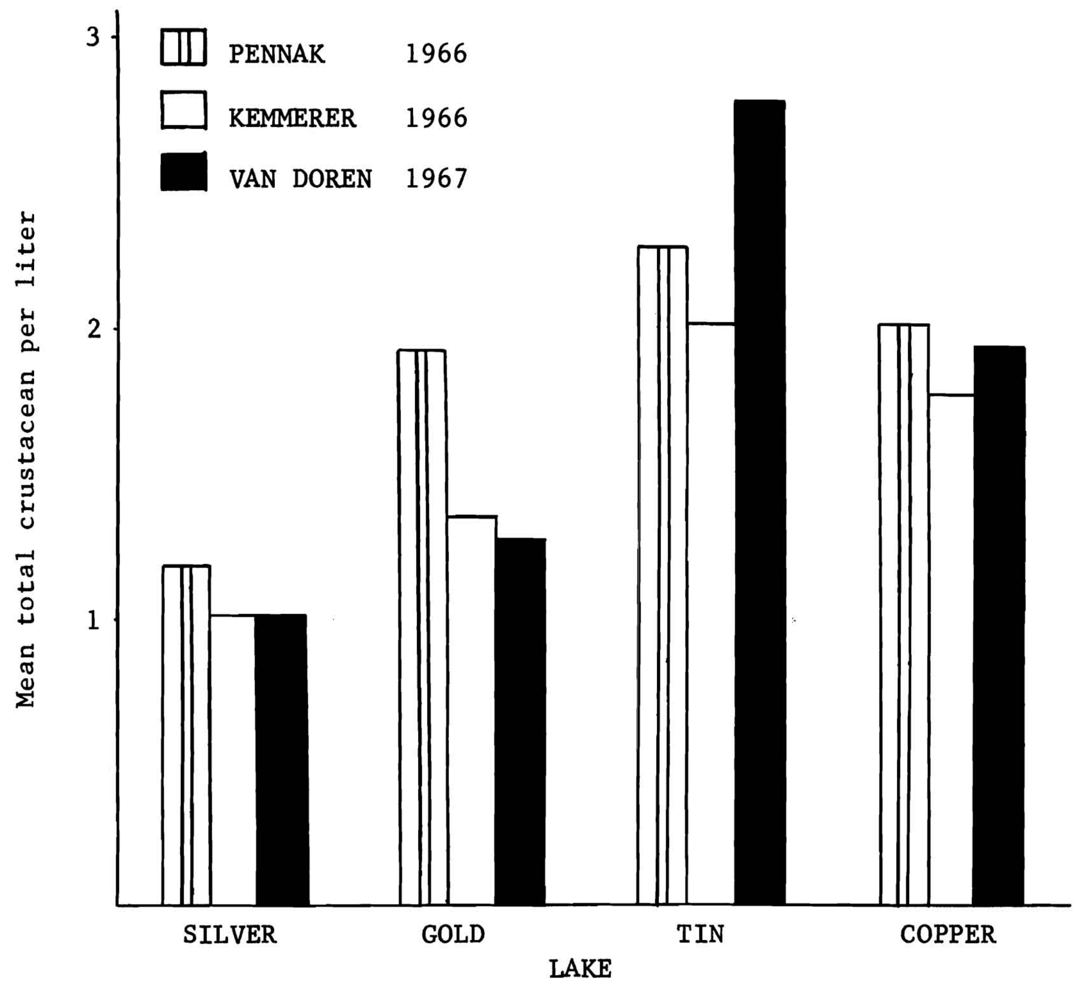


Figure 8. Comparison of methods.

Table 10. Types of horizontal dispersion for methods in lakes.*
I = Infradispersion, R = Random, S = Superdispersion.

		1966 KEMMERER d.f. 15	1966 PENNAK d.f. 15	1967 VAN DOREN d.f. 15
SILVER LAKE	$\bar{X}$	1.0	1.2	1.0
	S^2	0.3	0.2	0.1
	$S^2/\bar{X}$	0.3	0.2	0.1
	X^2	4.5	3.0	1.5
	P	~.995	~.995	~.995
	DISPERSION	I	I	I
GOLD LAKE	$\bar{X}$	1.4	1.9	1.3
	S^2	0.6	0.7	0.3
	$S^2/\bar{X}$	0.4	0.4	0.2
	X^2	6.0	6.0	3.0
	P	~.975	~.975	~.995
	DISPERSION	I	I	I
TIN LAKE	$\bar{X}$	2.0	2.3	2.7
	S^2	2.8	1.9	5.8
	$S^2/\bar{X}$	1.4	0.8	2.1
	X^2	21.0	12.0	31.5
	P	~.150	~.700	~.008
	DISPERSION	S	R > I	S
COPPER LAKE	$\bar{X}$	1.7	2.0	1.9
	S^2	1.7	1.2	1.6
	$S^2/\bar{X}$	1.0	0.6	0.8
	X^2	15.0	9.0	12.0
	P	~.450	~.850	~.700
	DISPERSION	R	R > I	R > I

* Expressed as mean number of total crustaceans per liter.

Table 11. Comparison of sampling methods within lakes, 1966 and 1967.*

SILVER LAKE			GOLD LAKE		
Van Doren	Kemmerer	Pennak	Van Doren	Kemmerer	Pennak
1.0	1.0	1.2	1.3	1.4	1.9

* Expressed as mean number of total crustaceans per liter.

The density and distributions of total crustaceans collected by the three methods in four lakes had a linear relationship. The correlation coefficient for $\bar{X}$ and $S^2/\bar{X}$ was found to be 0.897, which was significantly different from zero at the .05 level (Fig. 9).

D. Comparison of Sample Size

The relationship of sample size to density and coefficient of dispersion of total crustaceans was examined for variation. Silver Lake was selected because larger sample sizes could be taken from its deeper pelagic area. The Kemmerer, Van Doren, and a metered tow net were used to take large volume samples from the upper ten meter stratum. This information was compared to small volume samples from shallow depths (comparison of methods data for Silver Lake, Table 9).

The data for different sample sizes, methods and depths is presented in Table 12. The coefficient of dispersion and density of total crustaceans remained constant as the sample size and depth changed. An "F" test of total crustacean densities indicated no significant difference. Similarities of total crustacean densities and dispersion estimates from different sample volumes was attributed to the low crustacean density throughout the limnetic region of Silver Lake.

The low density of crustaceans indicates the need for larger sample volumes. The necessary sample size may be approximated by calculating the number of replications per station as described by

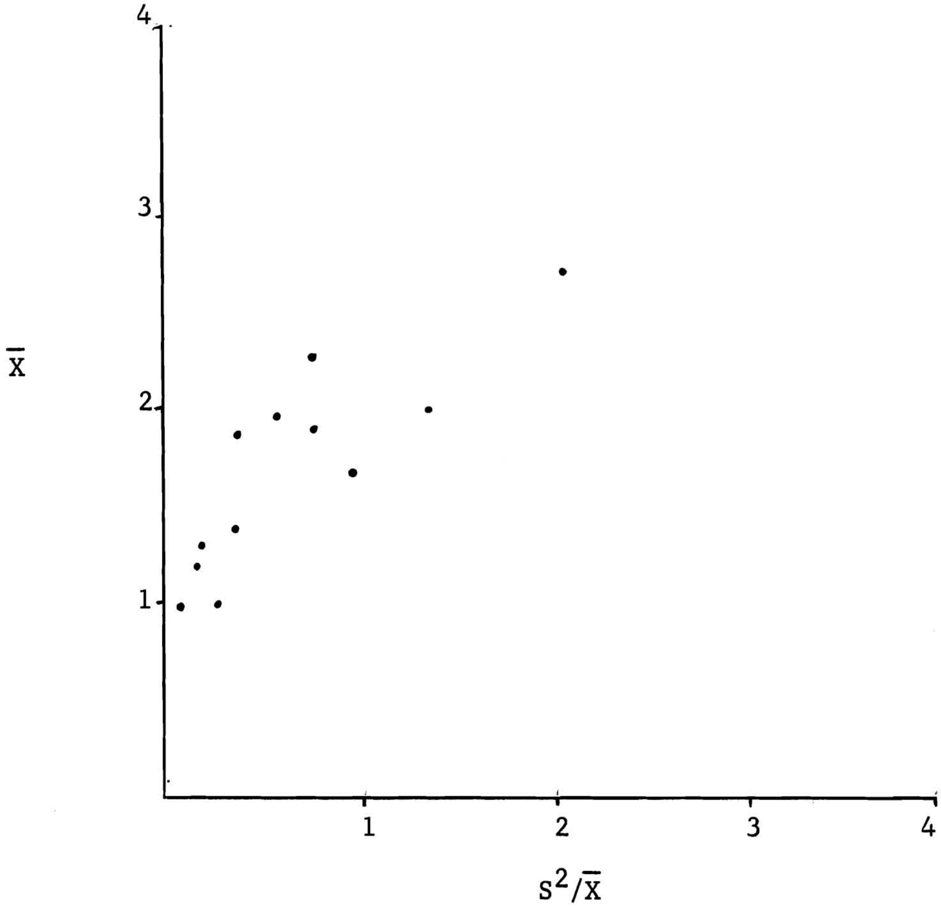


Fig. 9. Population densities plotted against Fisher's coefficient of dispersion for methods in lakes. Expressed as mean number of total crustaceans per liter.

Table 12. Types of horizontal dispersion in Silver Lake for sample sizes based on mean number of total crustaceans per liter.

Method	Sample Size* (liters)	Sample Depth (meters)	d.f.	$\bar{X}$	S^2	$S^2/\bar{X}$	X^2	P	DISPERSION
Pennak 1966	(120)	2	15	1.2	0.2	0.2	3.0	^.995	I
Kemmerer 1966	(40)	2	15	1.0	0.3	0.3	4.5	^.995	I
Van Doran 1967	(120)	2	15	1.0	0.1	0.1	1.5	^.995	I
Kemmerer 1966	(180)	11	15	1.4	0.5	0.4	6.0	^.975	I
Van Doran 1967	(720)	11	15	1.7	0.4	0.2	3.0	^.995	I
Metered Net 1967	(3280)	11	15	1.6	0.4	0.3	4.5	^.995	I

* Total sample volume for season.

Steel and Torrie (1960). S^2 is an estimate obtained from the previous

$$r \geq \frac{2\,(t_o + t_1)^2 S^2}{\delta^2}$$

experiment; δ is the size difference necessary; t_o is the t value associated with Type II error. The t_1 equals tabulated t for probability 2(1-P) where P is the required probability of detecting δ.

As an example, previous data are selected from two sample sizes of the Kemmerer method (Table 10). The variance of the two Kemmerer sample sizes is 0.4 based on 30 degrees of freedom. If a difference of 0.2 organisms per liter is desired between two stations, then the probability of Type I error equals 0.05 and Type II error 0.10. If 20 replications are required at each of the two stations, then error degrees of freedom are (2-1) (20-1) or 38. The calculated replications needed at each station are 274.4. If the volume of each replication is 110 liters (average of Kemmerer samples), 30,184.0 liters per station would be necessary to detect a difference of 0.2 organisms per liter.

The high degree of accuracy required in the above example (0.2 organisms per liter) is considered impractical because of the resultant large sample size. The sample size could be reduced by only detecting a difference of 1 organism per liter.

The collection of large volumes for comparison of limnetic crustaceans biomass in extreme oligotrophic waters may be accomplished with replicate vertical samples which eliminate variations caused by vertical distributions. Ricker (1938) found that plankton collected with vertical hauls were uniformly distributed in the limnetic reginn of a lake. Rawson (1953) stated vertical tows took sufficient quantities of plankton for convenient determinations of dry weight, ash and micro-kjeldahl determination of total organic nitrogen. Therefore, biomass estimates may be considered adequate when collected from the limnetic region where horizontal dispersion is essentially random.

The recommended sampler for collecting limnetic crustaceans is a simple tow net with a coarse meshed net (No. 14-15), large aperture, offset towing bridle, and a large net surface area. The tow rates might then be increased without causing turbulence in front of the net and avoidance by crustaceans.

Low density estimates may be due to avoidance behavior of the crustaceans. Fleminger and Clutter (1965) state that when samplers are preceded by a towing line, crustaceans may react to tactile stimuli or pressure waves which are created ahead of the moving samplers. They found that relatively more animals were collected in denser populations. This suggests that interindividual interference may be responsible for their restricted movements. The degree of avoidance is most likely related to behavior and locomotor capabilities characteristic of the species. In this study, avoidance may have been due to low crustacean density and high transparency of the water which provides additional space for movement and increased visibility.

SUMMARY

1. Four subalpine lakes in northeast Idaho were studied during the summers of 1966 and 1967. These lake areas ranged from 1.0 to 3.5 hectares and depths from 2 to 13 meters.
2. Limnetic crustaceans exhibited a simple species structure and low density.
3. Mean total crustacean density and horizontal dispersion appeared to approximate taxa density and horizontal dispersion.
4. Tin and Copper Lakes had higher densities of limnetic crustaceans than Silver and Gold Lakes, 1966 and 1967.
5. There was an indication that a positive linear relationship existed between total crustacean density and coefficient of dispersion in the four lakes.
6. There was an indication that a positive linear relationship existed between total crustacean density and coefficient of dispersion when sampled by three methods in four lakes.
7. The similarities of total crustacean density and dispersion estimates from different methods and sample sizes was attributed to the low density in the limnetic region of these waters.
8. Larger sample sizes are needed to increase the accuracy of density and dispersion estimates.
9. Sampling should be by repeated vertical hauls with simple tow nets.

10. Reliability of samples could have been affected by crustacean avoidance of samplers. Avoidance behavior may be high in these waters with low plankton density and high transparency.

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