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A comparative study of lake outlet ecosystems

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A COMPARATIVE STUDY OF LAKE OUTLET ECOSYSTEMS

By

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ABSTRACT

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A Comparative Study of Lake Outlet Ecosystems

Director: Andrew L. Sheldon

A comparative study was made of 13 lake outlets in Montana. The objective of the study was to examine correlations between the productivity of the lakes and the species richness and composition of the benthic insects in the outlet streams. Various measures of productivity were used. Benthic insects were collected and the presence and relative abundance of species were determined. The number of species at the outlet sites ranged from 18 to 40. Productivity indices which were based on the amounts of dissolved ions in the lakes (e.g. Ryder's morphoedaphic index) were not good predictors of the number of species of benthic insects in the outlet streams. Direct measures of productivity (chlorophyll and particulate carbon measurements made on lake effluent water) were good predictors of species richness. A significant positive correlation ($r = .606$, $p < .05$) was found between chlorophyll measurements and the number of species of insects in the outlet stream. A principal components analysis using the matrix of phi coefficients as the measure of similarity of the lakes showed significant differences in the faunal composition of the less versus the more productive lakes. The separation of lakes on the first three components of the principal components analysis was closely correlated with the division of lakes into productivity categories made on the basis of the chlorophyll and particulate carbon data. No differences were found in the number of species of filter-feeding insects in the less and more productive lake categories. Greater changes in faunal composition between the outlet site and the second study site 100 meters downstream were found in the more oligotrophic lakes than in the more productive lakes.

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CHAPTER 1

INTRODUCTION

Lake outlets can be viewed as transition zones between lentic and lotic types of water. Depending upon one's bias, lakes can be seen as perturbations of rivers, or outlet rivers can be looked at mainly as the overflow from lakes. The characteristics of both the lake and the outlet stream must be considered when studying lake outlet ecosystems.

Lake outlets have been studied by researchers who noted that lake plankton occurs in large amounts in outlet streams and declines downstream (Chandler, 1937; Reif, 1939; Beach, 1960; Cushing, 1963, 1964; Cowell, 1967; Maciolek and Tunzi, 1968; Ulfstrand, 1968; Gibson and Galbraith, 1975; Armitage and Capper, 1976). It has also been demonstrated that lake effluent waters sustain much larger populations of passive, filter-feeding invertebrates than areas of streams which are not influenced by limnoplankton discharge (Briggs, 1948; Knöpp, 1952; Müller, 1955, 1956, 1962; Illies, 1956; Cushing, 1963; Ulfstrand, 1968).

A more productive lake will provide more organic material for consumption by the benthic fauna in the outlet stream. The abundance of plankton would exert its primary effect on the filter feeders. However, lacustrine seston settles to the substrate and is utilized by grazers and detritivores, so it secondarily influences these components of the community. Due to the more abundant food source, benthic invertebrates should be more abundant in the outlet streams of the more productive lakes.

This study was done with the objective of examining correlations between the productivity of the lake and the species richness and faunal composition of the aquatic insects in the outlet stream. A number of factors affect the productivity of a lake. Nutrient enrichment is usually considered the main factor leading to the eutrophication of lakes. The natural nutrient load in a lake is a function of the geochemistry of the drainage basin, the morphometry and hydrology of the lake, and climatic conditions (Rawson, 1960). Superimposed on these factors are cultural influences (e.g. agricultural and domestic runoff, clearcuts, etc.). Other factors influence lake productivity by affecting the distribution, availability, and utilization of nutrients (Brezonik, 1969).

An attempt was made to find chemical and morphometric parameters which, due to their effect on the productivity of the plankton in the lake, would exert an influence on the benthos in the outlet community. It was proposed that these parameters could be used to predict species richness in the outlet streams. More directly, the amount of plankton in the effluent waters could be used as a predictor of the type of fauna which would be found in the lake outlet.

The type of fauna in the outlet stream is determined both by the type of lake which is above the stream and by conditions in the stream (substrate, current speed, etc.). In an attempt to minimize the effect of structural conditions in the stream, only outlet streams with stony substrates and a relatively steep slope were included in this study. Given comparable conditions in the streams, the effects of different productivity levels in the various lakes could be evaluated.

CHAPTER 2

REVIEW OF THE LITERATURE ON LAKE OUTLETS

Various researchers have found larger amounts of plankton in lake outlets as compared with similar non-outlet streams. Chandler (1937), Cushing (1964), and Ulfstrand (1968) found higher volumes of net plankton in lake outlets. Ulfstrand identified primarily plankton species characteristic of lakes in outlets, whereas, river bottom species were prominent elsewhere.

The term seston includes both plankton and non-living particles (detritus). Maciolek (1966) determined that without lacustrine contribution (phytoplankton characteristic of epilimnetic water), microseston in his study would be more than three-fourths detritus.

Maciolek and Tunzi (1968) included the microseston component, which constitutes more of the total suspended organic matter than the net catches. Blackflies, for example, are known to feed on bacteria and other particles which would be in this smaller size range (Freeden, 1964; Chance, 1970). Maciolek and Tunzi found the greatest concentration of suspended organic particles in the outlet of Laurel Lake, California, (greater than 12 gcal/l or nearly 3 mg/l dry weight) demonstrating that even an oligotrophic lake can have a profound influence on the abundance of microseston at the outlet. Approximately seven times as much particulate matter was found in the outlet as in the inlet water.

The quantity of lake plankton rapidly decreases with increasing distance from the outflow. Current speed, amount of silt, substrate type, amount of vegetation, and the number of filter feeders influence the rate of removal of lacustrine plankton.

A rapid current and high silt content were important factors in the destruction of phytoplankton in the Shenango River, which drains the highly productive Pymatuning Reservoir (Hartman and Himes, 1961). An average decrease in numbers of cells of 73% was found between the reservoir and a collecting station 10.6 miles downstream. Chandler (1937) also considered mechanical destruction by the grinding action of waters laden with silt to be a contributing factor to plankton decreases. However, he found that the greatest plankton decrease per unit of distance invariably occurred in heavily vegetated sections of the streams. He showed a decrease in phytoplankton of 70% within a distance of 20 meters in one river and a decrease of 60% within 15 meters in another river. Both streams were heavily vegetated in these sections, and when the vegetation was removed, plankton decrease was much reduced. Working in the Ocqueoc River system, Michigan, Beach (1960) also placed importance on the filtering effect of vegetation and periphyton. He found that plankton was removed still more rapidly in the section immediately below a dam.

Maciolek and Tunzi (1968) determined that the decrease in cellular microseston below the lake was due primarily to uptake by simuliid larvae, which removed 60% of the suspended algae in the first 0.4 kilometer section of the stream. Hydropsychids were important in the removal of zooplankton in the Vaal River in South Africa (Chutter, 1963). Zooplankton was removed within a distance of eight kilometers below the dam. Armitage and Capper (1976) found that when the microcrustaceans are at peak abundances in the Cow Green Reservoir, only 1-2% of the amount which drifted out of the reservoir was found 6.5 kilometers below the dam. In addition to the dipterans and trichopterans, in this river molluscs, oligochaetes (<u>Nais</u> <u>sp</u>.), and <u>Hydra</u> <u>sp</u>. were also abundant.

The effectiveness of the filter feeders in removing lake plankton is dependent on current speed. The influence of lake plankton was still significant 30 kilometers below the lake outflow in a large Swedish river with a discharge of 200 m^3/sec (Müller, 1956). In contrast, the influence of the lake outflow was insignificant 200 meters downstream in a smaller stream in Sweden with a discharge between 0.4 and 0.8 m^3/sec (Illies, 1956). The River Leven which flows out of Lake Windermere, has a relatively high discharge and plankton can be collected at the mouth 5.5 kilometers downstream (Elliott and Corlett, 1972).

Some taxa are eliminated more rapidly than others (Reif, 1939). Ulfstrand (1968) found a more rapid disappearance of phytoplankton. Chandler (1937) noted that the rate of disappearance of phyto- and zooplankton was about the same.

A number of workers have investigated seasonal and diurnal changes in the amounts of zooplankton leaving the lake. Gibson and Galbraith (1975) collected the largest amounts of zooplankton drift in June, July, and September in the Matamek River, Quebec. Armitage and Capper (1976) found that 98% of the total annual output of Copepoda, Cladocera, and Hydra occurred between July and October in the River Tees. Oswood (1976) obtained greater amounts of zooplankton at night in the outlet of Placid Lake, Montana.

It has been demonstrated that lake outlets can support much larger populations of passive filter-feeding invertebrates than downstream areas (Knöpp, 1952; Müller, 1955, 1956; Illies, 1956). This was related to the more abundant supply of lacustrine plankton at the outlet. Müller (1956) found hydropsychids in densities of over 50 million per hectare. Cushing (1963) recorded the highest densities of campodeiform Trichoptera larvae below a series of productive lakes (3,340 larvae per square foot in late August). Oswood (1976) recorded mean densities of hydropsychids of more than 1400 larvae/0.2 m^2 in the outlet of Placid Lake. The highest density found was greater than 5,000 larvae/0.2 m^2.

Briggs (1948) noted a doubling of the average density of the fauna below a dam in California. The caddisfly larvae accounted for most of the increased production below the dam. In the Matamek River, Quebec, net-spinning Trichoptera were twice as abundant and simuliid larvae were four times as abundant at the station below a lake as at a station four kilometers downstream (Gibson and Galbraith, 1975).

Ulfstrand (1968) did not find large numbers of hydropsychids, but found high production rates for blackflies (3 $g/m^2/day$ fresh weight). The total standing crop at the outlet was from 10 to 20 times higher than at nonoutlet stations. Scott (1958) concluded that the quantitative distribution of trichopteran larvae generally follows the quantitative distribution of food.

Dense populations of filter feeders are not associated only with lakes. Tsuda and Komatsu (cited in Hynes, 1970) found large numbers of hydropsychids in a river in Japan. Blackflies can also be found in great numbers in streams not associated with lakes. In the Bere Stream, Great Britain, Ladle (1972) measured production rates for _Simulium_ of 0.066 $g/m^2/day$ dry weight.

Many studies have shown that allochthonous material is the most important primary source of energy for stream fauna (Nelson and Scott, 1962; Minshall, 1967; King and Ball, 1967; Fischer and Likens, 1972, 1973). Lake outlet ecosystems are unique, then, not due to the fact that they have a large supply of allochthonous material, but because much of that material is plankton, which is nutritionally superior (Maciolek, 1966).

Ulfstrand (1968) referred to a lake outlet community. It differed from other localities with respect to the abundant supply of food from the lake, the large amounts of periphyton, and in the alteration of the temperature regime. He noted that total standing crops are greater at outlets, and that there is a peak of abundance during the summer, whereas seasonal fluctuations at non-outlets are barely discernible. The outlet communities Ulfstrand studied differed qualitatively from other communities only with respect to blackflies. He found blackfly species which were collected only or primarily at outlets, and noted that other blackfly species were not found at outlets. When the blackflies were subtracted from total standing crops, the outlets were essentially the same as other localities. A mayfly, Heptagenia sulphurea, also showed a distinct preference for lake outlets. He attributed this to the elevated fall water temperatures at outlets.

Hynes (1970a) thought that the restriction of certain blackfly and mayfly species to outlets in Swedish Lapland is possibly not universal, and that it may have nothing to do with food. He suggested that the pattern of temperature change is the important factor, and that these species are probably not confined to outlets elsewhere in their geographic ranges.

The increase in numbers and biomass of passive feeders may alter the numbers and biomass of other groups of insects. Illies (1956) found that active feeders at outlets were reduced in numbers and biomass compared to downstream areas. He found no qualitative difference between outlets and non-outlets in the occurrence of species of mayflies, stoneflies, and caddisflies. Müller (1955) saw no influence of outlet conditions on the densities of active feeders. Cushing (1963) found greater numbers of Ephemeroptera nymphs below the lakes, due to larger populations of *Baetis sp*. and *Tricorythodes fallax*. Baetid species were shown by Egglishaw (1964) to increase in numbers with increase in organic detritus. In contrast Illies (1956) found that large numbers of net-spinners reduced the numbers of *Heptagenia* and *Baetis*. Armitage, P. D. (1976) and Gibson and Galbraith (1975) both recorded greater numbers of mayflies at the downstream sites.

The species of Plecoptera were similar in outlet and non-outlet sites in the lake-river chain in Cushing's (1963) study. Similarly, Ulfstrand (1968) found no differences in the species composition of stoneflies in outlet versus non-outlet communities.

CHAPTER 3

DESCRIPTION OF STUDY SITES

The outlet streams of 13 Montana lakes were studied (eight lakes in the Clearwater River drainage, Lindbergh and Cygnet Lakes in the Swan River drainage, and Tally, Bowman, and Kintla Lakes in the Flathead River drainage) (Figure 1).

Some of the lakes have been little studied. Master's theses were done on Seeley Lake by Cladouhos (1971) and on Tally Lake by Hunter (1974). Juday and Keller (1974, 1976) have studied the lakes in the Clearwater chain (Rainy to Salmon) and have done more extensive work on Placid Lake. Streebin, et al. (1973), studied Rainy, Alva, Inez, Seeley, and Placid Lakes. The Montana Fish and Game Department has obtained morphometric data on some of the lakes. Few data are available for Bowman and Kintla Lakes in Glacier National Park. Morphometric data on the lakes are given in Table 1.

Several of the lakes have small dams associated with their outlet streams. Clearwater Lake has a beaver dam at the outlet. Inez and Placid Lakes have small regulatory dams right above the first sample sites.

Six of the lakes in the study are in a chain on the Clearwater River (Clearwater Lake to Salmon Lake). The Clearwater River originates at Clearwater Lake, which is

FIGURE 1

STUDY AREAS

Lakes

1. Kintla
2. Marshall
3. Lindbergh
4. Cygnet
5. Clearwater
6. Rainy
7. Alva
8. Bowman
9. Tally
10. Inez
11. Seeley
12. Placid
13. Salmon

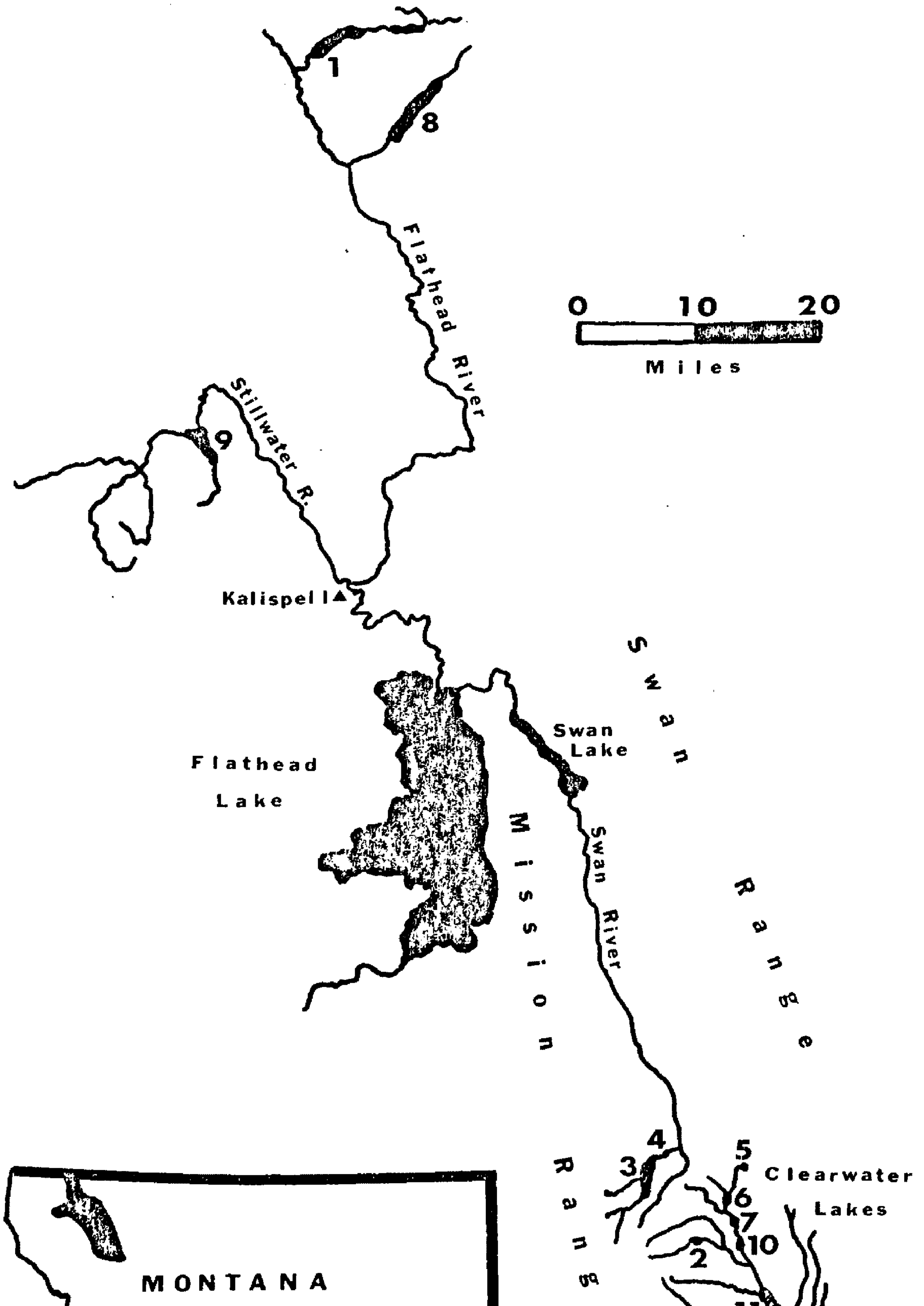

1
8
Flathead River
0 10 20
Miles
Stillwater R.
9
Kalispell
Swan Range
Swan Lake
Flathead Lake
Mission Range
Swan River
4
3
5
Clearwater Lakes
6
7
10
2
11
12
13
MONTANA

TABLE 1

MORPHOMETRIC DATA ON LAKES

(Lakes are ranked on the basis of the "productivity" index)

	ELEVATION (m)	MAXIMUM DEPTH (m)	(HECTARES) AREA	VOLUME (cu m)	LENGTH (Km)
KINTLA	1222	122.6	-	-	-
MARSHALL	1448	16.8	61	-	-
LINDBERGH	1318	38.1	294	-	6.5
CYGNET	1315	4.6	-	-	-
CLEARWATER	1460	13.7	51	3.44×10^6	-
RAINY	1250	9.2	28	1.46×10^6	-
ALVA	1244	24.4	118	18.24×10^6	-
BOWMAN	1226	80.5	-	-	-
TALLY	1021	150.1	537	-	5.6
INEZ	1237	21.4	116	13.11×10^6	-
SEELEY	1217	36.6	349	63.88×10^6	5.2
PLACID	1256	27.5	449	71.67×10^6	17.7
SALMON	1174	18.3	248	24.04×10^6	-

fed by underground springs, and drains south to the Blackfoot River. Marshall and Placid Lakes drain into the Clearwater River (See Figure 2).

The Clearwater drainage is bounded on the east by the Swan Range and on the west by the Mission Mountain Range. Both mountain ranges are predominately sedimentary carbonate rocks and were heavily glaciated during the Pleistocene (Alden, 1953). There are localized deposits of argillites and quartzites. Glacial till surrounds Rainy, Alva, Inez, and Seeley Lakes, while Salmon Lake occupies a rock basin in a narrow gorge.

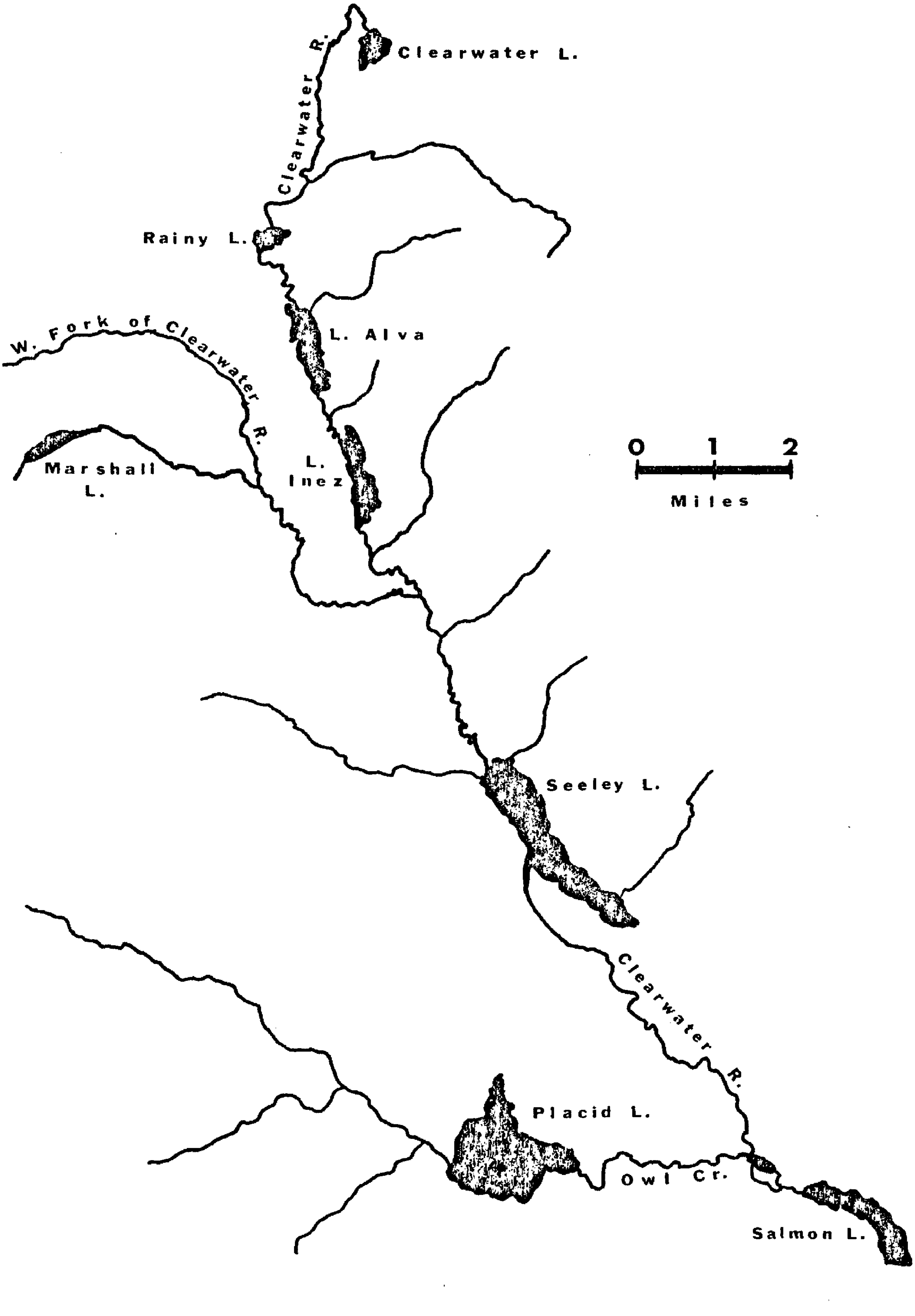
Due to the small change in elevation the Clearwater Valley is poorly drained. Approximately 50% of the land bordering the Clearwater River is marshy (Streebin, 1973), especially at the inlets to the lakes.

Lindbergh and Cygnet Lakes drain north into the Swan River. Cygnet Lake is just a few hundred meters below Lindbergh Lake. There are lakes in the Mission Mountains which drain into Lindbergh and Cygnet (Grey Wolf Lake, 2026 m, Lost Lake, 1898 m, High Park Lake, 1944 m, and Crystal Lake).

Bowman and Kintla Lakes, Glacier National Park, drain into the North Fork of the Flathead River, which flows south to Flathead Lake. Bowman and Kintla Lakes head in pre-Cambrian rocks and extend southwestward into a belt of soft Tertiary rocks (Alden, 1953). Upper Kintla Lake

FIGURE 2

CLEARWATER DRAINAGE STUDY SITES


Clearwater L.
Clearwater R.
Rainy L.
L. Alva
W. Fork of Clearwater R.
Marshall L.
L. Inez
0
1
2
Miles
Seeley L.
Clearwater R.
Placid L.
Owl Cr.
Salmon L.

(1332 m) is above Kintla Lake. Both Bowman and Kintla Lakes drain high mountain areas which have glaciers and permanent snow fields.

Tally Lake, Flathead National Forest, is west of the Rocky Mountain trench (8 miles west of Whitefish, Montana). The bedrock in the Flathead Valley is composed of carbonates, argillites, and quartzites which were worked upon by continental glaciation (Alden, 1953). The drainage area of Tally Lake is at a lower elevation than that of the other lakes.

Seeley, Salmon, Placid, and Tally Lakes have been affected by cultural eutrophication. Algal blooms of Anabaena flos-aquae have been observed in Seeley Lake (Cladouhos, 1971) and in the summer of 1972 in Tally Lake (Seastedt and Tibbs, 1974). A blue-green algal bloom occurred on Placid Lake during the summer of 1972 (Streebin, et al., 1973). Juday and Keller (1976) observed blooms on Salmon and Placid lakes during the summers of 1974 (Aphanizomenon flos-aquae) and 1975 (Anabaena flos-aquae).

It has been noted that Aphanizomenon flos-aquae blooms only in the presence of humic materials. Prakash, et al. (1973) has found that marine phytoplankton growth is stimulated by humic acids. Seeley, Placid, and Tally are the most highly colored lakes in this study.

Cladouhos (1971) attributed nutrient enrichment of Seeley Lake primarily to its morphometry, the dam on the outlet, and clear-cutting in the drainage basin. The lake drains poorly from its outlet, and it is confined to the north and west by low plains subject to spring flooding. The position of the outlet causes poor circulation and accumulation of nutrients. The bottom of the lake is heavily silted.

Hunter (1974) attributed the bloom in Tally Lake to nutrient enrichment from the large clearcuts in the drainage area and the cattle found in the basin, and to the positioning of both the inlet and outlet at the north end of the lake which would affect circulation patterns in the lake.

CHAPTER 4

METHODS

At each outlet stream benthic invertebrates were collected and certain chemical parameters were measured. Chlorophyll and particulate carbon were measured in an attempt to assess the amount of food entering the stream from the lake. The field work was done during a two and one half week period from July 25, 1976, to August 11, 1976.

Qualitative samples of benthic invertebrates were collected using kick nets (one with a mesh of eight threads per centimeter and one with sixteen threads per centimeter). Invertebrates were collected at two sites at each lake. The riffle area nearest the outlet was selected as site one and a second site was chosen at another riffle area approximately 100 meters downstream.

An attempt was made to thoroughly sample a cross section of the stream at each sample site. A minimum of five kick net samples (three with the coarser mesh net and two with the fine mesh net) were taken. Additional samples were taken as necessary to sample the entire range of habitats available at each site. The macroinvertebrates were preserved in 80% alcohol.

In the laboratory the samples were hand sorted, and the insect species were identified using the keys and description of Ross, 1944; Pennak, 1953; Walker, 1953;

Needham and Westfall, 1955; Edmondson, 1959; Stone, 1964; Jensen, 1966; Abdelnur, 1968; Smith, 1968, 1968a; Newell, 1970, 1971; Brown, 1972; Gaufin, et al., 1972; Usinger, 1974; Bauman, 1975; Hilsenhoff, 1975; Edmunds, et al., 1976. The occurrence and relative abundance of each species were recorded for each sample location. The categories used to indicate abundance were rare (only one individual), occasional (2-15 individuals), common (16 or more individuals), and abundant (a substantially greater number of individuals).

At each sampling location water temperature and time of day were recorded. Measurements were taken of the distance below the lake of the first and second sites and of the width and range in depth of the stream at site one.

Subjective data were noted on current velocity, light conditions, stone size and surface structure, amount of fine inorganic material, amount of organic deposits, periphyton, mosses, and attached algae.

Chemical analyses were done in the field on water collected at the outlet sites. The pH was measured using a Sargent-Welch, Model PBX pH meter, conductivity was measured with a Lab-Line Instruments, Inc. conductivity meter, and alkalinity was determined using Hach chemicals.

Water samples for laboratory analyses were collected at the outlet sites. The samples were taken from beneath the water surface by filling a one liter polyethylene bottle after rinsing it twice with water from the station. They were transported to the laboratory on ice and filtered the same day they were collected.

The water samples were analyzed for color (Juday and Keller, 1974, 1976), calcium and magnesium (APHA, 1971), particulate carbon (Strickland and Parsons, 1968; Maciolek, 1962) and total chlorophyll content (Goodwin, 1976; Golterman, 1969).

Water to be analyzed for color was filtered through 0.45 millimicron Millipore filters to remove suspended solids. Color was analyzed on a Beckman spectrophotometer (ACTA CIII) in the absorption spectrum between 340 and 550 millimicrons using a 10 centimeter cell length. Color is given in arbitrary units using the method of Juday and Keller (1974). Doubling the figures would approximate the Hazen scale. The numbers given for color are found by measuring the area under the curve between 340 and 550 millimicrons and dividing by the total area of one absorbance unit between 340 and 550 millimicrons.

Calcium and magnesium were analyzed on an atomic absorption spectrophotometer (Varian Techtron, Model 1000). A few drops of perchloric acid were added to the filtered water prior to analysis (EPA, 1971).

Quantitative analyses of total microseston were done by dichromate oxidation of filtered residues, generally following the procedure outlined by Strickland and Parsons

(1968), with modifications for fresh water. Either one or two liters of water were filtered through 4.5 centimeter Whatman GF/C glass filter paper fitted into standard Millipore filtration equipment. The filtration was done with a vacuum pump, which was held at 1/4 to 1/3 atmosphere. The filters had been freed from oxidizable material by placing them on aluminum foil in a muffle furnace at a temperature of 450-500 degrees C for 30 minutes.

Conditions of strong acidity and prolonged heating enable dichromate to oxidize nearly all organic compounds effectively, returning them to inorganic states. The theoretical aspects of quantitative dichromate oxidation have been extensively reviewed and applied to limnological analyses by Maciolek (1962). The extinction of the yellow dichromate solution after reduction by the organic matter was determined with a Coleman recording spectrophotometer (Hitachi EPS-3T). The particulate carbon in mg C/m^3 was calculated using the formulae of Strickland and Parsons (1968).

Chlorophyll content was used as an indicator of the biomass of plankton coming out the outlet. For chlorophyll analyses five liters of water were filtered through 4.5 centimeter Whatman GF/C glass filter paper with the use of a vacuum pump held below 1/3 atmosphere. The filter was rolled up and placed in a test tube in 10 milliliters of methanol and was kept in the dark at room temperature for

24 hours. After extraction was completed, the solution was put in a centrifuge at 4 degrees C. The optical density at 650 and 665 nm was determined by scanning the chlorophyll absorption peaks (Shimadzu MPS 50L recording spectrophotometer). The total chlorophyll concentrations were calculated using Holden's formula (Total chl (mg/l) = $25.5\ D_{650} + 4.0\ D_{665}$) (Goodwin, 1976).

The lakes were ranked using several indices of productivity. Many researchers have attempted to classify lakes. Hutchinson (1957, 1967) has reviewed the majority of schemes. Sheldon (1969, 1972) and Shannon (1969) have discussed the relative attributes of various multivariate techniques for the classification of lakes. Lake classifications based on productivity have placed the greatest importance on lake basin morphometry, on water chemistry, and on directly measured primary productivity or standing crops.

Rawson (1951) pointed out the usefulness of total dissolved solids as an indicator of edaphic conditions which affect productivity. A number of workers have found positive correlations between total dissolved solids (or correlates such as alkalinity and conductivity) and the productivity of plankton or bottom fauna (Slack, 1955; Northcote and Larkin, 1956; Armitage, K. B., 1958; Rawson, 1960; Egglishaw and Morgan, 1965). Rawson (1952) suggested that mean depth might be correlated with standing crops of plankton, bottom fauna, and fish in the lake. The depth of a lake is important for its effects on temperature, thermal stratification, and circulation and dilution of nutrient materials. Rawson's work, dealing with large lakes, pointed out the great influence of mean depth on fish yield. In a multiple regression analysis Northcote and Larkin (1956) found that total dissolved solids predominated over mean depth as a factor determining the level of productivity in smaller British Columbia lakes.

Both total dissolved solids and mean depth are incorporated into the morphoedaphic index (MEI) (Ryder, et al., 1974). The MEI is the ratio of total dissolved solids and mean depth of the lake. It has been found to be proportional to long term fish yields.

In the present study alkalinity/maximum depth and conductivity/maximum depth were used in the morphoedaphic index. The correlation of the MEI and the standing crop of plankton coming out the outlet (measured as total chlorophyll and particulate carbon) was examined. The MEI and other measures of productivity were analyzed to determine if correlations existed with the species richness of benthic invertebrates at the outlet study site.

Presence-absence data on insect species at the outlet sites were used to determine the degree of similarity between lakes. The phi coefficient (Siegel, 1956; Conover, 1971) was used as the measure of similarity. The matrix of phi coefficients for the lakes was used in a principal components analysis to get a preliminary grouping of lakes. The factors obtained in the principal components analysis were analysed for determining possible correlations with various physical and chemical parameters of the lakes.

CHAPTER 5

RESULTS

Morphometric data on the outlet streams are given in Table 2. Subjective data on substrate, current speed, and type of plants are in Tables 2 and 3.

Rawson (1960) grouped the factors affecting lake productivity into three broad categories - climatic, morphometric, and edaphic. Climatic factors were considered to be relatively constant in the lakes in this study. Morphometric data on the lakes are given in Table 1, page 13 (Montana Fish and Game Department; Konizeski, 1975 and pers. comm.).

Chemical data are given in Table 4. The pH values ranged from a low of 7.2 in Marshall Lake to highs of 8.4 in several of the lakes. Streebin, et al. (1973) found pH values for the five lakes in their study ranged from 7.4 at Seeley (May 22) to 8.4 in Inez (August 3). Cushing (1964) found that pH increased downstream in the lake-stream section of the Montreal River, Saskatchewan. This relationship was not found in the lakes in the Clearwater chain. Values ranged from 8.2-8.4, except for Seeley Lake which had a pH of 7.7.

Alkalinity values ranged from 20 ppm in Lindbergh and Cygnet Lakes to 110 ppm in Clearwater Lake. Similarly, conductivity ranged from 30 micromho/cm in Lindbergh and

TABLE 2

OUTLET STREAM DATA A

	DISTANCE OF SITE #2 BELOW OUTLET SITE (m)	WIDTH (m)	DEPTH (cm)	STONE SIZE (small, medium, large)	STONE SURFACE (smooth, rough)	FINER INORGANIC MATERIAL (little, average, much)	ORGANIC DEPOSITS (little, average, much)
KINTLA	90	20.0	20-45	S	S	A	L
MARSHALL	3.2 Km	6.0	20-35	M	S	A	L
LINDBERGH	130	28.0	20-50+	L	R	L	L
CYGNET	80	22.0	25-45	M	R	L	L
CLEARWATER	70	3.5	10-30	M	S	M	L
RAINY	80	6.0	10-20	S	S	L	L
ALVA	100	10.5	15-25	S	S	M	L
BOWMAN	100	27.5	25-45	S	S	A	L
TALLY	100	12.0	15-35	L	R	L	A
INEZ	90	13.0	15-25	S	S	M	L
SEELEY	95	21.0	15-40	L	S	A	M
PLACID	100	12.0	25-50	M	S	A	A
SALMON	260	15.5	20-30	M	S	A	A

TABLE 3

OUTLET STREAM DATA B

(Determinations are subjective)

	CURRENT	AMOUNT OF SHADING	PERIPHYTON	MOSSES	ALGAE
KINTLA	fast	partial	little	none	none
MARSHALL	medium	partial	average	many	some
LINDBERGH	fast	partial	average	many	some
CYGNET	fast	open	average	some	some
CLEARWATER	medium	partial	average	some	some
RAINY	medium	open	average	none	some
ALVA	slow	open	average	much	some
BOWMAN	fast	open	average	none	some
TALLY	medium	open	much	none	many
INEZ	medium	open	average	none	some
SEELEY	medium	open	much	none	much
PLACID	medium	open	average	none	some
SALMON	slow	open	much	many	some

TABLE 4

CHEMICAL DATA

(Lakes are ranked on the basis of the "productivity" index)

	DATE	TIME	TEMPERATURE (degrees C)	pH	CONDUCTIVITY (micromho/cm)	ALKALINITY (ppm)	Ca (ppm)	Mg (ppm)
KINTLA	8/7	3:30	17.5	8.0	90	60	13.2	3.6
MARSHALL	7/31	12:45	20.0	7.2	50	30	5.8	2.0
LINDBERGH	8/10	5 p.m.	18.5	7.5	30	20	4.2	1.1
CYGNET	8/10	7 p.m.	18.5	7.5	30	20	4.2	1.1
CLEARWATER	7/31	8:50	18.5	8.4	190	110	29.2	7.6
RAINY	7/25	8:30	18.0	8.3	180	100	28.4	7.3
ALVA	7/25	1:00	20.0	8.4	150	90	17.5	5.2
BOWMAN	8/7	9:30	16.0	8.1	90	40	13.8	3.9
TALLY	8/8	1:30	21.0	8.4	160	100	20.0	6.7
INEZ	7/25	3:00	23.0	8.4	140	60	23.4	5.9
SEELEY	8/1	8:15	21.5	7.7	75	40	9.1	3.2
PLACID	8/4	8:00	21.0	8.0	100	70	12.2	4.1
SALMON	8/4	12:00	20.0	8.2	110	60	13.2	4.6

Cygnet Lakes to a high of 190 micromho/cm in Clearwater Lake. The lower alkalinity and conductivity values in Lindbergh, Cygnet, and Marshall Lakes may indicate lower amounts of carbonates in the Mission Range. They may also represent climatic effects, since the drainage areas of these lakes are at higher altitudes than the lakes in the Clearwater chain. Lakes at higher altitudes where the winters are longer often have smaller amounts of dissolved ions than the edaphic conditions would indicate, because of the relatively short period of time available for the dissolution and transportation of minerals to the lake (Ryder, et al., 1975). Clearwater Lake is fed by underground springs so would be less affected by its higher altitude.

Calcium values varied from 4.2 to 29.4 ppm and Mg values were in the range of 1.1 to 7.6 ppm. Placid has values higher than Seeley but lower than Inez. Juday and Keller (1976) attribute this to the influence of Boles Creek, which has higher calcium and magnesium values than the upper Clearwater.

In the Clearwater chain (Clearwater, Rainy, Alva, Inez, Seeley, and Salmon Lakes) the amounts of dissolved ions generally decrease downstream (Juday and Keller, 1976; Streebin, et al., 1973). Streebin, et al. attribute the downstream decrease in alkalinity to the successive downstream dilution of the water from the upper reaches of the

Clearwater River. Cushing (1964) found that the concentrations of total dissolved solids decreased downstream in the Montreal River lake-stream system, Saskatchewan. He attributed the decrease to the assimilation of nutrients by phytoplankton in the lakes. Hynes (1960, 1970) suggested that lakes may act as "fertility traps" removing dissolved ions and depleting the supply of essential nutrients in the outlet stream.

Color values ranged from lows in Bowman (0.5), Kintla (0.5), and Clearwater (0.6) to highs in Seeley (6.8), Tally (7.8), and Placid (8.0) (Table 5). Color in natural waters is due to organic substances which include tannins, lignins, and humic acids from the decomposition of leaves and wood (Juday and Keller, 1976). Organic color may influence production by affecting pH, by chelating certain trace metal nutrients, and by absorbing light (Brezonik, 1969).

Particulate carbon values ranged from 79.58 mg C/m^3 in Kintla Lake to over 600 mg C/m^3 in Salmon Lake (Table 5). Particulate organic carbon, including planktonic organisms, generally accounts for about 10% of the total organic carbon, the remainder being in the dissolved form (Stumm and Morgan, 1970). The ratio of dissolved organic carbon to particulate organic carbon is almost universally in the range of 6:1 to 10:1 in both lake and stream systems (Wetzel, 1975).

TABLE 5

PRODUCTIVITY INDICES

(Lakes are ranked on the basis
of the productivity index)

	COLOR	CHLOROPHYLL (mg/m^3)	PARTICULATE CARBON (mg/m^3)	PRODUCTIVITY INDEX $(\text{Chl } \frac{x}{s})\cdot(\text{Part. C } \frac{x}{s})$	$\frac{\text{ALKALINITY (ppm)}}{\text{MAXIMUM DEPTH (m)}}$	$\frac{\text{CONDUCTIVITY (ppm)}}{\text{MAXIMUM DEPTH (m)}}$
KINTLA	0.5	0.536	79.6	0.678	0.489	0.734
MARSHALL	5.1	0.700	96.1	0.852	1.788	2.981
LINDBERGH	2.1	0.650	114.11	0.900	0.525	0.787
CYGNET	1.8	0.750	156.2	1.124	4.372	6.557
CLEARWATER	0.6	0.920	145.7	1.203	8.015	13.843
RAINY	1.4	0.936	222.2	1.499	10.929	19.672
ALVA	2.8	0.920	297.3	1.718	3.689	6.148
BOWMAN	0.5	0.980	285.3	1.738	0.497	1.118
TALLY	7.8	0.904	312.3	1.746	0.666	1.066
INEZ	4.2	1.120	342.3	2.034	2.810	6.557
SEELEY	6.8	1.144	528.5	2.555	1.093	2.049
PLACID	8.0	1.362	498.5	2.708	2.550	3.643
SALMON	4.3	2.680	600.6	4.169	3.279	6.011

Chlorophyll values were low and ranged from 0.536-2.680 mg chl/m^3 (Table 5).

Correlation coefficients for the relationship of the chemical, morphological, and biological parameters are given in Table 6. Log transformations were performed on the data as indicated before correlations were determined. Probability values are from a table in Steel and Torrie (1960).

A significant positive correlation was found between the number of species at the outlet sites (log S) and the biomass or productivity of plankton coming from the lake (log chlorophyll) ($r = 0.606$, 12 d.f., $p < .05$). There was also a weaker but significant positive correlation ($r = 0.578$, 12 d.f., $p < .05$) between the number of species at the outlet sites and a productivity index (Table 5). The productivity index combined the chlorophyll and particulate carbon data (the product of the standard variates (x_i/s_i) of total chlorophyll and particulate carbon values for each lake) (Figure 3). The logarithms of the chlorophyll and particulate carbon data were closely correlated ($r = 0.858$, 12 d.f., $p < .01$).

The logarithm of color was also positively correlated with the logarithm of the number of species ($r = 0.555$, 12 d.f., $p < .05$).

The edaphic and morphometric data were not well correlated with the indices of productivity. The logarithms of

TABLE 6

CORRELATIONS

* $p < .05$; ** $p < .01$

		r	d.f.
1.	log "productivity" - log maximum depth	-0.029	11
	log "productivity" - log S	0.578*	11
	log maximum depth - log S	-0.454	11
	R = .656, 10 d.f.		
2.	log chlorophyll - log particulate carbon	0.858**	11
	log chlorophyll - log S	0.606*	11
	log particulate carbon - log S	0.530	11
	R = .490, 10 d.f.		
3.	log color - log S	0.555*	12
4.	log alkalinity - log conductivity	0.971**	10
	log alkalinity - log maximum depth	0.222	10
	log alkalinity - log chlorophyll	0.290	10
	log conductivity - log maximum depth	0.217	10
	log conductivity - log chlorophyll	0.353	10
	log maximum depth - log chlorophyll	-0.143	10
	R = .203, 9 d.f.		
	Ryder index		
5.	alkalinity/maximum depth - log S	0.234	12
6.	alkalinity/maximum depth - log chl	0.086	12
7.	conductivity/maximum depth - log chl	0.117	12
8.	alkalinity/maximum depth - log S (non-Clearwater lakes)	0.531	6

TABLE 6 (continued)

CORRELATIONS

* p .05; ** p .01

		r	d.f.
9.	Clearwater chain only (Clearwater, Rainy, Alva, Inez, Seeley, Salmon)		
	log alkalinity - log maximum depth	-0.760	4
	log alkalinity - log chlorophyll	-0.448	4
	log maximum depth - log chlorophyll	0.110	4
	R = .350, 3 d.f.		
10.	particulate carbon/maximum depth - log S	0.622*	12
11.	log chlorophyll - % of total species in common at both outlet and downstream sites (Marshall not included)	0.613*	11
12.	log productivity index - % of total species in common at both sites (Marshall not included)	0.695**	11
	<u>Principal Components Analysis</u>		
13.	log chlorophyll - component 1	0.264	12
14.	log S - component 1	0.216	12
15.	log color - component 2	-0.580*	12
16.	elevation - component 2	0.541*	12
17.	log chlorophyll - component 2	-0.686**	12
18.	log S - component 2	-0.347	12
19.	log chlorophyll - elevation	-0.314	12
	<u>Partial Correlations</u>		
20.	log chlorophyll - component 2 (elevation held constant)	-0.647*	12
21.	elevation - component 2 (log chlorophyll held constant)	0.471	12

FIGURE 3

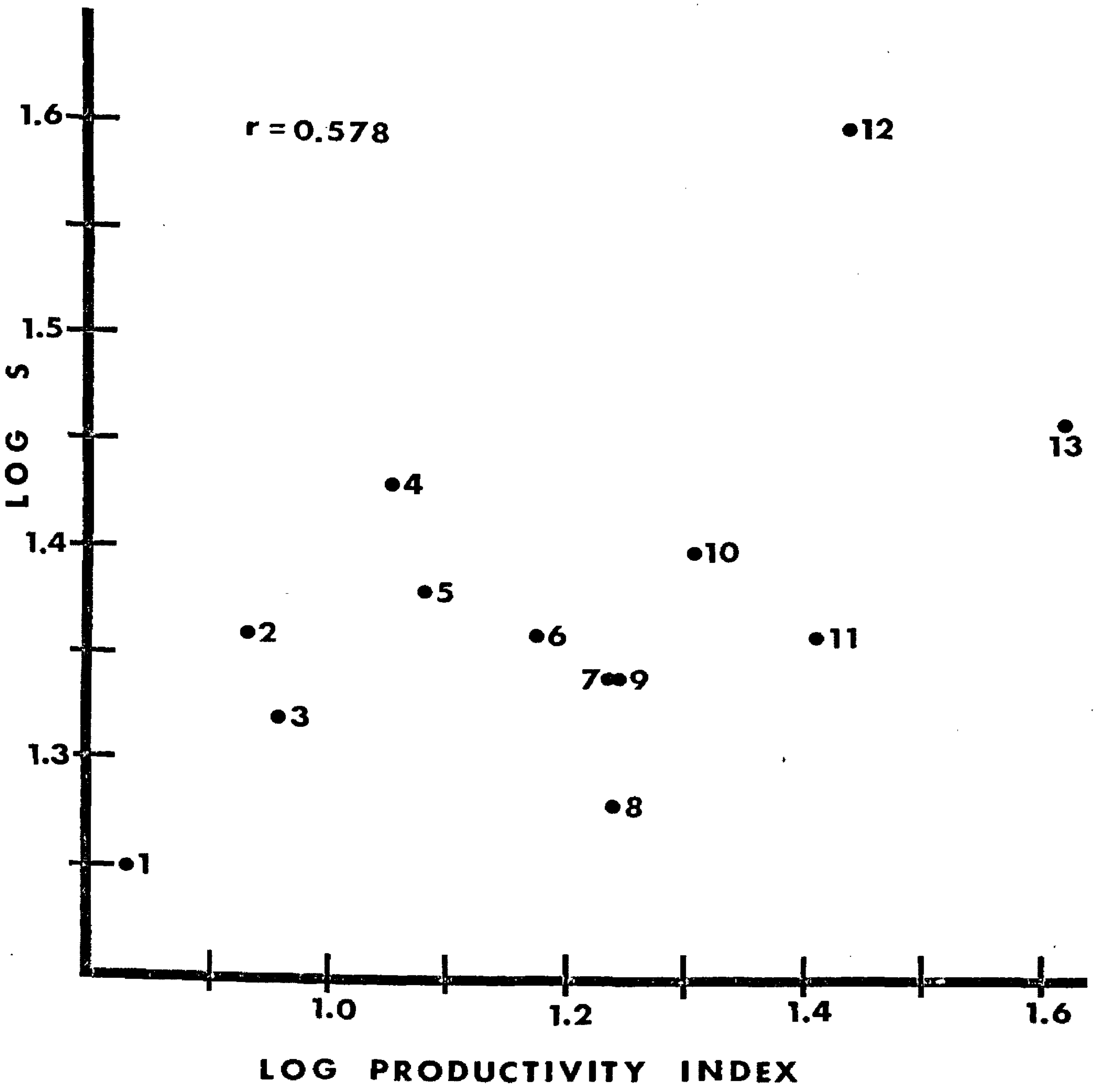
Correlation of Logarithms of Productivity Index and Logarithms of Numbers of Species at the Outlet Sites

Productivity Index =

$$\left(\text{Chlorophyll } \frac{x}{s}\right) \cdot \left(\text{Particulate C } \frac{x}{s}\right)$$

Lakes

1. Kintla
2. Marshall
3. Lindbergh
4. Cygnet
5. Clearwater
6. Rainy
7. Alva
8. Bowman
9. Tally
10. Inez
11. Seeley
12. Placid
13. Salmon


r = 0.578
LOG S
1.6
1.5
1.4
1.3
LOG PRODUCTIVITY INDEX
1.0
1.2
1.4
1.6
1
2
3
4
5
6
7
8
9
10
11
12
13

alkalinity and conductivity were highly correlated ($r = 0.971$, 11 d.f., $p < .01$). No significant correlations were found between the logarithms of either alkalinity or conductivity and the logarithm of chlorophyll. Similarly, no significant relationship was found between the logarithm of alkalinity or conductivity and the logarithm of the maximum depth.

In Ryder's (1974) morphoedaphic index (Table 5, p. 31) conductivity and alkalinity were used as correlates of total dissolved solids, and maximum depth was substituted for mean depth, since mean depth has not been determined for some of the lakes in the study. Alkalinity/maximum depth gave no significant correlation with either the logarithm of the number of species ($r = 0.234$, 12 d.f., $p < .82$) or with the logarithm of chlorophyll ($r = 0.086$, 12 d.f., $p < .92$) (Figures 4 and 5). Using conductivity/depth in Ryder's index gave a slightly higher correlation with the logarithm of chlorophyll ($r = .117$, 12 d.f., $p < .90$).

The Ryder index gave higher correlations with species richness at the outlet when applied only to the seven lakes outside the Clearwater chain ($r = 0.531$, 6 d.f., $p < .56$, for alkalinity/maximum depth and the logarithm of the number of species at the outlet).

Correlations using only the six lakes in the Clearwater chain showed a negative correlation for the logarithms of alkalinity and maximum depth ($r = -0.760$, 5 d.f.,

FIGURE 4

Correlation of Alkalinity/Maximum Depth and Logarithms of Numbers of Species

Lakes

1. Kintla
2. Marshall
3. Lindbergh
4. Cygnet
5. Clearwater
6. Rainy
7. Alva
8. Bowman
9. Tally
10. Inez
11. Seeley
12. Placid
13. Salmon

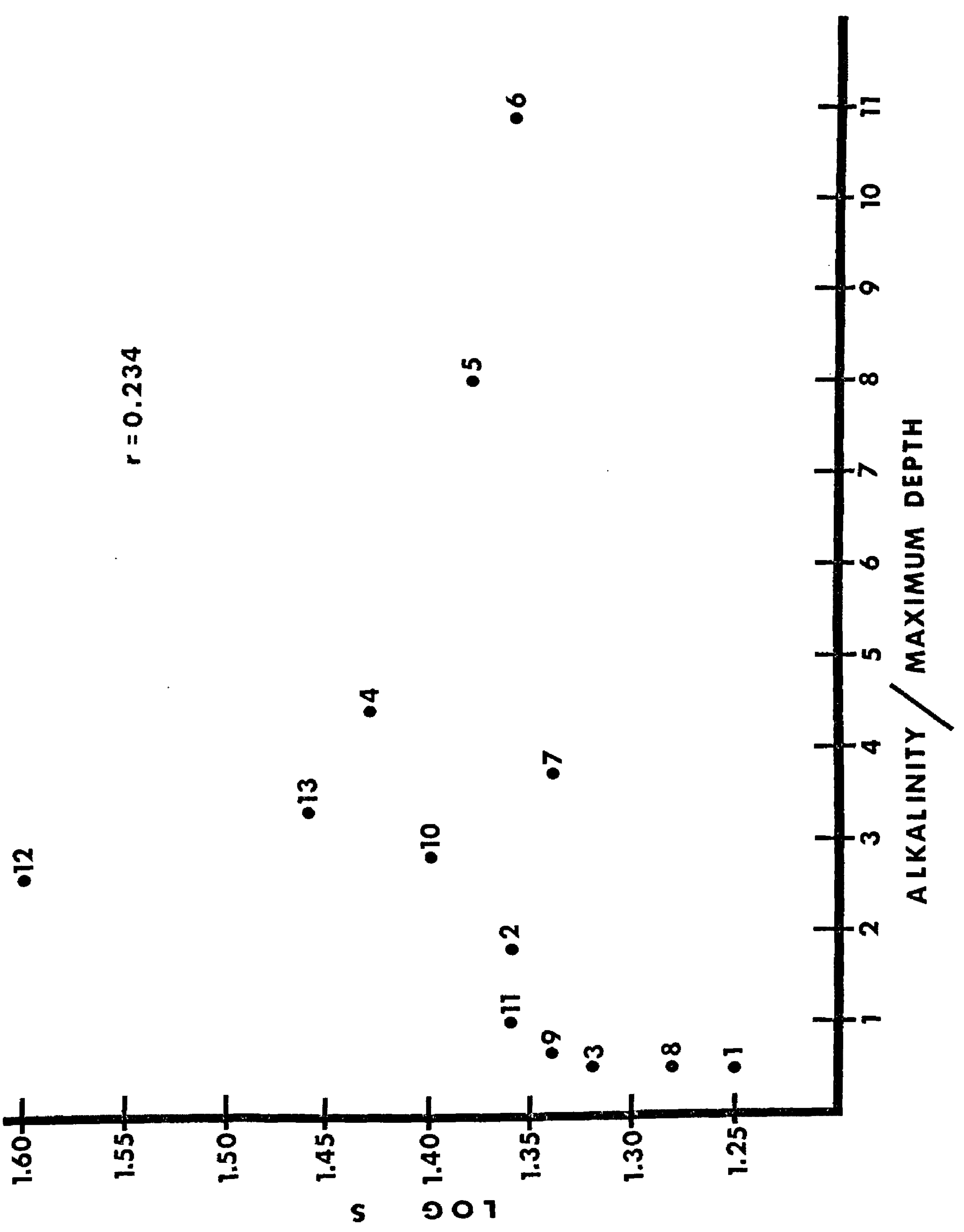
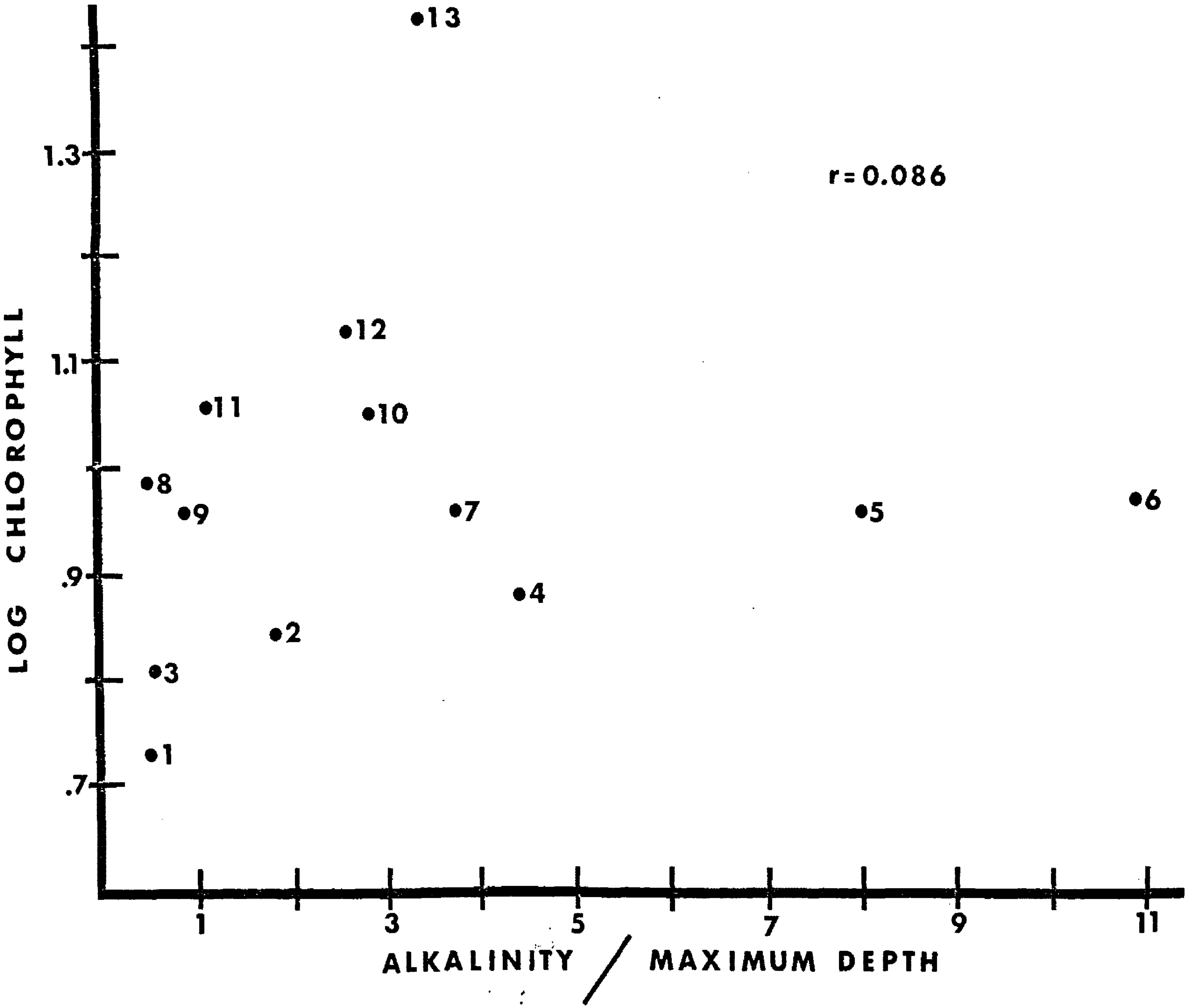

r = 0.234
LOG S
1.60
1.55
1.50
1.45
1.40
1.35
1.30
1.25
ALKALINITY / MAXIMUM DEPTH
1
2
3
4
5
6
7
8
9
10
11
1
2
3
4
5
6
7
8
9
10
11
12
13

FIGURE 5

Correlation of Alkalinity/Maximum Depth and Logarithms of Chlorophyll Content of Seston

Lakes

1. Kintla
2. Marshall
3. Lindbergh
4. Cygnet
5. Clearwater
6. Rainy
7. Alva
8. Bowman
9. Tally
10. Inez
11. Seeley
12. Placid
13. Salmon


r=0.086
LOG CHLOROPHYLL
1.3
1.1
.9
.7
ALKALINITY / MAXIMUM DEPTH
1
3
5
7
9
11
13
12
11
10
8
9
7
5
6
4
2
3
1

$p < .05$) and for the logarithms of alkalinity and chlorophyll ($r = -0.448$, 5 d.f., $p < .64$).

Another index (Hays and Anthony, 1964) which related area, mean depth, and methyl orange alkalinity to a productivity index based on standing crop of fish was applied to the 10 lakes in this study for which measurements of area were available. Essentially, the large lakes had low productivity indices and the small lakes had higher indices, which does not correspond to what was found in this study.

A total of 74 species of insects were identified - 68 species at the outlet sites and 69 species at the downstream sites. See Table 7 and Appendix Table A. Only 19 of the 68 outlet species were found at seven or more of the outlet sites (Table 8).

There were differences in the species composition between the outlet and downstream sites. *Hydropsyche oslari* (3 lakes), *Arctopsyche grandis* (3 lakes), *Wormaldia sp.* (1 lake), *Helius sp.* (1 lake), *Ephemerella doddsi* (1 lake), and *Stenelmis sp.* (5 lakes) were found only at downstream sites. *Epeorus albertae* was found at six downstream sites and only at the outlet site of Cygnet Lake. The six species found only at outlet sites were generally found only at one lake and were rare or occasional.

Generally, the 100 meters between the first and second sites was not a great enough distance to be away from the influence of outlet conditions, particularly in the more

TABLE 7

NUMBER OF SPECIES

	PLECOPTERA	TRICHOPTERA	(HYDROPSYCHID)	ODONATA	DIPTERA	(SIMULIIDAE)	EPHEMEROPTERA	LEPIDOPTERA	COLEOPTERA	TOTAL
OUTLETS										
Kintla	5	3	(1)	0	4	(3)	6	0	0	18
Marshall	3	7	(2)	1	3	(0)	6	0	3	23
Lindbergh	2	8	(3)	0	4	(2)	6	0	1	21
Cygnet	4	7	(3)	0	5	(4)	9	0	2	27
Clearwater	3	7	(1)	0	6	(4)	6	0	2	24
Rainy	2	6	(3)	1	3	(2)	7	1	3	23
Alva	2	8	(2)	2	1	(0)	6	0	3	22
Bowman	3	4	(1)	0	4	(3)	5	0	3	19
Tally	2	5	(2)	2	2	(1)	7	1	3	22
Inez	1	9	(3)	2	1	(0)	9	0	3	25
Seeley	2	6	(3)	1	3	(1)	7	1	3	23
Placid	4	11	(3)	2	6	(3)	12	1	4	40
Salmon	2	8	(2)	2	3	(1)	10	1	2	28
DOWNSTREAM										
Kintla	5	1	(0)	0	3	(2)	5	0	1	15
Marshall	4	10	(3)	0	3	(1)	9	0	5	31
Lindbergh	4	7	(2)	0	4	(1)	7	0	3	25
Cygnet	4	8	(4)	0	2	(0)	9	0	4	27
Clearwater	3	6	(2)	0	3	(2)	5	0	4	21
Rainy	3	4	(2)	2	2	(1)	8	1	3	23
Alva	4	8	(2)	2	2	(1)	7	1	3	27
Bowman	3	3	(1)	0	4	(3)	4	0	1	15
Tally	3	8	(2)	2	5	(2)	7	1	3	29
Inez	1	8	(3)	2	2	(1)	7	0	2	22
Seeley	2	8	(3)	2	4	(2)	10	1	2	29
Placid	4	8	(3)	2	5	(1)	8	1	3	31
Salmon	2	6	(2)	2	4	(0)	9	0	2	23

TABLE 8

SPECIES FOUND AT 7 OR MORE OUTLET SITES

Ephemeroptera	Number of sites
Ephemerella margarita	12
Baetis propinquus	7
B. tricaudatus	10
B. parvus	9
Tricorythodes sp.	8
Heptagenia criddlei	9
Trichoptera	
Hydropsyche cockerelli	8
H. occidentalis	9
Cheumatopsyche gracilis	11
Lepidostoma sp.	10
Athripsodes sp.	11
Plecoptera	
Acroneuria pacifica	11
A. californica	9
Amphinemura banksi	9
Diptera	
Hexatoma sp.	12
Simulium vittatum	10
Odonata	
Ophiogomphus morrisoni	7
Coleoptera	
Zaitzevia parvula	10
Optioservus sp.	12

productive lakes. In the less productive lakes the species composition at the downstream sites was sufficiently different to increase significantly the total number of species collected below that lake. This was particularly noticeable in Lindbergh (30 total species, 21 species at the outlet site), Cygnet (34 total species, 27 outlet species), and Marshall (38 total species, 23 outlet species), where the character of the downstream site was very different from the outlet site. In the case of Lindbergh the downstream site had a more suitable substrate than the outlet site, which was primarily bedrock and large boulders. The gradient of the outlet stream of Cygnet Lake becomes very steep at about 100 meters from the lake. The stream flowing out of Marshall Lake runs into a slow area with many logs and a great amount of silt, so it was necessary to sample 3.2 kilometers downstream. Therefore, the second site at Marshall is not comparable to those of the other lakes.

The number of species found at both the outlet and downstream sites was divided by the total number of species found at that lake (Table 9). When the relationship of the percent of the total species which were in common at the two sites and the logarithm of the productivity index was examined, the correlation coefficient was found to be highly significant ($r = 0.695$, 11 d.f., $p < .01$) (Figure 6). The correlation with the logarithm of chlorophyll was

TABLE 9

% OF TOTAL SPECIES FOUND:

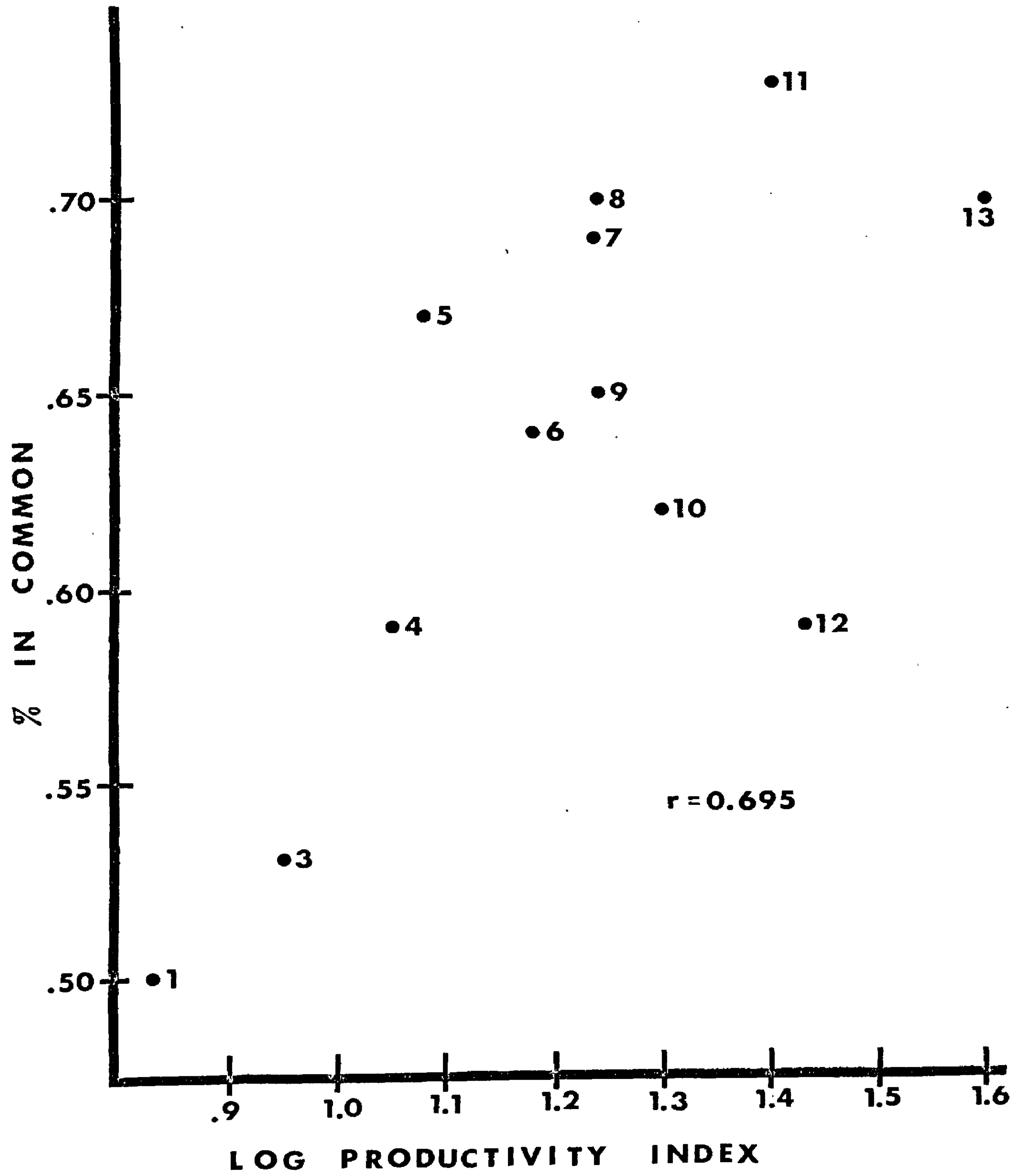
	DOWNSTREAM ONLY	OUTLET ONLY	IN COMMON
KINTLA (22 sp.)	.18	.32	.50
MARSHALL (38 sp.)	.39	.18	.42
LINDBERGH (30 sp.)	.30	.17	.53
CYGNET (34 sp.)	.21	.21	.59
CLEARWATER (27 sp.)	.11	.22	.67
RAINY (28 sp.)	.18	.18	.64
ALVA (29 sp.)	.24	.07	.69
BOWMAN (20 sp.)	.05	.25	.70
TALLY (31 sp.)	.29	.06	.65
INEZ (29 sp.)	.14	.24	.62
SEELEY (30 sp.)	.23	.03	.73
PLACID (44 sp.)	.11	.31	.59
SALMON (30 sp.)	.06	.23	.70

FIGURE 6

Correlation of Logarithms of Productivity Index and the Percent of Total Species Common to Outlet and Downstream Sites

Lakes

1. Kintla
3. Lindbergh
4. Cygnet
5. Clearwater
6. Rainy
7. Alva
8. Bowman
9. Tally
10. Inez
11. Seeley
12. Placid
13. Salmon



.70
.65
.60
.55
.50
% IN COMMON
.9
1.0
1.1
1.2
1.3
1.4
1.5
1.6
LOG PRODUCTIVITY INDEX
1
3
4
5
6
7
8
9
10
11
12
13
r = 0.695

significant at the .05 level ($r = .613$, 11 d.f.). Marshall Lake was not included in this analysis because of the greater distance between the two sites. This indicates that the seston is still present in great enough amounts in the downstream site of the more productive lakes to maintain the fauna which is associated with large amounts of lake plankton.

The lakes were separated into less productive and more productive categories on the basis of the index combining chlorophyll and particulate carbon data. Kintla, Marshall, Lindbergh, Cygnet, Clearwater, and Rainy Lakes were in the less productive category and Alva, Bowman, Tally, Inez, Seeley, Placid, and Salmon Lakes were in the more productive category.

Of the 68 species found at the outlet sites, 20 species were collected only in the six less productive lakes, 12 species were found only in the seven more productive lakes, and 36 species were found at some of the sites in both the productive and unproductive categories.

A Chi Square test showed a significant difference at the $p = .001$ level. $X^2 = 16.084$, 1 d.f.

	Less productive	Both	More productive
Observed	20.0	72.0	12.0
Expected	30.0	51.6	22.2

More species were observed to occur in both categories of productivity than the expected number. Fourteen of the 36 species found in both categories occurred primarily in either the less or more productive lakes, but also occurred in one lake in the other category. Rainy Lake contained species otherwise found only in the more productive lake category. Conversely, Placid Lake contained species otherwise found only in the less productive category. Bowman Lake contains species more characteristic of unproductive lakes, even though the various productivity indices dictated that it be placed in the productive lake category. When these borderline lakes are taken into consideration, the separation of species into those which occur in less productive or more productive lakes appears to be more of a real phenomenon.

Other factors such as altitude (due to its effect on temperature) may affect species distributions. For the most part, the lakes in the less productive category are at a higher elevation. In this study 19 species occurred only in the six lakes with the highest elevation. Jensen (1966) lists _Ephemerella_ _aurivilli_, _E_. _Doddsi_, and _Paraleptophlebia_ _heteronea_ as generally being found above 5,000 feet in Idaho.

The mean monthly temperatures and the temperature variance is not known for most of the lakes in this study. In the present study the colder temperatures were recorded in Kintla, Bowman, Lindbergh, Cygnet, Clearwater, and Rainy Lakes. However, temperature readings were not all taken at the same time of day, so are not comparable due to diel variations.

Streebin, et al. (1973) gave the following mean values for the summer months (May-August, 1972): Rainy outlet (11.5 C, s=3.85), Alva outlet (13.8 C, s=3.68), Inez outlet (14.6 C, s=3.45), Seeley outlet (14.7 C, s=5.00), and Placid outlet (17.4, s=4.08).

One can get an idea of the general range of temperatures from the distribution of insect species. Warmer water genera, such as _Ophiogomphus_, _Argia_, _Brachycentrus_, and _Helicopsyche_ (Armitage, K. B., 1961) are only found in Tally, Marshall, Rainy, Alva, Inez, Seeley, Placid, and Salmon outlets. However, other genera which Armitage lists as preferring warmer waters also occur in Lindbergh and Cygnet outlets (_Tricorythodes_, _Hydropsyche_, and _Antocha_).

The biological data on number of species was analyzed using principal components analysis (Cooley and Lohnes, 1962; Harman, 1976). The data from the outlet sites were first placed in 2x2 contingency tables for each pairwise combination of lakes. A is the number of species in common in both lakes, D is the number which occur in neither lake, and B and C are the numbers occurring in one lake but not in the other.

The phi coefficient ($\emptyset$) Siegel, 1956; Conover, 1971) was used as the measure of association.

$$\emptyset = \frac{AD - BC}{\sqrt{(A+B)\ (C+D)\ (A+C)\ (B+D)}}$$

The phi coefficient may vary from +1 when all of the species are in both of the lakes to -1 when all of the species are in neither of the lakes.

Only four phi coefficients had negative values (Kintla-Alva, Kintla-Inez, Bowman-Inez, and Marshall-Salmon). The lakes which had the most similar faunas ($\emptyset > 0.5$) were Marshall-Lindbergh, Lindbergh-Cygnet, Cygnet-Rainy, Rainy-Alva, Alva-Inez, Alva-Salmon, Tally-Seeley, Tally-Salmon, and Inez-Salmon (Table 10).

The Statistical Package for the Social Sciences (Nie, et al., 1975) program was used for the principal components analysis. The phi coefficients in matrix form were used in this program. The results of the principal components analysis are in Tables 11 and 12.

Communality is the proportion of the variance that a lake has in common with the average of all the lakes in the study. Clearwater (.465), Tally (.569), and Seeley (.595) had the lowest communalities and Placid (.790), Inez (.805), and Lindbergh (.824) had the highest communality values.

Component 1 accounts for 34.2% of the variation, Component 2 for 16.6%, Component 3 for 8.5%, and Component 4 for 7.8%.

When Components 1, 2, and 3 are graphed (Figure 7), six lakes are clearly separate from the rest (Kintla, Bowman, Lindbergh, Cygnet, Marshall, and Clearwater). These six lakes have positive values for Component 2.

TABLE 10

PHI COEFFICIENTS

	Kintla	Marshall	Lindbergh	Cygnet	Clearwater	Rainy	Alva	Bowman	Tally	Inez	Seeley	Placid	Salmon
Ki	1	.13	.30	.33	.25	.21	-.02	.37	.01	-.11	.13	.10	.04
Ma	-	1	.60	.35	.25	.21	.10	.32	.30	.04	.28	.22	-.03
Li	-	-	1	.63	.31	.33	.15	.17	.35	.27	.33	.13	.09
Cy	-	-	-	1	.41	.56	.27	.37	.34	.19	.37	.19	.11
Cl	-	-	-	-	1	.19	.02	.16	.15	.01	.06	.31	.08
Ra	-	-	-	-	-	1	.50	.32	.44	.42	.47	.35	.35
Al	-	-	-	-	-	-	1	.13	.46	.78	.37	.26	.54
Bo	-	-	-	-	-	-	-	1	.27	-.07	.25	.12	.15
Ta	-	-	-	-	-	-	-	-	1	.39	.57	.32	.51
In	-	-	-	-	-	-	-	-	-	1	.36	.20	.54
Se	-	-	-	-	-	-	-	-	-	-	1	.47	.48
Pl	-	-	-	-	-	-	-	-	-	-	-	1	.34
Sa	-	-	-	-	-	-	-	-	-	-	-	-	1

TABLE 11

PRINCIPAL COMPONENTS ANALYSIS A

COMPONENT	EIGENVALUE	% OF VARIATION	CUMULATIVE %
1	4.44944	34.2	34.2
2	2.16433	16.6	50.9
3	1.10885	8.5	59.4
4	1.01594	7.8	67.2
5	0.95697	7.4	74.6
6	0.68172	5.2	79.8
7	0.66250	5.1	84.9
8	0.59122	4.5	89.5
9	0.37123	2.9	92.3
10	0.33291	2.6	94.9
11	0.30275	2.3	97.2
12	0.24317	1.9	99.1
13	0.11898	0.9	100.0

TABLE 12

PRINCIPAL COMPONENTS ANALYSIS B

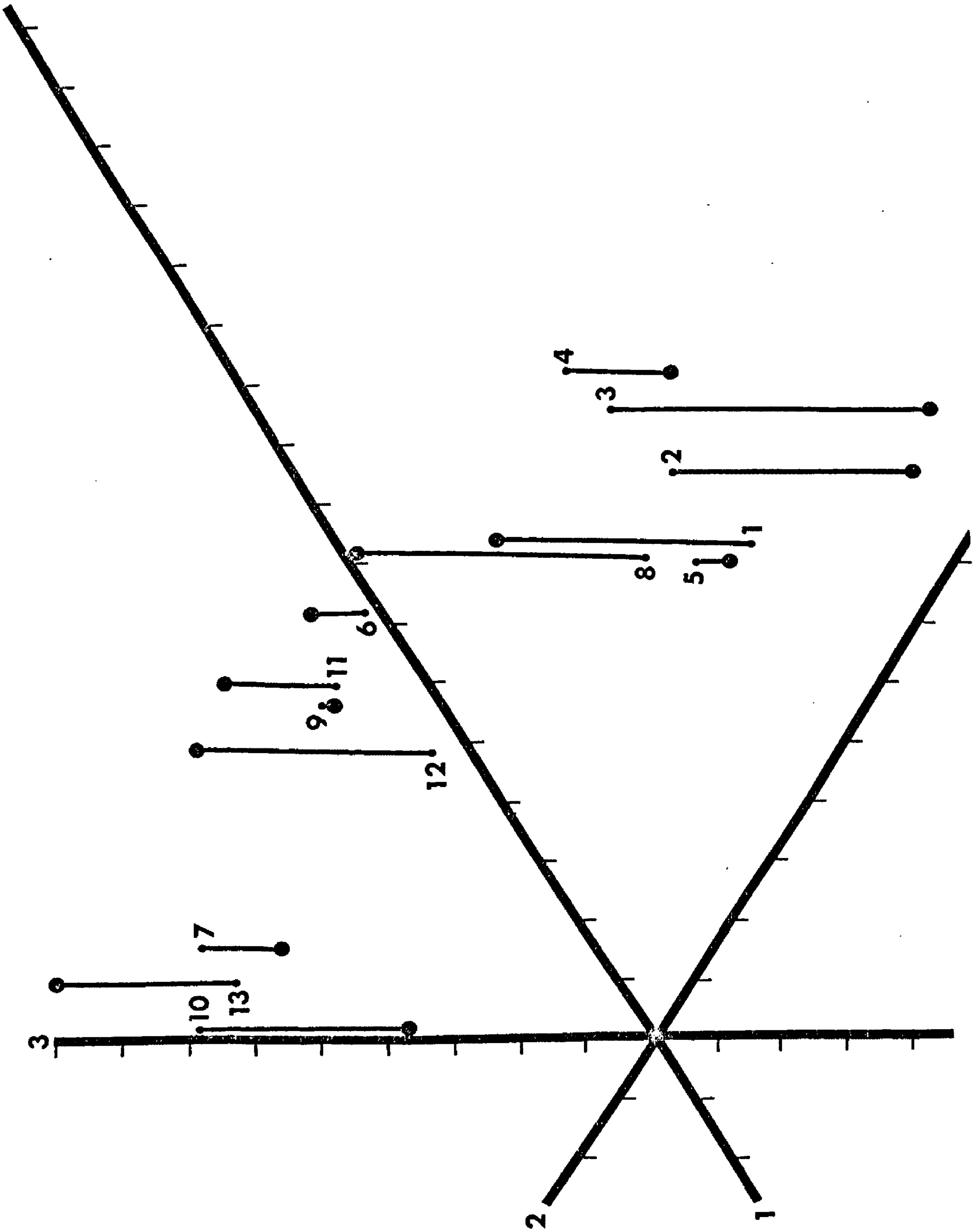
	COMPONENTS				COMMUNALITY
LAKE	1	2	3	4	
KINTLA	0.282	0.535	0.402	-0.337	0.642
MARSHALL	0.471	0.478	-0.372	0.238	0.646
LINDBERGH	0.606	0.447	-0.507	-0.024	0.824
CYGNET	0.577	0.429	-0.151	-0.204	0.707
CLEARWATER	0.357	0.443	0.063	0.370	0.465
RAINY	0.745	-0.030	0.079	-0.218	0.609
ALVA	0.659	-0.520	-0.106	-0.236	0.771
BOWMAN	0.425	0.389	0.447	-0.324	0.637
TALLY	0.724	-0.174	-0.010	0.121	0.569
INEZ	0.592	-0.582	-0.301	-0.158	0.805
SEELEY	0.724	-0.129	0.159	0.173	0.595
PLACID	0.527	-0.064	0.346	0.623	0.790
SALMON	0.592	-0.506	0.268	0.021	0.678

FIGURE 7

Components 1, 2, and 3 of the Principal Components Analysis

Lakes

1. Kintla
2. Marshall
3. Lindbergh
4. Cygnet
5. Clearwater
6. Rainy
7. Alva
8. Bowman
9. Tally
10. Inez
11. Seeley
12. Placid
13. Salmon



1
2
3
4
5
6
7
8
9
10
11
12
13
1
2
3

The correlation coefficient for the logarithm of chlorophyll and Component 2 is highly significant ($r = -0.686$, 12 d.f., $p < .01$) (Figure 8). Significant correlations are also obtained for the logarithm of color and Component 2 ($r = -0.580$, 12 d.f., $p < .05$) and for elevation and Component 2 ($r = 0.541$, 12 d.f., $p < .05$). The logarithm of chlorophyll and elevation do not give a significant correlation ($r = -0.314$, 12 d.f., $p < .74$).

Partial correlations were determined for the logarithm of chlorophyll, Component 2, and elevation. The partial correlation coefficient for the logarithm of chlorophyll and Component 2, holding elevation constant is -0.647, 12 d.f., $p < .05$). For elevation and Component 2, holding the logarithm of chlorophyll constant $r = 0.471$, 12 d.f., $p < .62$).

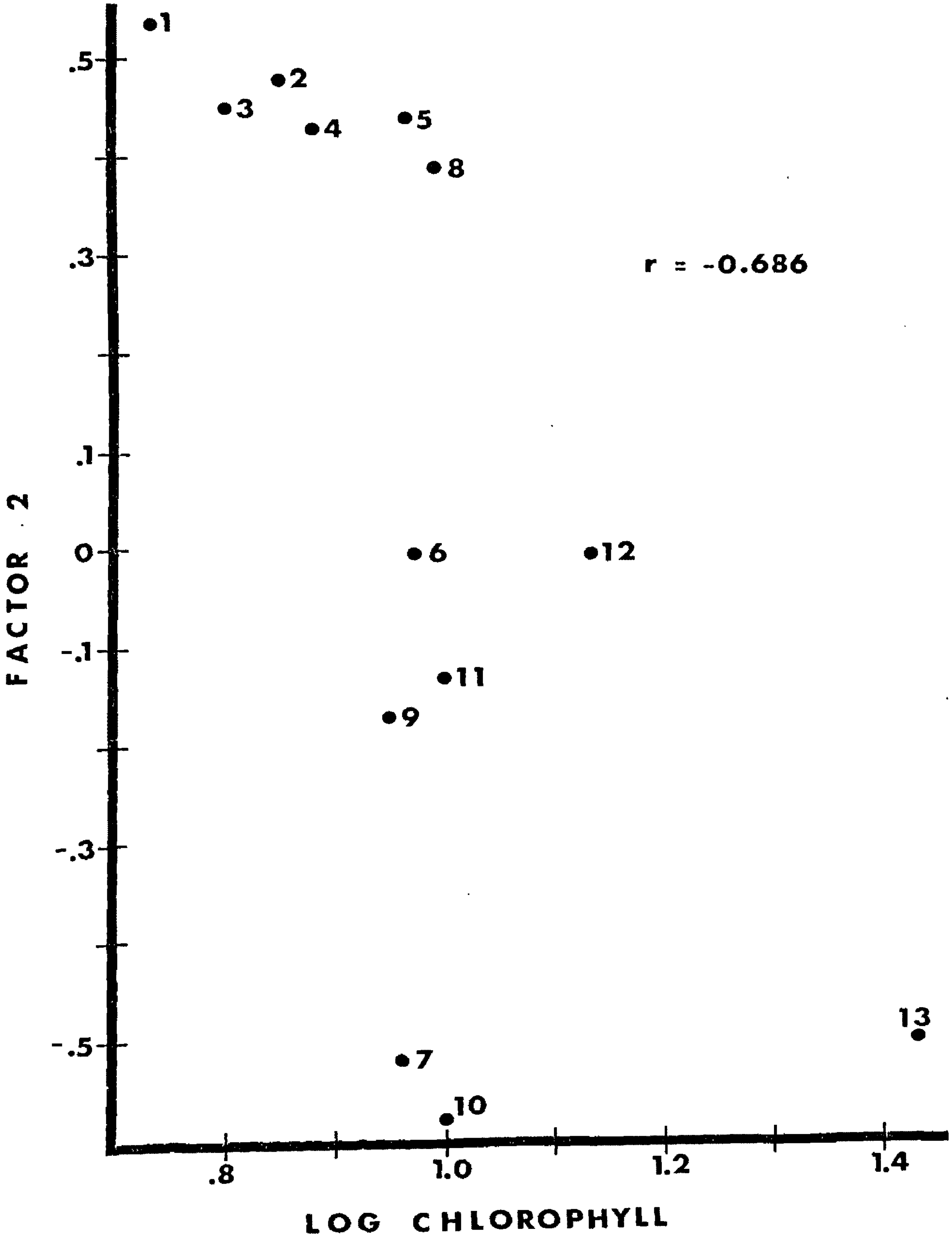
The six lakes with the positive values for Component 2 were considered to be the low productivity lakes because of the significant negative correlation between Component 2 and the logarithm of chlorophyll. These six outlets (Kintla, Bowman, Lindbergh, Cygnet, Marshall, and Clearwater) are similar in productivity (chlorophyll and particulate carbon) measurements, with the exception of Bowman, which had higher values for these parameters. They are higher in elevation, have colder temperatures, and generally have a fast current. They vary widely in such measurements as color, pH, alkalinity, conductivity, calcium,

FIGURE 8

Correlation of Logarithms of Chlorophyll Content
of Seston and Component 2 of the
Principal Components Analysis

Lakes

1. Kintla
2. Marshall
3. Lindbergh
4. Cygnet
5. Clearwater
6. Rainy
7. Alva
8. Bowman
9. Tally
10. Inez
11. Seeley
12. Placid
13. Salmon


FACTOR 2
LOG CHLOROPHYLL
r = -0.686
.5
.3
.1
0
-.1
-.3
-.5
.8
1.0
1.2
1.4
1
2
3
4
5
8
6
12
11
9
13
7
10

magnesium, lake depth, and the Ryder index, indicating that these parameters are not what is affecting the distribution of those insect species which these lakes have in common.

Salmon, Alva, and Inez also fall out together in the graph of Components 1, 2, and 3. These three lakes are close geographically and tend to have a number of factors in common. The current speed in the outlet stream is slower, and the streams have substrates of smaller particles. The maximum depth in the lakes is similar and they are close in elevation. They are warmer lakes and are in the more productive lake category. They also have similar values for pH, conductivity, alkalinity, magnesium, and the Ryder index.

Seeley and Tally also plot out close together in the graph of components from the principal components analysis. They differ in pH, conductivity, alkalinity, calcium, and magnesium. However, due to the greater depth of Tally, their Ryder indices are similar. They are two of the lower elevation lakes with warmer temperatures. Both are among the most highly colored lakes, and their productivity values are close. The streams are similar in current speed, substrate, and amount of periphyton.

Placid and Rainy plot out closest to Seeley and Tally Lakes. They tend to be intermediate in species composition and to have species which are found in both the less and more productive lake categories.

From comparisons of these three lake groupings, it appears that factors such as productivity and temperature are more important than the chemical composition of the water in determining what species will be found in the streams.

Based on feeding habits found in the literature (Muttkowski and Smith, 1929; Ross, 1944; Pennak, 1953; Chapman and Demory, 1963; Gilpin and Brusven, 1970; Thorup, 1970; Mecom, 1972; Cummins, 1973, 1974, 1975; Hall, R. J., et al., 1975) all of the species in this study were placed in the categories of filter feeders, detritivores, detritivore-periphyton grazers, periphyton grazers, and predators.

Some species are not well studied with regard to food preferences, and many forms change diets according to available food (Ross, 1944; Chapman and Demory, 1963), so it is not possible to list them with certainty without examination of the organisms' gut contents. Although the data on the food habits of these species is not extensive enough to determine the validity of placing some of them in their respective categories, some rough ideas on food web structure in the less productive versus the more productive lakes can be ascertained.

Kintla, Marshall, Lindbergh, Cygnet, Clearwater, and Bowman Lakes were included in the less productive category on the basis of their separation from the other lakes in the graph of Components 1, 2, and 3 from the principal components analysis.

The number of occurrences of each species in the lakes in each trophic category were tabulated (Table 13). The total number of species in the productive lakes was greater than would be expected if the species were distributed equally between the two categories. The filter feeders and predators had observed distributions very close to that which would be expected if they occurred equally in both categories.

The greatest differential is in the periphyton-grazer category, where the productive lakes have more than the expected number of occurrences. Combining the periphyton-grazer, detritivore, and detritivore-periphyton grazer categories would remove most of the uncertainty involved in the placement of species within categories. When this is done, there are more species in the productive lake category than would be expected. This is correlated with the greater amounts of organic deposits and periphyton observed in the more productive lakes (Tables 2 and 3, pages 26 and 27.

No correlation was found between the number of species of filter feeders and the productivity of the lake (r = .032

TABLE 13

OCCURRENCES

FILTER FEEDERS

Species	Less Productive	More Productive
Hydropsyche cockerelli	2	6
H. occidentalis	3	6
H. sp. 1	1	0
Cheumatopsyche gracilis	5	6
Simulium tuberosum	4	0
S. vittatum	5	5
S. articum	3	0
S. venustum	3	2
S. griseum	1	1
Brachycentrus sp.	1	1
	O = 28 E = 25.4	O = 27 E = 29.6

PREDATORS

Species	Less Productive	More Productive
Acroneuria pacifica	6	5
A. californica	3	6
Claassenia sabulosa	1	0
Alloperla sp.	3	1
Ophiogomphus morrisoni	0	7
Argia vivida	0	5
Perithemis sp.	1	0
Rhyacophila acropedes	4	1
R. angelita	2	0
	O = 20 E = 20.8	O = 25 E = 24.2

TABLE 13 (continued)

LARGELY DETRITIVORES

Species	Less Productive	More Productive
Ephemera	0	1
Pteronarcys californica	1	0
Amphinemoura banksi	6	3
Hexatoma sp.	5	7
Dicranota sp.	3	1
Wiedemannia sp.	1	0
Pericoma sp.	1	0
Antocha sp.	0	3
Lepidostoma sp.	5	5
	O = 22	O = 20
	E = 19.4	E = 22.6

LARGELY PERIPHYTON

Species	Less Productive	More Productive
Helicopsyche sp.	0	4
Neophylax sp.	1	1
Agapetus sp.	0	1
Hydroptila sp.	5	1
Leucotrichia sp.	0	2
Zaitzevia parvula	4	6
Optioservus sp.	5	7
Microcylloepus pusillus	0	2
Cleptelmis ornata	1	0
Lara sp.	1	0
Heterlimnius sp.	0	2
Brychius sp.	0	3
Donacia sp.	0	1
Tricorythodes	1	7
Paragyractis sp.	0	5
	O = 18	O = 42
	E = 27.7	E = 32.3

TABLE 13 (continued)

DETRITIVORES - PERIPHYTON

Species	Less Productive	More Productive
Caenis simulans	0	3
Paraleptophlebia debilis	2	1
P. bicornuta	1	4
P. heteronea	4	1
Heptagenia criddlei	4	5
Ephemerella margarita	5	7
E. tibialis	3	1
E. inermis	1	0
E. aurivilli	2	0
E. flavilinea	1	1
Baetis propinquus	3	4
B. intermedius	2	1
B. tricaudatus	4	6
B. parvus	4	5
B. sp. A	0	6
B. insignificans	0	1
Epeorus albertae	1	0
Pseudocleon sp. A	0	3
P. sp. B	0	1
Athripsodes sp.	5	6
Oecetis sp.	0	2
Limnephilus sp.	1	2
Ecclisomyia sp.	1	0
Dicosmoecus sp.	0	5
Platycentropus sp.	0	4
	O = 44 E = 52.15	O = 69 E = 60.85

PERIPHYTON, DETRITUS, DETRITUS-PERIPHYTON COMBINED

Less Productive	More Productive
O = 84 E = 99.25	O = 131 E = 115.75

TOTAL

Less Productive	More Productive
O = 131 E = 149.6	O = 184 E = 165.4

for the logarithms of the number of filter feeders at outlet sites and of the productivity index, 12 d.f., $p < .98$). Ten species of filter feeding insects were identified at the outlet sites (four hydropsychids, five Simulium species, plus Brachycentrus sp.). The number of filter feeders per outlet site varied from two species at Alva to seven species at Cygnet and Placid outlets.

Generally, there were more blackfly species in the less productive lakes and more hydropsychid species in the more productive lakes. The standing crop of hydropsychids was much greater in the productive lakes, but no quantitative data were obtained.

Hydropsychids were in the abundant category in Rainy, Inez, Seeley, Placid, and Salmon outlets (Appendix, Table A). Hydropsyche cockerelli was abundant in Cygnet Lake and Cheumatopsyche gracilis was abundant in Marshall Lake, both of which are in the less productive lake category. Seeley and Salmon Lakes still had large numbers of hydropsychids at the downstream sites.

Blackflies were abundant in Kintla, Bowman, Cygnet, and Clearwater outlets at the time the collection was made. Oswood (1976) also found them in abundance in Placid outlet at certain times of the year. They may have been less abundant in the warmer outlets due to the high temperatures at the time the study was done.

No taxonomic work was done on other invertebrate filter feeders. Sponges occurred at all outlet sites, with the exception of Cygnet outlet. Pisidium, which is also a filter feeder, occurred at all outlet sites but Kintla and Clearwater. Tally Lake outlet had extremely large numbers of Pisidium in the outlet stream.

Table 14 gives the percentage composition of insect species by order at each site. The mean values for each order are very similar at the outlet and downstream sites. The Plecoptera and Diptera constitute a higher percentage of the total species in the less productive lakes than in the productive lakes. Odonata, Coleoptera, and Lepidoptera constitute a greater percentage of the total species in the productive lakes. Trichoptera and Ephemeroptera are relatively constant in the two categories (slightly higher percentages in the productive lakes).

The Trichoptera and Ephemeroptera account for the greatest number of species, with 28.1% and 30.2% respectively. Diptera with 14.5%, Plecoptera with 11.7%, Coleoptera with 10%, Odonata with 3.8%, and Lepidoptera with 1.5% of the total account for the remainder of the species. Hydropsychidae and Simuliidae account for 9.2% and 8.1%, respectively.

TABLE 14

SPECIES COMPOSITION

(given in %)

	PLECOPTERA	TRICHOPTERA	(HYDROPSYCHIDAE)	ODONATA	DIPTERA	(SIMULIIDAE)	EPHEMEROPTERA	LEPIDOPTERA	COLEOPTERA
OUTLET									
Kintla	.28	.17	(.06)	0	.22	(.17)	.33	0	0
Marshall	.13	.30	(.09)	.04	.13	(0)	.26	0	.13
Lindbergh	.10	.38	(.14)	0	.19	(.10)	.29	0	.05
Cygnet	.15	.26	(.11)	0	.19	(.15)	.33	0	.07
Clearwater	.13	.29	(.04)	0	.25	(.17)	.25	0	.08
Rainy	.09	.26	(.13)	.04	.13	(.09)	.30	.04	.13
Alva	.09	.36	(.09)	.09	.05	(0)	.27	0	.14
Bowman	.16	.21	(.05)	0	.21	(.16)	.26	0	.16
Tally	.09	.23	(.09)	.09	.09	(.05)	.32	.05	.14
Inez	.04	.36	(.12)	.08	.04	(0)	.36	0	.12
Seeley	.09	.26	(.13)	.04	.13	(.04)	.30	.04	.13
Placid	.10	.28	(.08)	.05	.15	(.08)	.30	.03	.10
Salmon	.07	.29	(.07)	.07	.11	(.04)	.36	.04	.07
$\bar{x}$ =	.117	.281	(.092)	.038	.145	(.081)	.302	.015	.102
DOWNSTREAM									
Kintla	.33	.07	(0)	0	.20	(.13)	.33	0	.07
Marshall	.13	.32	(.10)	0	.10	(.03)	.29	0	.16
Lindbergh	.16	.28	(.08)	0	.16	(.04)	.28	0	.12
Cygnet	.15	.30	(.15)	0	.07	(0)	.33	0	.15
Clearwater	.14	.29	(.10)	0	.14	(.10)	.24	0	.19
Rainy	.13	.17	(.09)	.09	.09	(.04)	.35	.04	.13
Alva	.15	.30	(.07)	.07	.07	(.04)	.26	.04	.11
Bowman	.20	.20	(.07)	0	.27	(.20)	.27	0	.07
Tally	.10	.38	(.07)	.07	.17	(.07)	.24	.03	.10
Inez	.05	.36	(.14)	.09	.09	(.05)	.32	0	.09
Seeley	.07	.28	(.10)	.07	.14	(.07)	.34	.03	.07
Placid	.13	.26	(.10)	.06	.16	(.03)	.26	.03	.10
Salmon	.13	.26	(.09)	.09	.09	(0)	.39	0	.09
$\bar{x}$ =	.144	.259	(.089)	.042	.135	(.062)	.300	.013	.112

CHAPTER 6

DISCUSSION

The significant positive correlation between chlorophyll, which was used as a measure of the food supply and the number of species of insects at the outlet site ($r = 0.606$, 12 d.f., $p < .05$) requires a digression into the topic of species diversity.

Diversity is a function of the number of species present (species richness) and the evenness with which the individuals are distributed among these species (species equitability). Only species richness was measured in this study and the following discussion of diversity is not meant to synonymize species richness with species diversity. Although species diversity and species richness are often positively correlated, a positive correlation is not necessary (Hurlbert, 1971). Ulfstrand (1975) found that the diversity index of the stonefly communities was closely correlated with the species richness component. However, in the mayfly community, species diversity was correlated with equitability.

Diversity is a complex and much discussed subject. The relationship between production and diversity has not been well documented, and the evidence for relationships is conflicting. There is theoretical reason to expect areas of uniformly increased production to support more species. Growth in resources and the consequent reduction in utilization by the existing species, will allow an increased number of species (MacArthur, 1972). In extreme cases production clearly can affect the number of species. In the arctic, productivity may limit diversity (Hutchinson, 1959).

Productivity has, however, often been negatively correlated with diversity. In epipelagic waters with relatively great quantities of nutrient chemicals, production of the plankton is high but trends toward few species of organisms; in epipelagic waters with relatively small quantities of nutrients, plankton quantities are small but there are many species (MacArthur, 1972).

Yount (1956) studied the effect of productivity on species variety by counts of diatoms on glass slides at a high production and a low production station. Diatom productivity was measured by the rate of chlorophyll accumulation. He found that species variety was decreased by conditions of high productivity and attributed it to competition being greater where productivity is high. In low production areas the density remains low and the frequency of encounter also remains low, permitting relatively more species to coexist.

To some extent this may be operating in the outlet communities in this study. In outlets with a low biomass of insects (subjectively estimated by mass of insects per kicknet sample), the diversity was disproportionately high (e.g. Lindbergh, Marshall, Clearwater).

Margalef (1961) also pointed out that increases in nutrient supply may bring about a decrease in diversity. He suggests that initially diversity may increase with increases in nutrients, because species increase in numbers to take full advantage of the increased supporting capacity of the environment. Since various species differ in their capacity for increase in numbers, some multiply more rapidly than others and manifest dominance, thereby decreasing diversity. Changes in diversity taking place with an increase in nutrients, therefore, may be the result of some form of interspecific competition.

Moss (1973) found that diversity of phytoplankton decreased with increased fertility of the water on a seasonal basis, and also that diversity was greater in an oligotrophic than in two eutrophic lakes (Michigan and England). He explained the high diversity on the basis of greater overlap of populations of different species in oligotrophic lakes. Due to the slower growth rates and longer times necessary for attainment of peak populations in oligotrophic lakes, greater overlap between successive species populations occur, giving higher diversity values.

A number of cases have been documented where organic pollution reduces the number of species present while increasing productivity (Wilhm and Dorris, 1968; Warren, 1971; Cavins and Lanza, 1972). Yount (1956) states that the effects of pollution are to eliminate sensitive species and increase competition. MacArthur (1972) attributes the decrease in species diversity to the reduction in the diversity of the resources when one or a few nutrients become excessively common. Organisms using mainly the abundant nutrients will become very abundant.

One reason why a few species may not dominate in more productive lake outlet situations is that the filter feeders (which is the trophic group responding directly to increased amounts of phytoplankton coming out of the lake) have narrow habitat requirements. A number of workers have detailed the conditions of substrate and current speed required by the Simuliidae and Hydropsychidae because of their method of feeding.

Hydropsychids prefer larger substrate particles in shallow, fast-flowing water (Sprules, 1947; Edington, 1968; Philipson, 1969; Williams and Hynes, 1973; Gordon and Wallace, 1975; Wallace, 1975).

Blackflies are found in faster currents on bedrock, large rocks, or plants, generally within 10 centimeters of the water surface (Zahar, 1951; Peterson, 1956; Egglishaw and Morgan, 1965; Maitland and Penny, 1967; Ulfstrand, 1967; Maciolek and Tunzi, 1968).

The blackflies and caddisflies may indeed be the only species present where conditions are most favorable for them. But because streams are not uniform habitats, there is space for other organisms. Also, the quantities of organic matter passing through and cycling within stream ecosystems are very large and can sustain more varied populations of invertebrates than just the abundant filter feeders.

The present study was done during a time (late July and early August) when the hydropsychid filter feeders would occur in high densities. One would expect that if the diversity of other invertebrates were to be lower because of the numbers of filter feeders, that this would have been the case when this study was done.

In many cases in the literature where diversity decreased with increases in production, the habitat was more homogeneous (e.g. the open water habitats of plankton communities and the more uniform substrate conditions below pollution outflows). (See page 78 for a discussion of the effect of geometric complexity of the substrate on diversity.)

In their experimental ponds, Hall, Cooper, and Werner (1970) dealt with the complex of interrelated factors affecting aquatic environments under controlled conditions. They found that when the physical structure of the environment became more varied (e.g. by the growth of macrophytes), production and diversity of insects increased. Nutrients generally increased production of the zooplankton, but had little effect on number of species or equitability. The benthos increased production in response to nutrient additions the first year, but this was not born out in the two succeeding years. The bottom fauna initially showed a decrease in diversity at higher nitrogen and phosphorus levels. When subjected to a steady rate of nutrient input, production and biomass decreased while species numbers increased.

Watt (1973) considered the idea that diversity is proportional to the biomass/productivity ratio to be a fundamental principle of environmental science. Biomass/productivity increases in a stable environment. If productivity is held constant, diversity will increase with biomass. Carlander (1955) found a positive correlation between the standing crop of fish in different reservoirs and the number of species present. This would be expected if the productivity is fixed by the incoming energy from the sun.

Slobodkin and Sanders (1969) suggested that if high productivity is associated with high predictability, the result will be greater species diversity (see also Connell and Orias, 1964). They placed low diversity environments into the categories of new environments, severe environments, and unpredictable environments. Sanders (1969) found that in benthic marine communities, the greatest species diversity (number of species per sample of a fixed size) was found in habitats which had been stable over long periods of time.

Lake outlets can probably be considered highly predictable environments. The supply of plankton from the lake is predictable (in terms of pattern regularity and predictable seasonal changes of input). Fisher and Likens (1973) and Odum (1969) suggested that allochthonous matter lends stability to the stream ecosystem.

Also, the lake has a moderating effect on the temperature regime of the outlet. Lakes warm up more slowly, become warmer, and remain warm longer than streams (Ulfstrand, 1968).

Armitage, P. D. (1976) stated that stability increased in the River Tees after the building of the dam for the Cow Green Reservoir, and that algal growth increased. At times of high runoff the coarser particles settle in the lake and consequently do not have a marked scouring effect on the stream bottom.

Outlet communities are characterized by large amounts of periphyton growth. Some of the periphyton may be removed during periods of heavy runoff (personal observation on Salmon Lake), but the presence of large amounts of periphyton is an indication that scouring is not a major factor. Reduced turbidity after particles settle in the lake also enhances periphyton growth.

A few of the outlets in the study might be considered more severe environments. Temperature may limit the number of species in the coldest outlets. Some species are excluded from communities where temperature has low annual and diel amplitude (Ide, 1935). Since temperatures are warmer in outlet situations, this factor is probably not a significant one. It may, however, be operative in Kintla and Bowman Lakes, which drain mountain areas which have a continuous snow melt throughout the summer months, keeping temperatures lower.

However, temperature would also exert an effect on the productivity of plankton in the lakes, making it difficult to differentiate between the effects of temperature and productivity on the benthos at the outlet.

It may be that the chlorophyll measurement in Bowman Lake was higher than expected, because the "spring" plankton maximum occurred later in this lake due to the slower warming of the epilimnion. Photosynthetic rates may be high in cold mountain lakes, but the length of the growing season is greatly constricted (Wetzel, 1975).

Kintla, Bowman, and Lindbergh Lake outlets still had a heavy runoff at the time the study was made (Cygnet Lake outlet also was a rushing torrent in the center of the stream, but not where the sampling was done). The very fast current may limit the number of species that can occur in these outlets.

A lower temperature and a rapid current, then, may make a few of these outlets more severe environments. Although the effects would be predictable, the severity of the environment would lower species diversity.

Some factors that are known to increase the number of species are geometric complexity of the substrate, multiple predator-prey linkages, and narrow behavioral specializations resulting in spatial and temporal separation of populations. These factors are also involved in determining the number of species at each outlet, and in some cases may obscure differences based on productivity.

The diversity of the insect fauna in any area is related to the number of different microhabitats present (Sprules, 1947). Rubble and gravel offer more utilizable surface area than sand and bedrock.

The substrate in Cygnet outlet where the samples were taken was varied and of the cobblestone-rubble type, whereas Lindbergh outlet had a substrate consisting mainly of bedrock and large boulders due to the fast current. This probably accounts for the greater number of species at Cygnet than at Lindbergh outlet. These two lakes had identical chemical measurements and were close in amounts of chlorophyll and particulate carbon, so the productivity effect would be expected to produce similar numbers of species in the two lakes.

Diversity may also be related to the number of predators in the system and their efficiency in preventing single species from monopolizing some important limiting requisite (Paine, 1966). Leigh (1965) showed mathmatically (using Volterra's equations) that the stability of a community is maximized by maximizing the number of links in the food web. He theorized that for a community with the most stable food web structure, stability would increase with a decrease in productivity, with an increase in biomass, or with an increase in the number of species.

No study was made of the food webs at the various outlets. It does appear, however, that there are no great differences in the number of insect predator species at the various outlets. Other predators (e.g. fish) were not studied. It may be that the predator influence is held relatively constant, and that the changes in diversity can then be related to differences in food supply at the different outlets.

Ryder, et al., (1974) suggested that the morphoedaphic index might be used not only for estimating biomass or production of fish communities, but also of plankton and bottom fauna in the lake. In this study Ryder's index was not well correlated with estimates of plankton production determined by measuring the amount of chlorophyll in filtered residues. The use of maximum depth rather than mean depth may have had some effect on the determination of the

MEI, but in lakes where mean depth could be calculated, maximum depth was well correlated with mean depth.

The shallowest lakes (Cygnet, 3.05 meters, and Rainy, 9.15 meters) may be too small to be used in the MEI. Initially it was suggested that lakes be greater than 260 hectares in surface area and be located at altitudes less than 600 meters. Criteria for its use were subsequently relaxed, but the lakes in this study may be too high in altitude to fit well (all the lakes are at altitudes well above 600 meters).

Because of the proximity of the inlet and outlet in Tally Lake, the great depth of this lake may not exert its effect on reducing productivity. The chlorophyll measurements show the lake to be more productive than the MEI value predicts.

Indices such as the morphoedaphic index are based on large numbers of lakes. One might not expect to find significant correlations when only 13 lakes are used in the study.

Perhaps the single most important reason why the MEI does not work well for these lakes is that six of the lakes are in the Clearwater chain which does not conform to the usual situation (Hynes, 1969) of productivity increasing with increases in dissolved ions. Conductivity and alkalinity decrease as you go downstream, while productivity increases. Because the conductivity and alkalinity show an inverse correlation with productivity for these six lakes, it diminishes the usefulness of these correlates in the index. Probably the Ryder index cannot be used on chains of lakes.

Correlations between dissolved ions and production are often not precise, and some workers have not been able to show a significant correlation. McConnell and Sigler (1959) did not find good correlations between total dissolved solids or the individual ions measured and productivity (as measured by average chlorophyll quantity on concrete "rocks" in the Logan River, Utah.

The use of chlorophyll measurements as a means of estimating biomass and production is open to criticism (Ryther and Yentsch, 1957; Margalef, 1968). The chlorophyll concentrations in algal cells vary diurnally, with the type of algae involved, with environmental conditions, and with the physiological condition of the cell. Then too, there are errors in the measurement of chlorophyll, particularly at their lower limits of detectability. In the present study chlorophyll amounts were so low that it was necessary to filter five liters of water to get detectable readings.

There are errors inherent in any method of sampling aquatic insects. For example, it is difficult to remove simuliid larvae with a kick net. This fact, together with their patchy distributions might mean that they were not adequately sampled.

The two and one half week period over which the field work was done may have been too long to adequately compare the chemical conditions and insect fauna at the various outlets. Rains which occurred within the time period could have diluted the water and changed chemical conditions. The larger amount of particulate carbon in Tally Lake samples as compared with chlorophyll values may have been related to the fact that it was raining at the time the sample was taken. However, Ryder (1964) determined that a single surface water sample taken towards the end of July or in the first week of August closely approximated the mean TDS value for the entire year. (This was dependent on negligible wind and rainfall for about one week prior to the time the sample was taken.)

Generally chemical conditions could be expected to be stable in late July and early August when the study was done. However, the lakes draining areas of higher altitude were still receiving greater amounts of runoff.

The question of whether the outlets are comparable is perhaps of more importance as it involves the composition of the benthos. Two and a half weeks is a long enough time for species which would have been there at the beginning of the study to have emerged. Of greater import is the fact that species emerge later at higher altitudes (Elliott and Minshall, 1968).

Many of the species were in early instar stages, and in the higher altitude streams some species may have been too small to be taken by the collection methods used. Conversely, some of the species which were about to emerge in the higher altitude streams may have already done so in the streams at lower altitudes. The altitudinal differences in this study were not too great (1021 m to 1460 m), but perhaps were great enough to be of some significance, particularly since there were more substantial differences in the altitude of the drainage areas involved (which would affect stream temperatures).

Trophic characteristics of lakes are changing continuously and chlorophyll measurements could change substantially with time as a reflection of this. A bloom in one lake could radically alter the ranking of the lakes. This may have occurred in Bowman Lake, since the biotic indices do not indicate that it is as productive as the chlorophyll and particulate carbon measurements.

No taxonomic work was done on other invertebrate filter feeders (sponges, arthropods, molluscs) or on the species of Chironomidae which filter feed. Some of those groups were very abundant at certain of the outlets, and information on these groups would have given a more complete picture of the trophic situation at outlets.

The history of the streams in the study was not taken into account. Knowledge of events such as when a stream dried up might have some bearing on the interpretation of species composition. Furthermore, occasional limiting conditions may have a much greater effect upon the biota than do the usual conditions.

The ordination of biological species on a lake by lake basis was used in this study to indicate which lakes are similar in the species composition of benthos in the outlet stream. It also gives some idea of the patterns of interaction between physical and biological phenomena. In aquatic situations there is no simple cause and effect relationship between physical and chemical phenomena, as primarily causal, and biotic phenomena, as primarily effectual. Physical, chemical, and biotic factors interact in a relationship in which each factor is, to some degree, mutually determined by the others.

The result of this mutually determined complex of factors can perhaps best be viewed by looking at the species composition of the benthos. Benthic communities are more stable and more diverse than planktonic ones (Margalef, 1969). Therefore, some of the problems encountered in using planktonic species as indicator species in a comparative study might be circumvented. Taxonomic problems are still encountered, however, and the taxonomy of benthic insects has been little studied in the area where this research was done.

Diversity of benthic invertebrates may be a useful index. It integrates changes which occur over a period of time, and thus requires fewer samples for a given time period. Since communities with a large number of species may have a high stability, an index based on diversity may possibly be used to monitor changes in stability, such as those due to cultural eutrophication (Hooper, 1969).

CHAPTER 7

CONCLUSIONS

It was found that productivity indices based on the amounts of dissolved ions in the lake effluent water were not good predictors of the number of species or of the faunal composition of benthic insects in the outlet streams. Direct measures of productivity, such as chlorophyll and particulate carbon measurements made on lake effluent water, were better predictors.

The number of species of insects was greater in the outlet streams of the more productive lakes. This is correlated with the greater abundance of food (lacustrine plankton) in the outlet streams of the more productive lakes. No differences were found in the number of species of filter-feeding insects in the outlets of the less productive versus the more productive lakes.

Differences were also found in the faunal composition of the less productive as compared with the more productive lakes.

In the more oligotrophic lakes the faunal composition had changed more between the outlet and downstream sites than it had in the more productive lakes. This may indicate that in the less productive lakes the limnoplankton was not reaching the downstream sites in great enough amounts to maintain the type of fauna which is dependent upon it.

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APPENDIX

TABLE A

LIST OF SPECIES

Rare (R), Occasional (O), Common (C), Abundant (A)

	Kintla	Marshall	Lindbergh	Cygnet	Clearwater	Rainy	Alva	Bowman	Tally	Inez	Seeley	Placid	Salmon
PLECOPTERA													
Perlidae													
Acroneuria pacifica	C	C	C	C	C	.	R	C	C	.	O	C	O
downstream	C	C	C	C	C	.	O	C	C	.	O	C	O
A. californica	R	.	.	C	R	O	R	.	.	R	R	C	R
downstream	O	C	O	C	C	C	C	.	.	O	O	C	R
Claassenia sabulosa	.	.	.	O	.	.	.	.	.	.	.	.	.
downstream	R	.	.	O	.	.	.	.	.	.	.	.	.
Nemouridae													
Amphinemoura banksi	C	C	C	C	C	C	.	C	R	.	.	O	.
downstream	C	O	O	O	C	O	R	C	C	.	.	.	.
Chloroperlidae													
Alloperla sp.	O	O	.	.	.	.	.	R	.	.	.	R	.
downstream	R	O	O	.	.	O	O	O	R	.	.	O	.
Pteronarcidae													
Pteronarcys	R	.	.	.	.	.	.	.	.	.	.	.	.
californica	.	.	.	.	.	.	.	.	.	.	.	O	.
TRICHOPTERA													
Rhyacophila angelita	R	.	.	.	R	.	.	.	.	.	.	.	.
downstream	.	R	O	O	R	.	.	.	.	.	.	.	.
R. acropedes	.	R	O	R	O	.	.	.	.	.	.	R	.
downstream	.	O	O	O	O	.	.	.	.	.	.	.	.
Hydroptilidae													
Hydroptila sp.	R	C	C	O	.	.	.	C	.	.	R	.	.
downstream	R	O	C	C	.	.	.	R	C	.	O	.	.
Leucotrichia sp.	.	.	.	.	.	.	.	.	.	.	R	C	.
downstream	.	.	R	.	.	.	.	.	.	.	O	R	.

TABLE A (continued)

	Kintla	Marshall	Lindbergh	Cygnet	Clearwater	Rainy	Alva	Bowman	Tally	Inez	Seeley	Placid	Salmon
TRICHOPTERA													
Lepidostomatidae													
Lepidostoma sp.	.	O	O	R	O	O	C	R	C	.	.	R	C
downstream	.	C	O	O	O	O	C	.	C	C	.	.	O
Leptoceridae													
Athripsodes sp.	.	C	O	O	R	C	C	O	C	C	O	.	C
downstream	.	.	.	.	.	O	O	R	O	O	O	R	O
Oecetis sp.	.	.	.	.	.	.	O	.	.	C	.	.	.
downstream	.	.	.	.	.	.	O	.	.	C	O	.	.
Helicopsychidae													
Helicopsyche sp.	.	.	.	.	.	.	O	.	O	O	.	.	O
downstream	.	.	.	.	.	.	O	.	O	O	.	.	O
Brachycentridae													
Brachycentrus sp.	.	R	.	.	.	.	.	.	.	.	.	O	.
downstream	.	C	.	.	.	.	.	.	.	.	.	C	.
Limnephilidae													
Limnephilus sp.	.	.	.	.	R	.	.	.	.	R	.	.	R
downstream	.	.	.	.	R	.	.	.	.	.	.	.	.
Neophylax sp.	.	.	.	.	R	.	.	.	.	.	.	R	.
downstream	.	.	.	.	O	.	.	.	.	.	.	O	.
Ecclisomyia sp.	.	.	R	.	.	.	.	.	.	.	.	.	.
downstream	.	.	.	.	.	.	.	.	.	.	.	.	.
Dicosmoecus sp.	.	.	.	.	.	C	R	.	.	O	.	R	R
downstream	.	R	.	.	.	.	C	.	R	.	.	R	R
Platycentropus sp.	.	.	.	.	.	.	O	.	.	O	.	O	R
downstream	.	.	.	.	.	.	C	.	R	C	R	.	.
Glossosomatidae													
Agapetus sp.	.	.	.	.	.	.	.	.	.	.	.	R	.
downstream	.	.	.	.	.	.	.	.	.	.	.	.	.

TABLE A (continued)

	Kintla	Marshall	Lindbergh	Cygnet	Clearwater	Rainy	Alva	Bowman	Tally	Inez	Seeley	Placid	Salmon
TRICHOPTERA													
Philopotamidae													
Wormaldia sp.	.	.	.	.	.	.	.	.	.	.	.	.	.
downstream	.	C	.	.	.	.	.	.	.	.	.	.	.
Hydropsychidae													
Hydropsyche sp. 1	.	.	.	.	.	.	.	O	.	.	.	.	.
downstream	.	.	.	.	.	.	.	O	.	.	.	.	.
Hydropsyche oslari	.	.	.	.	.	.	.	.	.	.	.	.	.
downstream	.	O	.	R	O	.	.	.	.	.	.	.	.
H. cockerelli	.	.	C	A	.	A	C	.	.	A	A	A	C
downstream	.	.	C	C	.	C	C	.	.	O	A	C	C
H. occidentalis	.	C	O	O	.	O	O	.	O	C	R	A	.
downstream	.	C	O	O	.	C	C	.	C	O	O	C	.
Cheumatopsyche	R	A	R	R	C	R	.	.	A	O	C	A	C
gracilis	.	.	.	.	R	.	.	.	C	O	C	O	O
Arctopsyche grandis	.	.	.	.	.	.	.	.	.	.	.	.	.
downstream	.	C	.	C	.	.	.	.	.	.	.	.	.
ODONATA													
Gomphidae													
Ophiogomphus	.	.	.	.	.	C	C	.	C	C	C	C	C
morrisoni	.	.	.	.	.	C	C	.	O	C	O	C	O
Agrionidae													
Argia vivida	.	.	.	.	.	.	C	.	O	C	.	C	C
downstream	.	.	.	.	.	R	C	.	O	C	C	C	R
Libellulidae													
Perithemis sp.	.	O	.	.	.	.	.	.	.	.	.	.	.
downstream	.	.	.	.	.	.	.	.	.	.	.	.	.
DIPTERA													
Tipulidae													
Hexatoma sp.	O	O	O	C	.	C	O	O	O	C	O	C	O
downstream	O	O	O	C	.	C	C	O	R	O	O	C	O

TABLE A (continued)

	Kintla	Marshall	Lindbergh	Cygnet	Clearwater	Rainy	Alva	Bowman	Tally	Inez	Seeley	Placid	Salmon
DIPTERA													
Tipulidae													
Helius sp.	.	.	.	.	.	.	.	.	.	.	.	.	.
downstream	.	.	.	.	.	.	.	.	R	.	.	.	.
Dicranota sp.	.	O	R	.	C	.	.	.	.	.	.	O	.
downstream	.	.	R	.	C	.	.	.	.	.	.	R	.
Antocha sp.	.	.	.	.	.	.	.	.	.	.	R	C	R
downstream	.	R	O	R	.	.	.	.	C	.	R	O	O
Empididae													
Wiedemannia sp.	.	.	.	.	C	.	.	.	.	.	.	.	.
downstream	.	.	.	.	.	.	.	.	.	.	.	R	.
Psychodidae													
Pericoma sp.	.	R	.	.	.	.	.	.	.	.	.	.	.
downstream	.	.	.	.	.	.	.	.	.	.	.	.	.
Simuliidae													
Simulium tuberosum	A	.	O	A	.	.	.	A	.	.	.	.	.
downstream	C	C	O	.	.	.	.	C	.	.	.	.	.
S. vittatum	O	.	R	O	C	A	.	C	O	.	O	C	C
downstream	.	.	.	.	R	C	O	C	R	O	C	O	.
S. arcticum	O	.	.	R	O	.	.	.	.	.	.	.	.
downstream	O	.	.	.	.	.	.	.	.	.	.	.	.
S. venustum	.	.	.	O	C	O	.	O	.	.	.	O	.
downstream	.	.	.	.	.	.	.	O	O	.	R	.	.
S. griseum	.	.	.	.	A	.	.	.	.	.	.	O	.
downstream	.	.	.	.	O	.	.	.	.	.	.	.	.
EPHEMEROPTERA													
Leptophlebiidae													
Paraleptophlebia	O	.	.	.	R	.	.	.	.	.	.	R	.
debilis	R	.	.	.	R	O	.	.	.	.	.	.	.

TABLE A (continued)

	Kintla	Marshall	Lindbergh	Cygnet	Clearwater	Rainy	Alva	Bowman	Tally	Inez	Seeley	Placid	Salmon
EPHEMEROPTERA													
Leptophlebiidae													
Paraleptophlebia	.	.	.	.	.	.	.	C	O	.	O	O	C
bicornuta	.	.	.	.	.	.	.	O	O	.	C	.	C
P. heteronea	.	C	O	C	O	.	.	.	.	.	.	O	.
downstream	.	C	R	O	O	R	.	.	.	.	.	.	.
Ephemeridae													
Ephemera sp.	.	.	.	.	.	.	.	.	.	O	.	.	.
downstream	.	.	.	.	.	.	.	.	.	O	.	.	.
Caenidae													
Tricorythodes sp.	.	.	.	O	.	C	C	.	C	C	C	C	A
downstream	.	.	.	R	.	C	O	.	C	C	C	C	C
Caenis simulans	.	.	.	.	.	.	O	.	.	C	.	.	O
downstream	.	.	.	.	.	.	.	.	.	O	.	.	R
Heptageniidae													
Heptagenia criddlei	O	.	.	O	O	O	R	R	.	O	.	O	R
downstream	.	O	C	O	R	C	C	.	.	.	.	.	R
Epeorus albertae	.	.	.	O	.	.	.	.	.	.	.	.	.
downstream	.	C	O	C	.	.	O	.	O	.	R	.	.
Baetidae													
Pseudocleon sp. A	.	.	.	.	.	.	.	.	.	O	.	O	R
downstream	.	.	.	O	.	.	R	.	.	.	.	R	.
Pseudocleon sp. B	.	.	.	.	.	.	.	.	.	.	.	.	C
downstream	.	.	.	.	.	.	.	.	.	O	C	R	O
Baetis propinquus	C	R	.	.	.	R	.	C	.	.	O	C	O
downstream	C	.	.	.	.	.	O	C	.	R	O	C	R
B. intermedius	R	.	.	.	R	.	.	.	.	.	.	C	.
downstream	.	C	.	.	.	O	.	R	.	.	.	.	.
B. tricaudatus	.	C	C	A	O	C	C	.	C	O	O	A	.
downstream	O	C	C	C	C	C	C	.	C	.	R	C	.

TABLE A (continued)

	Kintla	Marshall	Lindbergh	Cygnet	Clearwater	Rainy	Alva	Bowman	Tally	Inez	Seeley	Placid	Salmon
EPHEMEROPTERA													
Baetidae													
B. parvus	.	O	O	C	O	.	.	.	O	O	O	C	R
downstream	.	O	O	O	C	.	.	.	O	.	O	O	R
B. sp. A	.	.	.	.	.	.	O	.	C	C	C	R	C
downstream	.	.	.	.	.	.	R	.	C	C	C	O	C
B. insignificans	.	.	.	.	.	.	.	.	R	.	.	.	.
downstream	.	.	.	.	.	.	.	.	.	.	R	.	.
Ephemerellidae													
Ephemerella doddsi	.	.	.	.	.	.	.	.	.	.	.	.	.
downstream	.	.	.	.	.	.	R	.	.	.	.	.	.
Ephemerella inermis	.	.	.	.	.	.	.	O	.	.	.	.	.
downstream	R	.	.	.	.	.	.	.	.	.	.	.	.
E. margarita	C	C	C	C	.	C	C	C	C	C	O	O	O
downstream	C	O	C	O	.	C	.	C	O	C	C	R	O
E. tibialis	R	.	O	O	.	R	.	.	.	.	.	.	.
downstream	.	.	O	O	.	.	.	.	.	.	.	.	.
E. aurivilli	.	R	R	.	.	.	.	.	.	.	.	.	.
downstream	.	.	.	.	.	.	.	.	.	.	.	.	.
E. flavilinea	.	.	.	R	.	C	.	.	.	.	.	.	.
downstream	.	O	.	.	.	O	.	.	.	.	.	.	.
LEPIDOPTERA													
Pyralidae													
Paragyractis sp.	.	.	.	.	.	R	.	.	O	.	R	C	O
downstream	.	.	.	.	.	R	R	.	R	.	O	C	.
COLEOPTERA													
Elmidae													
Zaitzevia parvula	.	O	.	C	C	C	R	C	O	O	O	C	.
downstream	O	C	O	C	C	O	C	C	O	.	O	C	.

TABLE A (continued)

COLEOPTERA	Kintla	Marshall	Lindbergh	Cygnet	Clearwater	Rainy	Alva	Bowman	Tally	Inez	Seeley	Placid	Salmon
Elmidae													
Optioservus sp.	.	C	C	C	C	C	C	O	O	C	C	C	R
downstream	.	C	C	C	C	C	C	.	.	C	C	C	.
Microcylloepus	.	.	.	.	.	.	.	.	C	.	.	.	O
pusillus	.	.	.	.	.	.	.	.	C	.	.	.	O
Cleptelmis ornata	.	C	.	.	.	.	.	.	.	.	.	.	.
downstream	.	O	O	R	.	.	.	.	.	.	.	.	.
Lara sp.	.	.	.	.	.	.	.	R	.	.	.	.	.
downstream	.	R	.	.	O	.	.	.	.	.	.	.	.
Heterlimnius sp.	.	.	.	.	.	.	.	.	.	.	C	C	.
downstream	.	.	.	.	.	.	.	.	.	.	.	O	.
Stenelmis sp.	.	.	.	.	.	.	.	.	.	.	.	.	.
downstream	.	R	.	C	O	.	.	.	R	.	.	.	R
Haliplidae													
Brychius sp.	.	.	.	.	.	O	C	.	.	O	.	.	.
downstream	.	.	.	.	.	O	O	.	.	R	.	.	.
Chrysomelidae													
Donacia sp.	.	.	.	.	.	.	.	.	.	.	.	R	.
downstream	.	.	.	.	.	.	.	.	.	.	.	.	.