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PRODUCTION OF CRUSTACEAN PLANKTON, BENTHIC MACROINVERTEBRATES
AND FISH IN SIX MOUNTAIN LAKES IN ALBERTA

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled PRODUCTION OF CRUSTACEAN PLANKTON, BENTHIC MACROINVERTEBRATES AND FISH IN SIX MOUNTAIN LAKES IN ALBERTA submitted by DAVID W. MAYHOOD in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

Annual production of crustacean plankton, benthic macroinvertebrates and fish was estimated in six alpine and subalpine lakes in Banff National Park, Alberta, to determine levels of secondary production likely to be encountered in Canadian Rocky Mountain lakes, and to identify which taxonomic groups are most productive. The six lakes chosen for study are representative of many Canadian Rocky Mountain lakes with respect to several important physical, chemical and biological attributes.

For invertebrates, life history and population dynamics data necessary for production calculations were obtained from instar and size-frequency analyses supplemented with data from the literature. Production was calculated by the Pechen-Shushkina method, a modification of Southwood's method for calculating numbers passing through an instar, or the Allen Curve method (crustacean plankton); or was estimated from mean biomass data by using production-to-biomass ratios per generation obtained from a review of the literature (benthic invertebrates). Potential production of trout was calculated from estimates of food production and estimates of the food requirements of model trout populations calculated by using Winberg's "balanced equation".

Total annual production of crustacean plankton ranged from 60 to 1460 mg m⁻³ dry weight (420 to 3240 mg m⁻²). Differences among the lakes were attributable primarily to differences in *Daphnia* production.

Annual production of benthic macroinvertebrates ranged from 5.0 to 26.9 g m⁻² preserved wet weight for nonpredaceous species. Production by predators was 33 to 54% of nonpredator production in the two lowest-elevation lakes, and was near zero in the remaining four lakes. Chironomids comprised most of the benthic macroinvertebrate production (60 to

77%) in four lakes, and were the single most productive taxonomic group in another. Amphipod production was substantial in three lakes, constituting 18 to 73% of total benthic macroinvertebrate production. Differences in benthic macroinvertebrate production among the six lakes were attributable mostly to differences in biomass.

In the two lowest-elevation lakes, crustacean plankton production was more than three times benthic invertebrate production, but in the remaining four lakes production by crustacean plankton was the same as, to less than one-quarter of, benthic macroinvertebrate production. Estimates of crustacean plankton and benthic macroinvertebrate production in most of the study lakes are similar to those published for these groups in other oligotrophic arctic or mountain lakes, and are much lower than published estimates for most mesotrophic or eutrophic lakes. Production of crustacean plankton in one lake could be termed moderately high.

Planktonic crustaceans comprised a volumetrically important part of the diet of some trout 10 g or less in weight, but were unimportant in the diets of most larger trout. Benthic invertebrates, particularly chironomids, amphipods and trichopterans, were the most important foods of trout generally. Allochthonous food was important to trout in only one lake, comprising less than 10% of the ration in the other five lakes.

Potential production of trout ranged from 3.8 to 23.7 kg ha⁻¹ wet weight, but only in one lake was production potential clearly greater than 10 kg ha⁻¹. The estimates of potential trout production in the study lakes are among the lowest reported for Salmonidae in the literature, but are comparable to the estimates published for salmonid faunas in other unproductive lake types, suggesting the calculations in this study are realistic.

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SECTION 1

INTRODUCTION, STUDY AREA AND METHODS

INTRODUCTION

The Rocky Mountains in southern Canada form a band 700 km long and 70 to 110 km wide along the Continental Divide between British Columbia and Alberta. Within this area lie thousands of lakes of a variety of types that reflect the climatically and geologically diverse nature of the surroundings (Northcote and Larkin 1963, Larkin 1974). The region as a whole is important for the recreation and extractive resource industries, both of which are to be greatly expanded in the near future (Parks Canada 1974; Alberta Energy and Natural Resources 1977; Alberta Recreation, Parks and Wildlife 1978). The lakes are one of the most important recreational resources of the region and are likely to be strongly affected by expansion in either type of industry.

The Rocky Mountain lakes are also a valuable research resource. Alpine and subalpine lakes tend to have simpler communities¹ than do lakes at lower elevations (Anderson 1974a), providing opportunities to analyze community and ecosystem² processes that in more complex situations would be nearly incomprehensible. In addition, the remoteness of some mountain lakes has protected them from human manipulation, making them useful benchmarks against which the effects of human activities on other similar lakes can be measured.

¹ Any group of interacting populations (Ricklefs 1973:590)

² A community and its environment in which there is a transfer of energy and matter (Whittaker 1975:2)

Most studies touching on the limnology of Canadian Rocky Mountain lakes have been limnological, floral or faunal surveys over large geographical areas, only a few of the investigations dealing with Rocky Mountain lakes extensively (e.g., Bajkov 1927, 1929; Bere 1929; Neave 1929a and b; Neave and Bajkov 1929; Wallis 1929; Rawson 1942, 1953; Reed 1959; Anderson 1968a, 1971, 1974a; Mudry and Anderson 1977). Some fishery biology and fishery management studies have also been published (Rawson 1940a and b, 1947, 1953; Rawson and Elsey 1950; McHugh 1940, 1941; Solman 1950; Cuerrier 1954; Cuerrier and Schultz 1957; Nelson 1965; Anderson 1975). Studies of lake dynamics have so far been confined to only a few subject areas: physical and chemical limnology (Wilcox 1899; Johnston 1922; Anderson 1968b, 1970a; Brown 1973), benthic fauna development in reservoirs (Nursall 1952; Fillion 1967), plankton community dynamics (Anderson 1967, 1968b, 1970b and c, 1972, 1977; Anderson and Raasveldt 1974; Anderson and Green 1975, 1976), and production. In the latter field a start has been made on the measurement of phytoplankton and planktonic bacteria production (Fabris 1966; Fabris and Hammer 1975; Anderson 1968b, 1974b; Anderson and Dokulil 1977), but only exploratory calculations of invertebrate and fish production have been published (Anderson 1975, 1977).

Production, defined as the total amount of tissue formed during a given period regardless of whether the tissue survives to the end of the period (Ivlev 1945), is part of the process of energy and matter transfer through ecosystems. Energy and matter are stored as tissue in organisms as a result of production. When the tissue is consumer, the contained energy and matter are passed to the consuming organisms. The

consumers use part of the energy and matter to build their own tissue (production), and are in turn consumed by yet other organisms. The greater the production of an organism the more energy and matter are available to its consumers. If the production of the organisms in an ecosystem could be measured and if it was known which organisms consume which, much would be known about how the ecosystem functions.

Because of the relative simplicity of their biological communities mentioned earlier (p.1), Rocky Mountain lakes are good ecosystems in which to study secondary production¹. In comparison to many other types of lakes there are usually few species with which to deal, and the expected long life cycles of animals in high mountain lakes would permit a low sampling frequency to be used. Both conditions would reduce the extensive data analysis usually required in secondary production studies. In addition, a knowledge of secondary production in Rocky Mountain lakes could be directly applied to managing the resource. For example, one of the most important uses of Canadian Rocky Mountain lakes is for sport-fishing. Knowing the potential trout production of the lakes, biologists could decide catch limits, and could help to determine the economic value of the fishery and the restrictions that should be placed on development in various watersheds.

As an initial step toward understanding production in Rocky Mountain lakes, it is the objective of this study to estimate secondary production in some important communities in a variety of lakes in the region. Specifically, the objectives are to estimate -

¹ Used in the broad sense of Waters (1977:93) to mean production of all heterotrophs.

- 1) production of crustacean plankton,
- 2) production of benthic macroinvertebrates, and
- 3) potential production of trout

in six representative Canadian Rocky Mountain lakes.

The crustacean plankton and benthic macroinvertebrate communities were selected for study because they are likely to play an important role in the transfer of energy and matter (Wetzel 1975), there are established procedures for studying them (e.g., Edmondson and Winberg 1971), and because they are probably the most important food sources of trout in the lakes (Mayhood and Anderson 1976). Potential production of trout was estimated because of its value in making resource management decisions. The results of the study were expected to show which taxa are the most important producers in these communities, and what levels of secondary production are to be expected in Canadian Rocky Mountain lakes. This information would indicate which taxa and what types of lakes would most profitably be studied in detail.

THE STUDY AREA

I selected six lakes near Lake Louise in Banff National Park for study because the Lake Louise area offers a variety of mountain lakes that are accessible by road or a short hike. The area is just two hours by car from the University laboratories, and inexpensive accommodation was available on site. The location and some features of the study area are illustrated in Figure 1.

Attributes of the General Study Area

The climate of the Lake Louise area has been summarized by Ander-

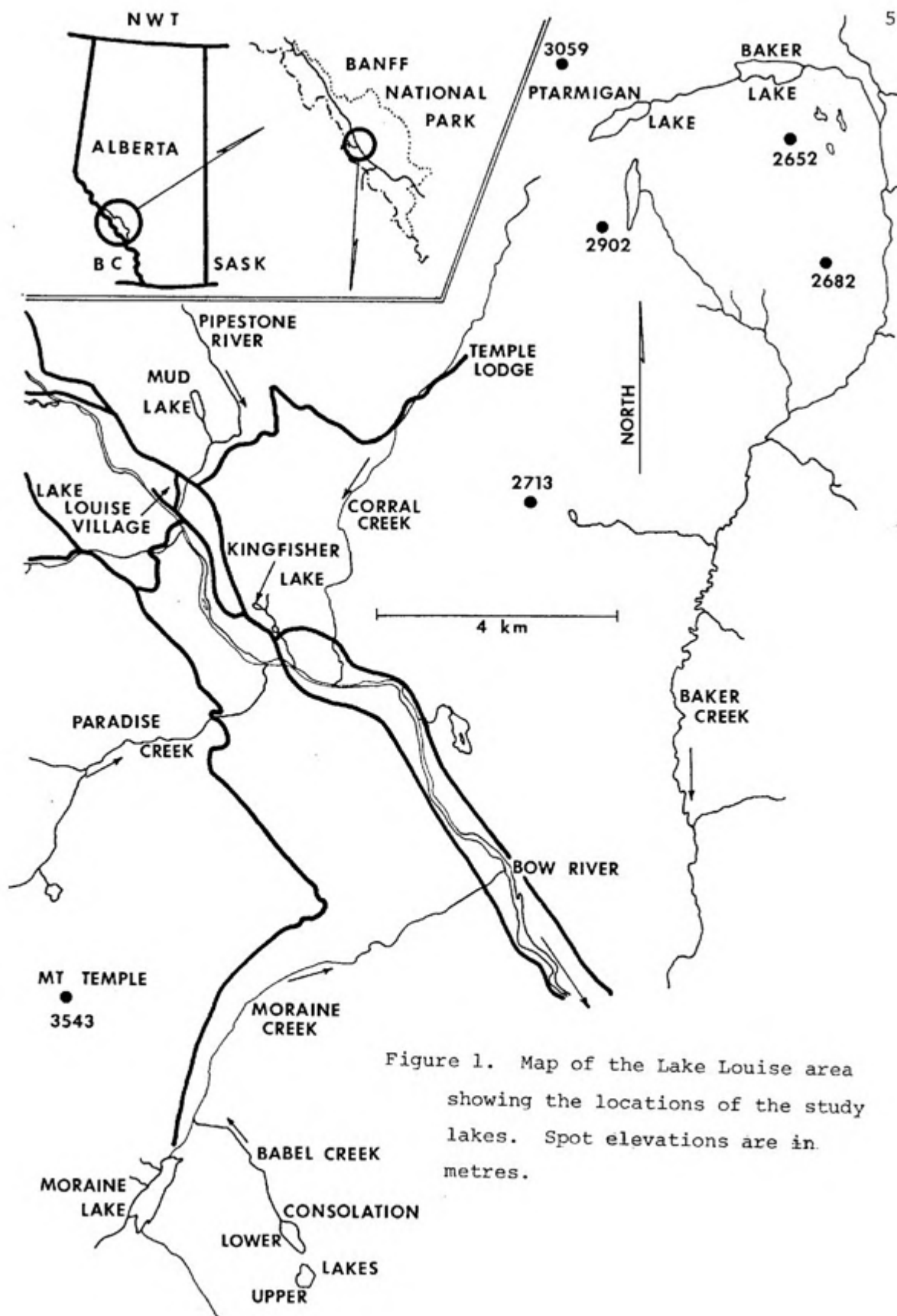


Figure 1. Map of the Lake Louise area showing the locations of the study lakes. Spot elevations are in metres.

son (1970a) and Gardner (1968) from weather records for Lake Louise village. Additional data are included in the report by Janz and Storr (1977) covering all of the contiguous mountain parks. The climate is classified as Dfc in the Köppen system, having long, dry winters and short, cool summers. The mean annual temperature is -0.2°C , with mean daily winter temperatures usually in the -8 to $+4^{\circ}\text{C}$ range, and mean daily summer temperatures usually in the 10 to 20°C range. Temperature extremes are 23 and -53°C (November to April) and 34 and -28°C (May to October). Temperatures well above freezing occur frequently in winter, reflecting the influence of Chinook winds. More than 60% of the mean annual precipitation of 71 cm water equivalent falls as snow. A snow cover of 1 to 3 m persists in the valleys for up to six months of the year.

The geology and geomorphology of the study area have been the subject of several reports and publications, that of Kucera (1974) being a good summary account. Precambrian Miette Group rocks (slate, pebble conglomerate, grits and some quartzite) underlie most of the Lake Louise area, outcropping on the forested slopes of the Bow Valley and between Ptarmigan and Baker Lakes at the Castle Mountain Thrust. Lower Cambrian Gog Group quartzites and some shale form the lower slopes of nearly all the mountains in the area, capping Panorama Ridge on the eastern side of the Consolation Valley. Middle Cambrian rocks of the Mt. Whyte, Cathedral, Stephen and Eldon Formations (mainly limestone and dolomite) form the middle slopes and summits of most peaks in the area. The Precambrian Miette Group rocks overlies much younger Devonian carbonates in the northeast corner of the study area at the Castle Mountain Thrust, points in the study area east of this fault lying on Devonian bedrock. Quater-

nary glacial and fluvial deposits cover the floor of the Bow Valley.

The geomorphology is typical of the Rocky Mountain region, being characterized by numerous high peaks, sheer cliffs, glaciers, cirques, hanging valleys, talus slopes, avalanche slopes, landslides, lateral, terminal and ground moraines, and other glacial and fluvial landforms (see map, Kucera 1974). The valley floor at the village of Lake Louise is about 1500 m above mean sea level. At 3543 m, Mount Temple is the highest point in the region, but many peaks exceed 3050 m, particularly along the Continental Divide.

Soils in the study area are primarily podzols, brunisols and luvisols, the types showing a complex distribution (Walker *et al.* 1976a). At high elevations soils are frequently thin and poorly developed. Topographic maps (NTS 82 N/8 East) and air photos indicate that a substantial proportion of the Lake Louise area, perhaps 25%, is bare rock, glacial ice or névé.

Forest cover in the Lake Louise area corresponds to the subalpine forest region of Rowe (1972), in which two subzones can be distinguished. The lower subalpine consists of dense, continuous closed-forest stands of Engelmann spruce (*Picea engelmannii* Parry), lodgepole pine (*Pinus contorta* Dougl.) and alpine fir [*Abies lasiocarpa* (Hook.) Nutt.]. The upper subalpine is typically a more open forest of Engelmann spruce, alpine fir and, at the highest elevations, alpine larch (*Larix lyallii* Parl.). Treeline in the study area is approximately 1900 m and 2300 m on north and south-facing slopes, respectively (Walker *et al.* 1976a). It is marked by patches of krummholz (stunted, knarled and twisted clumps of trees), the principal species being alpine fir and alpine larch. The treeless zone above timberline is the alpine zone.

Walker *et al.* (1976a,b) mapped landforms, vegetation and soils in a detailed land classification system that covers much, but not all, of the study area. Additional details of the study area features are covered in depth by them.

The Lakes and Their Drainage Basins

I chose Kingfisher, Mud, Moraine, Lower Consolation, Baker and Ptarmigan Lakes for study because they occupy a broad range of altitudes in the alpine and subalpine zones, in which most of the Banff Park lakes lie. All are accessible in summer by road or a short hike of no more than 8 km (Figure 1, Table 1), and all support trout populations, two other factors considered in their selection.

Kingfisher Lake lies in drift on the Bow Valley floor. Steep drift hills enclose it on the north and east except for a gap accommodating the temporary surface outlet, which shows evidence of being blocked at the lakeshore by an old beaver dam. Bedrock outcrops through a thin layer of drift on the south. To the north and west is floating bog and a low, wet area draining into the lake by temporary surface seepage. Miette Group bedrock underlies, and lodgepole pine forest covers the entire drainage basin (Table 2), the exact area of which could not be determined because the lake is fed mainly by groundwater.

Mud Lake lies in a depression in fluted ground moraine covered mainly by open lodgepole forest and underlain by Miette Group bedrock (Table 2). The north shore of the lake is floating bog. A low drift ridge closely parallels the east shore, but the west shore is nearly flat except near the outlet end. The exact area of the drainage basin

Table 1. Geographic coordinates, elevation and vegetation zones of the six lakes selected for study.

<u>Lake</u>	<u>Latitude</u>	<u>Longitude</u>	<u>UTM^a Grid Reference</u>	<u>Elevation (meters)</u>	<u>Vegetation Zone</u>
Kingfisher	51° 24' 40" N	116° 09' 40" W	11U/NG 583956	1539	lower subalpine
Mud	51° 26' 30" N	116° 10' 30" W	11U/NG 573989	1600	lower subalpine
Moraine	51° 19' 30" N	116° 11' 00" W	11U/NG 579858	1887	lower subalpine
Lower Consolation	51° 19' 00" N	116° 09' 00" W	11U/NG 592850	1951	upper subalpine
Baker	51° 29' 30" N	116° 02' 30" W	11U/NH 667047	2210	treeline
Ptarmigan	51° 29' 00" N	116° 04' 30" W	11U/NH 643039	2332	alpine

^a Universal Transverse Mercator.

Table 2. Some attributes of the drainage basins of the six lakes.

<u>Lake</u>	<u>Drainage Basin^a Area (ha)</u>	<u>Bedrock Composition (% total area)^b</u>				<u>Basin Coverage (% total area)^a</u>		
		<u>Miette</u>	<u>Gog</u>	<u>Cambrian Carbonates</u>	<u>Devonian Carbonates</u>	<u>Forest</u>	<u>Rock Low Plants</u>	<u>Glacier</u>
Kingfisher	?	100				100		
Mud	?	100				100		
Moraine	2630		74	26		13	68	19
Lower Consolation	1006	3	78	19		13	66	21
Baker	806	13	41	4	42	10	90	
Ptarmigan	195		85	15			100	

^a From National Topographic Service map 82 N/8 East, Edition 4 ASE, Series A 741, supplemented by aerial photograph and ground observations.

^b From data of Price and Mountjoy (1970), Aitken (1967), Belyea (1964), Baird (1967) and Kucera (1974), replotted on the map in footnote (a), and supplemented by ground observation.

could not be measured because the lake is fed mainly by groundwater.

Moraine Lake is dammed behind landslide debris in the glacial Valley of the Ten Peaks (Kucera 1974). Nine of the Ten Peaks of the Continental Divide form a continuous wall more than 6 km long and 2900 to 3400 m or more above sea level (about 1000 to 1500 m above lake level) along the southern and western boundary of the drainage basin. A shoulder of Mount Babel (3101 m) drops steeply into the west side of the lake. The rock-covered and stagnating Wenkchemna Glacier at the base of the Ten Peaks is the source of the largest tributary to Moraine Lake, Wenkchemna Creek. Active hanging glaciers on Mounts Fay and Bowlen, two of the Ten Peaks, contribute some meltwater, with most of the remaining input to the lake coming from small brooks entering on the west shore. The west shore of Moraine Lake slopes gently at first, then steeply upward to a wide alpine plateau (Larch Valley), Eiffel Peak (3078 m) and Pinnacle Mountain (3067 m), which mark the northern and western drainage basin boundary. Most of the bedrock in the drainage basin is Gog Group quartzite. Nearly 90% of the drainage basin is bare rock, low plants or glacier ice, even though the lake itself is in the lower subalpine zone (Table 2).

The Consolation Lakes lie in a narrow glaciated valley between Mount Babel on the west and Panorama Ridge (2824 m) on the east. Mount Quadra (3173 m) and Bident Mountain (3078 m) close off the head of the valley on the south except for 2469-m Consolation Pass and a narrow 2408-m pass leading to Taylor Lake to the southeast. A rock-covered glacier on the valley floor above the upper lake is fed by a spectacular hanging glacier on Bident and Quadra. The lakes are separated by debris of large angular stone blocks, but are connected through this leaky dam

by subsurface water flow. Large avalanche slopes open onto the lakes from Panorama Ridge, and debris slopes form the entire west shoreline of the lower lake. The lower lake is dammed behind drift: debris blocks derived from Mount Babel litter Babel Creek, the outlet, but do not significantly obstruct flow. As with Moraine Lake, the drainage basin of Lower Consolation Lake is nearly 90% bare rock, low plants and glacier ice. Gog Group quartzite dominates the bedrock in the drainage basin (Table 2).

Baker Lake lies in a wide valley that is treeless except for small patches of alpine fir near the outlet and below a sheltered ridge west of the lake. The valley and lake are flanked by Fossil Mountain (2926 m) on the north and Brachiopod Mountain (2652 m) to the south. The lake is dammed behind upturned Devonian strata at the east end, the outlet stream flowing around the north end of this dam to descend in a series of falls to the main Baker Creek valley. The east-west orientation of Baker Lake and the openness of its valley expose the lake to frequent strong westerly winds.

Ptarmigan Lake lies in the upper part of the Baker Lake drainage basin west of the Castle Mountain Thrust in a wide treeless valley oriented east to west. Ptarmigan Peak (3059 m) and Redoubt Mountain (2902 m) flank the lake on the north and the south, respectively. Ptarmigan is even more exposed to high winds than is Baker: the summit of Boulder Pass at the west end of Ptarmigan is only a few metres above lake level, providing virtually no protection from westerly winds. The lake is dammed behind quartzite Gog Group strata that dominate the drainage basin bedrock (Table 2) and dip gently westward, the outlet

stream spilling over these strata in a series of small waterfalls to Baker Lake about 3 km to the east.

METHODS

Sampling Schedule and Station Selection

A total of 65 visits to the six lakes was made for major sampling and observation in the period mid-May to early October of 1974 and 1975. In addition, numerous other visits were made to obtain data on ice conditions, temperatures, water renewal times and other general information. The study is principally based on 292 zooplankton vertical tows, 256 benthic collections and 14 collections of a total of 410 fish. The distribution of sampling effort among the lakes is summarized in Table 3.

The zooplankton of Kingfisher, Mud and Baker Lakes was sampled at approximately bi-weekly intervals during the 1975 study period; in Lower Consolation, Moraine and Ptarmigan Lakes the sampling frequency was approximately once per month. Benthic samples were collected at approximately monthly intervals during the sampling periods except in Mud Lake, where the 1975 samples were taken in May, June and July only. In Kingfisher Lake, benthic samples were taken only in 1974. Fish collections were made in 1974 in June, July and August in Kingfisher; June and July in Mud; June, August and September in Moraine; and July in Lower Consolation. One additional fish collection was made in October 1975 in Mud Lake.

Fish populations in Baker and Ptarmigan Lakes were not sampled in 1974 or 1975 because both waters had been extensively gillnetted in 1973 (Smiley 1976), and many of the samples and data collected then were available for analysis. I felt that the possible improvement in the

Table 3. Distribution of sampling effort among the six lakes. See also page 13, paragraph 2.^a

<u>Lake</u>	<u>Sampling Period</u>		<u>Number of Zooplankton Vertical Tows^b</u>	<u>Number of Benthic Collections</u>	<u>Number of Fish Collections</u>
	<u>1974</u>	<u>1975</u>			
Kingfisher	May to September	May to October	120	62 ^c	3
Mud	June to September	May to October	80	48	3
Moraine	June to September	July to September	18	36	3
Lower Consolation	July to September	June to September	18	33	1
Baker	July and August	July to September	35	34	2 ^d
Ptarmigan	July and August	July to September	21	35	2 ^d

^a Kingfisher and Mud Lakes were sampled most intensively because they had the longest ice-free seasons and were the warmest lakes. In addition, it was hoped that concentrated sampling in Kingfisher, the most accessible lake, would provide data of high precision for at least one of the lakes.

^b 1975 only.

^c 1974 only.

^d July 1973.

applicability and comparability of the data was likely to be too small to justify removing more fish from these lakes.

Stations for sampling zooplankton and benthos were selected according to the following procedure. In 1974, benthic samples from Baker, Ptarmigan, Lower Consolation and Moraine Lakes were collected on each sampling date from four to seven sites selected in the field to represent all areas of each lake. This survey procedure was used to determine which parts of the lakes could be sampled by Ekman grab (mud mostly) so that random-sampling stations could be established. All parts of Kingfisher and Mud Lakes were known to be suitable for Ekman grab sampling, so a bottom survey was unnecessary for them. Numbered grids were drawn on outline maps of all six lakes, and in all but Moraine Lake the area suitable for Ekman grab sampling was divided into two or three sampling strata. Six to twelve sampling stations in each lake were chosen from a table of random numbers, the number of stations in each stratum being allotted in proportion to the stratum area relative to the total lake area. Figures 2 to 4 illustrate the locations of the sampling sites in each lake.

Field Methods

Soundings of the lakes were made with a battery-powered echo sounder (Fish Lo-K-Tor, Lowrance Electronics Corp., Tulsa, Oklahoma). Readings were taken at regular, timed intervals along several transects across each lake while an assistant rowed at constant speed.

Flow rates in outlet and major inlet streams were measured with a propeller-type flow meter (GM Manufacturing Ltd.) calibrated by the Hydraulic Division, Canada Centre for Inland Waters, Burlington, Ontario.

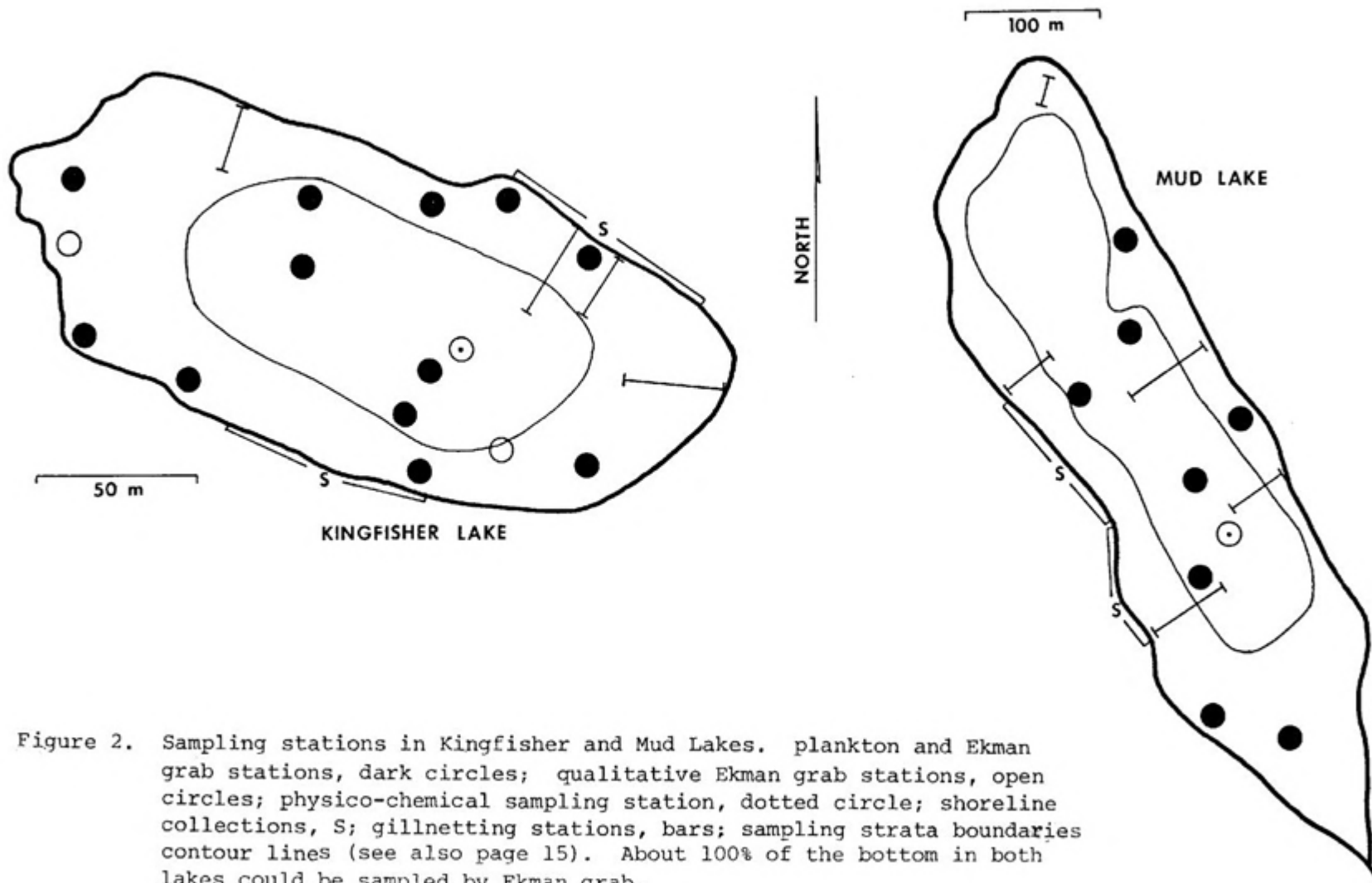


Figure 2. Sampling stations in Kingfisher and Mud Lakes. plankton and Ekman grab stations, dark circles; qualitative Ekman grab stations, open circles; physico-chemical sampling station, dotted circle; shoreline collections, S; gillnetting stations, bars; sampling strata boundaries contour lines (see also page 15). About 100% of the bottom in both lakes could be sampled by Ekman grab.

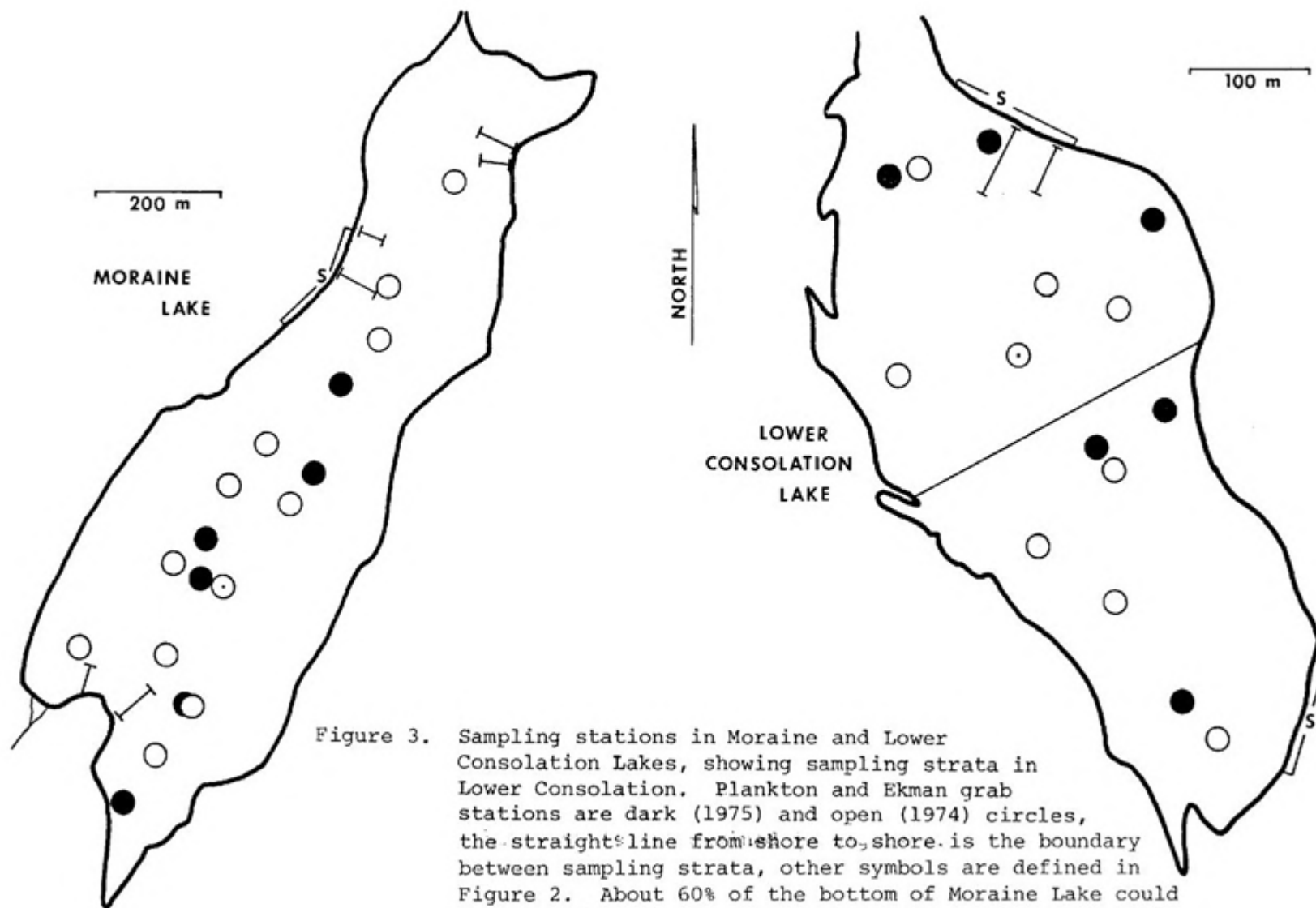


Figure 3. Sampling stations in Moraine and Lower Consolation Lakes, showing sampling strata in Lower Consolation. Plankton and Ekman grab stations are dark (1975) and open (1974) circles, the straight line from shore to shore is the boundary between sampling strata, other symbols are defined in Figure 2. About 60% of the bottom of Moraine Lake could be sampled by Ekman grab; in Lower Consolation Lake this proportion was about 80%.

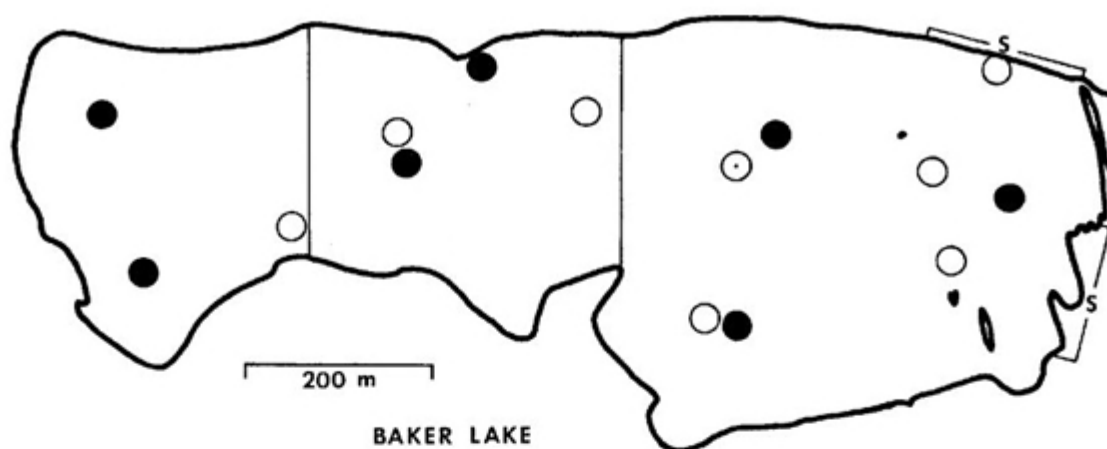
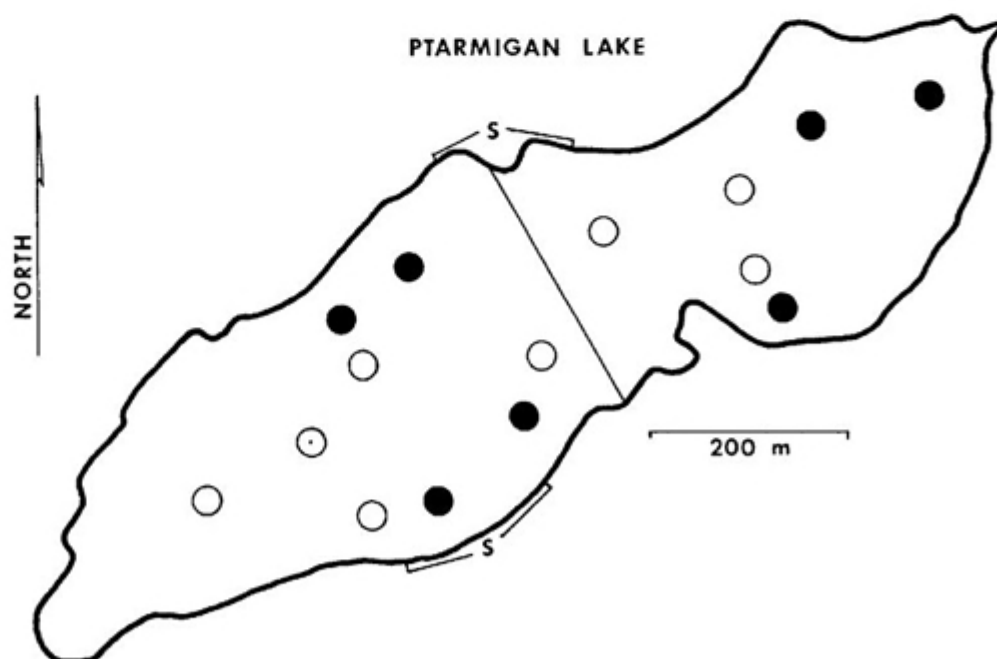


Figure 4. Sampling stations in Baker and Ptarmigan Lakes. Symbols as in Figure 3. About 90% of the bottom in Baker Lake could be sampled by Ekman grab; in Ptarmigan Lake this proportion was about 80%.



Thirty-second readings were taken at 60% of the site depth at several points across each stream. Width and mean depth were also measured to calculate stream discharge. In a few cases, when the flow meter was unavailable, floating wood chips were timed repeatedly over a stretch of stream of measured length, width and mean depth to estimate flow.

Water transparency was measured near the deepest point of each lake with a 20-cm black and white Secchi disc following the procedure described by Hutchinson (1957:399). Water colour was observed against the white part of the disc at half the Secchi depth.

Water temperatures were measured in the water column near the deepest point of each lake with a thermistor thermometer (Yellow Springs Instruments, Model 425C) calibrated at the beginning of each depth series against a mercury thermometer accurate to $\pm 0.1^{\circ}\text{C}$. The duration of the ice-free period was determined from my own observations of ice conditions in spring and fall, and from those of reliable observers working in the area (e.g., park wardens and scientists).

Mud samples were collected from near the deepest part of each lake with an Ekman grab and stored in double Ziploc[®] plastic bags for laboratory analysis of organic content.

Water samples for laboratory analysis were collected from approximately 30 cm below the surface near the center of each lake in acid-washed, double-rinsed two-litre polyethylene bottles. The bottles were shipped in dark iced coolers to the water quality laboratory of the Inland Waters Directorate, Calgary, for analysis. Water samples for analysis in the field were collected with a PVC or plexiglass Van Dorn sampler from selected depths, with a weighted and calibrated rubber-lined

hose to obtain an integrated sample from a column of water as described by Tonolli (1971), or from approximately 30 cm below the surface with double-rinsed one-litre polyethylene bottles. Conductivity was measured with a Dionic Series 3 portable meter, and pH with a Hellige colour comparator or an EIL Model 308 electronic meter. Hach methods (Hach Chemical Company, Ames, Iowa) were used for all other field determinations of water chemistry.

Zooplankton collections were made with a #20-mesh Wisconsin-style nylon plankton net (mouth diameter 25 cm, mesh aperture 65 to 70 μm) by making one vertical haul at each station on each sampling date. The net was lowered slowly until the weighted vial was felt to touch bottom, then the net was gently lowered a further 30 to 50 cm to bring the mouth within a few centimetres of the sediments. The net was retrieved at a constant rate of 0.5 m s^{-1} so that the adjustments for net filtration efficiency calculated by Anderson (1968b, 1970b) could be applied to the plankton counts. Samples were preserved at the time of collection with enough 37% formaldehyde solution to bring the final concentration of the sample to 5% formaldehyde.

Macrophytes were identified to genus in the field, and their locations and abundances were noted on sketch maps.

Qualitative shoreline collections were made by searching under rocks, sticks and debris along the shores of each lake, then sweeping the dislodged animals from the water with a small aquarium net or kitchen strainer. Collections were made for 15 to 30 minutes at each site sampled, then were preserved in 3.7% formaldehyde solution.

Benthic samples were collected with a 15.24-cm square Ekman grab, one grab sample being taken from each station on each sampling date.

Samples were sieved through a screened bucket (mesh aperture 0.36 mm x 0.52 mm) and the residue was stored in formaldehyde solution for final sorting in the laboratory.

Fish were collected with gangs of green nylon multifilament gill-nets, having 20 m each of 1.9-, 3.8-, 5.1-, 7.6-, and 10.2-cm mesh (stretched measure). In Kingfisher Lake, 10-m panels of each mesh size were used. The nets were set on the bottom overnight at the locations shown in Figures 2 to 4. Specimens were weighed to the nearest gram and their fork lengths were measured to the nearest millimetre. Stomachs were stored in 5.6% formaldehyde solution, and otoliths in a few drops of glycerol, for later study in the laboratory. In some cases the fish were frozen whole to be examined as above in the laboratory.

Laboratory Methods

Lake soundings were plotted on base maps drawn on enlarged aerial photographs, and were used to set the locations of contour lines. The photographs revealed considerable bottom detail in some cases, and were helpful in setting contours on the maps of some lakes. Scales of the aerial photographs were determined from the formula

$$\frac{\text{elevation of the aircraft} - \text{lake elevation}}{\text{lens diameter}}$$

Lake elevations were determined from 1:50,000-scale topographic maps (National Topographic Series 82 N/8 East, edition 4ASE, series A741, contour interval 30.5 m). Morphometric measurements were made from the lake maps using the methods described by Hutchinson (1957:164-167).

Water renewal times were calculated as the total lake volume at high water divided by the daily outflow or inflow, assuming no change in lake level over the time period. Sediment samples were homogenized by

thorough stirring, at least six subsamples being taken for analysis. Subsamples were dried for 24 h at 100°C, weighed, ashed at 650°C for two hours and reweighed. The weight loss on ignition was taken as a rough measure of the organic content of the sediments. No correction was made for carbonate or bicarbonate transformation.

Crustacean plankters were identified to species with the keys and descriptions of Wilson and Yeatman (1959), Brooks (1957, 1959), Brandlova, Brandl and Fernando (1972) and Deevey and Deevey (1971). Samples for each sampling date in each lake were pooled and subsampled with a Folsom plankton splitter for counting and measurement under a dissecting microscope. Cladocera and Copepoda were measured for size-frequency analysis and biomass determinations with an ocular micrometer, at a magnification of 25X except for the large *Diaptomus arcticus*, which was measured at 12X. The daphnids, bosminids and copepod nauplii were measured in the manner illustrated by Bottrell *et al.* (1976:440-444). *Polyphemus pediculus* was measured from the front of the eye to the furthest margin of the carapace. Copepod adults were measured from the tip of the rostrum to the base of the caudal rami.

Benthic samples were sorted from the residue left from field sieving under a dissecting microscope. Identifications of shoreline and benthic invertebrates were made with the following keys and descriptions:

General references: Pennak (1953), Edmondson (1959), Usinger (1956)

Ephemeroptera: Needham, Traver and Hsu (1935)

Odonata: Needham and Westfall (1955), Walker (1912, 1925, 1953)

Hemiptera: Brooks and Kelton (1967)

Trichoptera: Ross (1944)

Coleoptera: Larson (1975)

Diptera: Hamilton and Saether (pers. comm. MS keys), Saether (1969,

1971, 1975a and b), Hamilton, Saether and Oliver (1969), Pankratova (1970), Roback (1957), Stewart and Loch (1973), Mason (1973)

Mollusca: Burch (1972), Clarke (1973)

Representative specimens of aquatic beetles identified by Dr. D. Larson and chironomid specimens identified by Dr. A. Hamilton, Dr. O. Saether and Mr. R.L. Hare were used to verify some identifications. Individuals were counted and sorted into groups of easily-separable taxa. The groups were blotted on tissue to remove adhering preservative, then were weighed to the nearest 0.1 mg on an electronic balance. Molluscs were weighed with their shells intact.

Otoliths were immersed in glycerol and were examined under a dissecting microscope (up to 50X) against a dark background to determine fish ages. The number of hyaline rings observed on the otoliths was taken as the age of the fish in years. An additional annulus was assigned on the extreme edge of the otolith when the fish were taken early or late in the sampling season, on the assumption that growth had just begun (early season) or had just ended (late season).

Fish stomachs were examined and the contents were identified under a dissecting microscope (up to 50X). Taxa were sorted into separate piles in the sorting dish and the percentage of the total food volume consumed was estimated by eye (c.f. Windell 1971:217-219).

Details of the calculations used and evaluations of various methods are described at length in Sections 3, 4 and 5.

SECTION 2

PHYSICAL LIMNOLOGY AND WATER CHEMISTRY

In this section some physical and chemical attributes of the lakes are described, morphometric and temperature data required for some production calculations are presented, and the lakes are compared to others in the Canadian Rocky Mountains. Many of the features such as mean depth, temperature and total mineral content of the water may be related to secondary production (e.g., Ryder 1965, Johnson and Brinkhurst 1971), so the comparisons between the study lakes and other Canadian Rocky Mountain lakes provide an indication of how representative the study lakes are likely to be with respect to secondary production.

MORPHOMETRY AND DRAINAGE

Bathymetric maps and hypsographic curves of the six lakes are provided in Figures 5 to 7. Morphometric data are summarized in Table 4.

That the study lakes were selected to represent a wide range of altitudes in the Lake Louise area accounts for the wide altitudinal range they occupy among Canadian Rocky Mountain lakes in general (Figure 8A). A broad range of the areas and maximum depths found for Canadian Rocky Mountain lakes are also represented by the study lakes (Figures 8B, 8C). The volumes and mean depths of the six lakes are well within the ranges shown by the 20 Canadian Rocky Mountain lakes for which comparable data are available (Rawson 1942, 1953; Anderson 1968b, 1970a and b, 1975; Anderson and Dokulil 1977; Anderson and Green 1975). Because volume is largely determined by area and mean depth is correlated with maximum

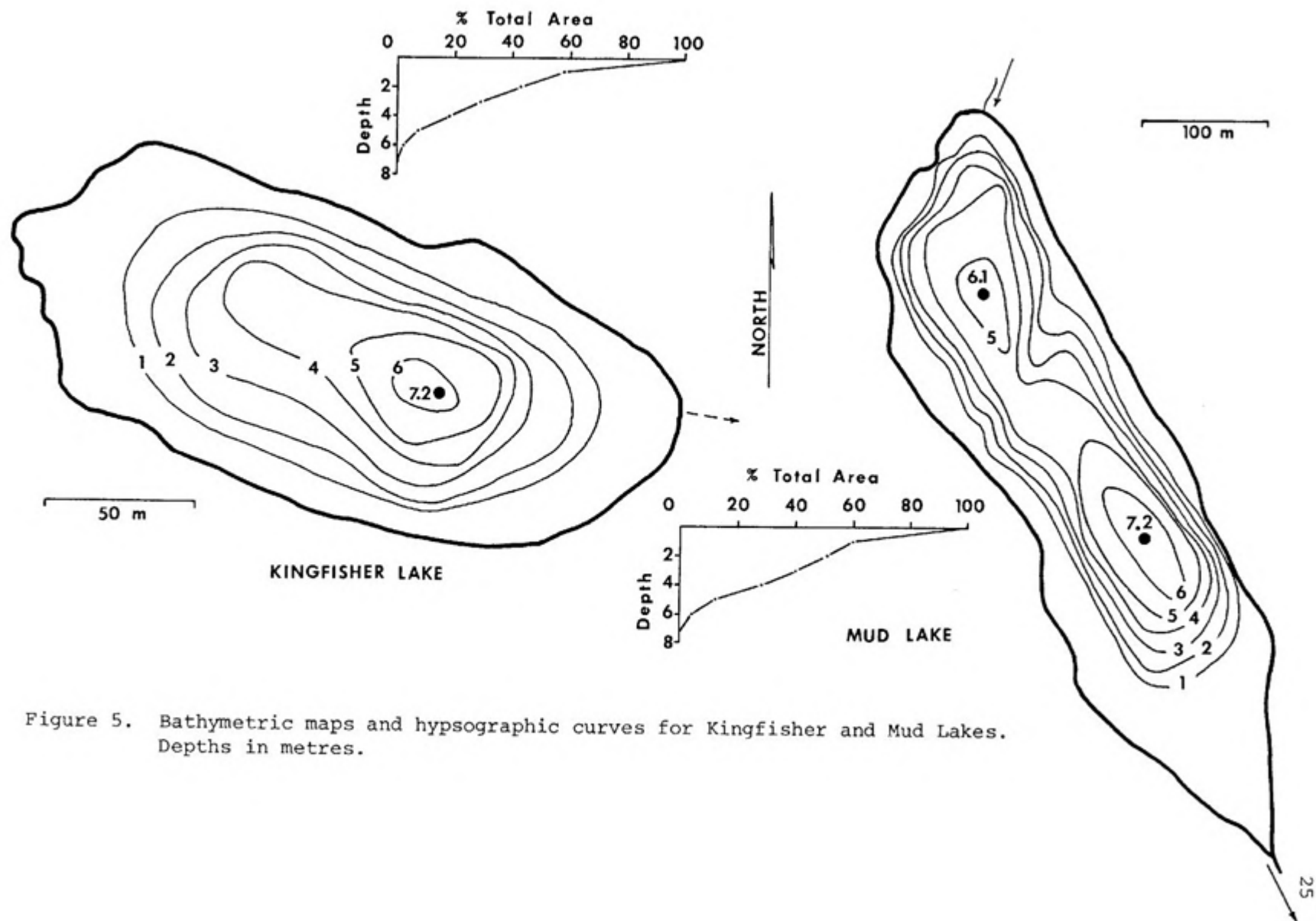


Figure 5. Bathymetric maps and hypsographic curves for Kingfisher and Mud Lakes. Depths in metres.

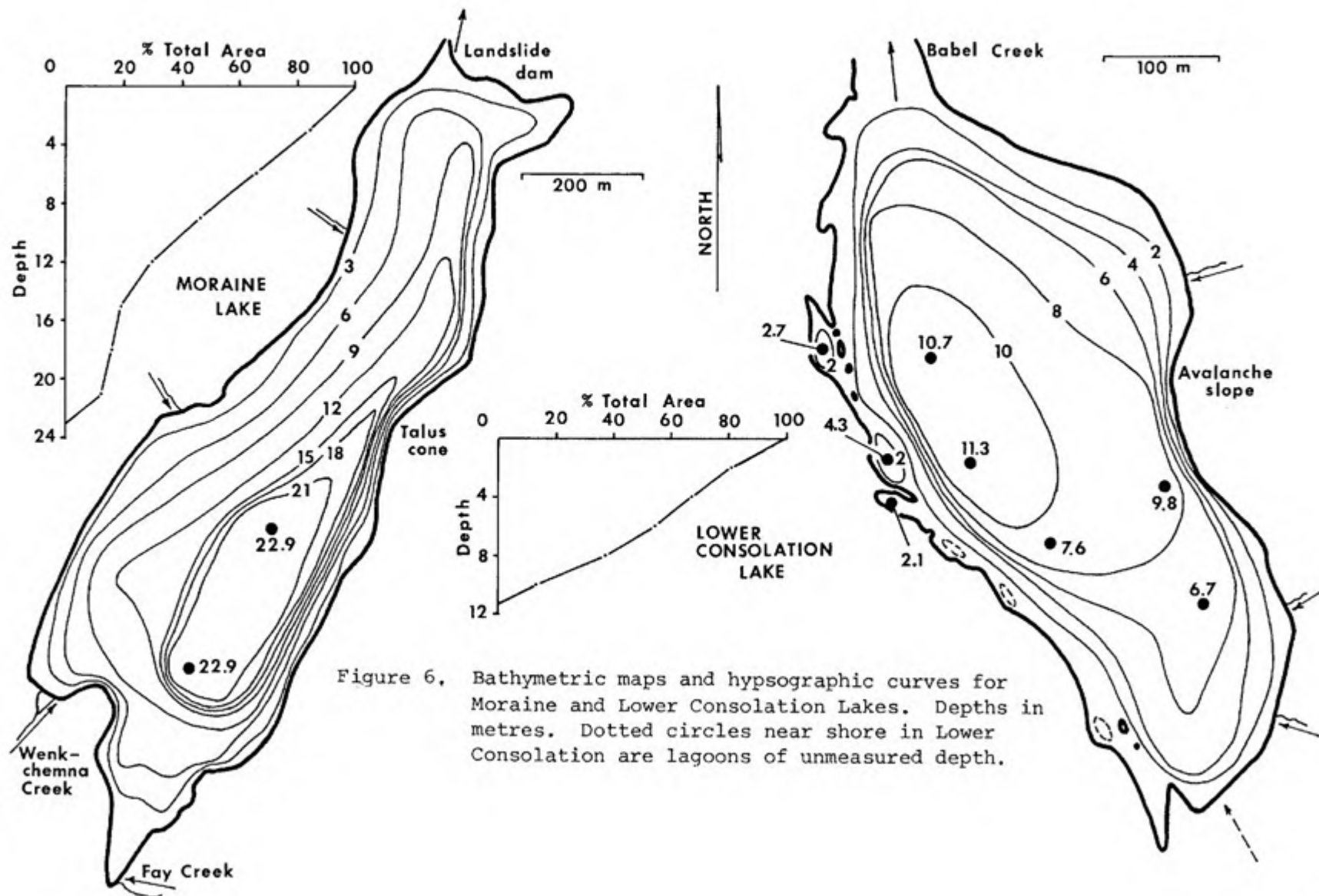


Figure 6. Bathymetric maps and hypsographic curves for Moraine and Lower Consolation Lakes. Depths in metres. Dotted circles near shore in Lower Consolation are lagoons of unmeasured depth.

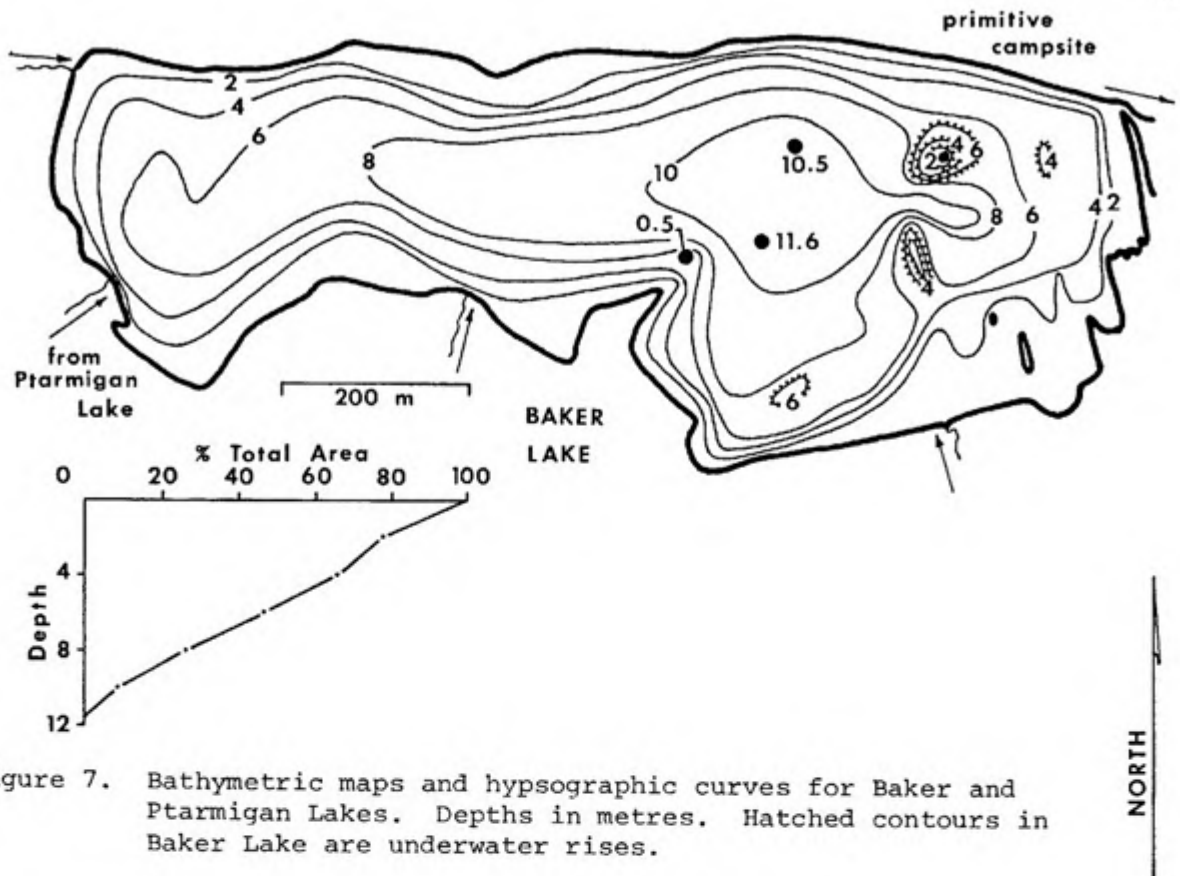


Figure 7. Bathymetric maps and hypsographic curves for Baker and Ptarmigan Lakes. Depths in metres. Hatched contours in Baker Lake are underwater rises.

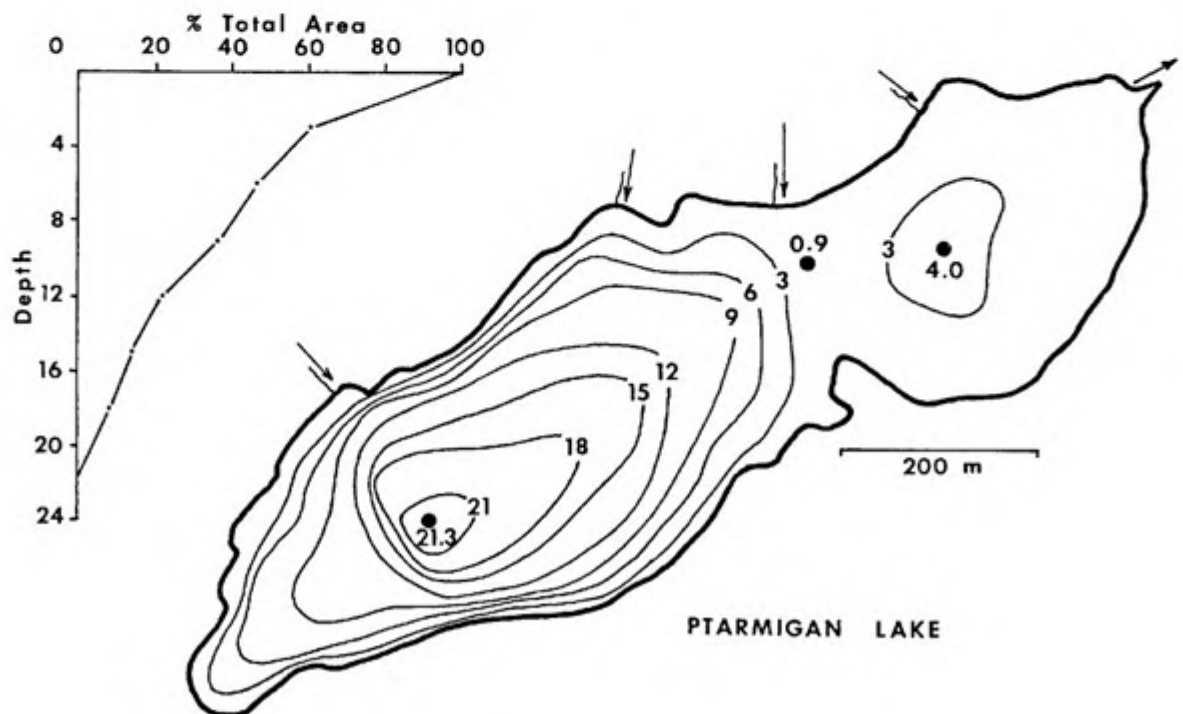


Table 4. Morphometry of the six lakes.

<u>Lake</u>	<u>Area (ha)</u>	<u>Depth (m)</u>		<u>Volume 10^4m^3</u>
		<u>max.</u>	<u>mean</u>	
Kingfisher	2.0	7.2	2.0	4.0
Mud	7.3	7.2	2.4	17.6
Moraine	41.3	22.9	9.6	397.1
Lower Consolation	14.5	11.3	5.9	85.7
Baker	36.4	11.6	5.4	198.6
Ptarmigan	27.9	21.3	7.0	195.0

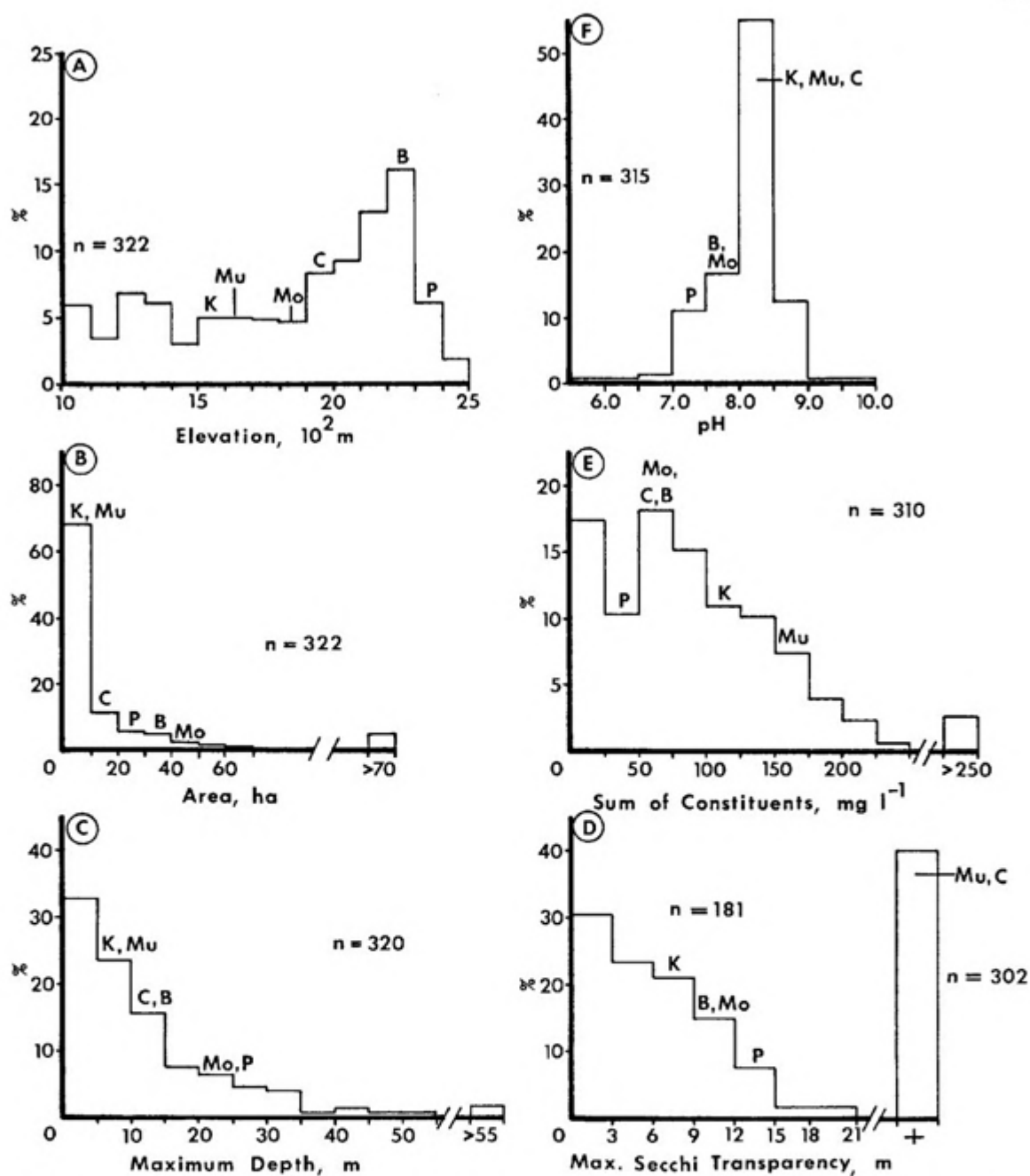


Figure 8. Some physical and chemical attributes of Canadian mountain lakes showing the ranking of the study lakes (data from Anderson (1974a)). Kingfisher Lake, K; Mud Lake, Mu; Moraine Lake, Mo; Lower Consolation Lake, C; Baker Lake, B; Ptarmigan Lake, P.

depth (Neumann 1959), the ranks of the six lakes in volume and mean depth must be near their respective ranks in area and maximum depth, shown in Figures 8B and 8C.

Table 5 summarizes the drainage data for the lakes and provides estimates of water renewal times. The times are only rough estimates because they are based on few outflow or inflow measurements, but are probably of the correct order of magnitude.

Because Kingfisher overflows for only a short time in spring and receives no measureable surface inflow, its water renewal time was estimated from the drop in water level in summer. Lake level declined by approximately 30 cm over a 90-day period in summer. The volume of water lost was 6000 m^3 (lake area times drop in water level), or about 67 m^3 per day, yielding an estimate of 600 days for the water renewal time. The effect of incoming seepage was not considered, so the actual renewal time must be less than 600 days.

Subsurface drainage is most important in Moraine Lake. The sum of discharges into the lake from the three principal inlets was 5.5 times the outlet discharge at the one time when flow measurements were made within a day of each other. In fact, the maximum outlet discharge was considerably lower than the minimum inflow measured. Since the lake level did not increase during the time the comparative measurements were taken (outlet discharge measurements from late June to early July suggest that, if anything, the lake level was dropping slightly at the time), at least 80% of the outflow from Moraine Lake is subterranean. The water leaks through the landslide dam at the north end of the lake, accounting for the overwinter drop in water level of six metres or more.

There is no evidence that subsurface drainage is important in Mud,

Table 5. Some drainage attributes of the six lakes.

<u>Lake</u>	<u>Outlet</u>	<u>Date</u>	<u>Discharge</u> <u>(m³s⁻¹)</u>	<u>Main Inlets</u>	<u>Date</u>	<u>Discharge</u> <u>(m³s⁻¹)</u>	<u>Mean Summer</u> <u>Water Renewal</u> <u>Time (days)</u>
Kingfisher	seepage			seepage			<600
Mud	Mud Cr.	74-06-19	0.02				
		74-09-20	similar to				
			above date	seepage,			81
		75-08-26	0.03	springs			
Moraine	Moraine Cr.	74-06-25	1.57	Wenkechewan Cr.	74-07-03	6.89	
		74-07-04	1.31		74-08-08	3.46	
		74-08-13	0.92		74-09-12	2.09	
		74-09-17	~0.0				
		75-07-02	~0.0	Fay Cr.	74-07-04	0.13	11
		75-09-12	~0.0		74-08-08	0.16	(inlet data)
					74-09-17	~0.16 est.	
				Larch Valley	74-07-04	0.13	
				Cr.	74-08-08	0.03	
Lower					74-09-17	~0.015 est.	
Consolation	Babel Cr.	74-07-03	2.04	subsurface			
		74-08-08	1.26	from upper			8
		74-09-12	0.57	lake			
		75-07-04	1.25				
Baker	Baker Cr.	74-07-30	0.55	Ptarmigan			61
		74-08-28	0.20	Cr			
Ptarmigan	Ptarmigan	74-08-01	0.24	surface			156
	Cr.	74-08-30	0.05	runoff			

Lower Consolation, Baker or Ptarmigan Lakes. Lower Consolation Lake water level can drop 30 cm or more during the summer, but drops in lake levels in Mud, Baker and Ptarmigan Lakes were no more than 30 cm in this study.

The drainage data were too incomplete to calculate precise annual rates of water renewal, but approximate rates were calculated by making some reasonable assumptions. Kingfisher Lake had no surface outflow during winter, and its water level did not drop appreciably after freeze-up. Outflow was restricted primarily to the 160-day ice-free period when the water renewal time was less than 600 days, so Kingfisher Lake had a water renewal rate of at least 0.6 times per year. The outlet of Mud Lake had approximately the same discharge in late fall as in summer, and may have flowed all winter; therefore, the water renewal rate could have been as high as 4.5 times per year (winter flow) or as low as 2 times per year (no winter flow). Water in Moraine drained out above the six-metre contour after September, there was little winter inflow so there was little water renewal in winter. The mean water renewal time of 11 days applied to the 110-day period mid-June to late September when the lake was overflowing through the surface outlet gives an estimated water renewal rate of approximately 10 times per year. Discharge from Lower Consolation Lake was much lower in fall than in mid-summer, but probably was maintained at a low level through the winter. If the mean water renewal time of 8 days is taken to apply only to the 150-day June to October period, the water renewal rate would be 19 times per year; but the true rate would be slightly higher because there is some winter replacement. If the mean water renewal time for Baker Lake of 61 days is taken to apply to the June to October period and winter discharge is

neglected (it is probably very low), the water renewal rate would be 2.5 times per year. The outlet of Ptarmigan Lake is just a trickle by late summer and probably does not flow at all in winter. The mean water renewal time of 156 days applied to the June to October period (150 days) yields an estimated water renewal rate of once per year for Ptarmigan Lake.

The limited comparable data available on Canadian Rocky Mountain lakes give no reason to believe the study lakes have unrepresentative water renewal rates. The water renewal rates of Kingfisher and Ptarmigan Lakes were close to the 0.7 to 0.8 times per year estimated for Upper Waterton Lake (Anderson and Green 1975, 1976) and the 1 time per year suggested for Herbert Lake (Anderson 1970a). The water renewal rates of Mud and Baker Lakes differed little from the 2 to 3 times per year estimated for Pyramid Lake (Anderson and Dokulil 1977). Moraine and Lower Consolation Lakes had water renewal rates greater than the 5.8 to 7.1 times per year of Lower Waterton Lake (Anderson and Green 1975, 1976) and the 7.7 times per year of Snowflake Lake (Anderson 1968b, 1970a), but much less than the 157 to 161 times per year of Knight's Lake (Anderson and Green 1975, 1976).

BOTTOM TYPES AND SEDIMENTS

Kingfisher and Mud Lakes have similar bottom types. Bottom areas less than two to three metres deep are covered by light-coloured flocculent sediments only slightly more dense than water; deep areas are covered by dark brown, jelly-like, flocculent mud of high organic content (78.1%, Kingfisher Lake; 70.0%, Mud Lake; $n = 0$ in both cases).

The bottom of the northern end of Moraine Lake is covered by coarse sand, gravel and talus; the bottom of the west side is covered by rock fragments usually no more than 30 cm in maximum dimension. The bottom in the central and southern parts of the basin is covered by cohesive or granular clay having an organic content of 7.0% ($n = 1$).

Talus and large rock debris cover the bottom of Lower Consolation Lake to near the maximum depth along the entire west side, some of the fragments reaching 2 m or more in maximum dimension. The bottom in shallow water elsewhere is covered by sandy sediments except at the avalanche slope on the east shore, where large rock rubble up to 50 cm in maximum dimension covers the bottom. The bottom in the central portion of the lake is covered by dark green-brown mud having an organic content of 28.4% ($n = 1$).

Much of the near-shore area of Baker Lake is sandy. Numerous rock ridges form reefs in the eastern third of the lake basin, and form the bedrock eastern and southeastern shoreline. The central portion of the lake bottom is covered mainly by black, silty sediment having a mean organic content of 12.8% (range 11.8 to 13.9%, $n = 2$).

The bottom of the shallow eastern basin of Ptarmigan Lake is covered by light-coloured mud. The bottom of near-shore areas elsewhere is covered by sandy deposits and rock fragments. Rock fragments are particularly abundant along the southwest shoreline, where a debris slope enters the lake. The deep sediments are mainly black, gritty mud having a mean organic content of 13.1% (range 12.4 to 13.8%, $n = 2$).

TEMPERATURE AND ICE COVER

Lake temperatures during the ice-free seasons of 1974 and 1975

are shown in Figures 9 to 11.

Moraine, Lower Consolation, Baker and Ptarmigan Lakes stratified weakly or not at all in the two years. Kingfisher Lake was distinctly stratified in June 1974, but stratification was weakly developed later that summer and throughout the ice-free period of 1975. Mud Lake was distinctly stratified in both years, particularly in June 1974.

Kingfisher and Mud Lakes were the warmest lakes, the former being warmer than the latter, most obviously at depths greater than four metres. Springs at the north end probably contribute the cool water to the depths of Mud Lake. Glacial meltwater inlets make Moraine and Lower Consolation the coldest of the lakes. Baker and Ptarmigan Lakes receive no glacial meltwater, so are warmer than Moraine and Lower Consolation Lakes. The greater elevations and depths of Baker and Ptarmigan Lakes causes them to be cooler than Mud or Kingfisher Lakes.

Temperature conditions in Kingfisher and Mud Lakes are similar to those in nearby Herbert Lake (Fabris and Hammer 1975; Anderson 1970a), and in Celestine Lake, Jasper National Park (Anderson 1970b) in that epilimnetic temperatures are greater than 15°C for prolonged periods, and near-bottom temperatures are well above 4°C through nearly all of the ice-free period. Moraine and Lower Consolation Lakes are among the coldest Canadian Rocky Mountain lakes, but the summer temperatures and weakly-developed thermal stratification of Baker and Ptarmigan Lakes are typical of alpine lakes in the region (cf. Anderson 1968a, b; 1970a; Fabris and Hammer 1975).

Kingfisher and Mud Lakes had an ice-free period of approximately 160 days, break-up occurring in mid-May and freeze-up in late October in 1974 and 1975. Ptarmigan Lake did not become free of ice until late or

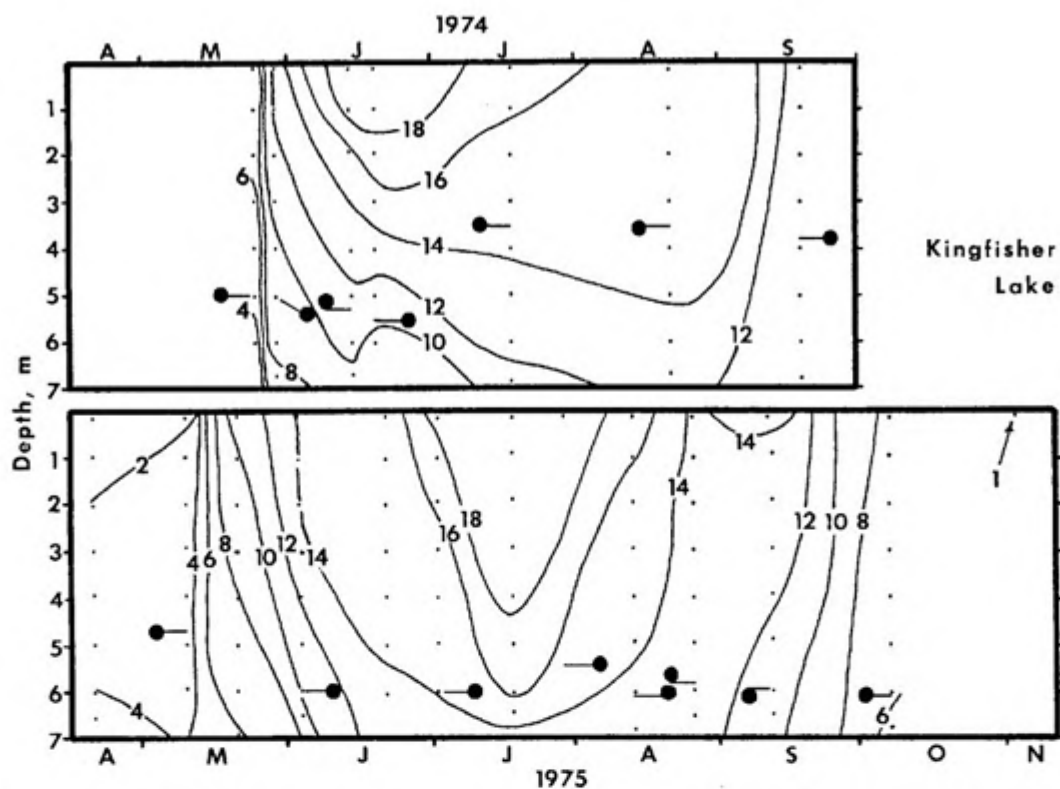
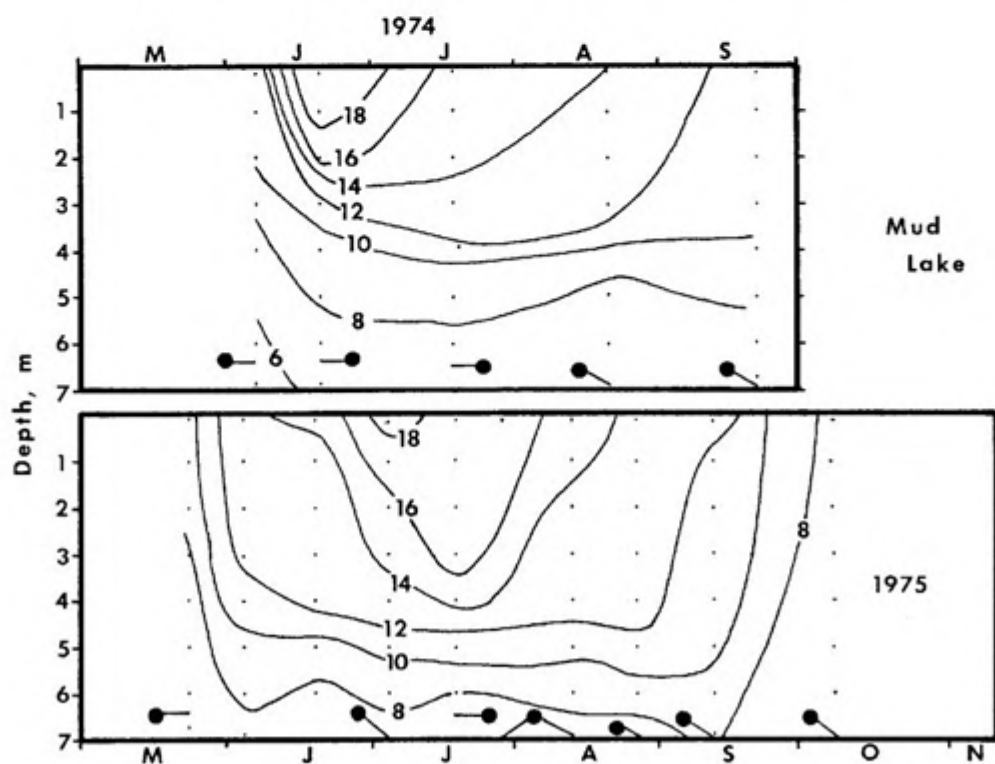


Figure 9. Secchi transparency (dark circles) and isotherm diagrams, Kingfisher and Mud Lakes. Temperatures in $^{\circ}\text{C}$.



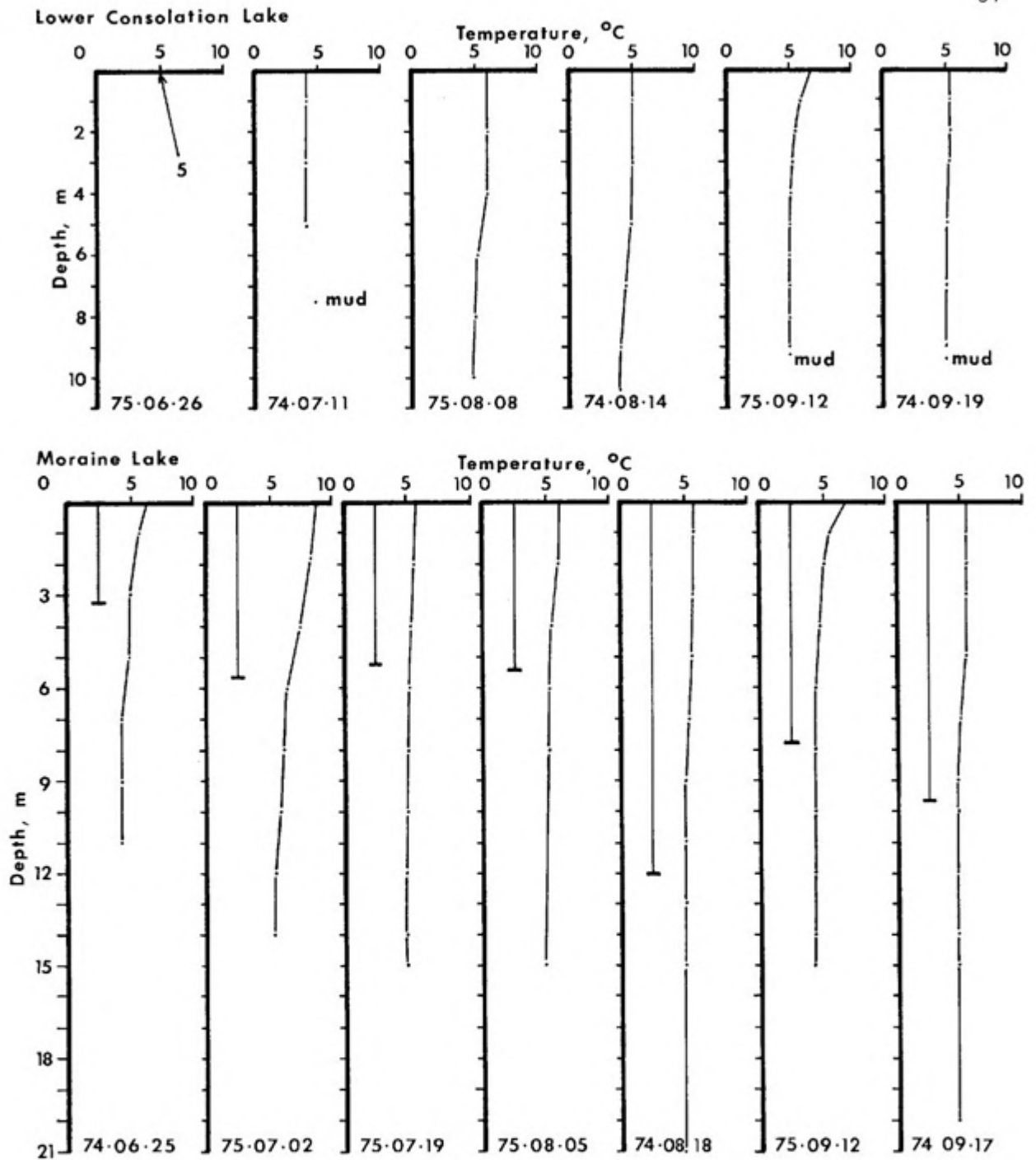


Figure 10. Secchi transparencies (inverted T-bars) and temperature profiles, Moraine and Lower Consolation Lakes.

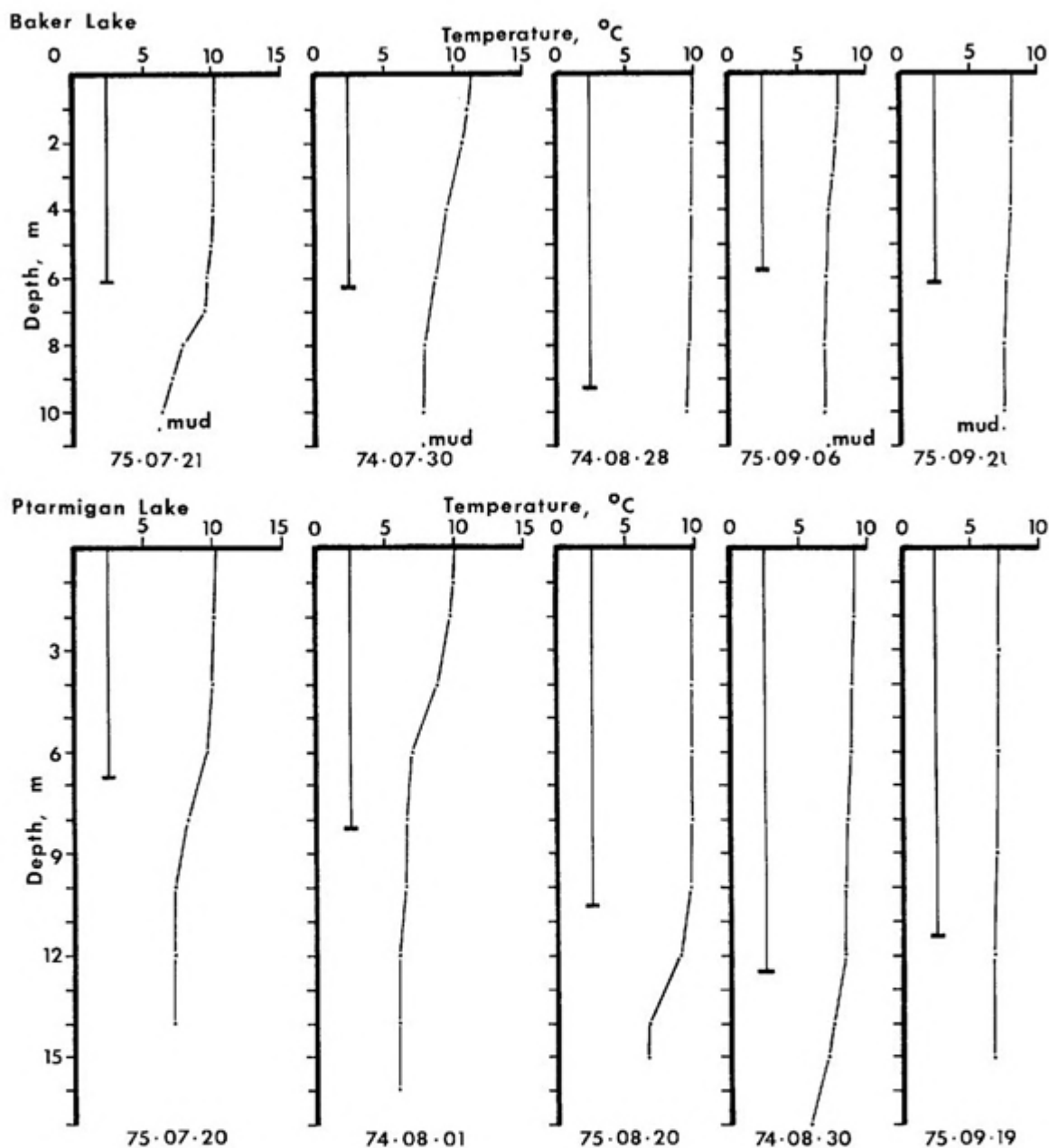


Figure 11. Secchi transparencies (inverted T-bars) and temperature profiles, Baker and Ptarmigan Lakes.

mid-July in 1974 and 1975, and is known to freeze over in late October or early November (G. Belland, pers. comm.; R.S. Anderson, unpublished data), yielding an estimated ice-free period of 110 days. Moraine became ice-free in late or mid-June, Lower Consolation in late June or early July and Baker in early or mid-July in 1974 and 1975.

Because it is so cold even in mid-summer, Lower Consolation Lake may freeze over about the same time (late October) as do shallower or higher lakes in the Canadian Rockies (Fabris and Hammer 1975; Anderson 1968a, 1970a). Moraine Lake may freeze over in early or mid-November because of its greater depth, even though it is slightly lower than Lower Consolation Lake. Baker Lake, only 122 m lower, is shallower, and breaks up one to two weeks earlier than Ptarmigan Lake, suggesting that it probably freezes over one to two weeks earlier also. Reasonable estimates of the duration of the ice-free periods are therefore 110 to 140 days for Lower Consolation Lake, 130 to 150 days for Moraine Lake and about 110 days for Baker Lake.

Kingfisher and Mud Lakes have ice-free periods identical to those of nearby Herbert Lake and Herbert Pond (Anderson 1970a, 1974b; Fabris and Hammer 1975) but slightly shorter than those of the lower elevation Jasper lakes, Patricia and Pyramid (Anderson 1974b; Anderson and Dokulil 1977). The ice-free period of Ptarmigan Lake is similar to that of alpine lakes and ponds (Anderson 1968a, 1974b; Fabris and Hammer 1975), but longer than that of the nearby alpine Eiffel and Helen Lakes (Fabris and Hammer 1975).

WATER TRANSPARENCY AND COLOUR

Secchi transparencies recorded on various dates are presented

with the temperature profiles in Figures 9 to 11. Among the lakes in which Secchi transparency was measurable the study lakes tended to have clearer waters than do Canadian Rocky Mountain lakes in general, but the tendency was not pronounced (Figure 8D).

Water colour was variable among the lakes, and within some lakes among sampling dates. Kingfisher Lake water was almost always yellow-green, but in September and October 1975 it was distinctly green. Mud Lake water was various shades of brown from May to early July, and was yellow-green from mid-July to September. Water colour in Moraine and Lower Consolation Lakes was blue; milky blue in the former and clear blue in the latter. Baker Lake had light- to medium-green water, and Ptarmigan Lake water was green to blue-green.

Laboratory analyses of colour in water samples collected on the dates shown in Table 6 ranged from 0 to 7 Hazen units; turbidity analyses done on the same samples at the same time ranged from 0.3 to 1.3 Jackson units in the various lakes. These colour and turbidity figures are very low.

As a rule of thumb the Secchi disc disappears at the level of 15% light transmission, and at about twice the Secchi depth light is effectively absent (Vollenweider 1974:176). According to this rule, light penetrates to the bottom of all of the lakes over most of their areas in summer, and at least occasionally penetrates to the maximum depth of all six lakes.

Secchi transparency is limited by the absorption properties of water and the quantity of dissolved and particulate matter in the water, particularly the latter (Wetzel 1975:63-64). The lower Secchi trans-

parencies in 1974 in Kingfisher Lake probably reflect higher quantities of suspended particulate matter in that year compared to 1975, because in neither year was the water highly coloured, nor was it silted. In Mud Lake Secchi transparency could have been limited by the brown colour of the water, especially early in the summer, and by plankton. Glacial siltation, although it was not as pronounced as in other glacial lakes nearby (e.g. Lake Louise), limited Secchi transparency in Moraine Lake. In Baker and Ptarmigan Lakes plankton probably limited Secchi transparency because colour was low and neither lake has a large source of silt.

WATER CHEMISTRY

Conductivity, sum of constituents, field pH, hardness and alkalinity all tended to decrease with increasing elevation among the six lakes (Table 6, compare to Table 1). Laboratory pH showed no trend with altitude, and laboratory figures for conductivity and alkalinity were lower than the field measurements. Phenolphthalein alkalinity was always zero in laboratory and field analyses.

All six waters were of the calcium-magnesium-bicarbonate type, calcium consistently forming slightly more than half the total cations, and bicarbonate always comprising at least three-quarters of the anions in milliequivalents (Table 7). Sulphate was the second most abundant anion in all six lakes.

The waters of the six lakes are representative of Canadian Rocky Mountain lakes in general with respect to their sums of constituents (TDS) and pH (Figure 8E, F), but tend to be more dilute than the average 142 mg l⁻¹ for North American river water (Livingstone 1963).

Table 6. Some physical and chemical features of water from the six lakes. Laboratory analyses were done on surface samples, field analyses on composite samples to 10 m. Field results ± 1 SE, 1974 - 1975

<u>Lake</u>		<u>Date</u>	Conductivity at 25°C ($\mu\text{S cm}^{-1}$)	Sum of Constituents (mg l^{-1})	pH	Total Hardness as CaCO_3 (mg l^{-1})	Total Alkalinity as CaCO_3 (mg l^{-1})
Kingfisher	lab	75-07-08	221	113.4	8.4	121	115
	field	June to Sept.	261 ± 9.4 n = 4		8.2 ± 0.05 n = 4		132 ± 3.4 n = 4
Mud	lab	70-06-25	272	155	8.0	146	125
	field	May, July to Sept.	290 ± 9.9 n = 4		8.2 ± 0.09 n = 3		126 ± 3.5 n = 4
Moraine	lab	67-09-20	124	65.0	7.9	63.4	54.9
	field	June to Sept.	140 ± 3.4 n = 4		7.8 ± 0.03 n = 4		67 ± 2.1 n = 4
Lower Consolation	lab	73-07-17	115	63.0	8.0	62.0	52.0
	field	July to Sept.	152 ± 6.7 n = 3		8.0 ± 0.15 n = 3		66 ± 2.0 n = 3
Baker	lab	66-07-22	104	54.7	8.1	49.8	39.3
	field	July and August	130 ± 6.7 n = 3		7.7 ± 0.03 n = 3		55 ± 0.0 n = 3
Ptarmigan	lab	66-07-22	53.3	26.6	7.4	26.3	22.1
	field	August	77 ± 5.0 n = 2		7.4 ± 0.05 n = 2		34 ± 0.0 n = 2

Table 7. Major ionic constituents of surface waters of the six lakes, determined from laboratory analyses (collection dates as in Table 6). Percentages are the proportion of anions or cations calculated from equivalent weights.

	Cations								Anions					
	Ca		Mg		Na		K		HCO ₃	SO ₄		Cl		
	mg l ⁻¹	%	mg l ⁻¹	%	mg l ⁻¹	%	mg l ⁻¹	%	mg l ⁻¹	%	mg l ⁻¹	%	mg l ⁻¹	%
Kingfisher	27.0	54.3	13.0	43.1	1.1	1.9	0.6	0.6	140.2	97.6	2.2	1.9	0.4	0.5
Mud	34.0	54.7	14.9	39.5	3.1	4.4	0.4	0.3	152	84.4	21.8	15.4	0.2	0.2
Moraine	15.7	60.7	5.9	37.6	0.4	1.4	0.2	0.4	66.9	87.2	7.6	12.6	<0.1	0.0
Lower Consolation	15.0	59.0	6.0	38.9	0.5	1.7	0.2	0.4	63.4	87.3	6.8	11.9	0.3	0.7
Baker	11.0	53.4	5.4	43.2	0.6	2.5	0.3	0.8	47.9	76.0	11.7	23.6	0.1	0.3
Ptarmigan	6.2	56.8	2.6	39.3	0.3	2.4	0.3	1.4	26.9	86.6	3.2	13.1	0.05	0.3

The major ionic composition of the water of the six lakes, with $\text{Ca} > \text{Mg}$ and $\text{HCO}_3 > \text{SO}_4$, is similar to that found in numerous other Canadian Rocky Mountain lakes (Anderson 1968b, 1970a, b, 1974a, b; Fabris and Hammer 1975), and is characteristic of the surface waters of the region as a whole (Water Quality Branch 1976). The dominance by these ions reflects the dominance (among soluble rock types) of limestone and dolomite formations in the Rocky Mountains (e.g. Baird 1967; Belyea 1964).

The differences between field and laboratory measurements were usually significant but were unimportant in that they did not lead to different ranking of the lakes. Part of the differences are attributable to the fact that laboratory samples were collected at the surface but field samples were a composite of water taken from the surface to a depth of up to 10 m¹. This would tend to give higher field conductivity and alkalinity values when the lakes are stratified, because deeper waters are then usually more highly mineralized than surface waters. Part of the differences could also be due to changes in the laboratory samples in transit: pH and alkalinity in particular are subject to rapid unpreventable changes with storage (Thomas 1953). Part of the differences could be due to differences in the accuracy of methods. For example, the method used for field alkalinity is accurate to only $\pm 7 \text{ mg l}^{-1}$ because of the concentration of the reagents used. In all cases the differences are within expected seasonal and depth variations (cf. Anderson 1970a), so the determinations are suitable for a general characterization of the water chemistry.

¹ Samples were collected by different agencies for different purposes.

SECTION 3

CRUSTACEAN PLANKTON

CALCULATIONS AND METHODS EVALUATION

Abundance and Biomass

Numbers of crustacean plankters per cubic metre were calculated from counts of one-eighth or one-thirty-second subsamples of the pooled field samples, the volume of the water column sampled, and estimates of the filtering efficiency of the net. The main sources of error in measuring abundance in this way are field variability (patchy distribution of individuals in the lake), sampler inefficiency and subsampling errors.

The collection of vertically-integrated samples from 6 to 12 randomly-selected sampling stations was an attempt to minimize the effect of field variability on the abundance estimates. No measurement of the error due to field variability was possible because the samples had to be pooled to reduce the work of plankton analysis to manageable proportions.

Filtration efficiency of plankton nets is considerably less than 100% because backpressure causes water and plankters to flow around the net rather than through it, and because some species may actively avoid the net. Anderson (1968b:111) calculated the mean filtration efficiency $\pm$ standard error (SE) of the style of net used in the present study to be $21.5\% \pm 1.10$ ($n = 16$). Filtration efficiency tends to be lower ($\bar{x} = 17\%$) in May and June in Alberta mountain lakes because of the greater degree of phytoplankton clogging typical of that period (Anderson 1970b). In this study a filtration correction factor of 5 was used

to convert plankton counts to numbers per cubic metre for samples taken in all months except May and June, when a factor of 6 was used.

McEwen *et al.* (1954) assessed the performance of a Folsom plankton splitter similar to that used in the present study, finding splitting errors to be random. Their data (their Tables 3 and 4) suggest that when more than 40 individuals are found in each subsample, the standard deviation will be 10 to 20% of the mean. When mean counts are more than 10, the expected distribution is approximately normal (Elliott 1971:31). In a normal distribution, 95% of the individual observations fall within 2 standard deviations of the mean, therefore 95% of the single-subsample counts will be within 20 to 40% of the mean count of all possible Folsom subsamples in which there are more than 40 individuals. In the present study more than 40 individuals of the most abundant species were counted in single subsamples, so these counts should have been within 20 to 40% of the number in the whole sample 95% of the time. Counts of the least abundant species would have been much less precise, but the absolute error would usually have been trivially small because the absolute abundance was low.

Individual dry weights of most crustacean plankters were calculated from the length-dry weight regressions of Bottrell *et al.* (1976: 438, 442) shown below:

Copepoda:	$\ln w = 1.9526 + 2.3990 \ln L$	± 0.0854
<i>Bosmina</i> :	$\ln w = 3.0896 + 3.0395 \ln L$	± 0.2123
<i>Ceriodaphnia</i> :	$\ln w = 2.5623 + 3.3380 \ln L$	± 0.6819
<i>Daphnia</i> :	$\ln w = 1.4681 + 2.8292 \ln L$	± 0.0723
Daphnidae:	$\ln w = 1.5072 + 2.7610 \ln L$	± 0.0683
(for <i>Scapholeberis</i>)		

where w is individual weight (μg dry weight), and
 L is individual length (mm)

Figures to the right are 95% confidence limits of the regression coefficients. For *Polyphemus* the length-wet weight regression of Sherbakov (1952, in Edmondson 1971a:141) was used to calculate individual wet weight in micrograms:

$$w^{0.33} = 4.4 L - 0.2$$

The footnote given by Edmondson in his Table 2.3.1 makes it clear that $w^{0.33}$, rather than the printed w^{-3} , is what is meant; otherwise w is impossibly large. Wet weights of copepod eggs were calculated from the equation relating the volume of a sphere to its radius

$$V = 4/3 \pi r^3$$

where r is the egg radius in mm, and

V is the egg volume in mm^3

on the assumption that the eggs had a density of 1 g cm^{-3} , the density of pure water at 4°C . Eggs of Cladocera were assumed to weigh no more than the calculated weight of the smallest individual in the smallest size class observed. Where necessary the wet weight - dry weight relationship shown by Bottrell *et al.* (1976:436) was used to convert wet weights to dry weights. Mean individual dry weights were multiplied by the abundance estimates to calculate the biomasses of the various taxa.

Instar Analysis

Instar analysis (Edmondson 1971b:149) was used to obtain the life-history data required for the production calculations. For copepods the abundance of eggs, nauplii, copepodids and adults were plotted separately against time. Cladocera do not have instars that are readily distin-

guishable, so arbitrary length-classes¹ were substituted for instars and the numbers of each were plotted against time.

Egg development times were calculated from the equations of Bottrell *et al.* (1976:445) relating development times to temperature. Development times were calculated at the maximum and minimum water temperatures observed on each sampling date, and the mean of the two calculations was taken as the mean development time for that date. The equations used were:

$$\begin{aligned} \text{Daphnidae:} \quad \ln D &= 3.3956 + 0.2193 \ln T - 0.3414 (\ln T)^2 \\ &\pm 0.3363 \quad \pm 0.0706 \end{aligned}$$

$$\begin{aligned} \text{all Cladocera: } \ln D &= 3.1457 + 0.4797 \ln T - 0.4003 (\ln T)^2 \\ \text{(used for Cladocera} & \\ \text{other than Daphnidae)} &\pm 0.3935 \quad \pm 0.0817 \end{aligned}$$

$$\begin{aligned} \text{Calanoida:} \quad \ln D &= 3.9650 - 0.4049 \ln T - 0.1909 (\ln T)^2 \\ &\pm 0.2738 \quad \pm 0.0817 \end{aligned}$$

where D is the development time (days), and

T is the water temperature (°C)

The 95% confidence limits are provided below their respective regression coefficients.

A source of error in the calculations of egg development times was the temperature estimate. Mud Lake in particular had a marked thermal gradient in the summer, but because the distribution of the plankton was not studied, the temperature to which the various species were subjected was unknown. Use of a mean figure could have led to a large under- or over-estimate of egg development times if the crustaceans all occupied the coldest or warmest water exclusively, but these possibili-

¹ Hereinafter referred to as instars because they were treated in exactly the same way.

ties seem unlikely. The other lakes had only slight thermal gradients in summer 1975, so the calculated egg development times of crustaceans in those waters could not be much in error. The influence of any possible error in egg development times on the production estimates was far exceeded by another error, largely correctable, which is discussed with the results.

The development times of other instars were calculated from the instar abundance graphs. Most of the instar curves (e.g., Figure 12), showed distinct pulses in abundance that could be traced through the population as the various instars developed. The mean time of pulse was determined for each instar, then the difference in the mean time of pulse was determined for successive instars. Where sufficient data were available the mean day of pulse was plotted against instar, a smooth curve was drawn by eye, and corrected mean days of pulse for each instar were read from the curve (e.g., Figure 16) (Rigler and Cooley 1974). For each instar the mean of the immediately preceding, and immediately following differences between the mean days of pulse was taken as the best estimate of the development time for the instar.

The method of calculating development times proposed by Rigler and Cooley (1974:640-641) was not used. The iterative calculations necessary when field data only are available are too time-consuming and do not justify the possible slight improvement in accuracy, particularly when other sources of error are likely to be more important. In this study boundaries of abundance pulses often had to be chosen subjectively. The shape of the pulse and the mean pulse data were frequently influenced by differential mortality during the pulse and by errors in the abundance estimates. The latter sources of error are probably characteristic of

all population data on planktonic crustaceans, and in most cases can be expected to be much more important than that arising from a failure to use Rigler and Cooley's theoretically more defensible calculation.

Production

No single method of calculating production was suitable for all taxa because of the many life-history differences among them. For populations having well-defined cohorts the Allen Curve method as described by Mann (1971:160) was used whenever the data permitted. The Allen Curve method is empirical, requiring no assumptions about the development times of instars or the type of growth experienced by individuals: it is therefore highly reliable when the data are suitable for its use. For populations in which continuous or prolonged reproduction made cohorts unrecognizable, the Allen Curve method could not be applied. Two calculations were then used:

- 1) Method of Pechen and Shushkina (1964, described by Winberg *et al.* 1971:304)

$$P = \sum_{i=1}^n (N_i \cdot \Delta w_i / D_i)$$

where P is production ($\mu\text{g dry weight d}^{-1}$),

N_i is the number of individuals per cubic metre in instar i on a given date,

Δw_i is the change in individual weight (growth) of instar i ($\mu\text{g dry weight}$),

D_i is the development time of instar i (days), and

n is the number of instars

The calculation was made for every sampling date on which the species was collected. The total production over a given period was calculated

by multiplying the mean daily P by the number of days in the period. The method assumes that the D_i 's as estimated from the instar pulse times are the same as the D_i 's on each sampling date.

- 2) Extension of Southwood's method for estimating numbers passing through an instar.

The area under the curve of instar abundance plotted against time has the dimensions numbers X days. Division of the area by the development time of the instar gives the approximate number reaching the median age of the instar (Southwood 1966:279). An estimate of production during any given period can be obtained from the equation

$$P = \sum_{i=1}^n (N_i \cdot \Delta w_i)$$

where N_i is the number passing through instar i during the period. The method is analogous to that of Pechen and Shushkina, but does not rely on a summation of instantaneous population growth estimates. It assumes no mortality within instars, only between instars. Because mortality must occur during the instar in nature, the estimate of N_i will be an underestimate of the number entering the instar but an overestimate of the number leaving it. Whether this leads to an over- or underestimate of P depends on the distribution of mortality in time within the instar.

Production had to be calculated by a variety of less satisfactory methods when data were unsuitable for analysis by the methods outlined above. Sometimes the maximum observed biomass was the only measure of production available; in other cases an estimated production-to-biomass ($P/\bar{B}$) ratio was used as a factor to convert observed mean biomasses to production estimates. In the results to follow the methods used are

specified in each case.

RESULTS

Kingfisher Lake

Species composition. The most common crustacean plankters in Kingfisher Lake were *Daphnia* (*pulex* group); *Scapholeberis kingi* Sars, 1903; *Ceriodaphnia affinis* Lilljeborg, 1900, *Bosmina longirostris* (O.F. Müller, 1785); *Polyphemus pediculus* (Linné, 1761); *Acanthodiaptomus denticornis* (Wierzejski, 1888); *Diaptomus leptopus* S.A. Forbes 1882; *Acanthocyclops vernalis* Fischer 1853 and *Orthocyclops modestus* (Herrick, 1883). Occasional specimens of *Alona* sp., *Chydorus sphaericus* (O.F. Müller, 1785) and *Macrocyclus albidus* (Jurine, 1820) occurred in the samples, but were never abundant. Several non-pectenate *Ceriodaphnia*, possibly *Ceriodaphnia quadrangula* (O.F. Müller, 1785) were found in the samples collected June 3, 1975, but all specimens dissected in subsequent samples were the pectenate *C. affinis*.

The *Daphnia* species could not be positively identified. All specimens examined had the large mid-pecten teeth characteristic of the *pulex* group, but showed a confusing range of head and body shapes. Mature females had heads with ventral margins ranging from the almost straight or slightly sinuate type characteristic of *Daphnia schødleri* Sars, 1862; through the concave-sinuate shape of *Daphnia pulicaria* Forbes, 1893 emend. Hrabáček, 1959; to the strongly concave shape diagnostic of *Daphnia pulex* Leydig, 1860 emend. Richard, 1896 (Brooks 1957, 1959; Brandlova, Brandl and Fernando 1972). Some specimens with *D. schødleri* head shapes had the rotund body shape, rounded back and short shellspine of

D. pulex; other specimens had the *D. pulex* head shape with the long shellspine and elongate body shape of *D. schødleri*. There seemed to be a gradual trend through the ice-free period, with small to medium-sized individuals with *D. schødleri* and *D. pulex* characteristics most common in May to July, and large individuals with the *D. pulicaria* head shape most common in August to October.

Instar analysis. Figures 12 to 15 illustrate the course of development of the most abundant species in summer 1975.

Most *Daphnia* size-classes had two peaks of abundance (Figure 12A), but the second peak may have been caused by a sampling error because it is coincident in all but one class. A substantial population was still present on the last sampling date, so the population may have continued to develop well into the fall.

Ceriodaphnia had two major pulses during the sampling period (Figure 12B). A small third pulse may have been generated by a small peak of eggs that appeared in late August, but the data are inconclusive. Only a small population of large individuals was present on the last sampling date and few *Ceriodaphnia* were present on the first sampling date, indicating that nearly all of the non-resting phase of the population cycle was sampled.

A single large pulse of *Bosmina* originated in June, and small numbers of eggs produced in late July through August generated a much smaller second pulse in late summer (Figure 13A). A single size-class dominated the population through August, indicating that development had virtually ceased. The data suggest that the entire non-resting phase of the annual population cycle was completed in the sampling period.

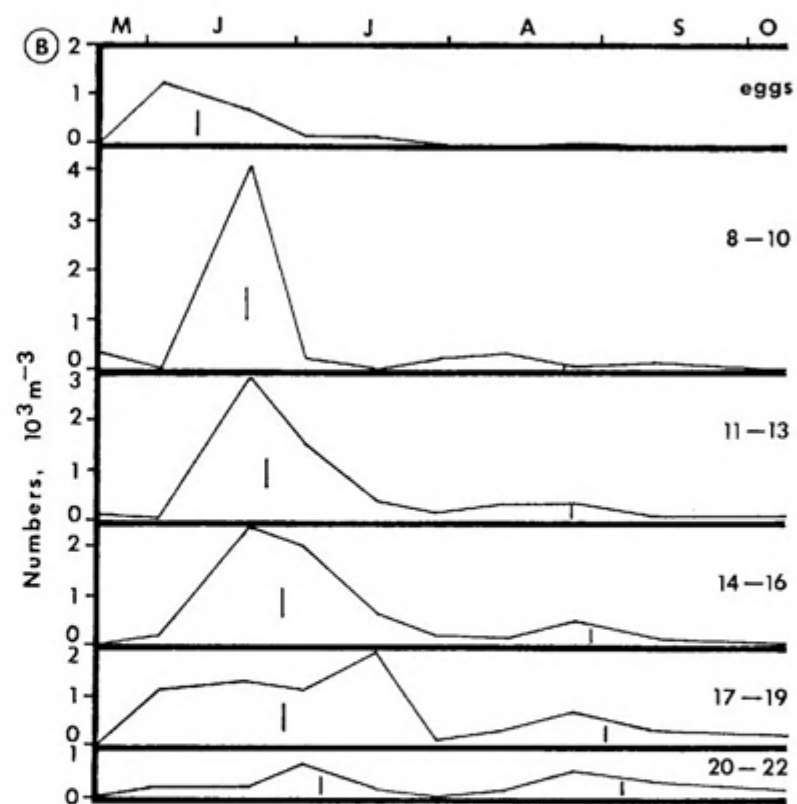
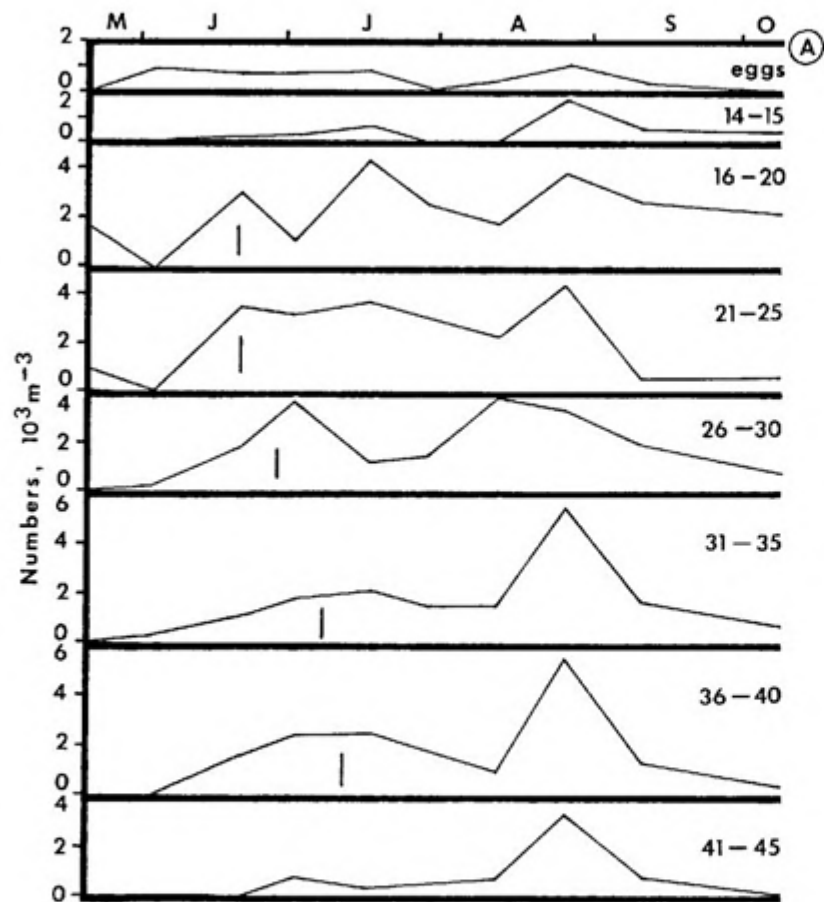


Figure 12. Size-class abundance curves and mean date of pulse (vertical bars) for *Daphnia* (left) and *Ceriodaphnia* (right) in Kingfisher Lake. Size-classes in micrometer units (m.u.).
 1 m.u. = 0.0398 mm

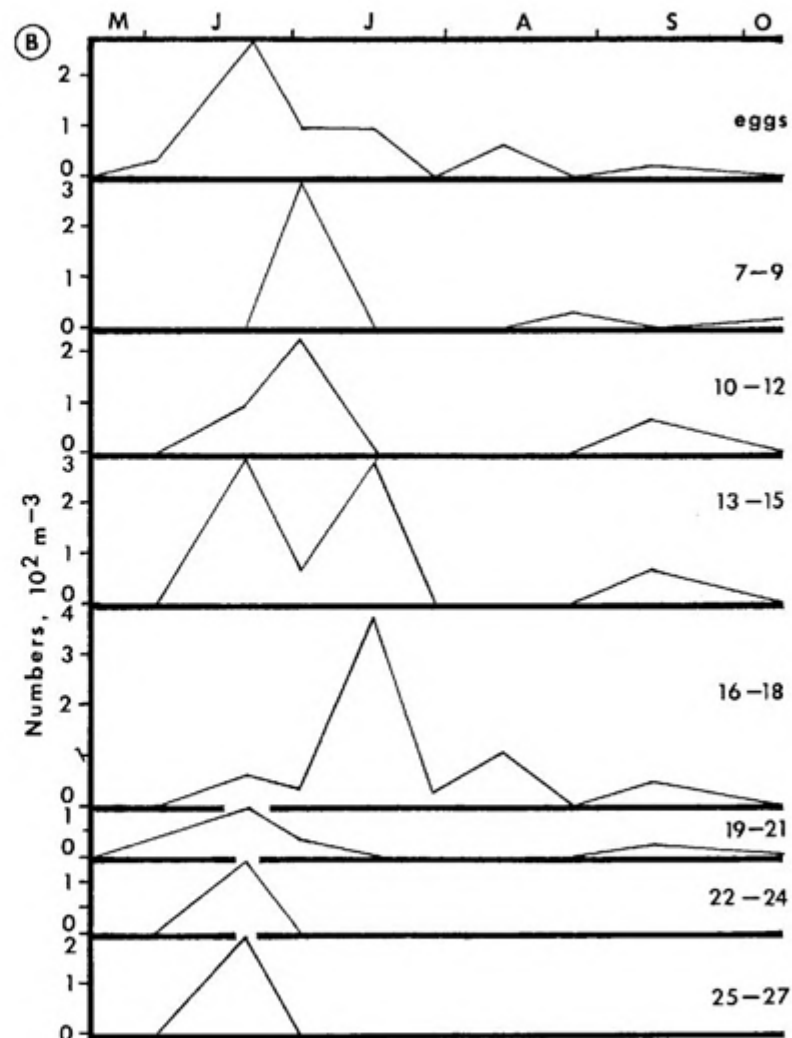
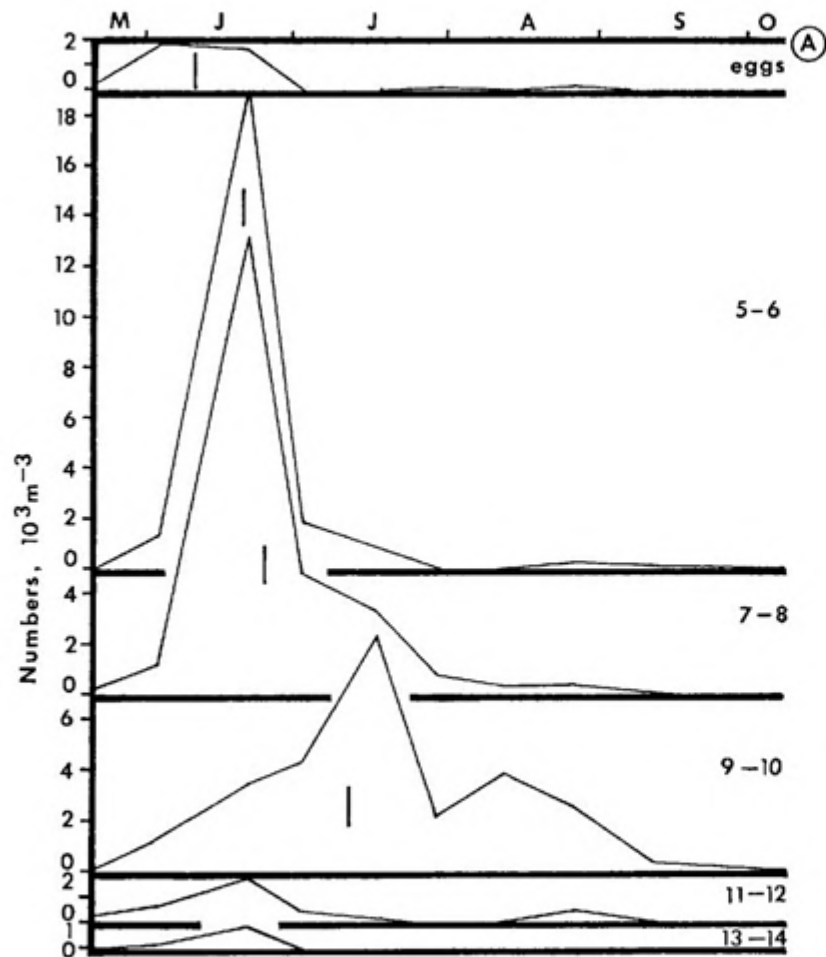


Figure 13. Size-class abundance curves and mean date of pulse (vertical bars) for *Bosmina* (left) and *Scapholeberis* (right) in Kingfisher Lake. Size-classes in m.u.
1 m.u. = 0.0398 mm

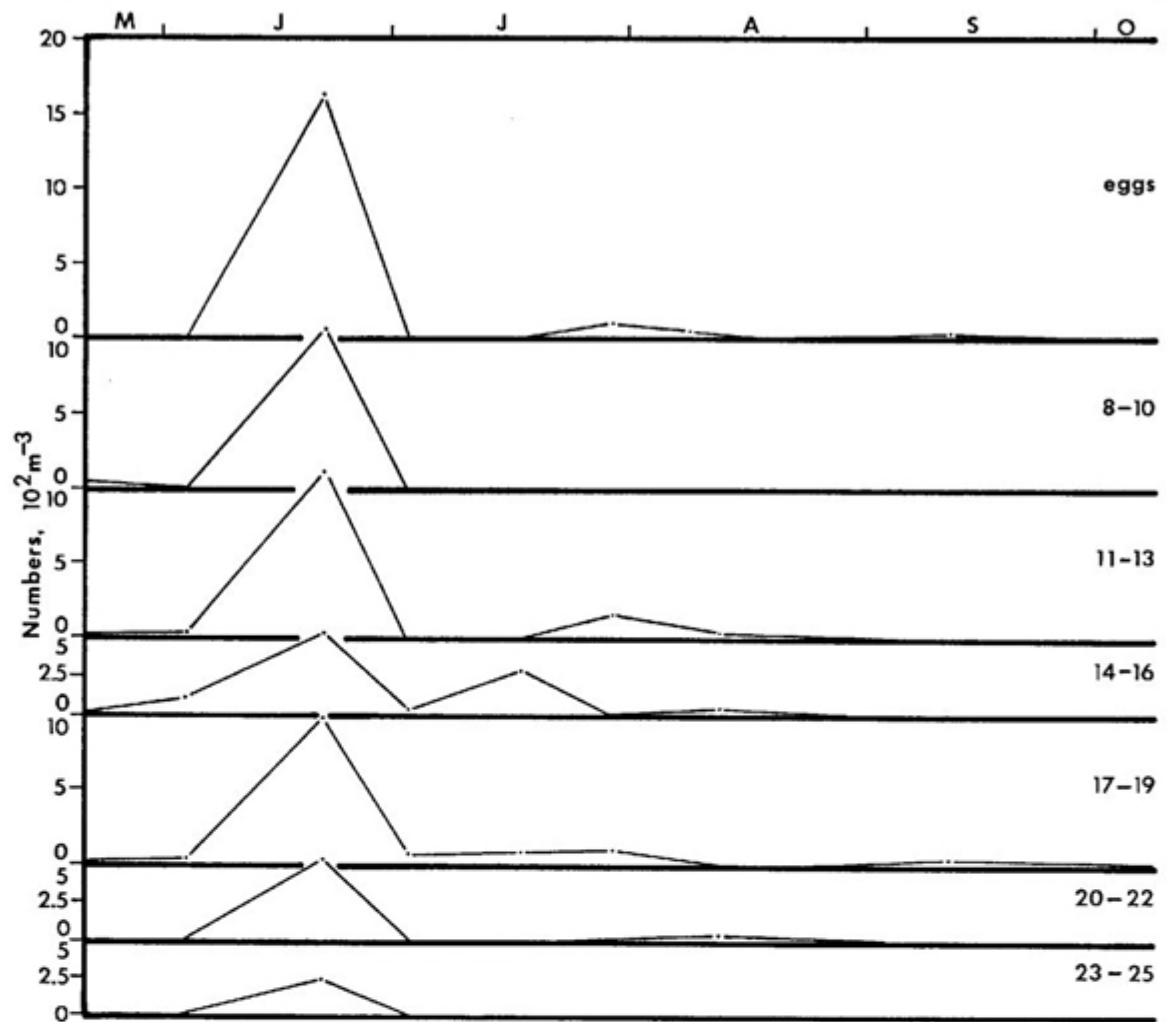


Figure 14. Size-class abundance curves for *Polyphemus* in Kingfisher Lake. Size-classes in m.u. 1 m.u. = 0.0398 mm

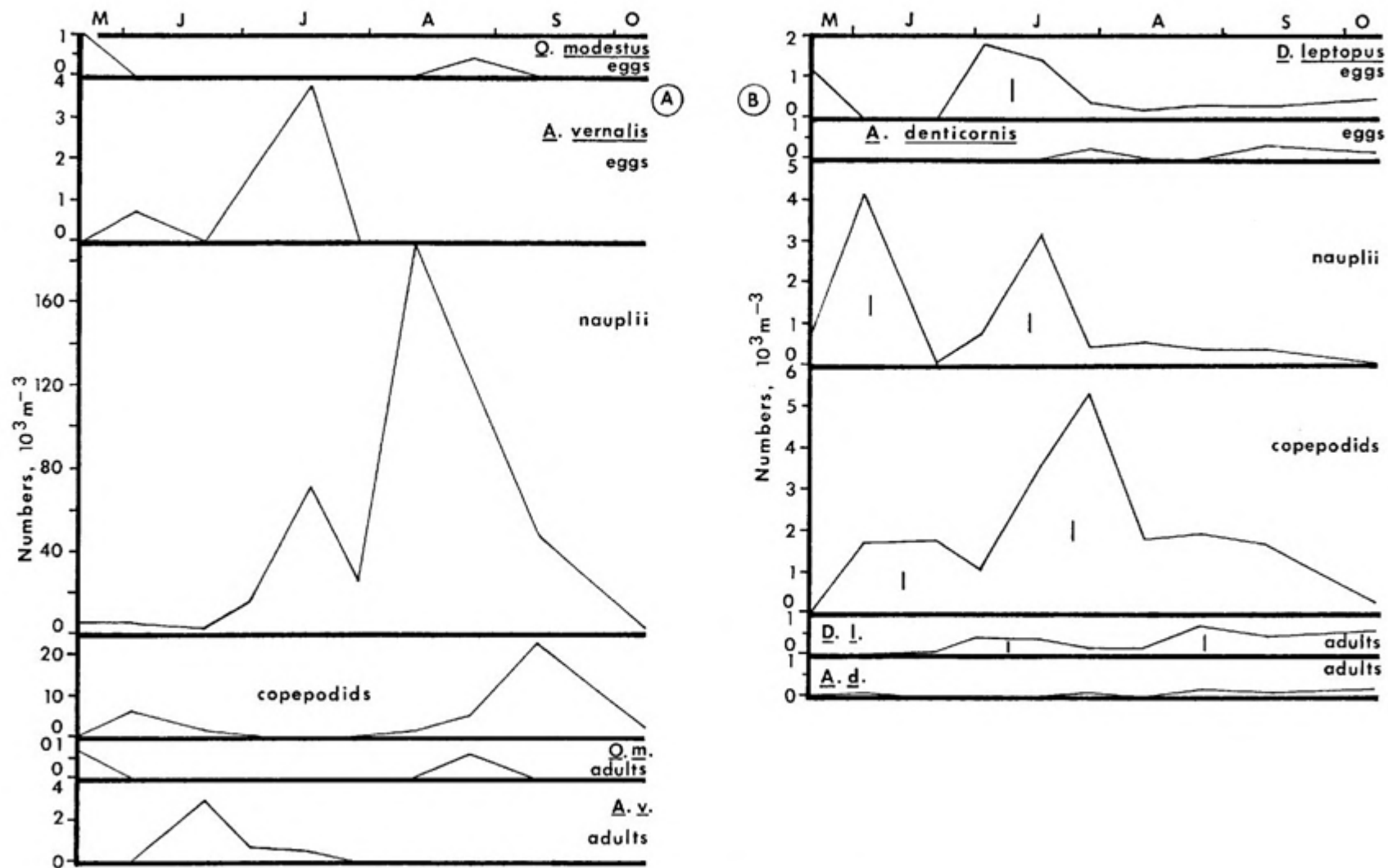


Figure 15. Instar abundance curves and mean dates of pulse (vertical bars) for Cyclopoida (left) and Calanoida (right) in Kingfisher Lake.

The Cyclopoida data revealed no consistent pattern of development (Figure 15A) partly because the different species of nauplii and copepodids could not be separated, but more importantly because all three species in the lake are at least partly benthic and so were not always susceptible to sampling. The nauplius and copepodid curves indicate that three generations of cyclopoids could have developed through the sampling period.

The Calanoida, chiefly *Diaptomus leptopus*, had two main generations during the ice-free period of 1975, one developing from eggs carried in May by winter adults, the other developing from eggs produced in July by the first generation (Figure 15B). It is not clear from Figure 15B whether eggs produced from August to October developed, or whether all instars ceased development, but in the calculations it was assumed that development continued.

The mean day of pulse for several instars could be determined for *Daphnia*, *Ceriodaphnia*, *Bosmina* and the Calanoida (Figures 12, 13A and 15B). These data were used to obtain the smoothed curves of mean pulse-date (Figure 16) and instar development time (Table 8) that yielded the number of individuals passing through each instar (Figure 17).

As Figure 17 clearly shows, the estimated total number of eggs produced cannot account for the number of later size-classes observed in the *Daphnia*, *Ceriodaphnia* or *Bosmina* populations. All three genera produce ephippial eggs (resting eggs) which are not quantitatively collected by vertical plankton tows, and which most likely make up the observed deficit. The number of neonatal *Daphnia* was under-estimated because the development time of the subsequent size-class was used to estimate the development time of neonates. The neonatal individuals had a narrower

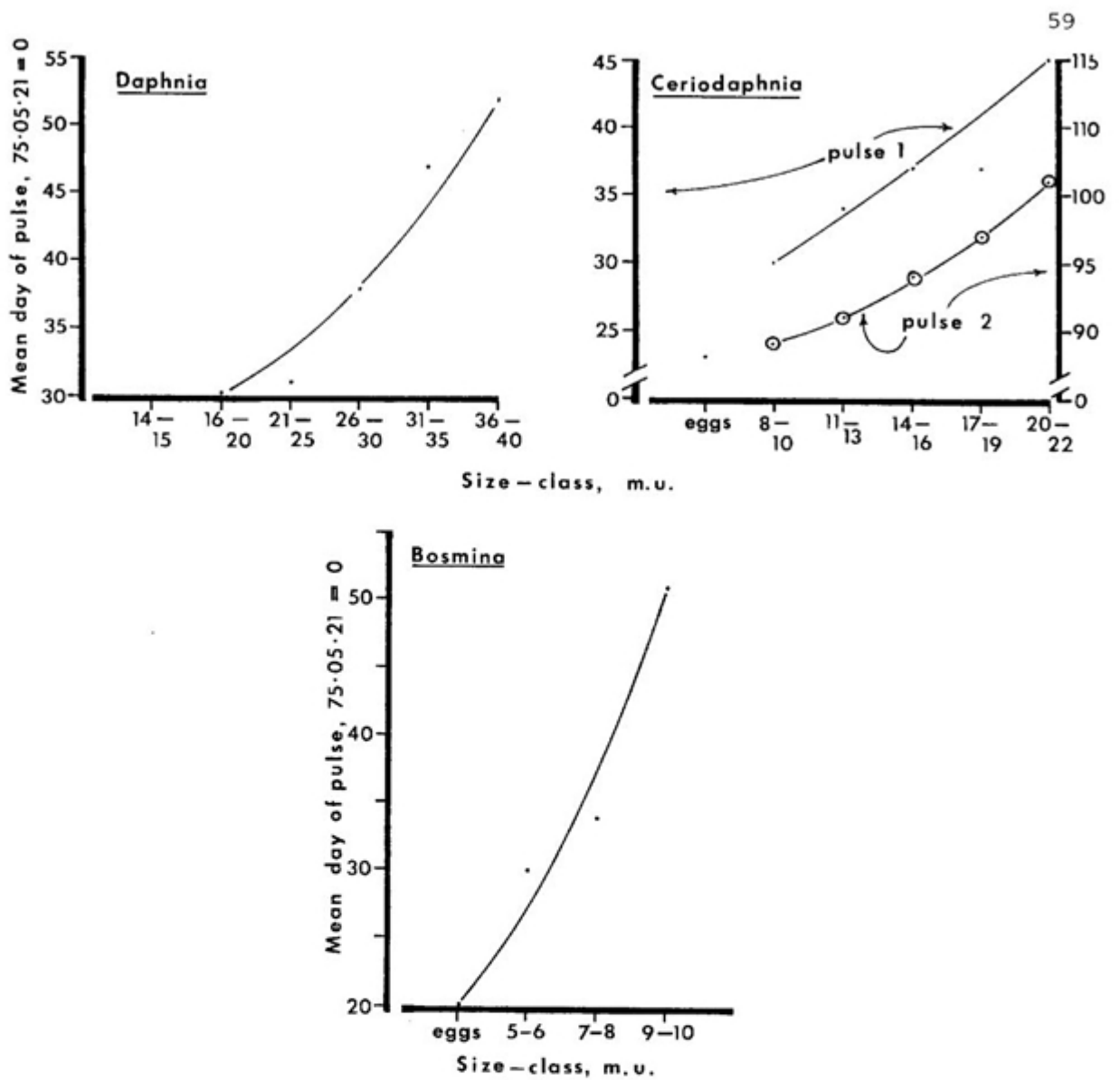


Figure 16. Smoothed curves for determining corrected mean dates of pulse for three Cladocera in Kingfisher Lake.

Table 8. Development times for the instars of four planktonic Crustacea, Kingfisher Lake, May to October 1975. Asterisks indicate estimated times. m.u.: ocular micrometer units (0.0398 m.u. = 1 mm).

<u>Taxon</u>	<u>Size-class (m.u.) or instar</u>	<u>Development time (days)</u>		
		<u>Pulse 1</u>	<u>Pulse 2</u>	<u>Mean</u>
<i>Daphnia</i>	eggs			4.7
	14-15	3.2*		
	16-20	3.2		
	21-25	4.0		
	26-30	5.4		
	31-35	7.0		
	36-40	8.0		
	41-45	8.0*		
<i>Ceriodaphnia</i>	eggs			5.3
	8-10	3.5	2.0	2.8
	11-13	3.6	2.2	2.9
	14-16	3.8	3.0	3.4
	17-19	3.9	3.8	3.8
	20-22	4.0	4.0	4.0
<i>Bosmina</i>	eggs			7.0
	5-6	8.5		
	7-8	12.0		
	9-10	14.0		
	11-12	14.0*		
	13-14	14.0*		
Calanoida	eggs			5.8
	nauplii	9	8	8.5
	copepodids	17.5	21.5	19.5
	adults	26	32	29.0

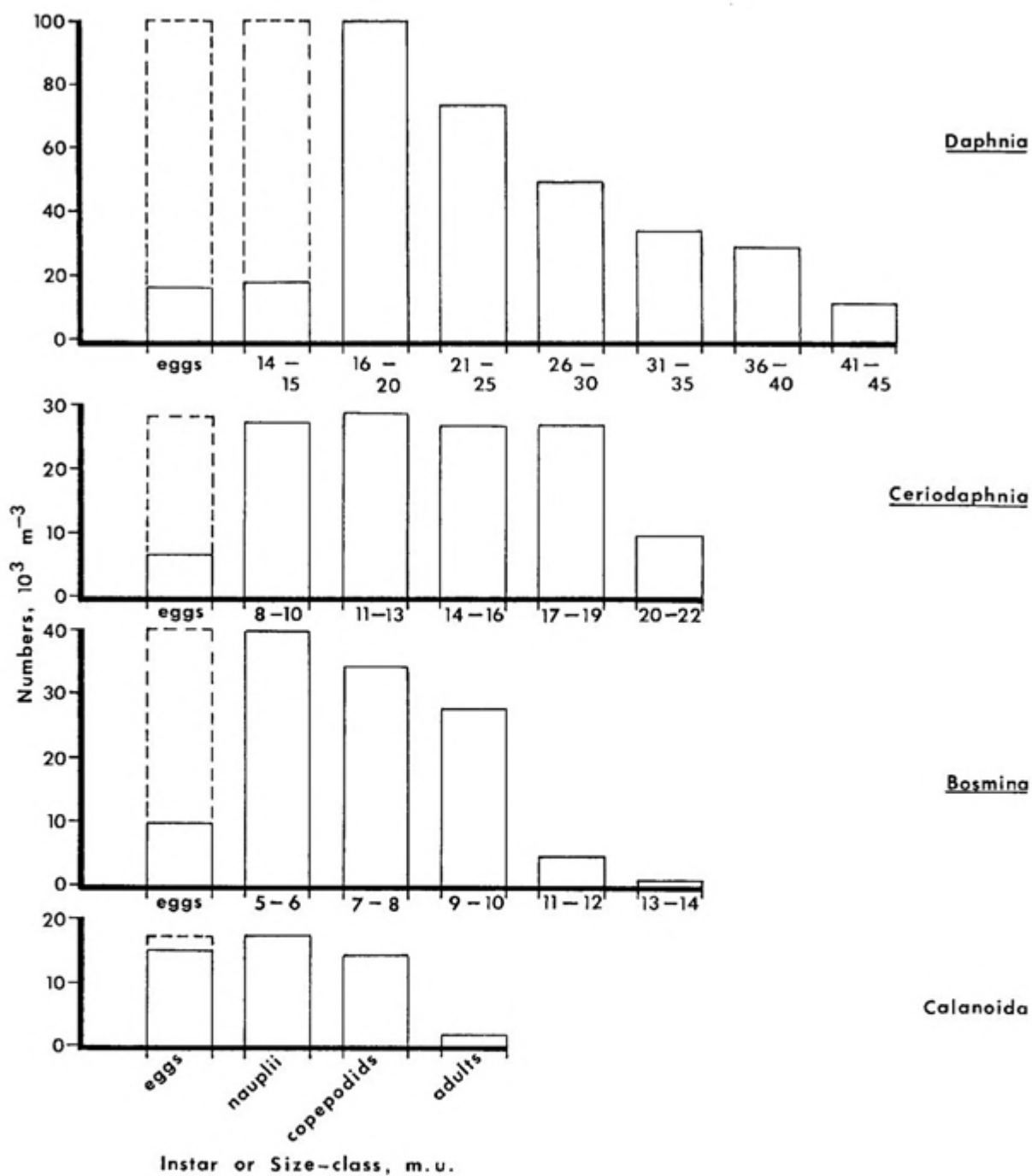


Figure 17. Numbers passing through the instars or size-classes of four planktonic Crustacea in Kingfisher Lake, as calculated by the Southwood method. Dotted lines show adjusted estimates. (see page 58).

size-range so they must have developed much faster than did the subsequent size-class. Calanoida egg numbers may have been slightly underestimated because some eggs were produced before the first sampling date, so were missed in the counts (Figure 18B).

Development times could not be determined for the instars of *Scapholeberis*, *Polyphemus* or the Cyclopoida because the instar abundance data were too sparse or erratic (Figures 13B, 14 and 15A).

Production. Mean summer biomass, mean daily production, total summer production and P/B's for the most abundant Crustacea are summarized in Table 9. Production calculated by the extension of the Southwood method has been adjusted for the minimum number of ephippial eggs (and neonates, in the case of *Daphnia*) that must have developed to produce the maximum number observed in later instars as shown in Figure 17. A similar adjustment to the calculations made by the Pechen-Shushkina method was not possible because the error is not detectable when the method is used alone, and because production is first calculated on a daily basis but the error could not be attributed to individual days.

The Pechen-Shushkina and unadjusted Southwood methods yielded very similar results; in the case of *Bosmina* results were identical. Both methods, however, provide underestimates because they fail to account for production from ephippial eggs to at least the neonatal size-class. The error is relatively small despite the large difference in estimated egg numbers, amounting to less than 11% in the case of *Daphnia*, where the discrepancy between unadjusted and adjusted values was greatest. Even the adjusted Southwood estimates are at least slightly low because zero mortality was assumed for the developing ephippial eggs.

Table 9. Production and biomass (dry weight) of planktonic Crustacea in Kingfisher Lake, May to October, 1975 (140 days). Asterisks indicate assumed values. P: production, $\bar{B}$: mean biomass.

<u>Taxon</u>	<u>Method</u>	mean summer biomass <u>mg m⁻³</u>	mean daily production <u>mg m⁻³</u>	total summer production <u>mg m⁻³</u>	summer P/ $\bar{B}$
<i>Daphnia (pulex group)</i>	Pechen-Shushkina	76.3	5.6	780	10.2
	Southwood (unadjusted)	76.3	6.0	840	11.0
	Southwood (adjusted)	76.3	6.7	940	12.3
<i>Ceriodaphnia</i>	Pechen-Shushkina	7.1	1.3	180	25
	Southwood (unadjusted)	7.1	1.4	190	27
	Southwood (adjusted)	7.1	1.4	200	28
<i>Bosmina longirostris</i>	Pechen-Shushkina	6.4	0.42	59	9.4
	Southwood (unadjusted)	6.4	0.42	59	9.4
	Southwood (adjusted)	6.4	0.46	64	10.1
<i>Scapholeberis kingi</i>	maximum observed biomass	0.5	≥ 0.02	≥ 2.6	≥ 5
	estimated maximum P/ $\bar{B}$	0.5	≤ 0.14	≤ 20	35*
<i>Polyphemus pediculus</i>	maximum observed biomass	1.9	≥ 0.1	≥ 15.7	≥ 8
	estimated maximum P/ $\bar{B}$	1.9	≤ 0.5	≤ 70	$\leq 35^*$
Cyclopoida	maximum observed biomass	9.1	≥ 0.3	≥ 41.4	≥ 4
Calanoida	Pechen-Shushkina	17.5	1.1	150	8.5
	Southwood (unadjusted)	17.5	1.1	160	9.1
	Southwood (adjusted)	17.5	1.1	160	9.1

Only crude estimates of production of *S. kingi* and *P. pediculus* were possible because instar development times could not be measured. Both species had at least one generation through the summer, so the maximum observed biomass provides a minimum estimate of summer production. Calculations of *P. pediculus* production in Mud Lake showed that summer $P/\bar{B}$'s for Cladocera in Lake Louise area lakes could be as high as 30 to 40, so $35\bar{B}$ should give a reasonable estimate of maximum summer P for *P. pediculus* and *S. kingi* in Kingfisher Lake.

The production and biomass figures for Cyclopoida are minimum estimates. The summer P given in Table 9 is the sum of the maximum observed biomasses of each of three cohorts. It is based on the assumption that no individuals died or were missed by the sampler. Since neither assumption is likely to be true, the actual summer P must be larger.

Daphnia had by far the greatest production of any crustacean in the Kingfisher Lake plankton, followed by *Ceriodaphnia* and the Calanoida. *Bosmina*, *Polyphemus* and probably the Cyclopoida had similar summer production, each ranking after the Calanoida. *Scapholeberis* was the least important planktonic crustacean in terms of production.

Mud Lake

Species composition. *Daphnia* (*pulex* group) *Bosmina longirostris*, *Polyphemus pediculus*, *Acanthodiaptomus denticornis* and *Acanthocyclops vernalis* were the most common crustacean plankters in Mud Lake. *Chydorus sphaericus* was occasionally found in the samples, but was never common. A single specimen of *Daphnia rosea* Sars, 1862 emend Richard 1896 was also found.

The *Daphnia* species could not be positively identified. As was the case in Kingfisher Lake, there were many intergrading specimens showing characters of two or more of *Daphnia pulex*, *D. schødleri* and *D. pulicaria*.

Instar analysis. The courses of development of the largest populations of Crustacea are shown in Figures 18 and 19.

The three cladoceran populations each had a single large pulse beginning in June or July. *Bosmina* had disappeared from the plankton by August and *Polyphemus* had become uncommon by then, but *Daphnia* continued to be common until at least early October.

Acanthocyclops vernalis had three generations during the summer, but only the first produced a large number of copepodids and adults: few second-generation, and practically no third-generation copepodids and adults appeared in the samples despite the large numbers of nauplii present through the summer.

Acanthodiaptomus denticornis, the other common copepod in Mud Lake, had two generations through the summer of 1975. The first hatched from resting eggs in May and June, reaching maturity in late June and early July. It then produced eggs giving rise to the second generation that reached maturity in late July or early August. Eggs produced by the second generation accumulated in the population and were presumably resting eggs.

The mean days of pulse could be determined for the three cladoceran species (Figure 18). These data for *Daphnia* and *Polyphemus*, were plotted against size-class (Figure 20). The smoothed values so obtained plus the pulse dates calculated for *Bosmina* (Figure 18B) were used to calculate the development time of each size-class (Table 10), the development times being used in turn to determine the number of individuals passing through each instar (Figure 21).

As Figure 21 shows, the estimated number of eggs (and neonates in the case of *Daphnia*) were too low to account for the number of indi-

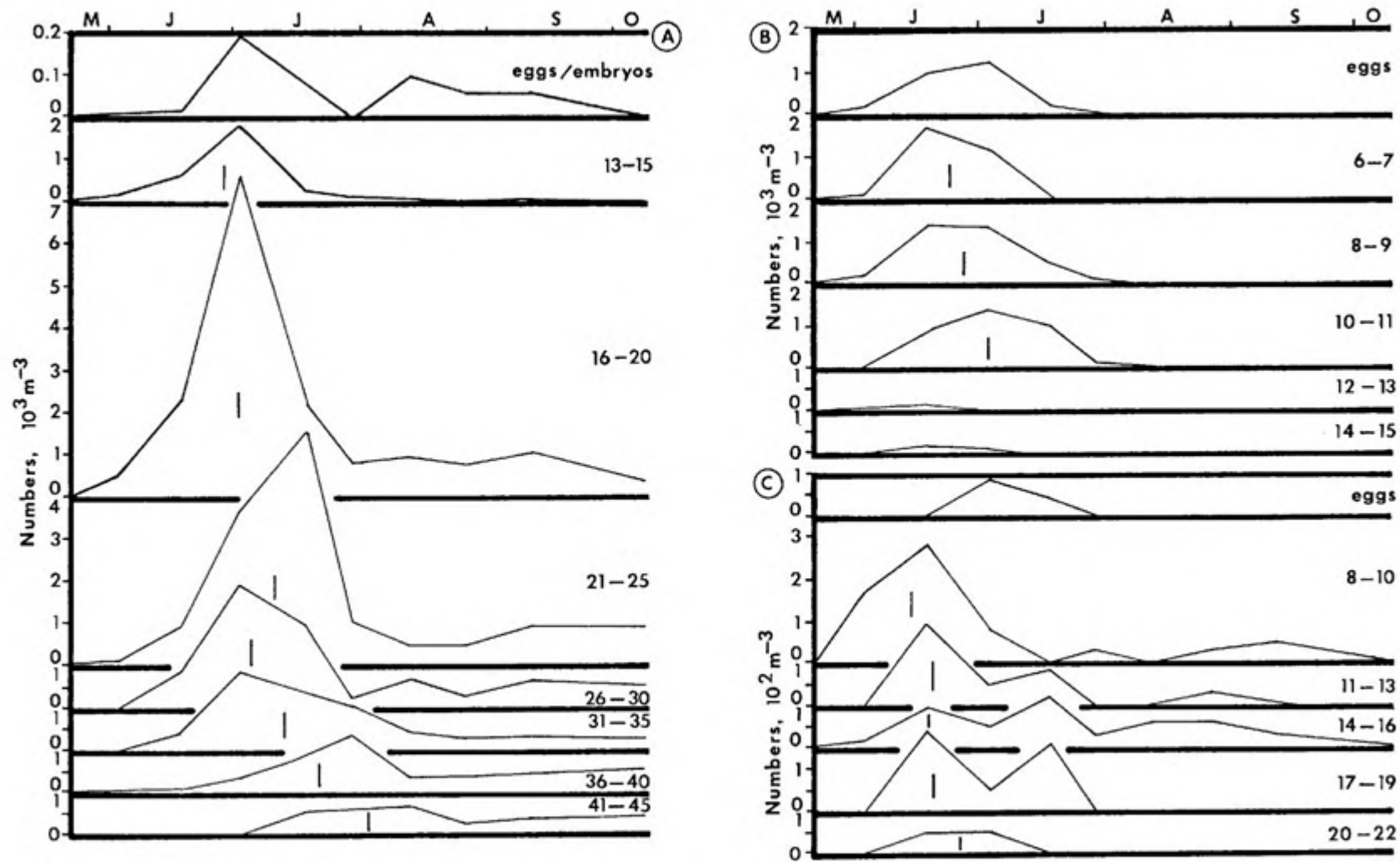


Figure 18. Size-class abundance curves and mean date of pulse (vertical bars) for *Daphnia* (A), *Bosmina* (B) and *Polyphemus* (C) in Mud Lake. Size-classes in micrometer units (m.u.). 1 m.u. = 0.0398 mm

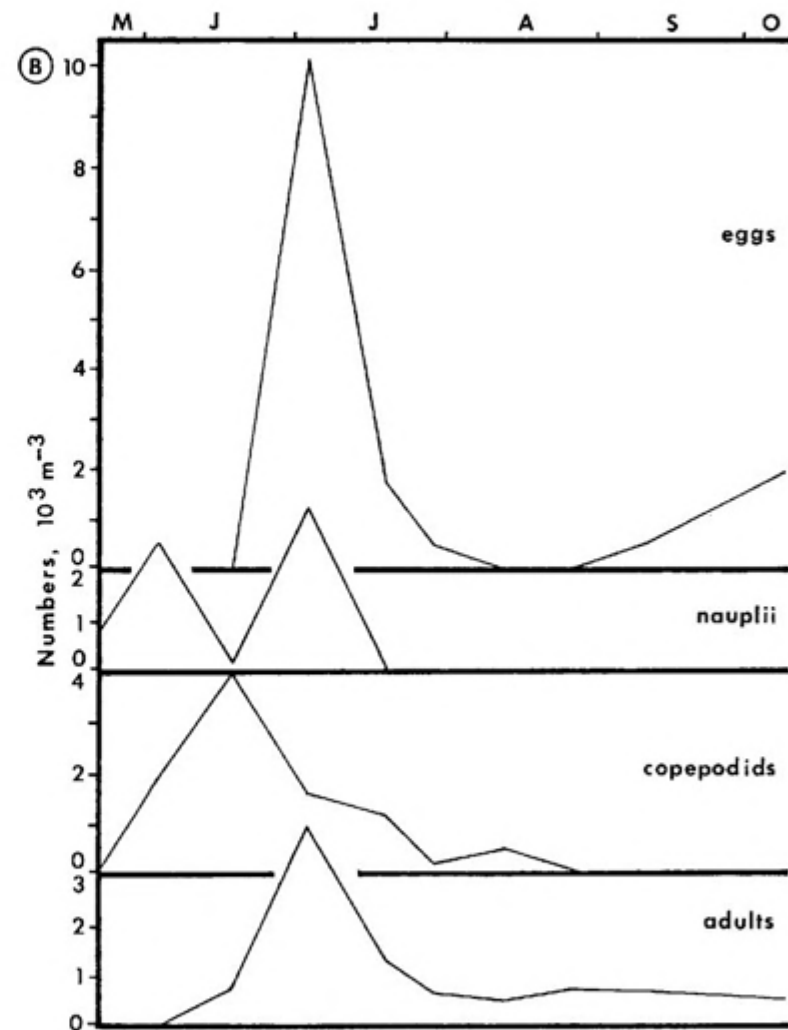
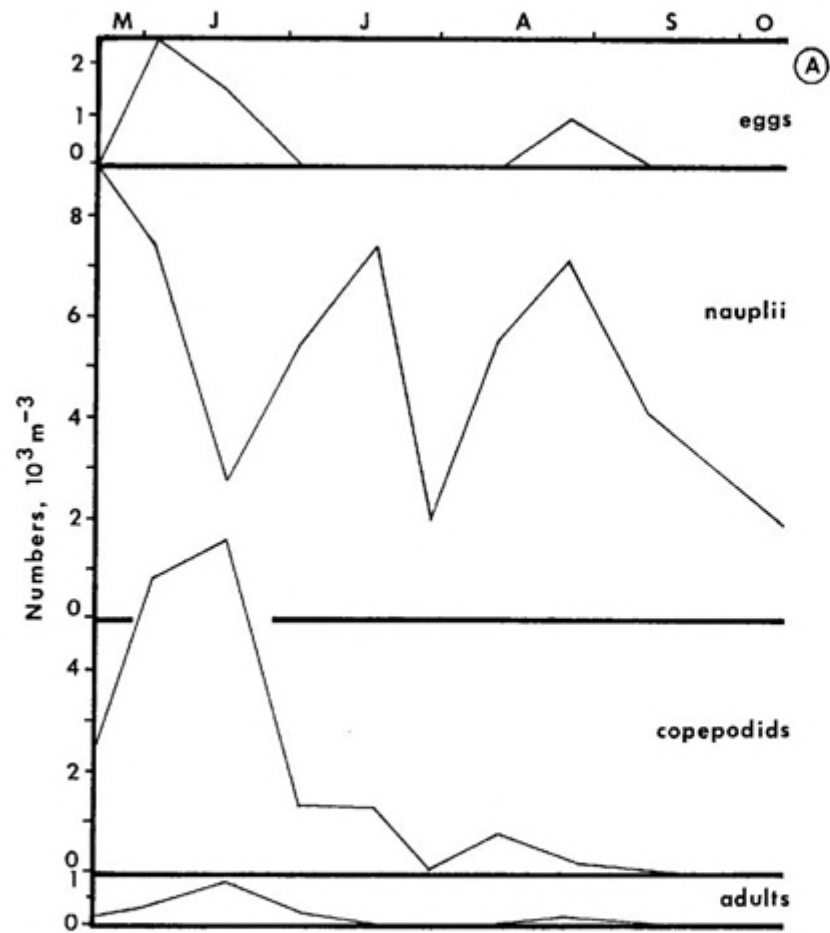


Figure 19. Instar abundance curves for *Acanthocyclops vernalis* (left) and *Acanthodiaptomus denticornis* (right) in Mud Lake.

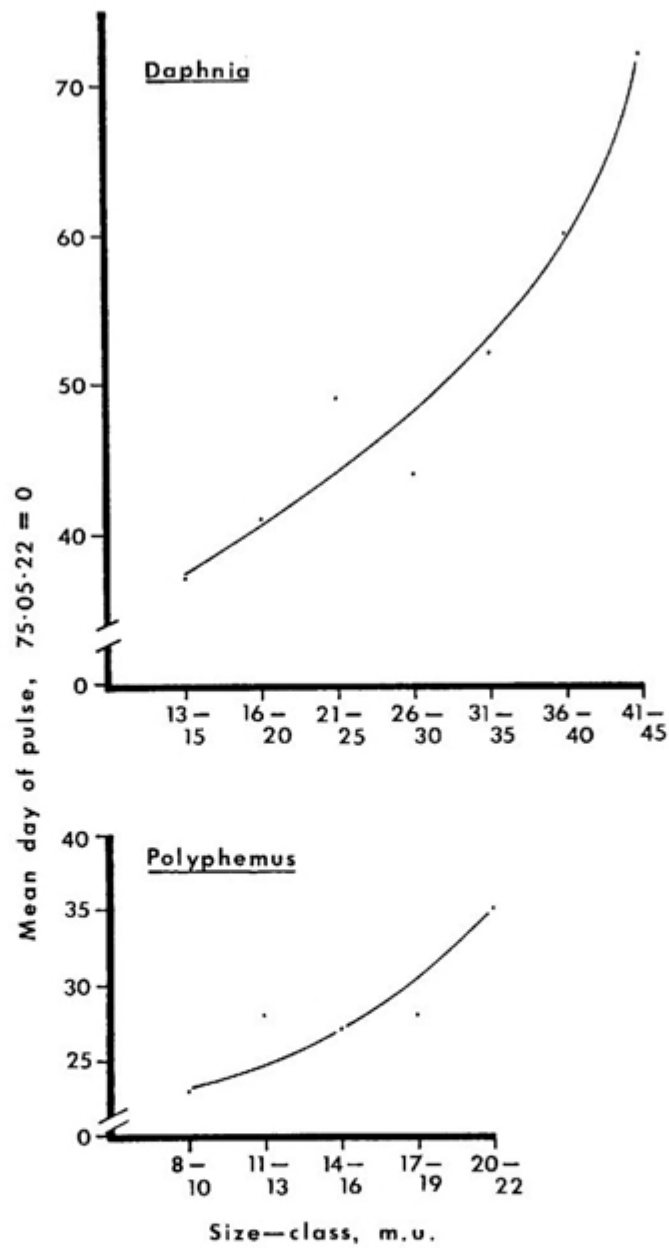


Figure 20. Smoothed curves for determining corrected mean dates of pulse for two Cladocera in Mud Lake.

Table 10. Development times for the size-classes of three species of planktonic Crustacea, Mud Lake, May to October, 1975. Asterisks indicate estimated values. m.u.: ocular micrometer units (0.0398 m.u. = 1 mm)

<u>Taxon</u>	<u>Size-class (m.u.) or instar</u>	<u>Development time (days)</u>
<i>Daphnia</i>	eggs	7.0
	13-15	3.0
	16-20	3.2
	21-25	3.8
	26-30	4.5
	31-35	5.8
	36-40	9.5
	41-45	12.5
<i>Bosmina</i>	eggs	7.5
	6-7	4
	8-9	5
	10-11	6
	12-13	6*
	14-15	6*
<i>Polyphemus</i>	eggs	7.0
	8-10	1.8
	11-13	2.0
	14-16	2.8
	17-19	4.0
	20-22	4.5

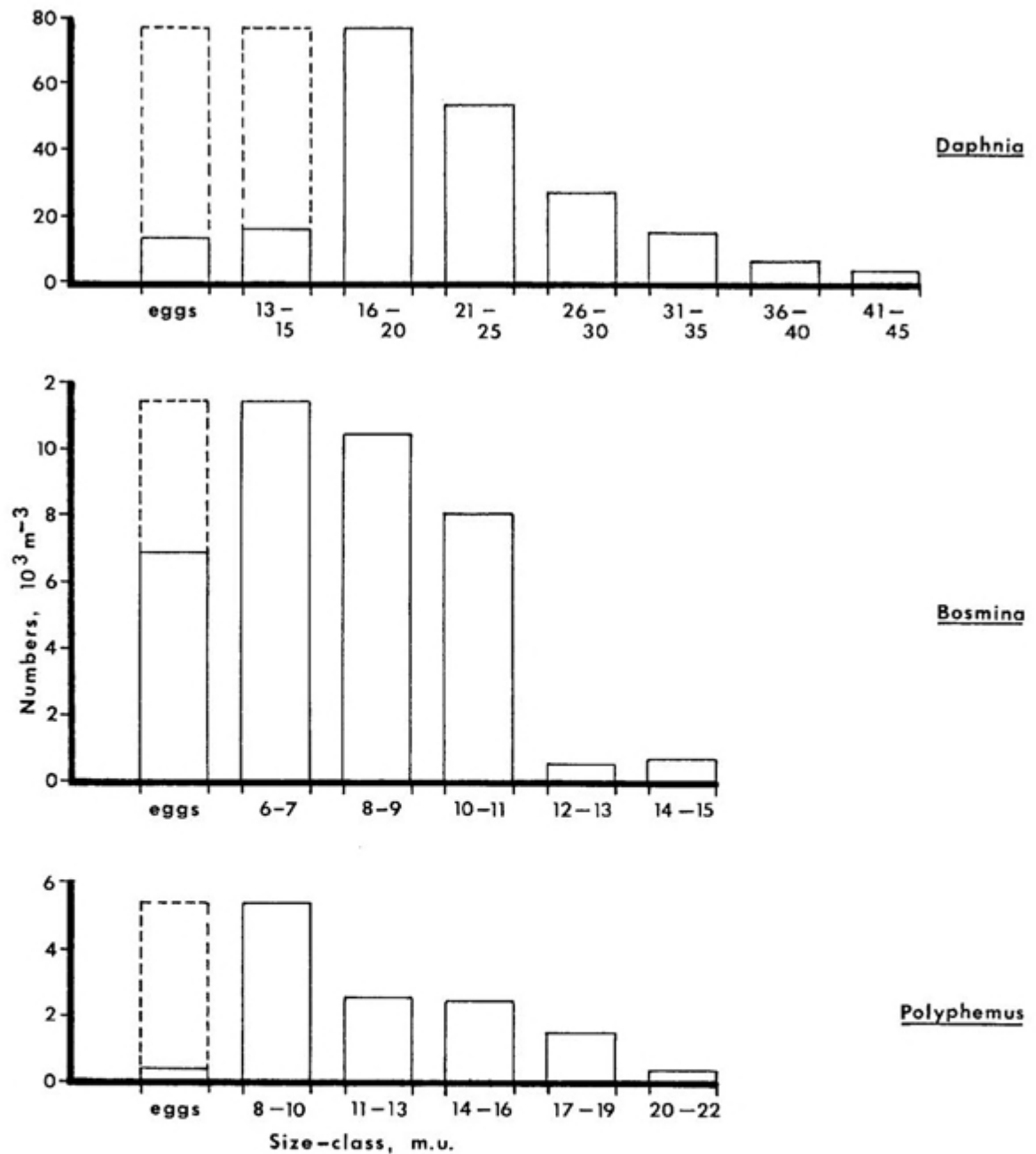


Figure 21. Numbers passing through the size-classes of three Cladocera in Mud Lake as calculated by the Southwood method. Dotted lines show adjusted estimates.

viduals passing through later instars, the difference presumably being made up by the hatching of resting eggs. *Daphnia* neonate numbers were underestimated because the neonate size range was narrower than that of the following instar. Individuals would have passed quickly through the neonatal instar and much more slowly through the next instar. The time between the mean days of pulse of the two stages, used to estimate development time, would have been spent mostly in the later instar.

The data on *Acanthocyclops* instar abundance were unsuitable for determining instar durations (Figure 19A), so total numbers passing through each instar could not be calculated.

The adequacy of the *Acanthodiaptomus* data was checked during the production calculations (Figure 22). The first generation suffered virtually no mortality until maturity was reached. In contrast, the second generation showed high mortality initially, but little in the late instars. Estimated egg numbers were adequate to account for the numbers of later instars observed.

Production. Biomass and production measurements are presented in Table 11. The Pechen-Shushkina and unadjusted Southwood methods were in reasonably good agreement but both underestimated production because they did not account for production from ephippia to the first size-class. The degree of error in the unadjusted Southwood method was about 16% in the case of *Daphnia*, but was less for *Bosmina* and *Polyphemus*, when the adjusted and unadjusted figures were compared.

The sum of the maximum biomasses observed in each of the three generations was the only measure of production available for *Acanthocy-*

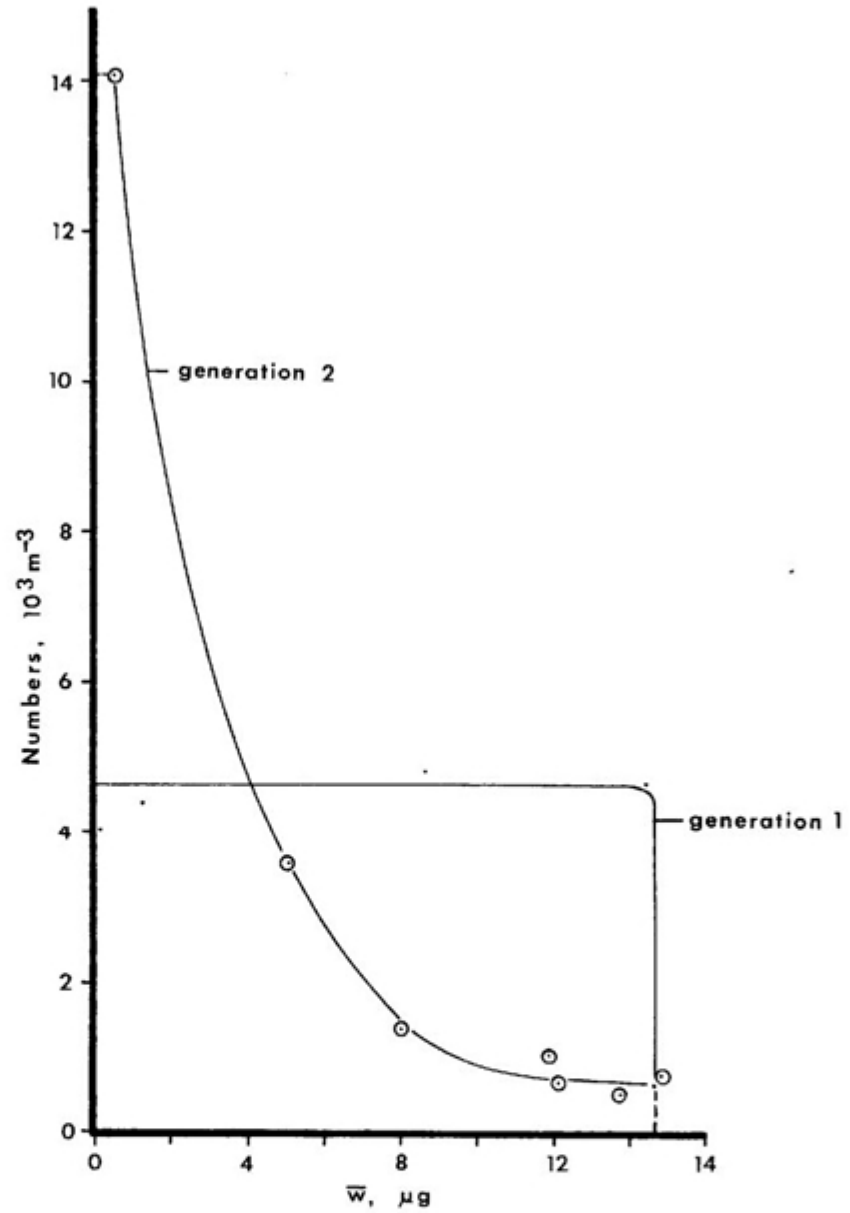


Figure 22. Allen Curves for two generations of *Acanthodiptomus denticornis* in Mud Lake. $\bar{w}$ is in dry weight.

Table 11. Production and biomass (dry weight) of planktonic Crustacea in Mud Lake, May to October, 1975 (139 days).

<u>Taxon</u>	<u>Method</u>	mean summer biomass <u>mg m⁻³</u>	mean daily production <u>mg m⁻³</u>	total summer production <u>mg m⁻³</u>	summer P/ $\bar{B}$
<i>Daphnia</i> (<i>pulex</i> group)	Pechen-Shushkina	34.8	3.0	420	12.1
	Southwood (unadjusted)	34.8	3.2	440	12.6
	Southwood (adjusted)	34.8	3.7	520	14.8
<i>Bosmina longirostris</i>	Pechen-Shushkina	1.1	0.13	18	16
	Southwood (unadjusted)	1.1	0.17	23	21
	Southwood (adjusted)	1.1	0.17	24	22
<i>Polyphemus pediculus</i>	Pechen-Shushkina	0.5	0.11	15	30
	Southwood (unadjusted)	0.5	0.12	17	34
	Southwood (adjusted)	0.5	0.14	19	38
<i>Acanthocyclops vernalis</i>	maximum observed biomass	3.4	≥ 0.1	≥ 15	≥ 4.4
<i>Acanthodiaptomus denticornis</i>	Allen Curve, generation 1	33.4 ^a		67	2.0 ^a
	Allen Curve, generation 2	13.0 ^a		53	4.1 ^a
	whole summer	20.1	0.9 ^b	120	6.0

^a Biomass calculated from Allen Curves (Figure 22) as the mean for each cohort; therefore P/ $\bar{B}$'s are per cohort.

^b Production not referable to a precise period; calculation assumes 139-day production period.

clops vernalis. Actual production must have been at least equal to the sum of maximum biomasses, and was probably greater because production by many individuals that died before reaching maturity was not included.

Despite the great difference in the pattern of mortality between the two generations of *Acanthodiaptomus*, production of both generations was similar. The greater production of early instars of the second generation was largely compensated for by a higher mortality rate.

Daphnia had by far the greatest production among the planktonic crustaceans, followed by *Acanthodiaptomus*. Actual production of *Acanthocyclops* could have been near that of *Bosmina* and *Polyphemus*, which had similar summer production, ranking third and fourth, respectively.

Moraine Lake

Diaptomus arcticus Marsh, 1920 was by far the most abundant crustacean in the plankton, *Daphnia middendorffiana* Fischer, 1851 being sparsely represented in the samples on all three sampling dates. Only one specimen of the cyclopoid *Acanthocyclops vernalis* was found.

Copepodids dominated the *Diaptomus arcticus* population in July and August, but by September almost the entire population was mature and eggs were being produced (Figure 23A). Up to 910 *D. arcticus* per square metre were present on or in the bottom sediments (see Moraine Lake benthic data, Section 4), but no more than 5% of the population was benthic on any one sampling date.

Annual production by *Diaptomus arcticus* estimated from the Allen Curve in Figure 23B was 65 mg m^{-3} dry weight, including the benthic portion of the population. The observed summer $\bar{B}$ for 1975 including benthic

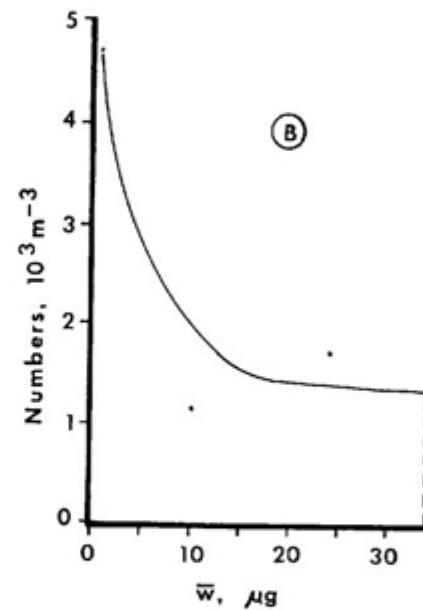
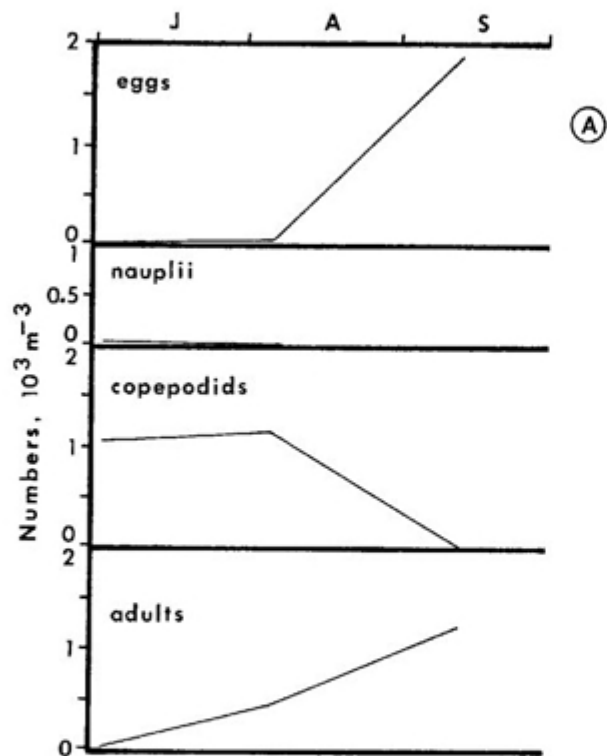


Figure 23. Instar abundance diagrams and an Allen Curve for *Diaptomus arcticus* in Moraine Lake. $\bar{w}$ is in dry weight.

D. arcticus, was 33.9 mg m^{-3} dry weight, giving a summer $P/\bar{B}$ of 1.9. The cohort $\bar{B}$ calculated from Figure 23B was 26.3 mg m^{-3} dry weight, yielding a $P/\bar{B}$ of 2.5 per cohort.

Too few *Daphnia middendorffiana* were collected for an adequate instar analysis: the maximum observed abundance was only 117 m^{-3} . The only available estimate of production was the product of the observed summer $\bar{B}$ and an assumed summer $P/\bar{B}$. In Baker Lake *D. middendorffiana* had a summer $P/\bar{B}$ near 8.5 (see below), so the $\bar{B}$ of 1.81 mg m^{-3} for the same species in Moraine Lake was multiplied by 8.5 to obtain an estimated summer P of approximately 15 mg m^{-3} dry weight.

Lower Consolation Lake

The calanoid copepod *Diaptomus tyrrelli* Poppe, 1888 was the only crustacean present in the plankton in significant numbers. The only other planktonic crustacean present was *Acanthocyclops vernalis*, of which one specimen was found in the samples.

D. tyrrelli nauplii and copepodids co-dominated the population in June (Figure 24A). By early August, many had matured and some eggs were produced. In September nearly all of the population was mature and many females were carrying eggs.

The method used to estimate the number of eggs giving rise to the *D. tyrrelli* population yielded an underestimate (Figure 24B). The true number of eggs must have been at least the number of individuals observed on the first sampling date, so this was taken to be the best available estimate of egg numbers and production was calculated accordingly.

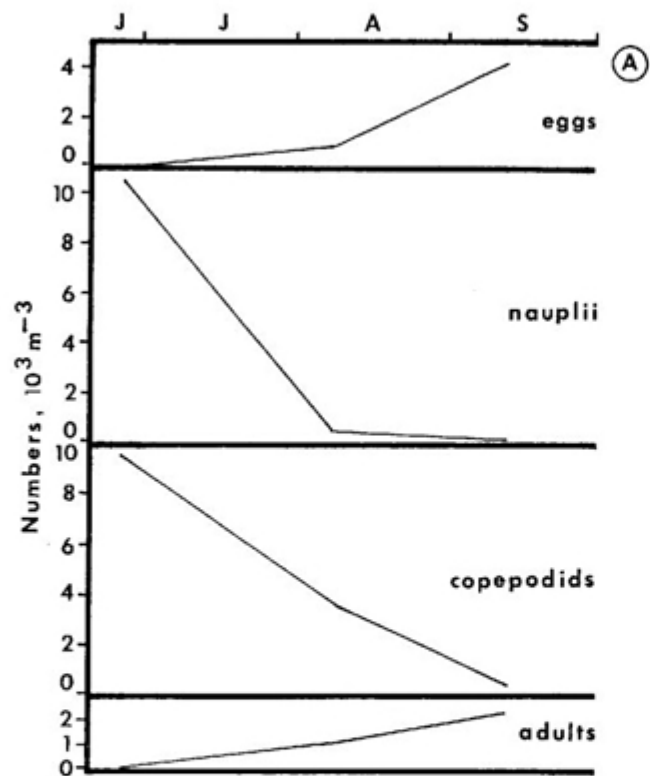
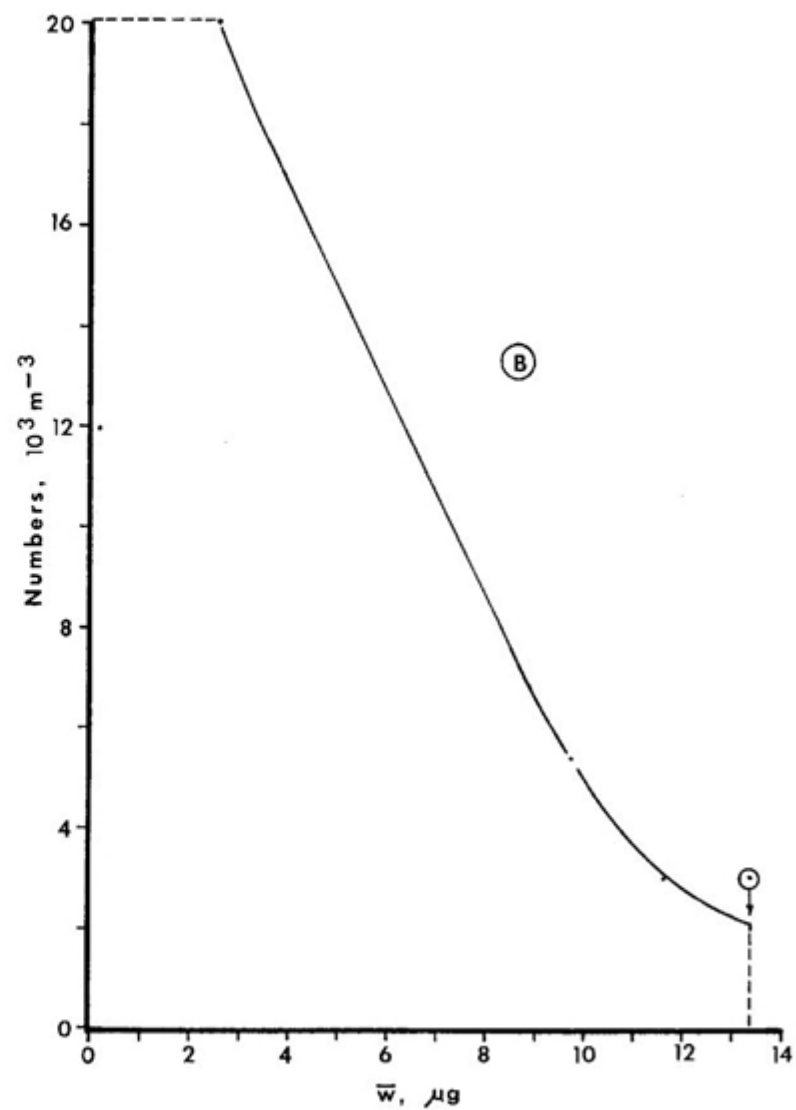


Figure 24. Instar abundance diagrams and an Allen Curve for *Diaptomus tyrrelli* in Lower Consolation Lake. $\bar{w}$ is in dry weight.



Annual production of *D. tyrrelli* was at least 150 mg m^{-3} dry weight. Mean biomass calculated from the samples was 46.2 mg m^{-3} dry weight, yielding a $P/\bar{B}$ of $= 3.3$. Mean biomass calculated from the Allen Curve was 53.12 mg m^{-3} dry weight, giving a $P/\bar{B}$ of 2.9 per cohort.

Baker Lake

The most abundant crustacean species in the Baker Lake plankton were *Daphnia middendorffiana*, *Diaptomus tyrrelli* and *Diaptomus arcticus*. *Chydorus sphaericus* and *Acanthocyclops vernalis* occurred infrequently in the samples.

Daphnia middendorffiana produced a single pulse of eggs in August (Figure 25A). Pulses in later instars appear to be a composite of animals present in July and animals arising from the August egg pulse; consequently only crude estimates of size-class development times were possible.

The mean water temperature of Baker Lake must not have exceeded 10°C (Figure 11), yielding a calculated egg development time of 8.1 days. Among four size-classes, the intervals between mean days of pulse were 6, 8 and 3 days (Figure 25A), or approximately 6 days on the average. The area under each size-class curve was divided by 6 days to obtain a first estimate of the numbers passing through each class (Figure 25B). As expected, numbers in some size-classes were overestimated and others were underestimated, the line drawn through the points by eye, providing the best available estimate of number in each class (comparable to Richards and Waloff's first method; Southwood 1966:281). Egg numbers were underestimated because animals present on the first sampling date had hatched

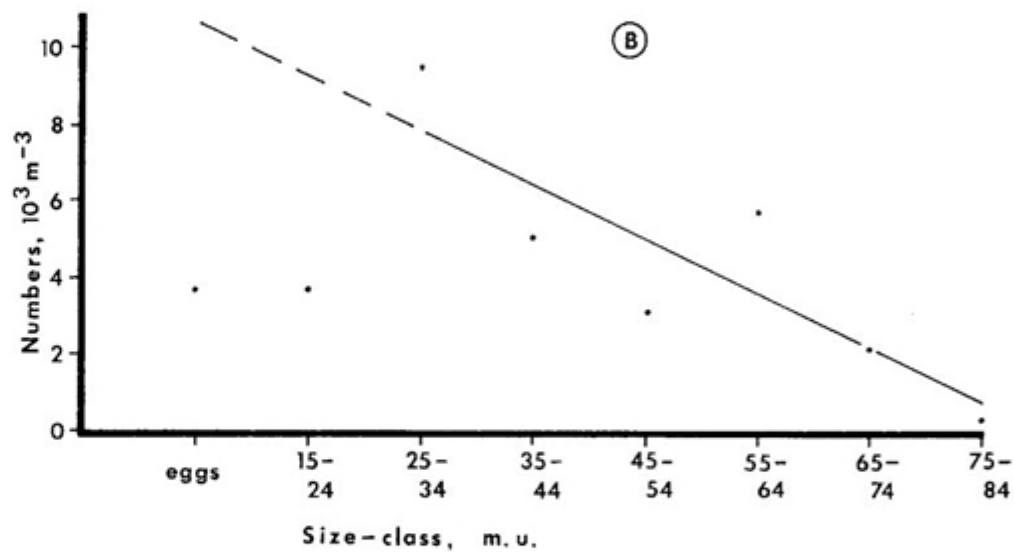
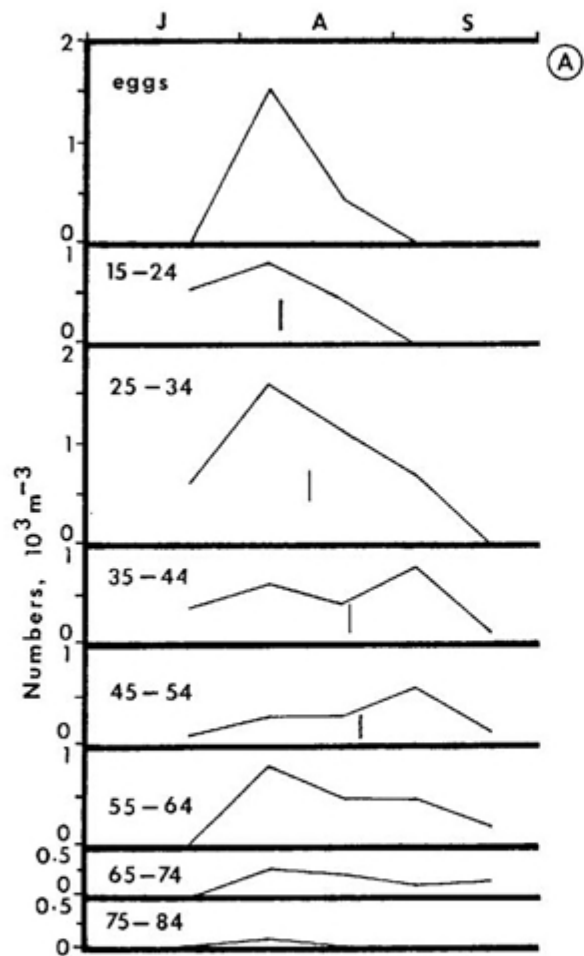


Figure 25. Size-class abundance curves for *Daphnia middendorffiana* in Baker Lake, and estimated numbers passing through each size-class.

prior to that date from eggs that were not sampled. Similarly, the neonatal size-class may have been underestimated in part because of an overestimated development time, and in part because many in the class developed before the first sampling date.

The numbers passing through each size-class were read from the line in Figure 25B and production was calculated by the Southwood method. To the nearest 50 mg, summer production of *D. middendorffiana* was 450 mg m⁻³ dry weight. Mean summer biomass was 52.73 mg m⁻³, yielding a summer $P/\bar{B}$ of 8.5.

The *Diaptomus tyrrelli* population consisted mostly of copepodids in late July, but by late August most of the population was mature. The adults produced a peak of eggs in early September (Figure 26A).

Annual production of *D. tyrrelli* calculated from Figure 26B was 57 mg m⁻³ dry weight. Mean summer biomass was 31.6 mg m⁻³ dry weight, resulting in a $P/\bar{B}$ of 1.8. From the Allen Curve $\bar{B} = 24.62$ mg m⁻³ dry weight, giving a cohort $P/\bar{B}$ of 2.3.

By the time Baker Lake was first sampled in late July, 1975, the *Diaptomus arcticus* population consisted mainly of copepodids (Figure 27). By late August almost the entire population was mature, but as of the late September sampling date no eggs had been produced. Much of the *D. arcticus* population ($\bar{x} = 24\%$, range 8 to 35%) was benthic (see Section 4), but both parts of the population are included in the production calculation here.

Without either an estimate of the number of eggs giving rise to the generation or the number of early nauplii produced, it was not possible to construct an Allen Curve for *Diaptomus arcticus*. The only

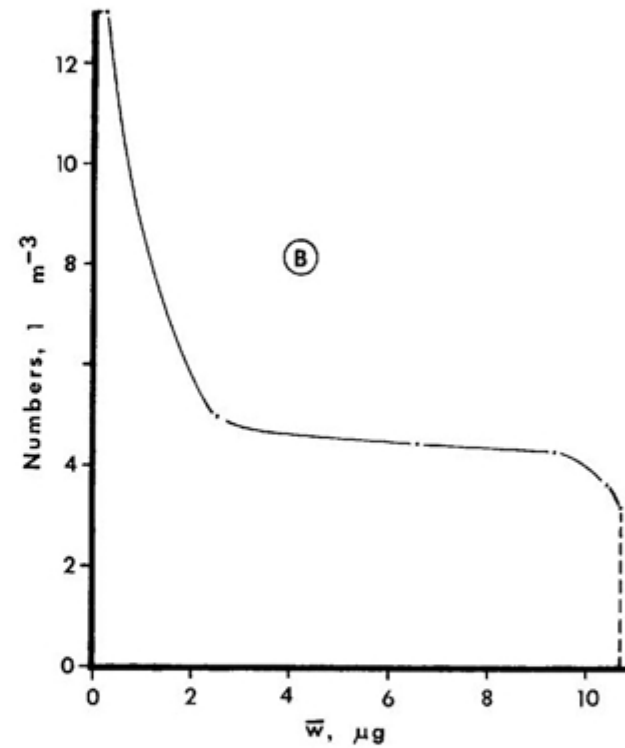
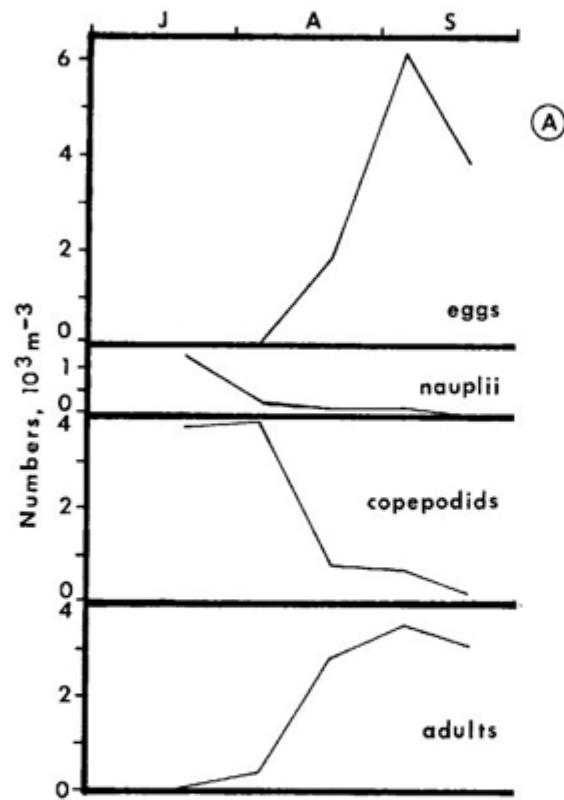


Figure 26. Instar abundance curves and an Allen Curve for *Diaptomus tyrrelli* in Baker Lake. $\bar{w}$ is in dry weight.

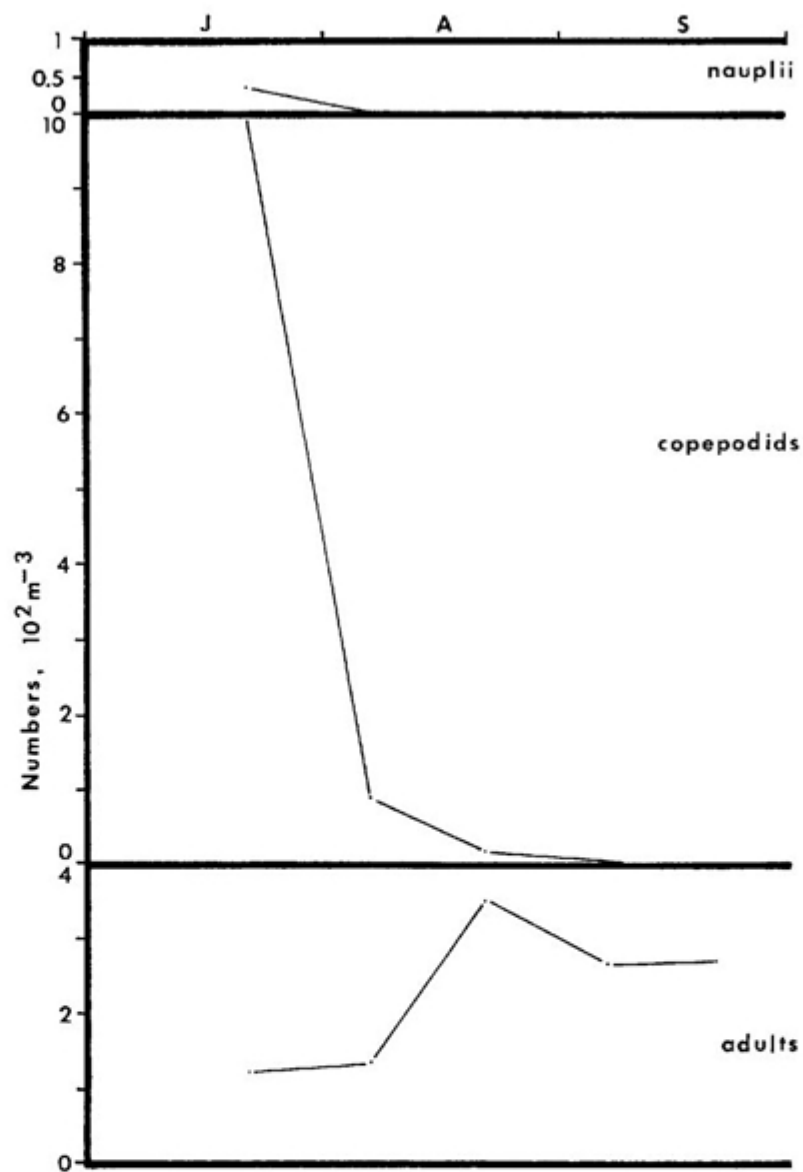


Figure 27. Instar abundance diagrams for *Diaptomus arcticus* in Baker Lake.

available estimate of production was the product of the mean observed biomass and an estimated $P/\bar{B}$. The mean $P/\bar{B} \pm \text{SE}$ for four calanoid populations in the present study plus one calculated for Snowflake Lake *Diaptomus tyrrelli* (see Discussion) was 2.24 ± 0.28 . The summer $\bar{B}$ for *D. arcticus* in Baker Lake of 41.5 mg m^{-3} dry weight was multiplied by 2.24 to obtain an estimated annual production of 90 mg m^{-3} .

Ptarmigan Lake

Diaptomus tyrrelli was the only crustacean that was at all abundant in the plankton of Ptarmigan Lake. Specimens of *Daphnia middendorffiana* and *Chydorus sphaericus* were rarely found (not more than two per one-eighth subsample).

The *Diaptomus tyrrelli* population was composed of nearly equal numbers of nauplii and copepodids in late July, 1975 (Figure 28A). By late August most individuals were in the copepodid stage, and by late September most were mature, many of the females carrying eggs.

Production by the cohort as calculated from Figure 28B was approximately 60 mg m^{-3} dry weight. Cohort $\bar{B}$ calculated from the Allen Curve was 24.30 mg m^{-3} dry weight and observed summer $\bar{B}$ was 27.3 mg m^{-3} dry weight, yielding a cohort $P/\bar{B}$ of 2.6, or a $P/\bar{B}$ of 2.3 (observed $\bar{B}$).

DISCUSSION

Annual Production

Data on annual production would improve the comparability of the zooplankton production estimates. Most of the calculations, however, estimated only summer production.

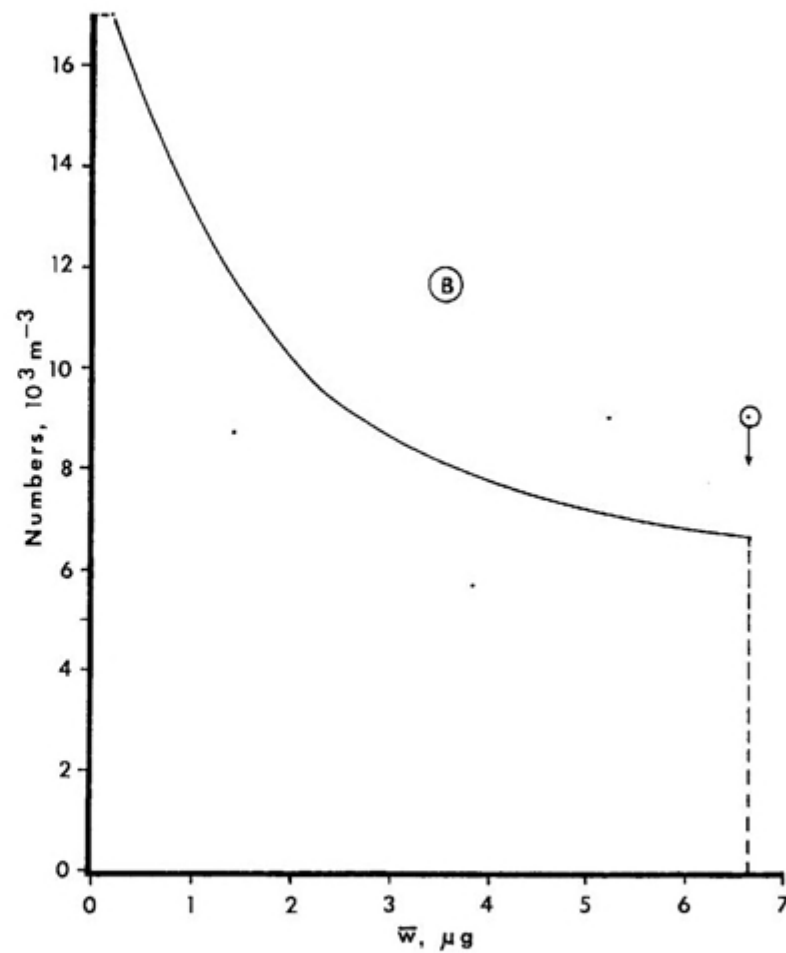
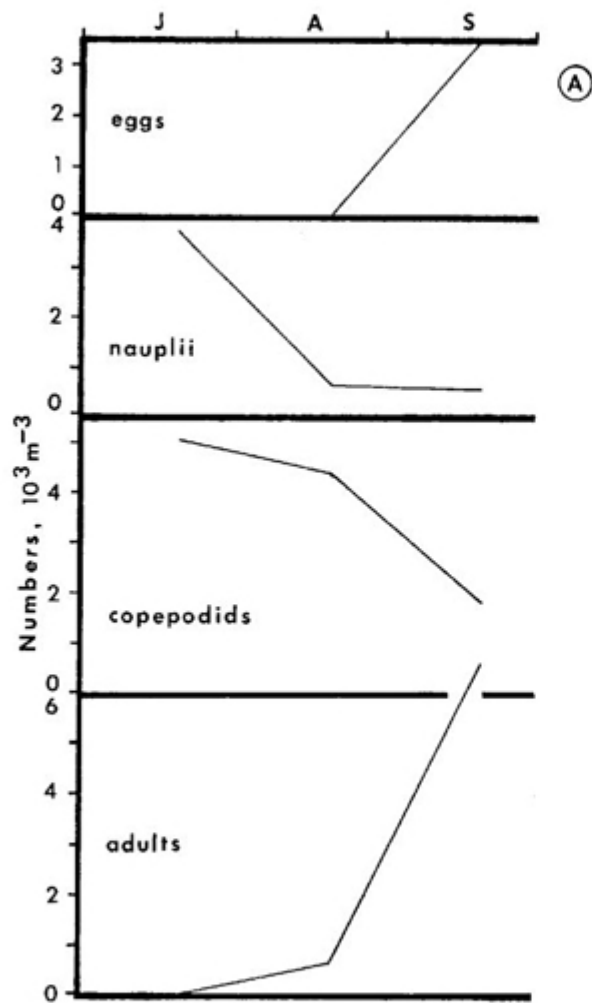


Figure 28. Instar abundance diagrams and an Allen Curve for *Diaptomus tyrrelli* in Ptarmigan Lake. Circled point in the Allen Curve is a maximum estimate made by assuming that all immatures present on the last sampling date survived to adulthood.

The instar abundance data suggest that most of the cladoceran populations completed most or all of their annual production during the sampling period. In Kingfisher and Mud Lakes, few or no *Ceriodaphnia*, *Bosmina*, *Scapholeberis* or *Polyphemus* were present on the earliest and latest sampling dates (Figures 12B, 13, 14, 18B and C). *Daphnia* was present in both lakes on either the earliest or latest sampling dates, but at much lower abundance than in mid-summer (Figures 12A, 18A). In Baker Lake, however, *Daphnia middendorffiana* was common in the earliest sample, indicating that some early-season production was missed (Figure 25A).

Because of the way the Allen Curve method was used, the calanoid production measurements made by the method are estimates of annual production. The methods used to calculate calanoid production in Kingfisher Lake provide estimates only of summer production, but the instar abundance data suggest that little calanoid production took place outside the sampling period (Figure 15B). The maximum biomass estimates of cyclopoid production are minimum estimates of summer production and therefore of annual production as well.

Species counts of 3 Canadian Wildlife Service winter collections (Anderson, unpublished data) tend to support the conclusion that summer P equals annual P for species of crustacean plankton in Kingfisher and Mud Lakes. In Kingfisher Lake, *Daphnia* and *Ceriodaphnia* can be common in late fall (1700 m^{-3} and 1500 m^{-3} , respectively; 71-11-09), but are scarce or absent in mid-winter (74-02-15). *Scapholeberis* and *Polyphemus* were absent on both of these dates. *Bosmina* was absent from the late fall sample and uncommon (850 m^{-3}) in the mid-winter sample.

Cyclopoids were uncommon at most under the winter ice and were all adult (450 m^{-3} ; 74-02-15). *Diaptomus leptopus* was the only calanoid present in winter, existing only as copepodids and adults in both November and February, so it appears that little or no calanoid production occurs in winter. In a mid-winter sample from Mud Lake (74-02-15), *Acanthodiaptomus* was absent, *Daphnia* and *Orthocyclops* were rare ($<100 \text{ m}^{-3}$) and *Acanthocyclops* nauplii, copepodids and adults were uncommon ($<1000 \text{ m}^{-3}$), so there could have been little winter production in Mud Lake. On the basis of the above considerations, the summer P values were accepted as satisfactory estimates of annual production for all further calculations and comparisons. Some slight upward adjustment of summer P could have been made to estimate annual P of certain species, but in view of the probable small difference between the two, and of the probable magnitude of the errors in abundance and biomass determinations, small-scale adjustments were considered to be superfluous.

Comparison of Pechen-Shushkina and Southwood Methods

For the 7 populations in which Pechen-Shushkina and adjusted Southwood estimates were compared, the former were from 6 to 25% lower than the latter ($\bar{x} = 15\%$). Almost half of this difference resulted from the adjusted to the Southwood estimates, because the Pechen-Shushkina method gave results averaging only 8% lower than the unadjusted Southwood figures (range 0 - 23%). The difference in results from the unadjusted Southwood and Pechen-Shushkina methods are due to the use of abundance data integrated over the entire season in the Southwood method as opposed to the use of seasonal means of point estimates in the Pechen-Shushkina method, because both methods use identical daily abundance,

growth and development time data in an analogous way. The Southwood method has the advantage of readily revealing errors in abundance estimates, such as the underestimates of cladoceran egg numbers in this study, which the Pechen-Shushkina method does not do. The adjusted Southwood estimates are the most reliable because they include production by eggs or early instars that were missed in the sampling, so it is these adjusted estimates that have been used in subsequent calculations.

P/B Ratios

There is now considerable evidence that assumed production-to-biomass ratios (P/B's) can be used in conjunction with biomass determinations to make reasonable estimates of production in many invertebrate populations (Waters 1969,1977; Mann and Brylinsky 1975; see also Part 4 of this study). Estimates of production from P/B and biomass data are commonly used by eastern European limnologists (e.g. Gak *et al.* 1972, Kajak *et al.* 1972), but the method has been rarely used in North America. Data from this study provide information on P/B for several crustacean plankton populations that could help in estimating crustacean plankton production in similar Rocky Mountain lakes.

The $P/\bar{B}$ per cohort was remarkably similar among the calanoid populations studied, ranging from 2.0 to 4.1 for the populations in which production was calculated from Allen Curves (6 cohorts). In Kingfisher Lake, calanoids which had $P/\bar{B} = 9.2$ had two principal generations of about equal size, so $P/\bar{B}$ per cohort was 4.6. A cohort $P/\bar{B}$ of 2.1 was obtained for *Diaptomus tyrrelli* in Snowflake Lake when production was calculated from Anderson's (1968b) raw data by the Allen Curve method

(see below). The mean $\pm$ SE of these eight $P/\bar{B}$ estimates was 2.89 ± 0.34 .

In five of the calanoid populations a generation lasted one whole year (see also Anderson 1971, 1972), but measured summer $\bar{B}$ (as opposed to $\bar{B}$ calculated from Allen Curves) was available for only the ice-free period. Since summer $\bar{B}$ was taken near the end of the life cycle in these populations, it is possible that summer $\bar{B}$ was a biased estimator of cohort $\bar{B}$. Mean summer $P/\bar{B}$ for these five populations was 2.24 ± 0.28 , slightly lower than the mean cohort $P/\bar{B}$ calculated above, and was used to estimate *Diaptomus arcticus* production in Baker Lake.

Calanoid cohort $P/\bar{B}$ found in this study are similar to those reported in the literature. *Limnocalanus macrurus* Sars had a 4-year average cohort $P/\bar{B}$ of 2.98 in Char Lake, N.W.T. (Rigler *et al.* 1974; Rigler 1975). Rey and Capblancq (1975) reported an annual $P/\bar{B}$ of 2.5 for univoltine *Mixodiaptomus laciniatus* (Lilljeborg) in a Pyrenees subalpine lake. It appears that a reasonable estimate of calanoid cohort production is about 3 times the mean biomass, and that if the number of cohorts (generations) per year is known, $P/\bar{B}$ times mean biomass would provide a rough estimate of annual production.

Cladocera, which were significant producers in three of the six lakes, had much more variable $P/\bar{B}$'s than did the Calanoida, probably because the lack of discrete cladoceran generations made it impossible to calculate cohort $P/\bar{B}$. Summer $P/\bar{B}$'s ranged from 8.5 for *Daphnia middendorffiana* in Baker Lake to 38 for *Polyphemus* in Mud Lake. Summer $P/\bar{B}$'s for a single species, *Bosmina longirostris*, ranged from 10.1 in Kingfisher Lake to 22 in Mud Lake.

A similar broad range exists in the literature, even when only

other mountain or unproductive lake types are considered. In a Russian arctic lake *Daphnia cristata* Sars had a summer $P/\bar{B}$ of 26.2 (Alimov *et al.* 1972); in Lake Port-Bielh in the Pyrenees, *Daphnia longispina* (O.F. Müller) had a $P/\bar{B}$ of 2.5 (Rey and Capblancq 1975), values widely bracketing those observed for the same genus in this study (8.5 to 14.9). The summer $P/\bar{B}$ for *D. cristata* cited above is comparable to that calculated for *Ceriodaphnia* in Kingfisher Lake (28) and that found for *Bosmina* in Mud Lake (22). The very high summer $P/\bar{B}$ of 38 found for Mud Lake *Polyphemus* is also not unknown for a predatory cladoceran: values as high as 46 have been reported, although values from 15 to 20 appear to be more typical (Winberg *et al.* 1972; Gak *et al.* 1972; Alimov *et al.* 1972; Andronikova *et al.* 1972).

The mean $\pm$ SE summer $P/\bar{B}$ for all 7 cladoceran populations in this study for which reliable data were available was 19.1 ± 4.1 , with a coefficient of variation of 56.6%. For the nonpredatory cladocerans only the mean was 16.0 ± 3.1 , with a coefficient of variation of 47.4%, a slight improvement in precision. It is possible that additional detailed work on unproductive lakes will reveal consistencies in the $P/\bar{B}$'s of their cladoceran populations; however the data from this study and that in the literature show that at present the possibility of considerable error must be accepted if assumed $P/\bar{B}$'s are used to calculate cladoceran production.

Community Production

In calculating community production, it is theoretically permissible to add together production of individual species populations only if none of the species preys on others within the community: to add pre-

dator production to that of its prey in effect counts predator production twice (Winberg 1971:5; Winberg *et al.* 1971:296). To overcome the problem, predaceous and non-predaceous production should be calculated separately. It is difficult to do this in practice because many planktonic animals feed at more than one trophic level. Many predators are predaceous for only part of their life cycles, may prey partly outside the plankton community, or may be only partly predaceous within the community. For example, late instars of cyclopoids are often predaceous but the early instars are non-predaceous (McQueen 1969). The large calanoid *Diaptomus arcticus*, important in Baker and Moraine lakes, preys on *D. tyrrelli* (Anderson 1970c), but its early instars must be nonpredaceous, and even its late instars probably consume non-planktonic food and are omnivorous (Anderson 1970c).

In calculating production of the crustacean plankton communities in each lake, the production of at least partly predaceous and nonpredaceous species were presented separately, then production by the two groups was summed to obtain a measure of total annual community production (Table 12). This procedure yields a maximum estimate, but the error involved is unlikely to be large because production by at least partly predaceous species was usually small relative to that of nonpredaceous species. Furthermore, most species classified as predaceous (cyclopoids, *Diaptomus arcticus*) undoubtedly consumed food from outside the crustacean plankton community, and this fraction of their production should logically be added to non-predaceous production.

On the basis of annual production per unit of lake volume, Kingfisher Lake had the most productive crustacean plankton community.

Table 12. Annual production and mean biomass (dry weight) of planktonic Crustacea in the six Lake Louise-area lakes compared to that in selected lakes throughout the world. Asterisk indicates assumed value.

Lake	BIOMASS			PRODUCTION							Source and Comments
	$\bar{B}$ (mg m ⁻³)			NonPredators		Predators		Total			
	NonPredators	Predators	Total	P mg m ⁻³	P/ $\bar{B}$	P mg m ⁻³	P/ $\bar{B}$	P mg m ⁻³	P/ $\bar{B}$		
Kingfisher	108.0	11	119	1380	13	80	7	1460	2920	12	This study
Mud	56.0	3.9	59.9	660	12	30	8	690	1660	12	This study
Moraine	35.7		35.7	80	2			80	770	2	This study <i>D. arcticus</i> non-predaceous
Lower Consolation	46.2		46.2	150	3			150	880	3	This study
Baker	84.3	41.5	126	510	6	90	2.24*	600	3240	5	This study <i>D. arcticus</i> predaceous
Ptarmigan	27.3		27.3	60	2			60	420	2	This study
OTHER MOUNTAIN LAKES											
Snowflake, Alberta				80				80	490		Anderson (1975) alpine lake
Snowflake, Alberta	52		52	100	1.9			100	600	1.9	Recalculated from Anderson (1968b) Allen Curve
Teardrop, Alberta								980	580		Anderson (1975) alpine pond
V. Finstertalersee Austria								8	120		Pechlaner <i>et al.</i> (1972) alpine lake plank- tonic portion of population only
Port-Bielh, France								210	1900	2.5	Rey & Capblanc (1975) approximate data
FAR NORTHERN LAKES											
Char, N.W.T.	8.7			26	3			26	270		Rigler <i>et al.</i> (1974) & Rigler (1975) polar lake P range 17-31 mg m ⁻³
Krivoe, U.S.S.R.	9.6	5.2	15	130	14	26	5.0	160	1910	11	Alimov <i>et al.</i> (1972) arctic lake vegetative periods
Krugloe, U.S.S.R.	65	19	84	810	12	236	12	1050	1570	12	Alimov <i>et al.</i> (1972) arctic lake vegetative season
CANADIAN SHIELD LAKES											
Clear, S. Ontario	200			2990	15						Schindler (1972) Predaceous cyclopoid abundant
239, N.W. Ontario	20			190	10						Schindler (1972) Predaceous cyclopoid abundant
A UNIQUE LAKE											
Baikal, U.S.S.R.	21	16	37	280	13	36	2.2				Moskalenko & Votinsev (1972) 0-50m
PRODUCTIVE LAKES											
Red, U.S.S.R.	120	22	142	2200	18	180	8.2				Andronikova <i>et al.</i> (1972) May-Oct. boreal
Severson, Minn.				3400							Comita (1972) prairie lake
Myastro, U.S.S.R.	280	42	322	3700	13	500	12				Winberg <i>et al.</i> (1972) May-Oct. Byelorussia
Batorin, U.S.S.R.	440	120	560	6870	16	1480	12				Winberg <i>et al.</i> (1972) May-Oct. Byelorussia

The Baker and Mud Lake planktonic crustacean communities had similar productivities, but were less than half as productive as those in Kingfisher Lake. Crustacean plankton production was approximately the same in Moraine, Lower Consolation and Ptarmigan Lakes, being one-quarter or less than that in Baker and Mud Lakes, and one-tenth or less than that in Kingfisher Lake. Overall, there was a 24-fold difference in crustacean plankton production between the most and the least productive lakes.

The relative productivities of four of the six communities can be readily accounted for. Ptarmigan Lake is the highest in elevation of any of the lakes, is one of the deepest, has one of the shortest ice-free periods, has water with the lowest mineral content, and is among the coldest of the lakes. Moraine and Lower Consolation, the other two low-productivity lakes with respect to their crustacean plankton communities, are very cold, have waters with low mineral content, have a short ice-free season and have short water renewal times. In addition, Moraine Lake is the deepest of the six lakes. Kingfisher Lake, on the other hand, is the warmest, shallowest, lowest in elevation, has one of the longest ice-free periods, has water with one of the highest mineral contents, and probably has the longest water renewal time.

There is no obvious explanation for the relative productivities of the remaining two lakes with regard to their crustacean plankton. Despite being the second highest of the lakes with one of the shortest ice-free seasons, short water renewal time, and having the second most dilute water, Baker Lake annual crustacean plankton production was near that of Mud Lake, a lake 600 m lower, shallower, warmer, with a longer

ice-free season and water with the highest dissolved solids of the six lakes. Furthermore, although Baker Lake is only 122 m lower than Ptarmigan Lake, and is only slightly shallower, slightly warmer, has only slightly less dilute water, and is within 2 km of Ptarmigan Lake in similar terrain, the crustacean plankton annual production in Baker Lake was 10 times that in Ptarmigan Lake.

Similarly, the more than two-fold difference in crustacean plankton production of Mud and Kingfisher Lakes is difficult to explain in view of the considerable physical similarity of the two lakes. Although Mud Lake is more than three times the area of Kingfisher Lake, the lakes have similar mean depths, are located at about the same elevation, in similar terrain and in the same geological formation within 4 km of each other, have similar bottom types, light penetration, water colour and water chemical composition.

The differences in crustacean plankton production among the six lakes were due almost entirely to differences in cladoceran production, particularly that of *Daphnia* spp. Cyclopoid production was low or absent in all six lakes, and calanoid production was relatively constant regardless of species, voltinism or number of species, ranging from 60 to 160 $\text{mg m}^{-3} \text{ yr}^{-1}$ ($\bar{x} \pm \text{SE} = 117.0 \pm 18.1$, $n = 6$).

On the other hand, total nonpredaceous cladoceran production ranged from 0 to 1200 $\text{mg m}^{-3} \text{ yr}^{-1}$, and the range for *Daphnia* production alone was nearly as large (0 to 940 $\text{mg m}^{-3} \text{ yr}^{-1}$). In the three most productive lakes *Daphnia* was by far the most productive crustacean plankton (64 to 75% of total production), reaching abundances much greater than 10,000 m^{-3} on individual sampling dates in Kingfisher and Mud Lakes,

and greater than 1000 m^{-3} for the much larger species in Baker Lake. In contrast, *Daphnia* was rare in or absent from the three least productive lakes.

Whatever factors are controlling the distribution and abundance of *Daphnia* spp. are responsible for most of the variation in crustacean plankton production among the six lakes. The identity of these factors remains to be determined, but two possibilities seem worth investigating. The six lakes have all been heavily stocked with trout in the past (Parks Canada stocking records), and marked reductions or elimination of large species of *Daphnia* have been associated with trout introductions in high Rocky Mountain lakes (Anderson 1972). A second possibility is suggested by the work of Allan (1976), who hypothesized that in a nutritionally-dilute environment copepods should have a competitive advantage over cladocerans because copepods are able to capture a wider range of particle sizes. Carbon-14 experiments done in the six lakes (Mayhood and Anderson 1976, and unpublished data) suggest that planktonic primary productivity is higher in the three lakes having the highest *Daphnia* production than it is in the three lakes having little or no *Daphnia* production, the principal crustacean producer in the latter lakes being a calanoid.

The foregoing discussion compared the six lakes on the basis of crustacean plankton production per unit of lake volume. From the point of view of assessing fish food productivity this is the most relevant unit for comparison: fish predators must search a volume of water, so the concentration of plankton organisms and their productivity is of greatest importance. The lakes can also be compared on the basis of crustacean plankton production per unit of lake surface, which is the

more relevant measure from some points of view; for example, in assessing the supply of dead plankton available to benthic organisms. According to the latter measure, Baker Lake is the most productive of the six lakes, the remaining lakes retaining their ranks relative to each other (Table 12). The reason Baker Lake crustacean plankton production surpasses that of Mud and Kingfisher Lakes on a unit area basis is that Baker Lake is deeper than the other two waters, so that its smaller production per cubic metre adds up to more under one square metre of surface. The remaining lakes do not change rank because the differences in depth are insufficient to completely compensate for their differences in production per cubic metre. There is considerable compensation, however, so that the 24-fold difference in crustacean plankton production per cubic metre between the most and least productive lakes is reduced to less than an 8-fold difference on an areal basis.

Table 12 compares crustacean plankton productivity in the 6 Lake Louise-area lakes with that in several other mountain, northern and Shield lakes. Figures for four moderately to highly-productive waters are given to provide an indication of the range that has been found for the world's natural lakes. The following discussion refers to nonpredator production per unit volume.

Ptarmigan, Moraine and Lower Consolation Lakes had annual crustacean plankton production similar to that in nearby alpine Snowflake Lake, Banff National Park, and to that in the Russian Arctic Lake Krivoe; higher than that in Char Lake, Cornwallis Island, N.W.T., and Vorderer Finstertalersee, an Austrian alpine lake; but lower than that in several other low-productivity lakes. Annual crustacean plankton production in

Mud and Baker Lakes was comparable to that in Krugloe, a shallow Russian arctic lake. Crustacean plankton production in Kingfisher Lake was lower than that found in productive lakes, but was high enough to label it moderately productive. In short, Ptarmigan, Moraine and Lower Consolation are among the least productive lakes studied with respect to their crustacean plankton production; Mud and Baker Lakes appear to be near the mid-range for oligotrophic lakes, and Kingfisher Lake has a moderately productive zooplankton community.

The data on Snowflake Lake in Table 12 provide a valuable check on the Allen Curve method used for calculating calanoid production in this study. Anderson (1975) estimated the production of *Diaptomus tyrrelli* mostly from primary productivity data (Anderson 1968b) and some determinations of *D. tyrrelli* filtering rate. I used his raw data on *D. tyrrelli* population size, biomass and clutch size (Anderson 1968b) to construct an Allen Curve in the same way as was done for the Lake Louise-area calanoids, assuming dry weight was 15% of fresh weight (Bottrell *et al.* 1976:436). The two estimates agree.

It was shown in Section 2 that the six lakes of this study are representative Canadian Rocky Mountain lakes with respect to several of their physical and chemical attributes. Moraine, Lower Consolation, Ptarmigan and Baker Lakes have crustacean plankton communities that occur commonly in lakes of the Rocky Mountain region, with respect both to species composition and population abundance (Anderson 1971, 1974a), so can be considered as having representative crustacean plankton communities. The zooplankton communities of Mud and Kingfisher Lakes are similar to others in Rocky Mountain lakes, particularly those in the mon-

tane zone; but one of their species, *Acanthodiaptomus denticornis*, is apparently restricted to the Bow River valley (Anderson 1974a) in the Rocky Mountain area. *A. denticornis* was relatively scarce in Kingfisher Lake in 1975, however, its place being taken by *Diaptomus leptopus*. Because there was little difference in the annual calanoid production between Mud and Kingfisher Lakes, it seems unlikely that the presence of *A. denticornis* in either lake is influential enough to rate the crustacean communities as atypical with respect to production. On grounds of their physical, chemical and biological similarities to other Rocky Mountain lakes, the six Lake Louise-area lakes studied likely showed a broad range of the crustacean plankton production to be expected in alpine and subalpine trout-inhabited lakes of the region.

BENTHOS

The objective in this section is to describe the benthos of the six lakes and to estimate the production of benthic macroinvertebrates. The section is divided into three parts. The first shows which taxa are most important in abundance and biomass in the various lakes, and presents the biomass data required for the production calculations. The second analyzes some of the most important macroinvertebrate populations in each lake to provide data on voltinism required for the production calculations. The third analyzes published data on macroinvertebrate P/B for use in the production calculations and presents the production estimates.

SPECIES COMPOSITION, ABUNDANCE AND BIOMASS

Calculations and Methods Evaluation

The mean abundances of benthic fauna were calculated from the counts of animals collected by Ekman grab. The mean biomasses of major taxa were calculated for each sampling date from the preserved wet weights of the groups in the Ekman grab collections.

Sampler efficiency. A standard Ekman grab of the size used in this study was evaluated by Flannagan (1970). When compared with diver-collected cores in mud substrate, the Ekman grab significantly underestimated oligochaete abundance (approximate efficiency 65%), but provided satisfactory abundance estimates for chironomids, sphaerids and total macroinvertebrates. Among eight samplers tested the standard Ekman grab was second only to the FRB multiple-corer in its efficiency in col-

lecting total macroinvertebrates, and was the most efficient in collecting chironomids.

The standard Ekman is subject to "wash-out" (loss of animals from the top of the sample) when nearly full if the top shutters open even slightly on ascent. Also, a frontal wave may push invertebrates aside as the grab approaches the sediments. An attempt was made to minimize frontal wave and wash-out effects by locating the lake bottom with the grab, lowering the grab gently nearby, then raising the sampler carefully at a constant rate after tripping the release. Wash-out was probably unimportant in shallow samples because it could be directly observed and the sample could be re-taken.

Sieve efficiency. Invertebrates were sorted from the substrate by passing the sample through a sieve having apertures of 0.36 x 0.52 mm, the taxa retained being arbitrarily defined as macroinvertebrates. According to Jonasson (1955), sieves with a pore size of 0.51 mm may fail to quantitatively retain Tubificidae and chironomids as large as 6 mm in length, but satisfactorily retain *Chaoborus* larvae, tubificid cocoons and sphaerid clams. Head capsule dimensions are thought to determine whether chironomids are retained: Jonasson found chironomids having head capsule widths of approximately 0.5 mm or greater did not pass through the 0.51-mm mesh aperture. In contrast, Maitland *et al.* (1972) found that the 0.5-mm mesh aperture retained virtually all *Stictochironomus* larvae more than 3.5 mm in length¹, but retained only 0 to 7% of the

¹ The units of their Figure 2 must be millimetres, not centimetres as marked. Chironomid larvae do not attain a length of 14 cm as the Figure shows, but lengths of 14 mm are typical of numerous species.

smallest size-classes up to 2 mm in length.

According to Jonasson's (1955) hypothesis, retention of chironomids in this study would presumably have been limited by the relationship of head depth and the smaller dimension of the mesh aperture. Head depths of many small species such as *Tanytarsus*, *Micropsectra*, *Corynoneura* and *Pagastiella* were less than 0.36 mm, so these species may have been largely missed if Jonasson's hypothesis is correct. If the relationship observed by Maitland *et al.* (1972) applies, all but the first or second instars of most chironomid species would have been collected quantitatively, because third, fourth and usually second-instar larvae exceeded 3.5 mm in length.

Regardless of the effect of sieve aperture size on the abundance estimates, probably little macroinvertebrate biomass was lost through the sieve used. Maitland *et al.* (1972) reported that summer production of *Stictochironomus* estimated by using the 0.5-mm aperture sieve was 90.6% of the total, and that over the entire year the underestimate was just 2.7%. Similarly, Zelt and Clifford (1972) noted that a net of 0.72 mm mesh aperture underestimated the biomass of stream insects by only 5%, but abundance by 50%, when compared to a net of 0.32 mm mesh aperture.

In general, one would expect that failure to include small individuals would not seriously underestimate total biomass because of the large number of small individuals that equal the weight of one large individual. If, as Waters (1977:112) suggests, the ratio of maximum to minimum weight in freshwater animals is usually in the range of 100:1 to 500:1, then about 100 to 500 small individuals would have to be lost for every large individual retained by the sieve for the biomass to be

underestimated by 50%. Put another way, the efficiency of the sieve would have to be approximately 1% or less with respect to abundance to cause a 50% underestimate of biomass. Such low efficiencies (1 to 25%) with respect to numbers were sometimes approached in the data of Jonasson (1955) and Maitland *et al.* (1972) for particular species on particular days, but for larger taxonomic groups such as Chironomidae in which cohorts overlap, or over long time intervals, such low sieve efficiencies are highly unlikely. A more realistic estimate would be that overall sieving efficiencies are likely to be in the order of 50% with respect to numbers (Jonasson 1955; Maitland *et al.* 1972), and 90% with respect to biomass.

Effect of preservatives on wet weight. Recent studies have demonstrated a strong effect of preservatives on the wet or dry weight of benthic invertebrates (Howmiller 1972; Stanford 1973; Hare 1976; Donald and Paterson 1977), although the wet and dry weights of planktonic invertebrates are apparently unaffected by preservation in 10% formalin (Bottrell *et al.* 1976). In the present study, the effect of formalin preservation on the wet weight of three benthic invertebrates was tested to determine if preserved wet weight accurately represented live weight, and if not, to obtain correction factors with which the biomass measurements could be adjusted.

Tests were run on Oligochaeta, *Hyalella azteca* (Saussure) and *Gammarus lacustris* Sars. The animals were weighed alive, preserved in 3.7% formaldehyde (Shawinigan Brand stock formalin solution, McArthur Chemical Company, 37% formaldehyde and 63% water and methanol) in Cal-

gary tapwater (mean conductivity $\pm$ standard deviation = $380 \pm 47 \mu\text{S cm}^{-1}$ @ 20°C , $n = 71$, Water Quality Branch 1975), and weighed at various intervals up to 1405 days afterward. Triplicate weights were obtained on each occasion with the weighing technique described previously (Laboratory Methods, p. 23), by replacing the animals in preservative for one minute after each weighing, then repeating the weighing procedure.

The blot-dry weighing method provided reproducible weights (Table 13). The 17 coefficients of variation for the triplicate weighings ranged from 0.81 to 3.39%, and had a mean $\pm$ standard deviation (SD) of 1.80 ± 0.82 . Since 95% of individual weight measurements should fall within 2SD of the true mean, fewer than 5% of the weight determinations of the benthic macroinvertebrates should differ from the true values by more than approximately 7% (i.e., $2 \times 3.39\%$), if it is assumed that the test data are representative of all samples weighed.

Weight determinations made four to five months after fixation underestimated live weights of the three test taxa by 2 to 22% (Table 13). Weights measured 3.5 to 4 years after fixation underestimated live weights of *Gammarus* and *Oligochaeta* by 17 and 25%, respectively. All three taxa showed an immediate 5 to 12% drop in weight upon fixation (the animals were weighed within 10 minutes of death from the preservative).

Of the four previous studies on the effect of preservatives on wet weight of benthic invertebrates cited earlier, only that of Donald and Paterson (1977) employed both a weighing method and preservative similar to that used here. Donald and Paterson, studying chironomids, found a *Chironomus* species to have gained 10 to 15% in wet weight after

Table 13. Changes in the wet weight of three macroinvertebrates preserved in 3.7% formaldehyde solution. SD: standard deviation.

Days After Preservation	Oligochaeta		13 <i>Hyaella azteca</i>		30 <i>Gammarus lacustris</i>	
	Mean weight $\pm$ SD (g) n = 3	Proportion of Live Weight	Mean Weight $\pm$ SD (g) n = 3	Proportion of Live Weight	Mean Weight $\pm$ SD (g) n = 3	Proportion of Live Weight
0 (live)	0.0547 $\pm$ 0.0008	1.00	0.0448 $\pm$ 0.005	1.00	0.4270 $\pm$ 0.0061	1.00
0 (preserved)	0.0505 $\pm$ 0.0013	0.92	0.0393 $\pm$ 0.0012	0.88	0.4071 $\pm$ 0.0033	0.95
1			0.0383 $\pm$ 0.0013	0.85		
2					0.4286 $\pm$ 0.0063	1.00
16					0.4129 $\pm$ 0.0048	0.97
50	0.0573 $\pm$ 0.0016	1.05				
74			0.0370 $\pm$ 0.0010	0.83		
85					0.3818 $\pm$ 0.0053	0.89
125			0.0349 $\pm$ 0.0008	0.78		
134	0.0534 $\pm$ 0.0006	0.98				
250					0.3790 $\pm$ 0.0069	0.89
1356					0.3552 $\pm$ 0.0038	0.83
1405	0.0411 $\pm$ 0.0004	0.75				

being preserved for 100 days, and found *Procladius* sp. and *Metriocnemus* to have lost approximately 15% of their live weight after 100 days in preservative. Beyond 100 days weights of *Chironomus* had stabilized, but those of *Procladius* and *Metriocnemus* fluctuated about a level of 10% weight loss. A fourth species of chironomid tested by Donald and Paterson lost 45% of its live weight after preservation, but these specimens had been transferred from an extremely saline habitat (conductivity 42,000 to 45,000 $\mu\text{S cm}^{-1}$ @ 20°C) to distilled water plus 10% formalin, so osmotic stress may account for the very large weight loss.

Available results have not provided a correction factor that can be generally applied to data on preserved wet weight to estimate live weight. The data of Donald and Paterson (1977) and those of the present study suggest that the live biomass of individual taxa may be underestimated by 10 to 25%, or overestimated by as much as 15%, when 10% formalin-preserved wet weight is obtained by a blot-dry technique after 200 to 500 days in preservative, as was done in this study. Community biomasses and biomasses of taxa with many species may be underestimated by only 5 to 10%, however, because weight gains by a few taxa would partially compensate for weight losses by most taxa. After the many uncertainties in the available information were considered, no attempt was made to adjust the biomass or production estimates made in this study.

Results

Kingfisher Lake. Emergent sedges (*Carex* L.) occurred sparsely around the shoreline of Kingfisher Lake, as did *Sparganium* (Tourn.) L. A small, dense clump of *Chara* Valliant grew at the 2-m contour at the

southeast end of the lake, and a smaller clump of *Myriophyllum* L. occurred within 1 m of the northwest shore. *Potamogeton* sp., either *P. pectinatus* L. or *P. filiformis* Pers., was sparsely distributed throughout the 0- to 2-m zone, and *Menyanthes trifoliata* L. projected into the water from shore in several places. Total coverage by macrophytes in Kingfisher Lake was no more than 5% of the bottom area.

Hyalella azteca was the most abundant macroinvertebrate in the samples, followed distantly by the chironomids *Cladotanytarsus*, *Tanytarsus* and *Pagastiella*, and by ceratopogonids (Table 14). Nearly all taxa were less abundant in samples taken from below 2 m than they were in the 0- to 2-m zone, but *Tanytarsus* and *Micropsectra* were about equally abundant in both, tubificids were somewhat more abundant in the deep zone, and *Chironomus* was found only in the deep zone. Few additional taxa were found in the shoreline collections (Table 15).

Figure 29 illustrates mean summer biomasses and changes in biomass of major taxonomic groups through the summer of 1974 in Kingfisher Lake. Only *H. azteca* showed a clear trend in biomass, increasing from May to September; the other taxa remaining constant or nearly so over the same period. *H. azteca* formed more than half the biomass of benthic macroinvertebrates in Kingfisher Lake (Figure 30). The mean summer biomass for the entire fauna was 2.756 g m^{-2} wet weight, the mean for the 8 shallow stations being 4.8 times that for the 4 deep stations.

Mud Lake. In Mud Lake, as in Kingfisher, emergent *Carex* spp. were sparsely distributed around the shoreline, and *Potamogeton pectinatus* or *P. filiformis* was sparsely distributed throughout the 0- to

Table 14. Benthic macroinvertebrate abundance m^{-2} in Kingfisher Lake, means of 5 collections dates, 1974. + indicates taxon was found in fewer than 5 samples, was represented by fewer than 10 animals, or was present in the macrophyte beds. Standard errors are provided only as an index of variability. They cannot be used to set confidence limits because samples were taken at approximately regular, not random, time intervals.

Taxon	Macro- phyte Beds	8 Shallow Stations n = 40		4 Deep Stations n = 20		Whole Lake n = 60		
		$\bar{x}$ $\pm$ SE		$\bar{x}$ $\pm$ SE		$\bar{x}$ $\pm$ SE		
Coelenterata								
<i>Hydra</i> Trembley	+							
Turbellaria			+		+			
Nematoda			+		+			
Mollusca								
<i>Gyraulus</i> Charpentier			+					
<i>G. parvus</i> (Say)	+				+			
<i>Pisidium</i> Pfeiffer	+		+					
Oligochaeta								
Naididae			+					
<i>Nais barbata</i> (Müller)	+							
Tubificidae	+	12.9	5.39	45.2	28.7	23.7	9.26	
<i>Tubifex templetoni</i> Southern			+					
Lumbriculidae	+	39.8	11.7	4.3	2.96	28.0	7.11	
Hirudinoidea								
<i>Helobdella stagnalis</i> (L.)	+		+		+			
Hydrocarina			+					
Crustacea								
<i>Scapholeberis kingi</i>					+			
<i>Simocephalus vetulus</i> Schödler			+					
<i>Eurycercus lamellatus</i> (O.F.M.)	+		+					
<i>Alona affinis</i> (Leydig)			+					
Ostracoda	+		+					
Diaptomidae			+		+			
<i>Acanthocyclops vernalis</i>			+					
<i>Macrocyclus albidus</i>	+		+					
<i>Hyaella azteca</i> (Saussure)	+	1300	210	118	96.3	906	130	
Ephemeroptera								
<i>Caenis</i> Stephens	+		+					
Baetidae			+					
Odonata								
<i>Aeshna</i> Fabricius	+		+					
Libellulidae	+		+					
<i>Somatochlora</i> Selys			+					
<i>Cordulia</i> Leach			+					
Coenagrionidae			+					
<i>Coenagrion</i> Kirby	+							

- continued

Table 14 - cont'd.

Taxon	Macro- phyte Beds	8 Shallow Stations n = 40		4 Deep Stations n = 20		Whole Lake n = 60	
		$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$
Odonata (cont'd.)							
<i>Ischnura</i> Charpentier	+						
Trichoptera							
Leptoceridae		+					
<i>Oecetis</i> McLachlan		28.0	6.82	0		18.7	4.12
Limnephilidae		+					
Phryganeidae		+		+			
Coleoptera							
<i>Acilius</i> Leach		+					
Diptera							
Chironomidae							
<i>Ablabesmyia</i> Joh.	+	22.6	11.6	0		15.1	7.03
<i>Procladius</i> s.s. Skuse	+	61.4	13.3	8.6	5.93	43.8	8.26
<i>Clinotanytus</i> Kieff.		7.5	3.04	0		5.0	1.84
<i>Psectrocladius</i> (Kieff.)	+	+					
<i>Cricotopus</i> (v.d.Wulp.)	+						
<i>Pagastiella</i> Brund.		267	43.5	0		178	26.3
<i>Chironomus</i> (Meig.)	+	0		32.3	12.0	21.5	5.15
<i>Cryptocladopelma</i> Lenz		21.5	11.4	0		14.3	6.91
<i>Cryptochironomus</i> Kieff.		11.8	5.56	4.3	4.3	9.3	3.60
? <i>Harnischia</i> Kieff.		+					
<i>Dicrotendipes</i> Kieff.	+	+		+			
<i>Glyptotendipes</i> Kieff.				+			
<i>Cladotanytarsus</i> Kieff.		422	310	8.6	6.70	284	187
<i>Tanytarsus</i> v.d.Wulp.	+	212	54.6	151	82.5	192	41.3
<i>Micropectra</i> Kieff.		7.5	5.53	10.8	10.8	8.6	4.66
<i>Zavrelia</i> Kieff.		+					
<i>Paratanytarsus</i> Kieff.	+	+		+			
Ceratopogonidae							
? <i>Culicoides</i> Latreille		11.8	6.72	0		7.9	4.06
<i>Palpomyia</i> Meig., <i>Bezzia</i> Kieff. or <i>Johannsenomyia</i> Malloch	+	200	32.3	10.8	8.8	137	19.7
Tabanidae							
<i>Tabanus</i> L. or		+					
<i>Chrysops</i> Meig.							

Table 15. Shoreline fauna of the six lakes. Numbers are numbers of individuals in the collection. + indicates the animal was present. Numbers in parentheses after the date are times of the collections in minutes.

TAXON	74-06-19(15) Kingfisher	74-07-16(30)	74-06-18(15) Mud	74-07-18(20)	Moraine 74-09-17(30)	74-07-12(30) Lower Consolation	74-08-14(30)	74-07-30(30) Baker	74-08-28(30)	74-07-31(30) Ptarmigan	74-08-30(30)
Hydrozoa											
<i>Hydra</i>		2									
Turbellaria					5					20	
Bryozoa		+									
Gastropoda											
<i>Lymnaea</i> Lamarck									4		
<i>Gyraulus parvus</i> (Say)	9	4	5								
Pelecypoda											
Sphaeridae						1	1	7	25		2
Oligochaeta		4			22		3	2	6	2	70
Hirudinoidea									2		
Hydracarina											
<i>Lebertia</i> Newman								5	3	3	1
<i>Hydrobates</i> Koch											11
<i>Hydrochoreutes unguatus</i>			2								
Cladocera (Koch)											
<i>Polyphemus pediculus</i>			1								
<i>Simocephalus vetulus</i>	25	15									
<i>Scapholeberis kingi</i>				1							
<i>Eurycercus lamellatus</i>	13	1	17								
Ostracoda		1									
Copepoda											
<i>Diaptomus arcticus</i>					10				15		
<i>Eucyclops agilis</i> (Koch)						1					
<i>Macrocyclus albidus</i>			2								
Amphipoda											
<i>Hyalella azteca</i>	8	4	40	1							
<i>Gammarus lacustris</i> Sars							4	59			1
Ephemeroptera											
<i>Caenis</i>	1			1							
<i>Ameletus</i>						8	2				
<i>Parameletus</i>						4		3			
<i>Siphonurus</i>							4		42		

- continued

Table 15 - cont'd

	74-06-19 (15)	Kingfisher	74-07-16 (30)	74-06-18 (15)	Mud	74-07-18 (20)	Moraine	74-09-17 (30)	74-07-12 (30)	Lower Consolation	74-08-14 (30)	74-07-30 (30)	Baker	74-08-28 (30)	74-07-31 (30)	Ptarmigan	74-08-30 (30)
Odonata																	
Coenagrionidae				2		1											
<i>Enallagma</i> Charpentier	1																
<i>E. borealis</i> (Selys)	1	2															
<i>Aeshna</i>	3	1		3													
<i>Aeshna palmata</i> Hagen						1											
Libellulidae	1			1													
<i>Somatochlora cingulata</i>				1													
Plecoptera																	
<i>Megarcys</i> Klapálek									1								
<i>Isoperla</i> Banks									1								
<i>Yoraperla mariana</i> (Ricker)										1							
Hemiptera																	
<i>Gerris notabilis</i> Drake &		4															
Trichoptera /Hottes									1								
Limnephilidae	1	1		9		5			6			11			1		3
<i>Oecetis</i>	3	5															
unidentified small larvae		53															
unidentified pupae																	
Coleoptera																	
<i>Hydroporus compertus</i> Brown									1								
<i>Rhantus</i> DeJean or <i>Colymbetes</i>														1			
Diptera /Clairville																	
Tipulidae																	
<i>Dicranota</i> Zetterstedt												1					
Chironomidae												1		1			
Tanypodinae	7	2								2							
Orthoclaadiinae	10	1						1	4	8	2					1	
Chironomini	1	4															
Tanytarsini	56																
<i>Thienemannimyia</i> Fittk.gr.				4		+											
<i>Corynoneura</i> (Winn.)															1		
<i>Cricotopus</i> (v.d.Wulp.) or																	4
<i>Orthocladus</i> (v.d.Wulp.)																	

- continued

Table 15 - cont'd

	74-06-19 (15)	Kingfisher	74-07-16 (30)	74-06-18 (15)	Mud	74-07-18 (20)	Moraine	74-09-17 (30)	74-07-12 (30)	Lower Consolation	74-08-13 (30)	74-07-30 (30)	Baker	74-08-28 (30)	74-07-31 (30)	Ptarmigan	74-08-30 (30)
<i>Paracladius</i> Hirv.																1	
<i>Psectrocladius</i>																1	
<i>Cryptochironomus</i> Kieff.												1	1				
<i>Endochironomus</i> Kieff.				1													
<i>Phaenopsectra</i> s.s. Kieff.																10	
<i>Paratanytarsus</i>				+													
Ceratopogonidae																	
<i>Culicoides</i>				1													
<i>Palpomyia</i> pupae	1																

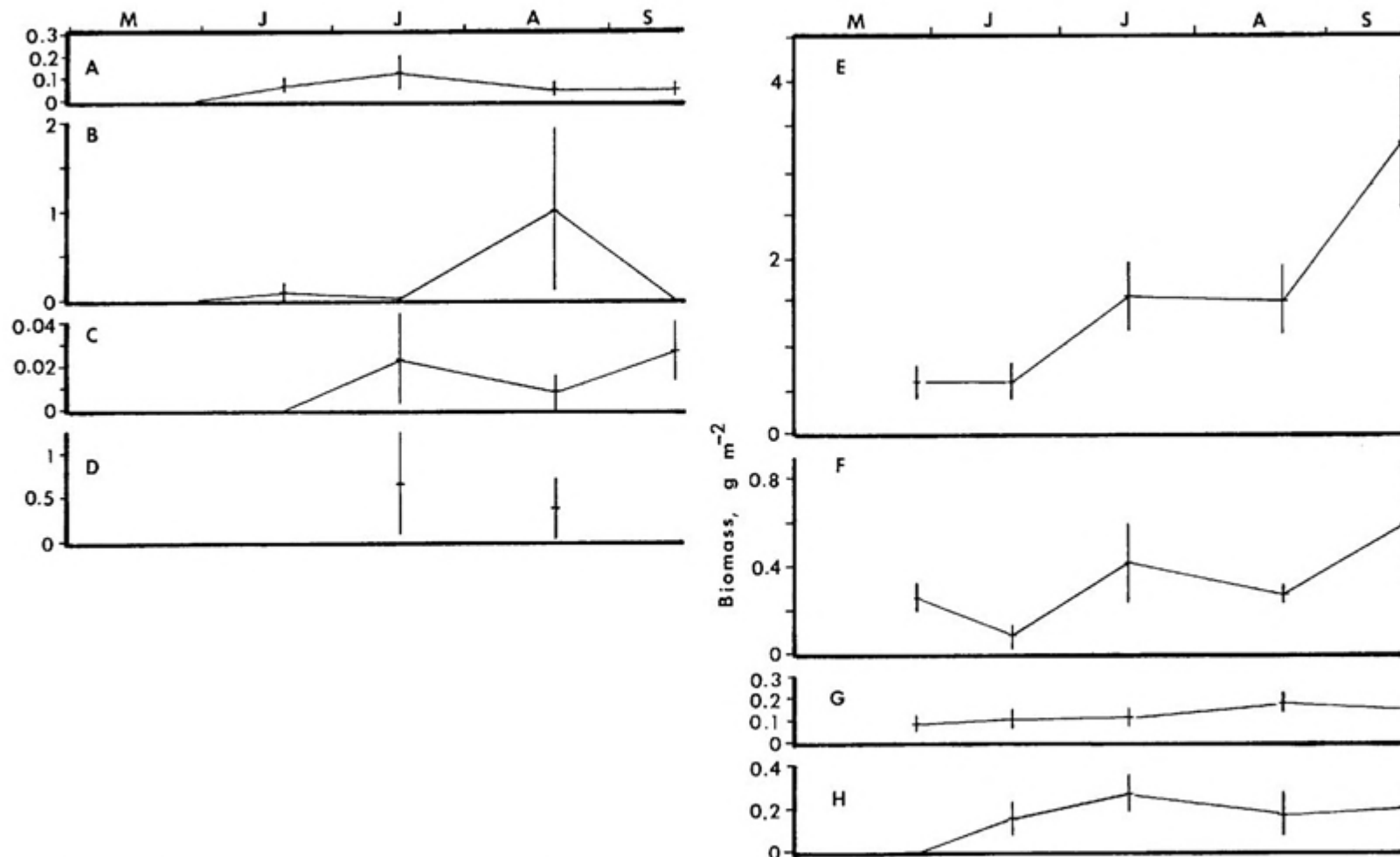
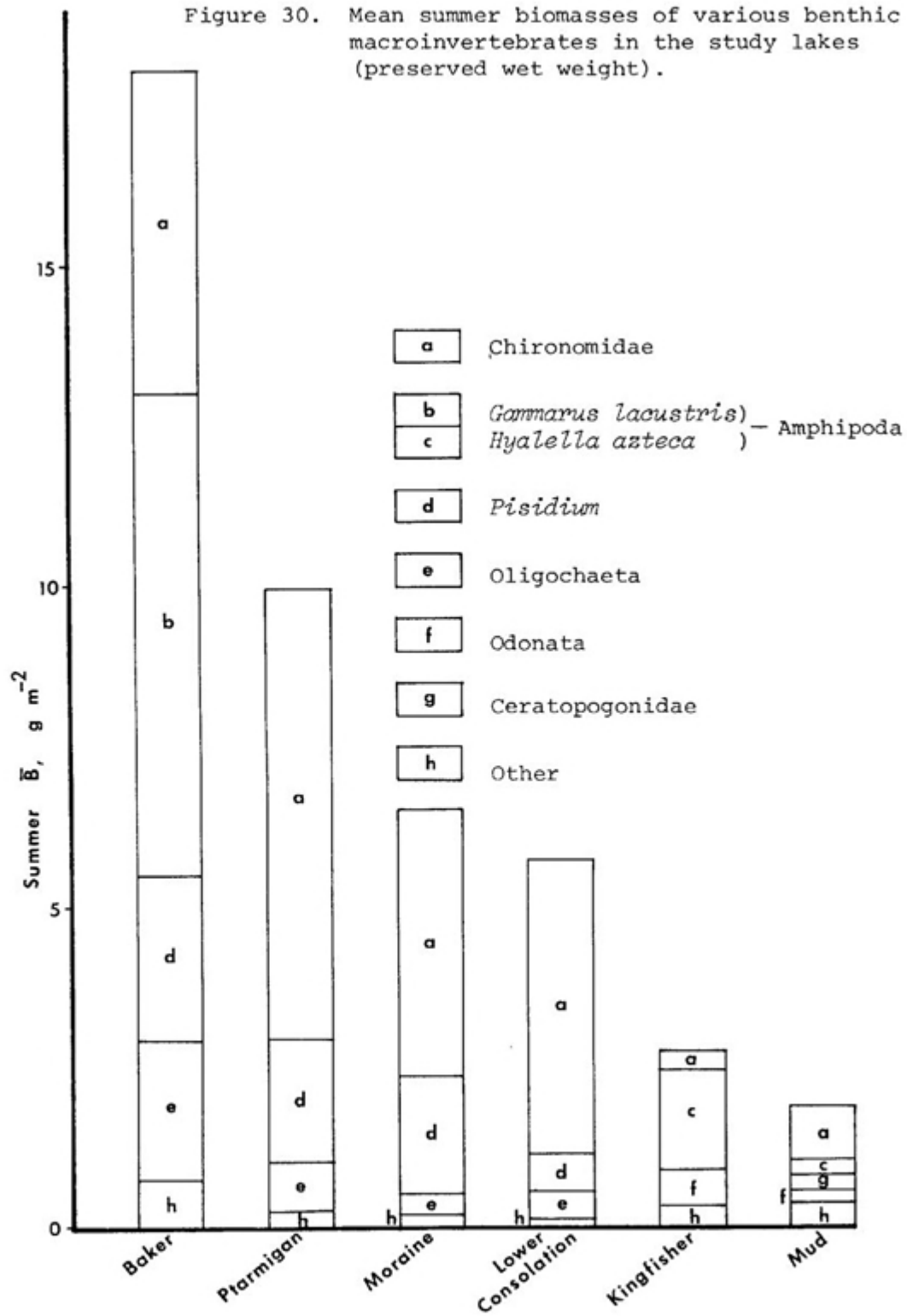


Figure 29. Variations in estimates of mean biomass $\pm$ SE of Trichoptera (A), Coenagrionidae (B), *Helobdella stagnalis* (C), Aeshnidae (D), *Hyaella azteca* (E), Chironomidae (F), Ceratopogonidae (G), and Oligochaeta (H) in Kingfisher Lake, 1974 (preserved wet weight).

Figure 30. Mean summer biomasses of various benthic macroinvertebrates in the study lakes (preserved wet weight).



2-m zone. Dense clumps of *Chara* occurred in several places, particularly at the south end of the lake straddling the 2-m contour, and was sparsely distributed throughout the 0- to 2-m zone. *P. natans* L. was found at one point along the east shore. Coverage by macrophytes, mainly *Chara*, might be as high as 10% of the bottom area in Mud Lake.

The most abundant macroinvertebrates were the chironomid *Micropsectra*, and ceratopogonids, especially ?*Culicoides* followed by *Tanytarsus*, *Dicrotendipes* and *Polypedilum* (Table 16). Most taxa were more abundant in the shallow than in the deep zone, but a few (*Dicrotendipes*, *Psectrocladius*, *Guttipelopia*, *Chironomus*) were at least as abundant in the deep as in the shallow zone. Some large insects (*Aeshna*, Limnephilidae) appeared in the shoreline samples (Table 15) but not in the Ekman grab samples.

Unlike the same species in Kingfisher Lake, *H. azteca* in Mud Lake showed no clear trend in biomass through the summer. Chironomid and ceratopogonid biomass varied widely (Figure 31). Other macroinvertebrates had stable biomasses or appeared infrequently in the benthic samples. Chironomids formed nearly half of the mean total macroinvertebrate biomass (Figure 30), which was 3.5 times higher in the shallow zone than in the deep zone.

Moraine Lake. No macrophytes were found in Moraine Lake.

The sphaerid *Pisidium*, the chironomids *Micropsectra* and *Paracadius* and the calanoid *Diaptomus arcticus* were the most abundant macroinvertebrates in the Moraine samples (Table 17). ?Enchytreidae were extremely abundant on certain dates in the bay entered by Fay Creek, but

Table 16. Benthic macroinvertebrate abundance m^{-2} in Mud Lake, means of 6 collection dates, May to September 1974-75. + indicates taxon was present in qualitative samples, or occurred in fewer than 5 samples or that fewer than 10 were found in all 45 samples.

Taxon	Qualitative Samples 74-07-18	4 Shallow Stations n = 21		4 Deep Stations n = 24		Whole Lake n = 45	
		$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$
Nematoda							
Mollusca							
<i>Pisidium</i>	+	121	61.8	39.5	34.3	77.5	34.2
Oligochaeta							
Tubificidae	+	99.4	42.4	0		46.4	19.8
<i>Limnodrilus udekemianus</i>	+						
Lumbriculidae /Clap.							
Hirudinoidea							
<i>Helobdella stagnalis</i>	+	+					
Hydracarina							
<i>Hydryphantes</i> Koch		+					
<i>Lebertia</i>		+		+			
Crustacea							
<i>Daphnia</i> O.F.M.				+			
<i>Simocephalus vetulus</i>		+		+			
Ostracoda		+					
<i>Acanthodiaptomus denticornis</i>		+		+			
<i>Hyalella azteca</i>	+	160	53.0	14.3	9.58	82.3	25.2
Ephemeroptera							
<i>Caenis</i>		61.9	26.8	5.4	2.97	31.8	12.6
Odonata							
<i>Somatochlora</i>		+					
Coenagrionidae				+			
Trichoptera							
? <i>Leptocella</i> Banks	+						
<i>Oecetis</i>	+						
Phryganeidae							
Diptera							
Chironomidae							
<i>Ablabesmyia</i>	+	63.6	28.4	7.2	5.6	33.5	13.6
<i>Procladius</i> s.s.	+	165	41.2	52.0	19.6	105	21.9
<i>Guttipelopia</i> Fittk.		70.7	42.2	93.3	68.0	82.8	41.3
<i>Psectrocladius</i> spp.	+	96.4	42.8	115	54.5	106	35.3
<i>Cricotopus</i>		+					
<i>Dicrotendipes</i>	+	119	43.6	122	56.4	121	36.3
<i>Cryptochironomus</i>		33.8	12.1	0		15.8	5.66

- continued

Table 16 - cont'd.

	Qualitative Samples 74-07-18	4 Shallow Stations n = 21		4 Deep Stations n = 24		Whole Lake n = 45	
		$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$
Diptera (cont'd)							
Chironomidae (cont'd)							
<i>Pagastiella</i>		96.3	28.0	5.4	5.4	47.8	13.4
<i>Polypedilum</i> (<i>Pentapedilum</i>)Kieff.		240	113	12.6	7.98	119	52.9
? <i>Harnischia</i>		+		+			
<i>Chironomus</i>		2.0	2.0	28.7	19.7	16.2	10.5
<i>Endochironomus</i>		32.3	16.8	1.8	1.8	16.0	7.90
<i>Cryptocladopelma</i>	+	+		+			
<i>Micropsectra</i>		1060	332	102	87.5	549	162
<i>Tanytarsus</i>		340	136	88	36.3	206	66.4
<i>Paratanytarsus</i>		+		+			
Ceratopogonidae							
? <i>Culicoides</i>	+	834	288	17.9	11.3	399	134
<i>Palpomyia</i> , <i>Bezzia</i> or <i>Johannsenomyia</i>	+	217	36.6	10.8	4.67	107	17.2
<i>Tabanus</i> or <i>Chrysops</i>		+					

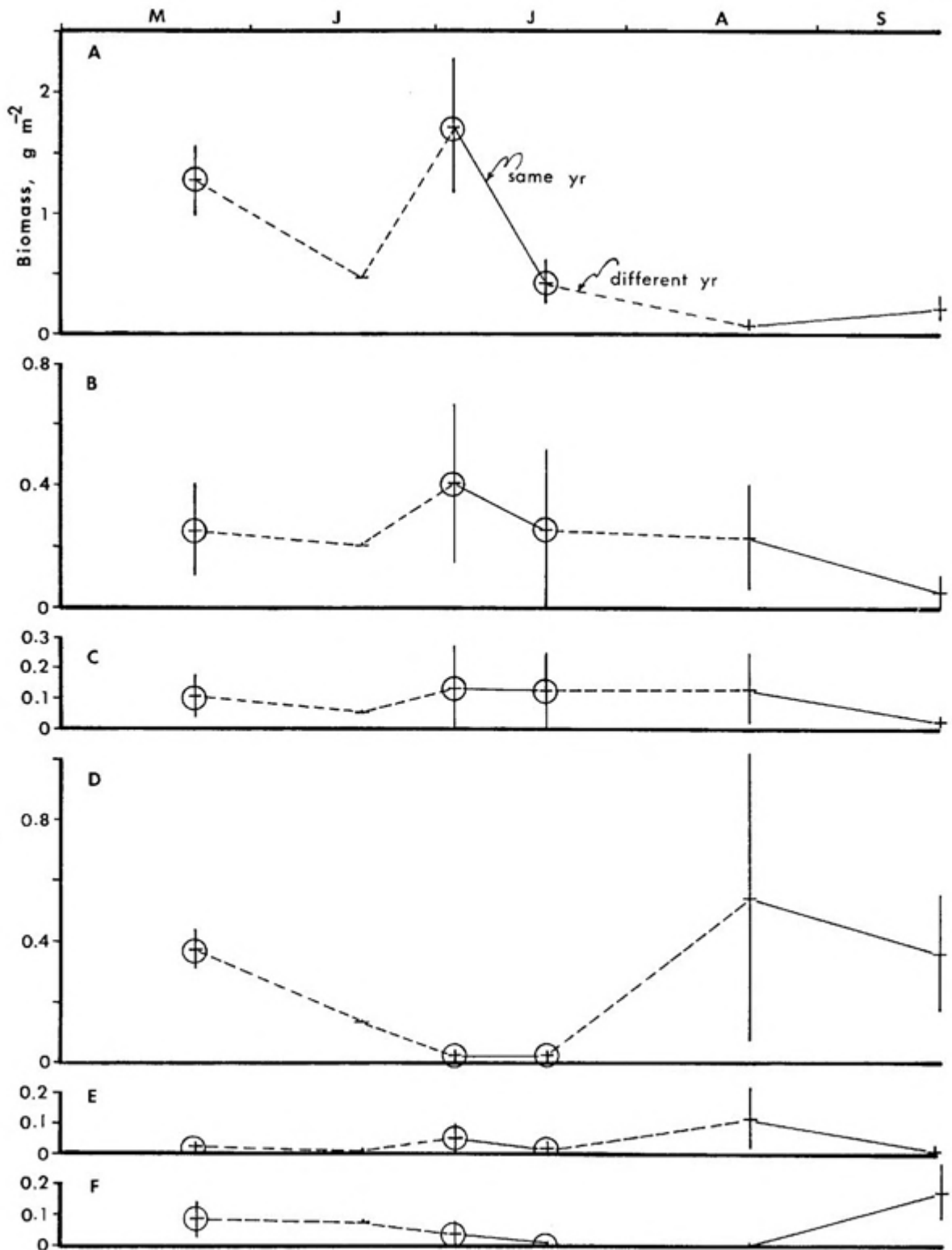


Figure 31. Variations in estimates of mean biomass $\pm$ SE of Chironomidae (A), *Hyaella azteca* (B), Oligochaeta (C), Ceratopogonidae (D), *Caenis* (E), and *Pisidium* (F) in Mud Lake (preserved wet weight). Plain points, 1974; circled points, 1975.

Table 17. Benthic macroinvertebrate abundance m^{-2} in Moraine Lake, means of 6 collections, June to September 1974-75. + indicates occurrence in fewer than 5 samples, or fewer than 10 found.

Taxon	Whole Lake n = 36	
	$\bar{x}$	$\pm SE$
Nematoda	46.6	19.0
Mollusca		
<i>Pisidium</i>	1310	240
Oligochaeta		
?Enchytreidae	350	245
Tubificidae	132	82.6
<i>Limnodrilus hoffmeisteri</i> Clap.		
Lumbriculidae	+	
Hydracarina		
<i>Lebertia</i>	33.5	10.1
Crustacea		
<i>Daphnia</i>	+	
Ostracoda	+	
<i>Diaptomus arcticus</i>	583	112
<i>Acanthocyclops vernalis</i>	+	
Plecoptera	+	
Trichoptera		
Limnephilidae	39.5	32.2
Chironomidae		
<i>Procladius</i> ss	+	
<i>Procladius</i> <i>caudatus</i> Edw.gp.	27.5	7.7
<i>Pseudodiamesa</i> nr. <i>branickii</i> Now.	136	41.8
<i>Heterotrissocladius subpilosus</i> (Kieff.) gp.	120	50.6
<i>Orthocladius</i> or <i>Cricotopus</i>	+	
<i>Rheocricotopus</i> (Thien.and Harn.)	+	
<i>Paracladius</i>	628	201
<i>Parakiefferiella</i> (Thien.)	90.9	37.8
? <i>Hydrobaenus</i> (Fries)	+	
? <i>Zalutschia</i> (Lipina)	+	
<i>Psectrocladius</i>	+	
<i>Corynoneura</i>	+	
<i>Phaenopsectra</i> s.s	77.8	37.1
<i>Stictochironomus</i> Kieff.	352	84.9
<i>Chironomus</i>	136	39.7
<i>Micropsectra</i>	649	220

occurred elsewhere in much lower numbers. Small numbers of Turbellaria were the only addition to the species list from the shoreline collection (Table 15).

Chironomid, oligochaete and *D. arcticus* biomasses varied little from their mean values through the two summers, although chironomid biomass appeared to increase slightly from June to September 1974 (Figure 32). One *Pisidium* biomass was far below the summer mean. Chironomids constituted more than 60%, and *Pisidium* nearly 30%, of the mean summer biomass (Figure 30).

Lower Consolation Lake. No macrophytes were found in Lower Consolation Lake, but masses of attached filamentous algae were conspicuous on large submerged boulders at the inlet and outlet ends.

The most abundant macroinvertebrates were *Procladius* and *Psectrocladius*, followed distantly by *Tanytarsus* and *Pisidium* (Table 18). Most taxa were about equally abundant in the two sampling zones, but *Pisidium* and *Stictochironomus* were more abundant in the north zone than in the south. Two mayflies, *Ameletus* and *Siphonurus*, were found in the shoreline collections but not in the grab samples, and are potentially important fish food organisms (Table 15).

Apart from one chironomid and one *Pisidium* collection, each with very large standard errors due to unusually large single catches, biomasses on each sampling date were close to the mean and showed no strong trends (Figure 32). Chironomids comprised approximately 80% of the summer biomass of macroinvertebrates in Lower Consolation Lake (Figure 30).

Baker Lake. A *Potamogeton* species, possibly *P. praelongus*

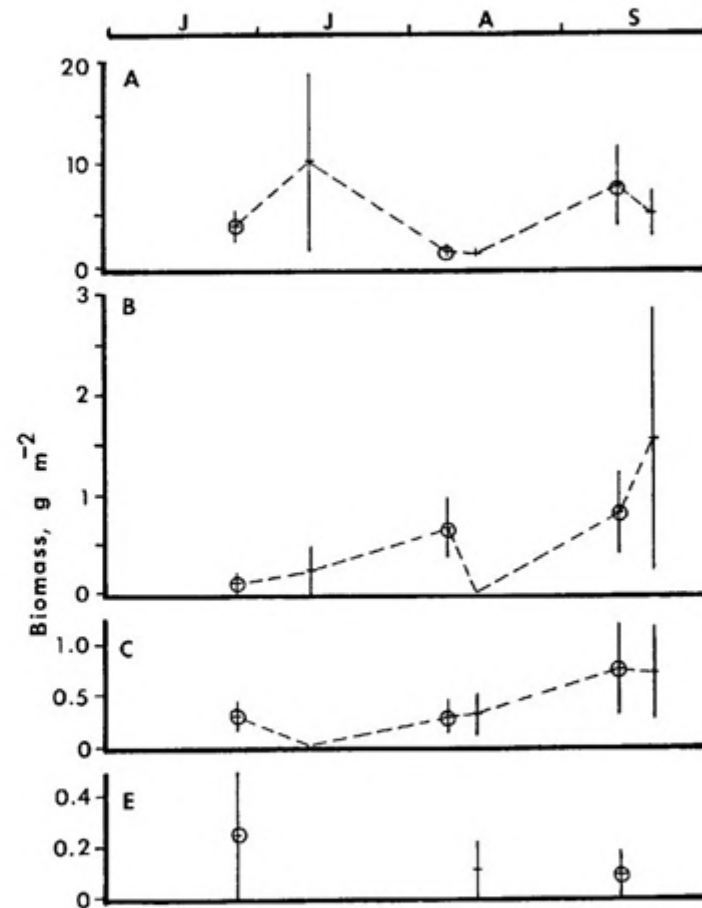
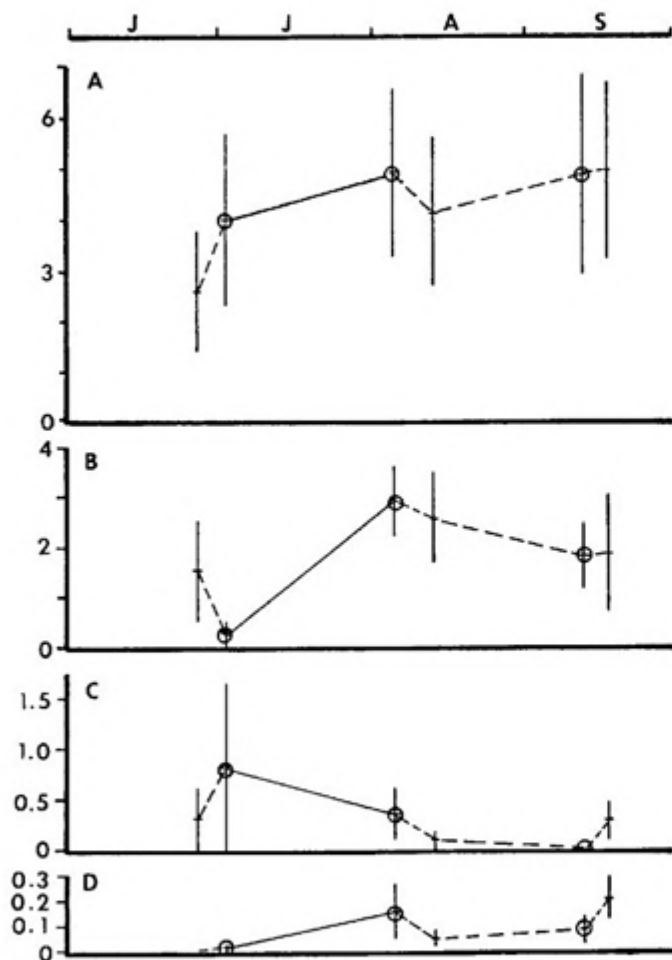


Figure 32. Variations in estimates of mean biomass $\pm$ SE of Chironomidae (A), *Pisidium* (B), Oligochaeta (C), *Diaptomus arcticus* (D, benthic portion of population only), and *Gammarus lacustris* (E) in Moraine Lake (left) and Lower Consolation Lake (right) (preserved wet weight). Plain points, 1974; circled points, 1975. Broken lines connect collections made in different years, solid lines connect collections made in the same year.

Table 18. Benthic macroinvertebrate abundance m^{-2} in Lower Consolation Lake, means of 6 collections, July to September 1974-75.
+ indicates occurrence in fewer than 5 samples, or that <10 were found.

Taxon	North Zone n = 17		South Zone n = 16		Whole Lake n = 33	
	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$
Turbellaria	+					
Nematoda	22.8	9.8	18.8	7.8	20.9	6.3
Mollusca						
<i>Pisidium</i>	514	199	113	66.5	320	107
Oligochaeta	58	32.6	167	93.3	111	48.2
Tubificidae						
Lumbriculidae						
Crustacea						
Ostracoda	+		+			
<i>Diaptomus tyrrelli</i>			+			
Cyclopoida	+		+			
<i>Gammarus lacustris</i>	+					
Trichoptera						
Limnephilidae	+		+			
Diptera						
Chironomidae						
<i>Procladius</i> s.s.	831	321	1040	305	932	222
<i>Protanypus</i> (Kieff.)	+		+			
<i>Pseudodiamesa nr. branickii</i>	+		+			
<i>Psectrocladius</i>	585	289	864	477	720	275
<i>Paracladius</i>	139	79.4	21.5	11.8	82.0	41.3
<i>Cricotopus</i>	+		+			
<i>Corynoneura</i>	+		+			
<i>Orthocladius</i> s.s.			+			
<i>Phaenopsectra</i> s.s.	32.9	15.5	26.9	10.3	30.0	9.4
<i>Stictochironomus</i>	65.9	39.6	0		34.0	20.4
<i>Tanytarsus</i>	405	185	253	88.1	331	104
<i>Micropectra</i>	27.9	10.4	13.5	13.5	20.9	8.4

Wulf., appeared frequently in Ekman grab samples taken from the west end of Baker Lake, and an unidentified Characeae occurred frequently in samples taken in the large bay along the south shore. Although not a macrophyte, thin masses of the branched, filamentous green alga *Cladophora* Kutz. appeared in Ekman grab samples taken from several points in the lake.

The most abundant macroinvertebrates were *Tanytarsus* and *Pisidium* followed by *Diaptomus arcticus* and *Procladius* (Table 19). *Gammarus lacustris* and several chironomid genera were also numerically important. Mean abundances for several taxa appeared to differ widely among the three sampling zones, but it is doubtful if many of the apparent differences are real because of the considerable sampling variability associated with each mean. Shoreline sampling added a few additional taxa to the species list, including the mayflies *Parameletus* and *Siphonurus*, both potentially important as fish food organisms (Table 15).

Oligochaeta and *Diaptomus arcticus* biomass showed little variation through the summer, but chironomid biomass was higher in September than in July or August (Figure 33). *Pisidium* biomass was lower in September 1975 than any of the four July or August sampling dates. The very high mean biomass of *Gammarus lacustris* recorded in September was caused by a single catch of 84 amphipods at a site in the western zone. Without this extreme sample, the mean $\pm$ SE September biomass would have been $5.32 \pm 1.64 \text{ g m}^{-2}$, similar to the July and August biomasses. *G. lacustris* comprised about 42%, and chironomids 28%, of the mean summer biomass of macroinvertebrates in Baker Lake (Figure 30).

Table 19. Benthic macroinvertebrate abundance m^{-2} in Baker Lake, means of 5 collections, July to September 1974-75. + indicates occurrence in fewer than 5 samples, or that less than 10 individuals were found.

Taxon	West Zone n = 8		Central Zone n = 10		East Zone n = 16		Whole Lake n = 34	
	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$
Turbellaria	+		+		+			
Nematoda			+		+			
Mollusca								
<i>Pisidium</i>	2010	723	1230	619	875	259	1250	277
Oligochaeta	215	46.0	30.1	14.4	37.7	14.1	77.2	13.4
Tubificidae								
Lumbriculidae								
Hirudinoidea								
<i>Nepheleopsis obscura</i>					+			
Hydracarina /Verrill								
<i>Lebertia</i>	+		+		+			
Crustacea								
<i>Daphnia</i>			+		+			
Ostracoda	+		+		+			
<i>Diaptomus arcticus</i>	405	206	487	228	710	353	573	185
<i>Diaptomus tyrrelli</i>	+		+		+			
Cyclopoida	+		+		+			
<i>Gammarus lacustris</i>	840	427	439	121	151	36.0	398	108
Trichoptera								
Limnephilidae	+				+			
Chironomidae								
<i>Procladius</i> s.s.	958	458	508	116	401	94.6	563	122
<i>Procladius</i>	10.8	7.0	21.5	13.2	35.0	13.7	25.3	7.7
<i>Cricotopus</i>	21.5	11.5	0		151	109	76.1	51.1
<i>Corynoneura</i>	+		+					
<i>Paracletidius</i>	+							
<i>Psectrocladius</i>					+			
<i>Phaenopsectra</i> s.s.	538	302	250	156	256	92.6	320	95.2
<i>Chironomus</i>	436	395	151	114	48.4	22.2	170	99.2
<i>Stictochironomus</i>	684	224	822	418	191	160	492	154
<i>Paracletopelma</i> Harn.	+		+		+			
<i>Tanytarsus</i>	1020	424	1290	316	1660	317	1400	202
<i>Cladotanytarsus</i>	0		25.8	18.4	80.7	56.4	45.6	27.0
<i>Paratanytarsus</i>	274	204	108	90.2	35.0	32.2	113	56.8
<i>Micropsectra</i>	211		870	452	61.9	41.6	335	140

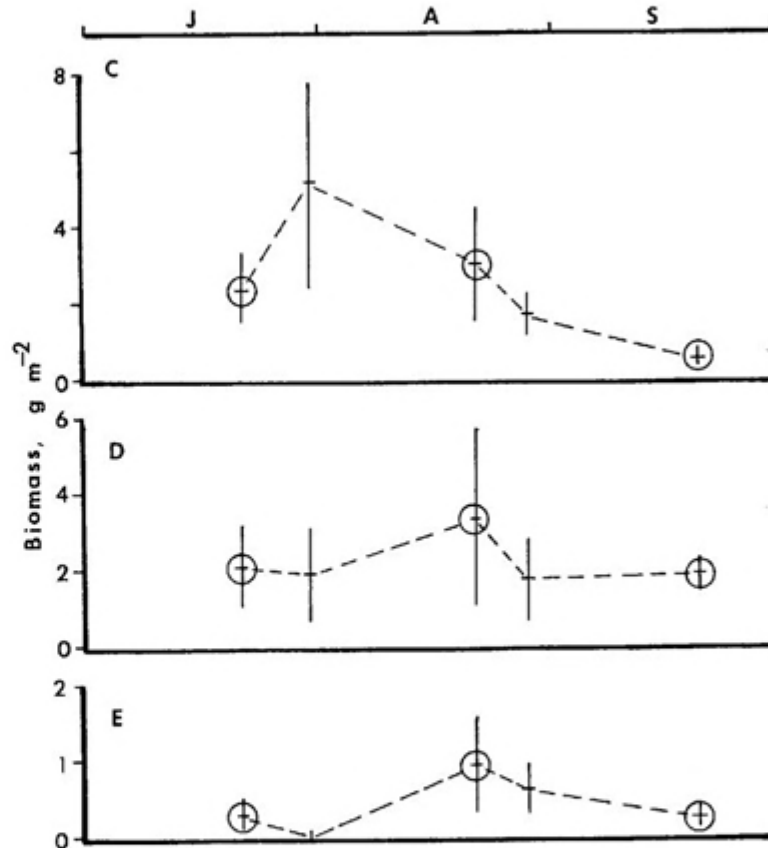
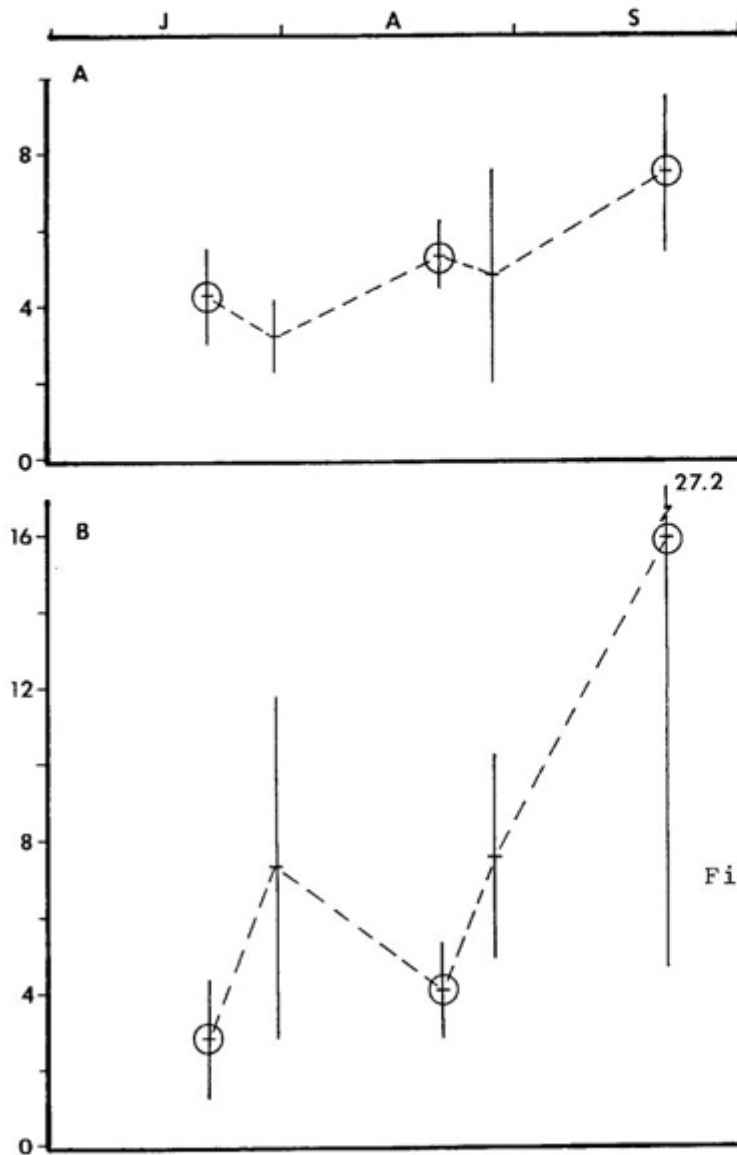


Figure 33. Variations in estimates of mean biomass $\pm$ SE of Chironomidae (A), *Gammarus* (B), *Pisidium* (C), Oligochaeta (D), and *Diaptomus arcticus* (E, benthic animals only) in Baker Lake (preserved wet weight). Plain points, 1974; Circled points, 1975.

Ptarmigan Lake. A species of *Equisetum* L. was rare along the shoreline of Ptarmigan Lake. Clumps of an unidentified Characeae similar or identical to that in Baker Lake were common near the 2-m contour in the east basin of Ptarmigan, but covered no more than 5% of the total lake bottom.

Tanytarsus was by far the most abundant macroinvertebrate in the benthic fauna, followed by *Pisidium* (Table 20). *Micropectra*, *Phaenopsectra*, *Stictochironomus*, *Paratanytarsus* and *Procladius* were also abundant. The marked physical differences between the east and west basins were reflected in the species composition of the benthic fauna. Lumbriculidae, *Psectrocladius*, possibly *Phaenopsectra*, *Tanytarsus* and *Paratanytarsus* were more abundant in the shallow east basin than in the deeper west basin; while *Protanypus*, *Heterotrissocladius*, *Parakiefferiella*, *Paracladius*, *Stictochironomus*, *Chironomus* and *Micropectra* were more abundant in the deep west basin. The shoreline collections added only the water mite *Hygrobates* to the species list of macroinvertebrates in Ptarmigan Lake (Table 15).

The biomass of chironomids and oligochaetes showed no strong trends or large fluctuations from July to September, but *Pisidium* biomass was higher in September than in July or August (Figure 34). Although only occasional *Gammarus* specimens were collected, when they occurred they formed a sizeable portion of the biomass because of their large individual size. Despite the differences in the composition of their benthic faunas, the two basins of Ptarmigan Lake had similar mean biomasses: for the east basin the mean macroinvertebrate biomass for the summer was 10.765 g m^{-2} ; for the west, 9.350 g m^{-2} . Chironomids con-

Table 20. Benthic macroinvertebrate abundance m^{-2} in Ptarmigan Lake, means of 5 collections, July to September 1974-75. + indicates occurrence in fewer than 5 samples, or that fewer than 10 specimens were found.

Taxon	West Basin n = 20		East Basin n = 15		Whole Lake n = 35	
	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$	$\bar{x}$	$\pm SE$
Turbellaria	+					
Nematoda	17.2	7.9	71.8	36.1	40.6	16.1
Mollusca						
<i>Pisidium</i>	1150	329	1270	462	1200	273
Oligochaeta						
Naididae	+					
Tubificidae	40.9	15.1	8.6	6.2	27.1	9.0
Lumbriculidae	8.6	5.0	54.5	11.5	28.3	5.7
Hydracarina						
<i>Lebertia</i>	6.5	3.5	34.5	17.9	18.5	7.9
Crustacea						
Ostracoda	+		+			
<i>Diaptomus tyrrelli</i>			+			
<i>Acanthocyclops vernalis</i>	+		+			
<i>Gammarus lacustris</i>			+			
Trichoptera						
Limnephilidae	+					
Diptera						
Chironomidae						
<i>Procladius</i> s.s.	336	78.6	551	208	428	99.8
<i>Thienemannimyia</i> group	+		+			
<i>Protanypus hamiltoni</i>	40.9	11.0	0		23.4	6.3
<i>Psectrocladius</i> ^a /Saeth.	0		192	54.3	82.3	23.3
<i>Cricotopus</i> }	+		+			
? <i>Acricotopus</i> }	+					
<i>Corynoneura</i>	2.1	2.1	175	98.3	76.2	42.2
<i>Heterotrissocladius</i> ^b	189	45.1	2.9	2.9	109	25.8
<i>Parakiefferiella</i>	58.1	19.1	5.7	3.9	35.6	11.0
<i>Paracladius</i>	47.3	21.4	0		27.0	12.2
<i>Phaenopsectra</i> s.s.	293	111	1100	590	639	261
<i>Stictochironomus</i>	921	281	74.6	45.9	558	162
<i>Chironomus</i>	297	108	2.9	2.9	171	61.7
<i>Tanytarsus</i>	183	63.1	5510	1860	2466	798
<i>Paratanytarsus</i>	114	26.3	884	319	444	138
<i>Micropectra</i>	973	194	195	151	640	128

^a At least 2 spp., one near *barbimanus* (Roback 1957).

^b Larvae in the *marcidus*, *maeeri* groups, and *H. sp. E* (Saether 1975b) were found.

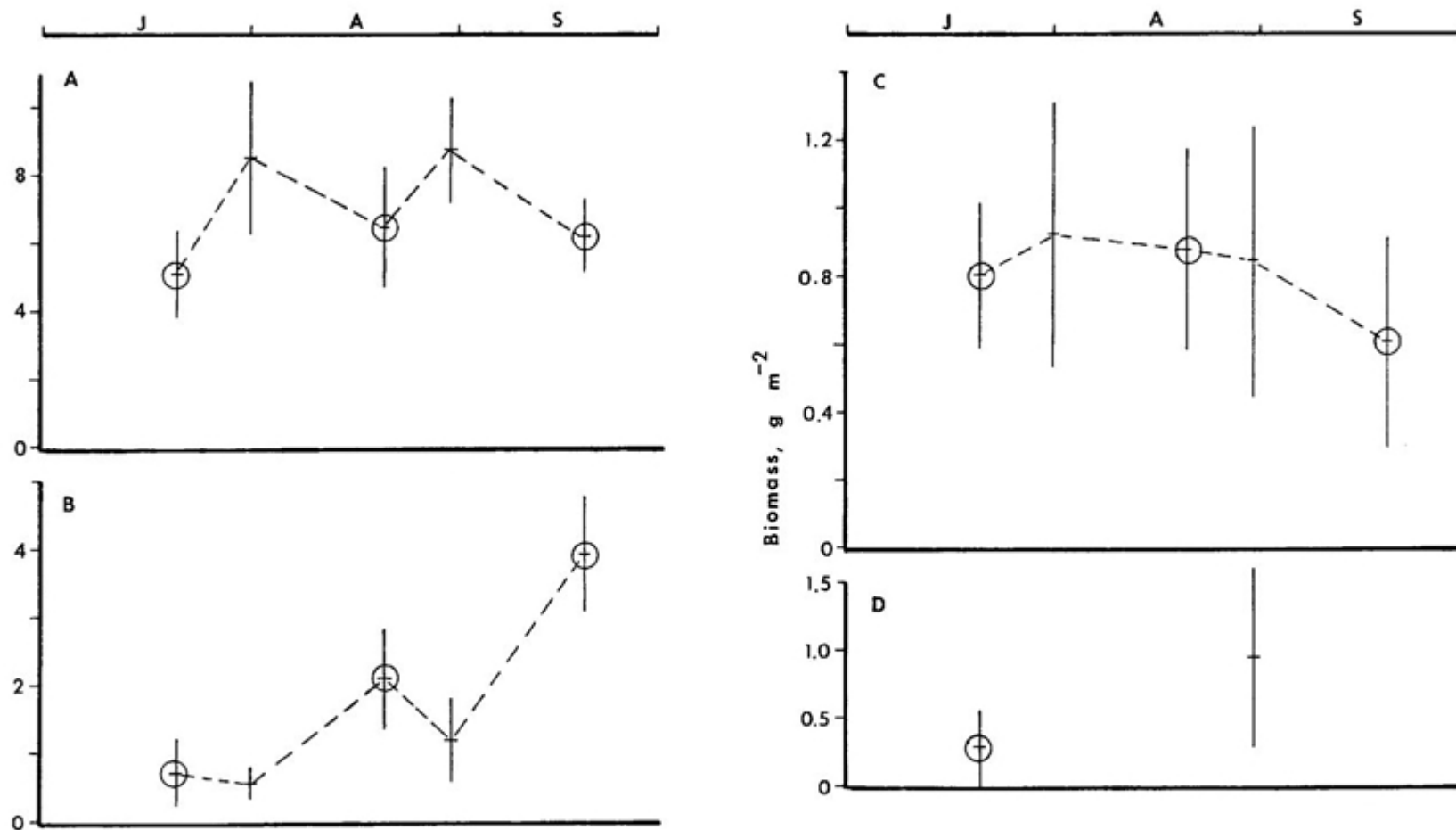


Figure 34. Variations in estimates of mean biomass $\pm$ SE of Chironomidae (A), *Pisidium* (B), *Oligochaeta* (C), and *Gammarus lacustris* (D) in Ptarmigan Lake (preserved wet weight). Plain points, 1974; circled points, 1975.

stituted about 70% of the mean summer biomass of macroinvertebrates (Figure 30).

Discussion

Of the 146 alpine and subalpine lakes in the Canadian Rocky Mountains studied by Anderson (1971), only a few lower subalpine lakes and ponds supported benthic macrophytes. Kingfisher, Mud, Moraine and Lower Consolation Lakes thus appear to be typical subalpine lakes of the region with respect to the occurrence of macrophytes. The occurrence of macrophytes in Ptarmigan and Baker makes these lakes unusual, but not unique. Macrophytes are found in Amethyst Lake (1967 m), Jasper National Park (Rawson 1953) and I have observed extensive beds of *Carex* spp. in Boom Lake (1893 m), sprigs of *Myriophyllum* in Lake Louise (1731 m), and a submergent moss in Redoubt Lake (2392 m), all in Banff National Park.

Odonata and Ceratopogonidae, two groups important in the benthic or shoreline samples from Mud and Kingfisher Lakes, were absent from the four highest lakes. Most other major taxonomic groups were common to all six lakes, but the species or genera often differed, as the Chironomidae data well illustrate. Diamesinae were absent from Mud and Kingfisher Lakes, and Orthoclaadiinae were represented only by the genera *Cricotopus* and *Psectrocladius*, only the latter in Mud Lake being numerically important. In contrast, one or both of the diamesids *Protanypus* and *Pseudodiamesa*, and 4 to 9 orthoclad genera, some of them abundant, occurred in the four highest lakes. Both diamesids and orthoclads are considered to be primarily cold-adapted forms (Oliver 1971). Species of *Heterotrissocladius*, *Paracladius*, *Protanypus* and *Pseudodiamesa*, common orthoclads or

diamesids in some or all of the four highest lakes, are considered characteristic of oligotrophic to ultraoligotrophic habitats (Saether 1975c). Among the Chironomini, *Stictochironomus* and *Phaenopsectra* were common in the four highest lakes but were absent from Mud and Kingfisher Lakes. On the other hand, the two lowest lakes had numerous Chironomini and Tanypodinae genera that were absent from the four highest lakes. Some species of these in the genera *Pagastiella* and *Cryptocladopelma* are held to be characteristic of oligotrophic to mesotrophic or dystrophic habitats (Saether 1975c). The tanypod *Procladius* and the Tanytarsini genera *Micropsectra*, *Tanytarsus* and *Paratanytarsus* were present in most or all the lakes.

There are insufficient data available to determine if the benthic macroinvertebrate communities of the study lakes are representative of those in Canadian Rocky Mountain lakes in general. The only published account of the species composition of benthic fauna in natural Canadian Rocky Mountain lakes is that of Rawson (1953), who found the Amethyst Lake benthos to be numerically dominated by *Pisidium conventus* Clessin (61%) and the chironomids *Stictochironomus*, *Tanytarsus*, *Psectrocladius* and *Procladius* (20%). The Amethyst Lake macroinvertebrate fauna appears to be most similar to that of the west basin of Ptarmigan Lake in the present study. Rawson (1942, 1953) published the only data on biomass of benthic invertebrates in Canadian Rocky Mountain lakes, but failed to specify his sieve mesh aperture, weighing methods or whether preserved or fresh specimens were weighed, so his data are not comparable to those of this study.

INSTAR ANALYSIS

Procedure

Amphipods collected in the Ekman grab samples were measured to the nearest millimetre from the tip of the rostrum to the base of the telson by straightening each specimen against a plastic ruler. The presence of eggs, embryos and spinous oöstegites on females was noted. Length frequencies and the proportions of reproductively-active females were plotted in sequence to determine life-cycle lengths.

Head depths of chironomids were measured on unmounted specimens at 25X with an ocular micrometer, and the numbers of pupae and prepupae of each taxon in each sample were noted. Larvae were assigned to instars on the basis of a size-frequency analysis of head depth measurements and instar frequencies were plotted sequentially to determine the lengths of the life cycles.

Life histories of ceratopogonids were studied in a similar manner to those of chironomids except that head length instead of depth was used. For other invertebrates that were not abundant in the samples, the times of occurrence of pupae (e.g., Trichoptera) or darkened wingpads (e.g., Ephemeroptera) were recorded, and note was taken of larval or nymphal sizes for several taxa.

Results

Amphipoda. Changes in the size distribution of *Hyaletta azteca* in Kingfisher Lake through the ice-free period of 1974 are illustrated in Figure 35. Most of the generation present in May, measuring 5 to 6 mm in length, grew slightly through June and produced eggs and embryos

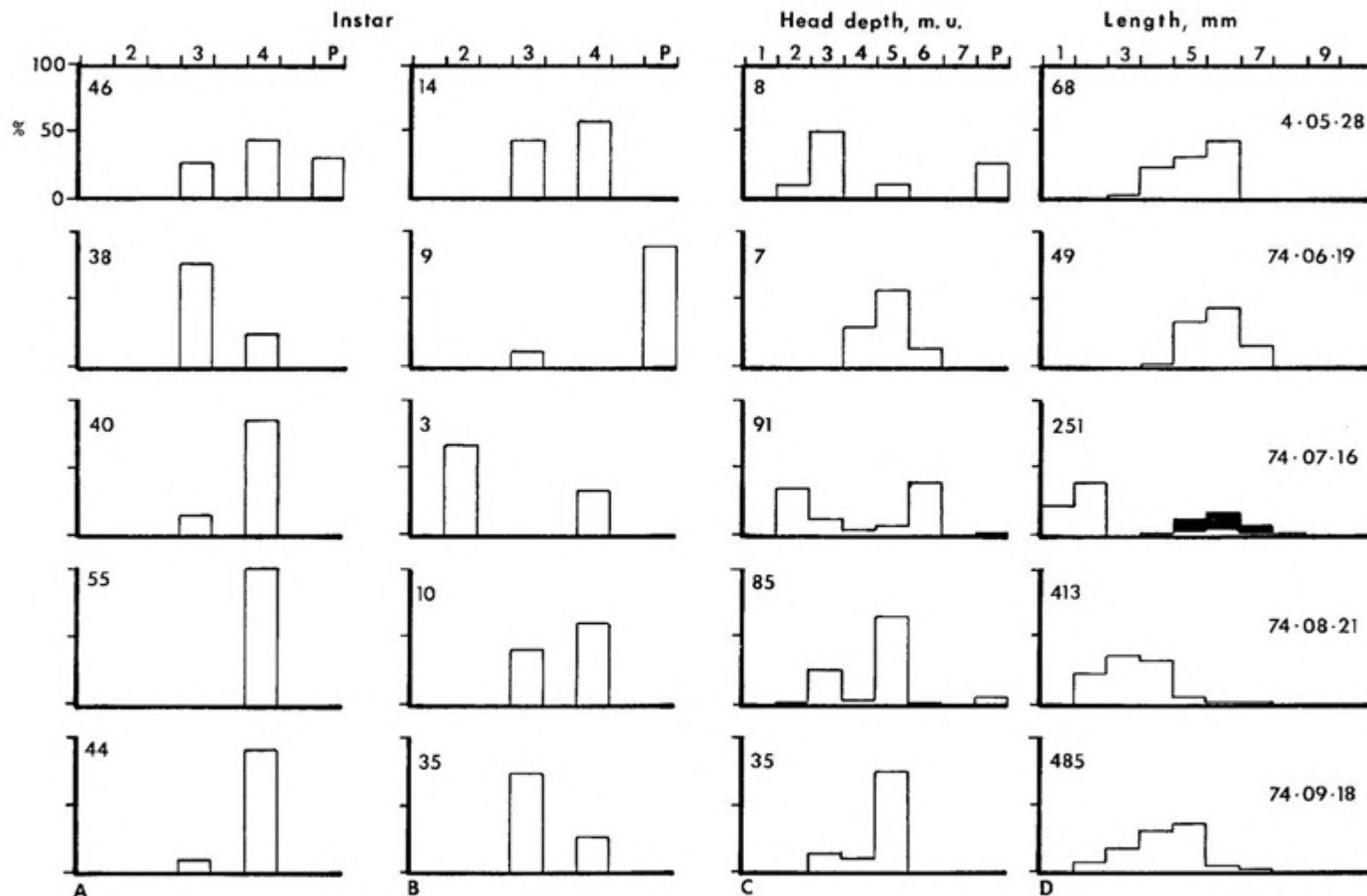


Figure 35. Instar and size-frequency analyses of *Pagastiella* (A), *Procladius* spp. (B), *Tanytarsus* spp. (C), and *Hyaella azteca* (D) in Kingfisher Lake. Numbers examined in upper lefthand corner. Pupae and prepupae, P. Dark areas, reproductive-condition females. 1 m.u. = 0.0398 mm.

in mid-July at a length of 5 to 7 mm. Most, if not all, of this generation disappeared from the population by mid-August. Young amphipods released in July grew until at least mid-September, when most of the animals measured 4 to 5 mm in length. There appears to be little winter growth, judging from the length distributions of the May and September samples.

The course of events in the life cycle of *H. azteca* in Mud Lake in 1974-75 is less clear (Figure 36). It is definite, however, that the overwintering animals produced eggs and embryos by at least the beginning of July, and that eggs, embryos or both were present until at least mid-July. By mid-July young *H. azteca* were entering the free-living population.

Four size-classes can be discerned in the 1975 size-frequency distributions for *Gammarus lacustris* in Baker Lake (Figure 37), each class showing slow growth through the summer. The histograms for 1974 tend to confirm that there are four size-classes in the Baker Lake population at any one time, although the smallest class was absent from the July 1974 samples. Only a very few females showed evidence of reproductive activity, and all of these were in the two largest size-classes.

Populations of amphipods in the remaining three lakes were either absent or numbers were too low to provide reliable life history information.

Chironomidae. Representative head-depth frequency histograms for several chironomid populations are illustrated in Figure 38. Most frequently, three larval instars could be distinguished in each taxon; however, in a few (Lower Consolation *Psectrocladius*, Kingfisher *Procladius*

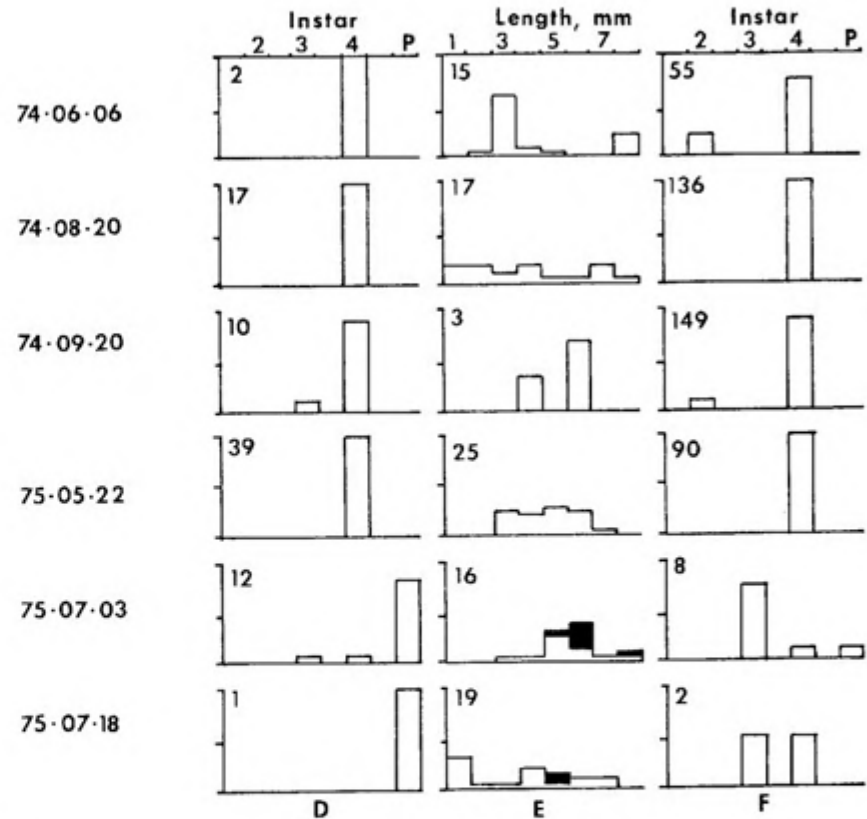
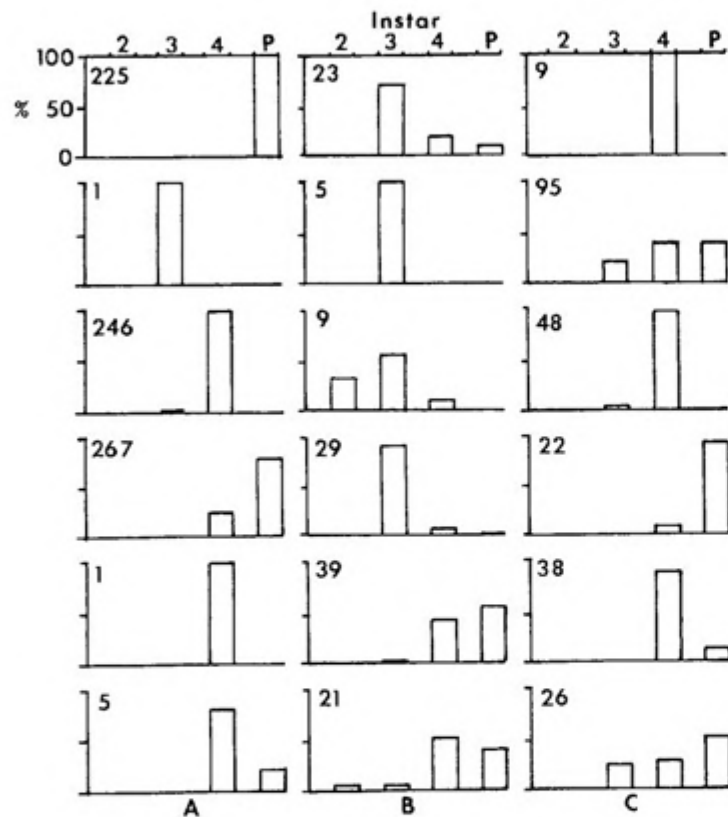


Figure 36. Instar analyses of *Micropsectra* (A), *Dicrotendipes* (B), *Tanytarsus* (C), *Guttipelopia* (D), and *?Culicoides* (F); and size-frequency analysis of *Hyalella azteca* (E) in Mud Lake. Numbers examined in upper lefthand corner. Pupae and prepupae, P. Dark areas, reproductive-condition females.

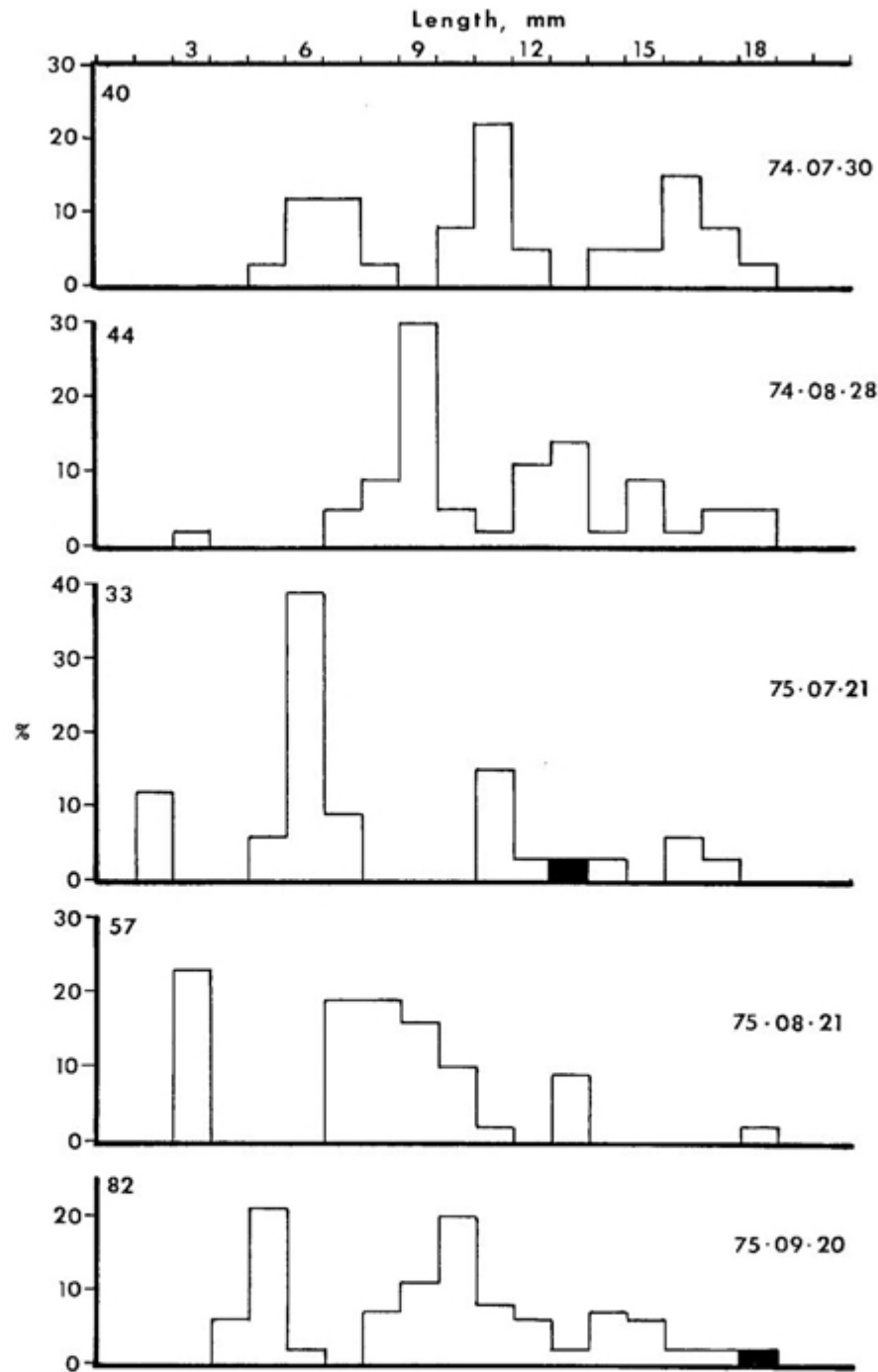


Figure 37. Size-frequency analysis of *Gammarus lacustris* in Baker Lake. Numbers examined in upper lefthand corner. Dark areas, are reproductive condition females.

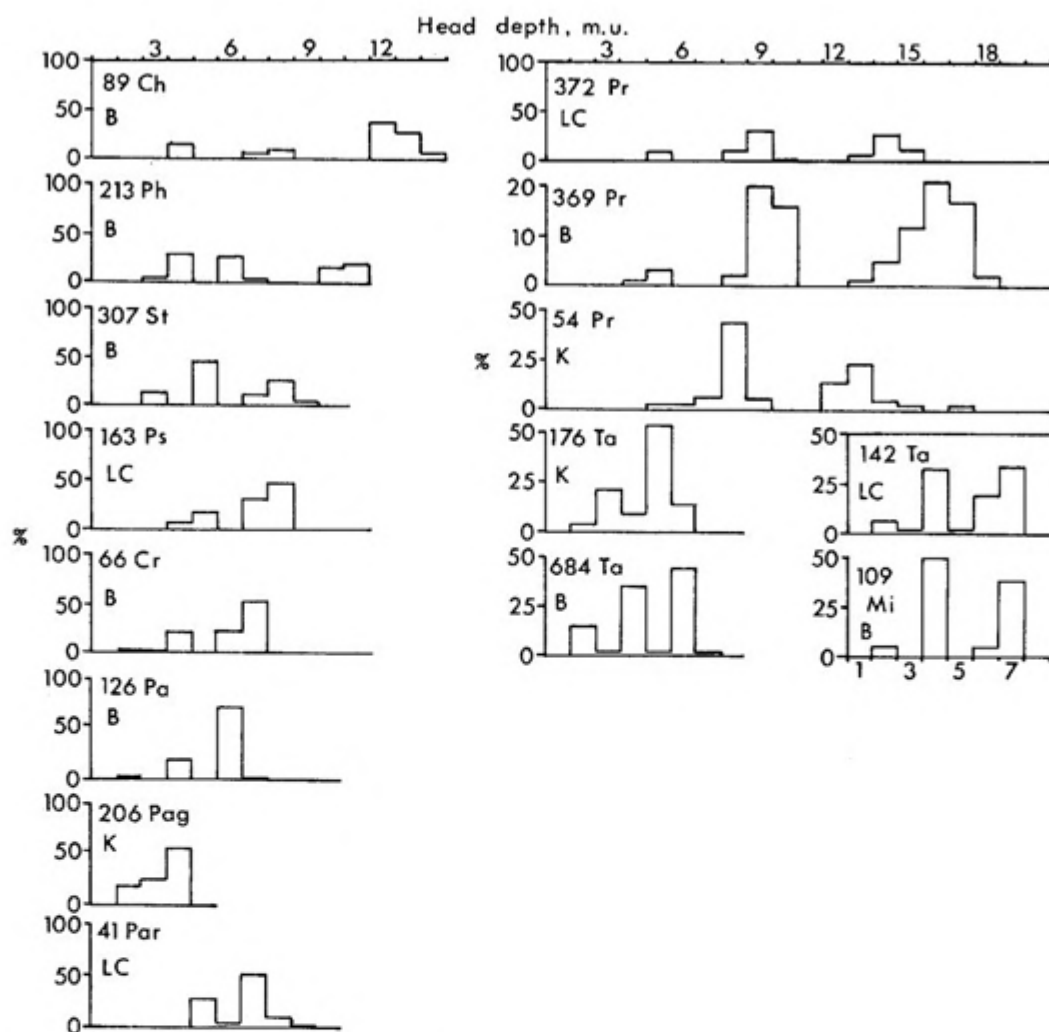


Figure 38. Size-frequency analyses of chironomid head depths to identify instars. Ch, *Chironomus*; Ph, *Phaenopsectra* s.s.; St, *Stictochironomus*; Ps, *Psectrocladius*; Cr, *Cricotopus*; Pr, *Procladius* s.s.; Ta, *Tanytarsus*; Mi, *Micropsectra*; Pa, *Paratanytarsus*; Pag, *Pagastiella*; and Par, *Paracladius*. Baker Lake, B; Lower Consolation Lake, LC; and Kingfisher Lake, K. 1 m.u. = 0.0398 mm. Numbers examined in upper lefthand corner.

ius and *Tanytarsus*) only two instars were obvious. In very small species such as *Corynoneura* (not shown) only the final larval instar was found, almost always in the prepupal stage. *Pagastiella* in Kingfisher Lake appears as only a single size-class in the histogram, but included two instars, one of 2 micrometer units (m.u.) head depth and the other of 3 to 4 m.u. head depth. Most specimens in the larger instar measured about 3.5 m.u. but those that were slightly less were classed as 3; those slightly more as 4.

It was possible to distinguish larval instars without having to actually measure head depths of all larvae because there was virtually no overlap of head depth in most populations (Figure 38). For populations in Moraine, Mud and Ptarmigan Lakes only a few individuals of each size-class encountered in each grab sample were measured, then the remaining larvae were allocated to size-classes by eye.

Instar analyses for the chironomid populations are illustrated in Figures 35, 36 and 39 to 42. It is apparent that the great majority of chironomid populations had only a single emergence per year, as indicated by the presence of pupae or prepupae; therefore these populations had at least one-year cycles. Several populations had young instars present during the emergence period that did not emerge then: these populations had at least two-year cycles. Finally, in a few populations shifts in instar distribution were so slow that these populations must have had cycles of at least three years.

The probable life-cycle durations of the various populations analyzed are listed in Table 21. Populations in Kingfisher and Mud Lakes had the shortest life cycles (0.5 to 1 year), Baker and Ptarmigan Lake

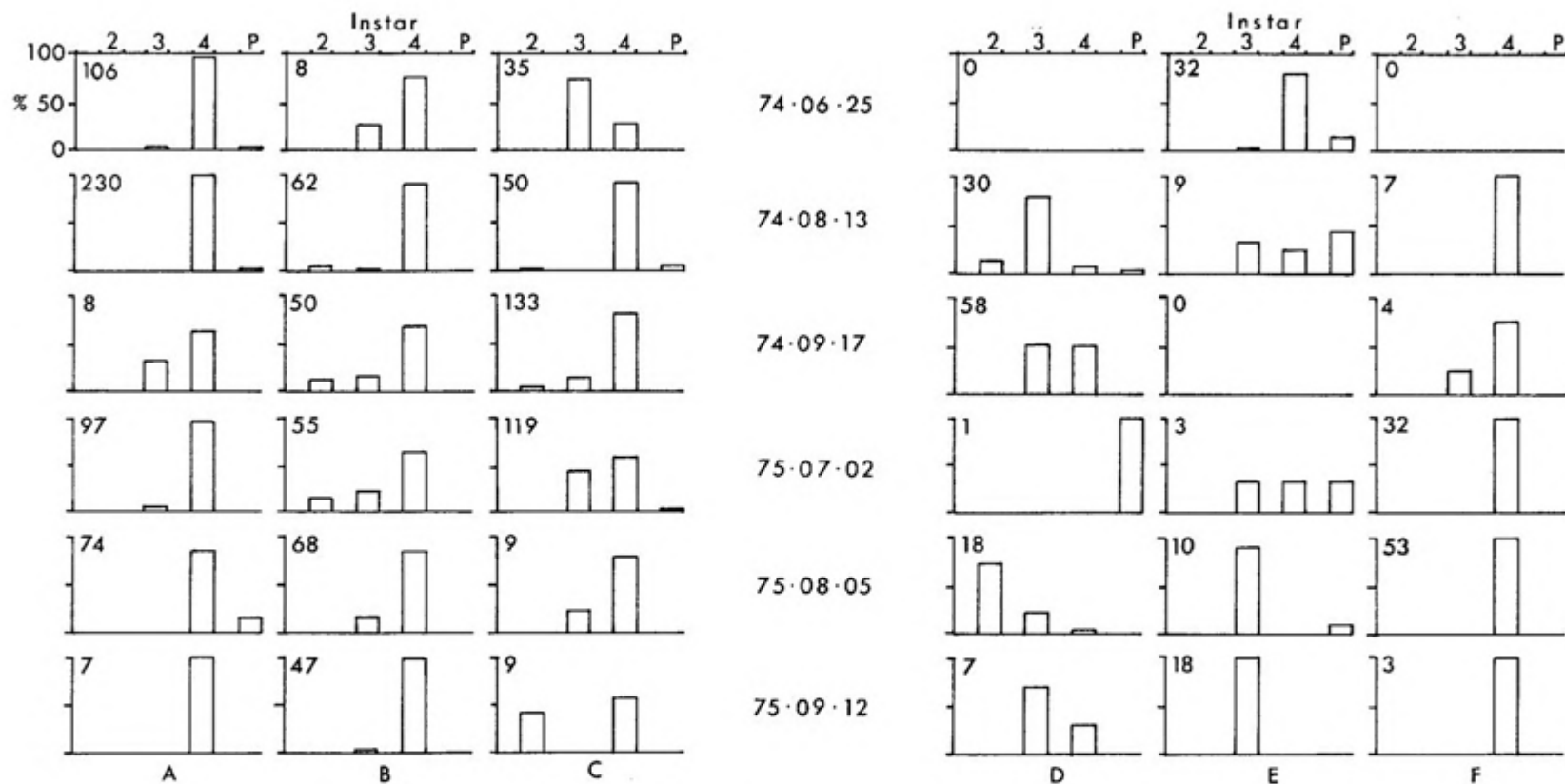


Figure 39. Instar analyses of *Paracladius* (A), *Stictochironomus* (B), *Micropsectra* (C), *Pseudodiamesa* (D), *Parakiefferiella* (E), and *Heterotrissocladius* (F) in Moraine Lake. Numbers examined in upper lefthand corner. Pupae and prepupae, P.

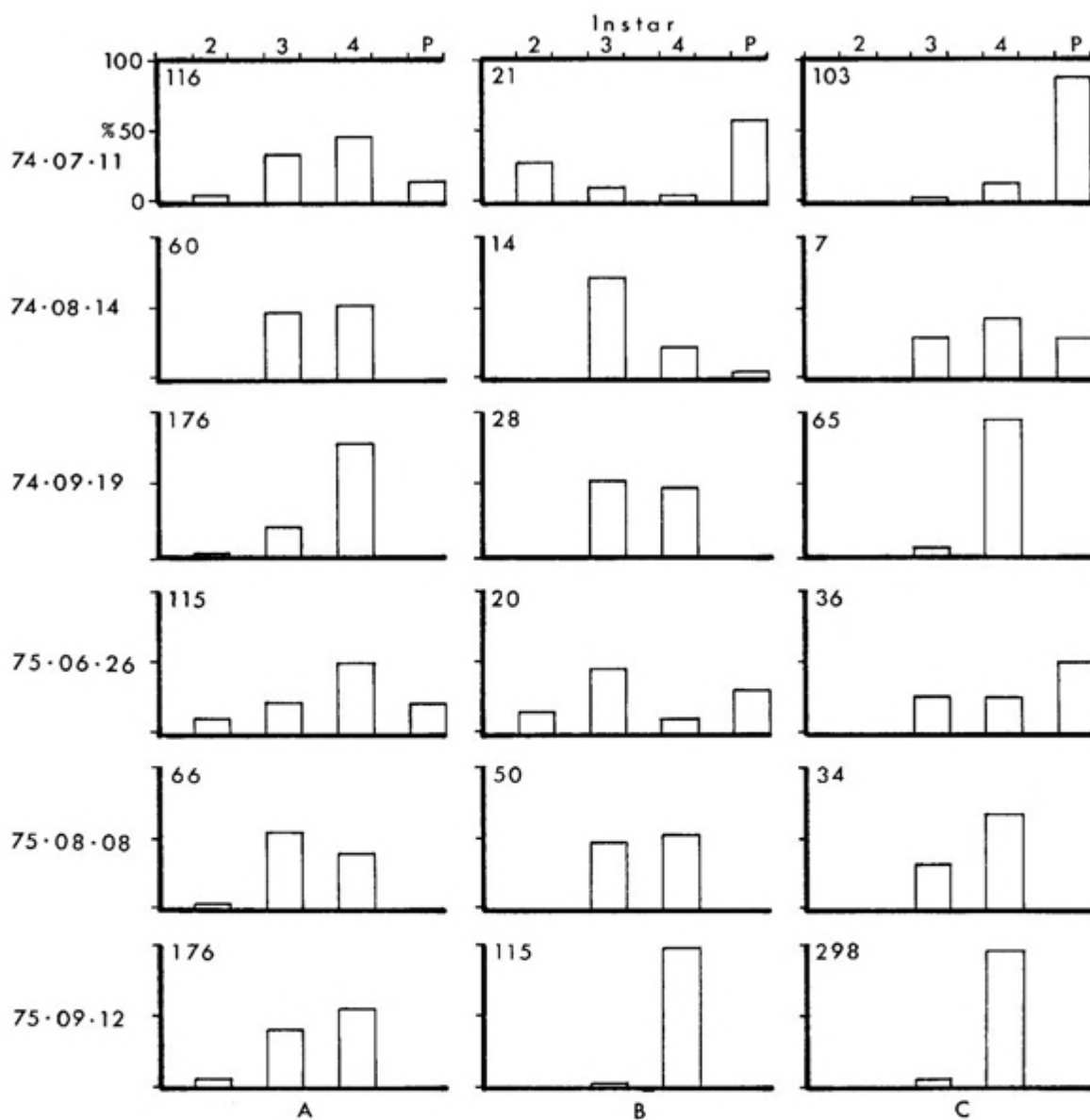


Figure 40. Instar analyses of *Procladius* (A), *Tanytarsus* (B) and *Psectrocladius* (C) in Lower Consolation Lake. Numbers examined in upper lefthand corner. Pupae and prepupae, P.

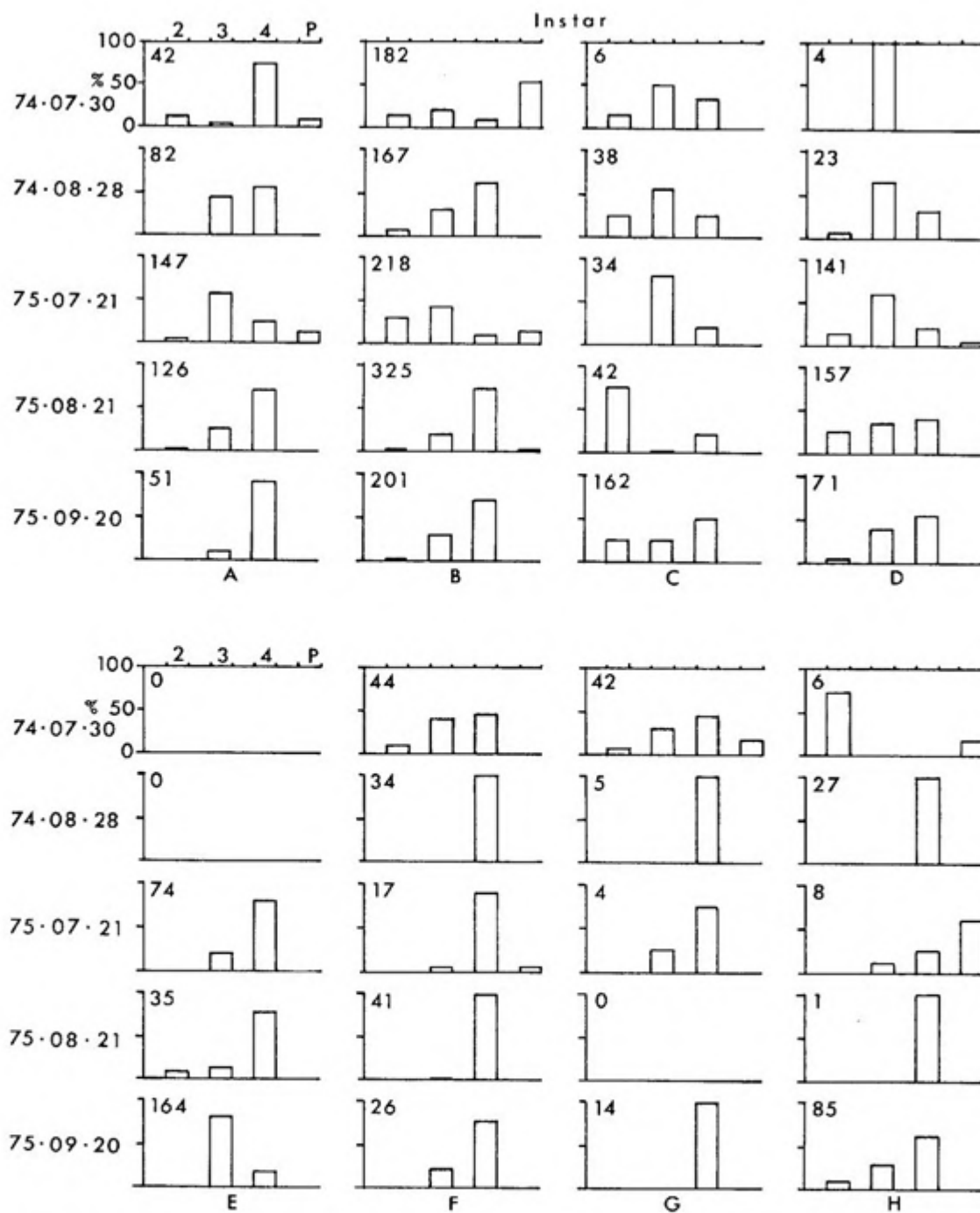


Figure 41. Instar analyses of *Procladius* (A), *Tanytarsus* (B), *Phaenopsectra* (C), *Stictochironomus* (D), *Micropsectra* (E), *Paratanytarsus* (F), *Cricotopus* (G), and *Chironomus* (H) in Baker Lake. Numbers examined in upper lefthand corner. Pupae and prepupae, P.

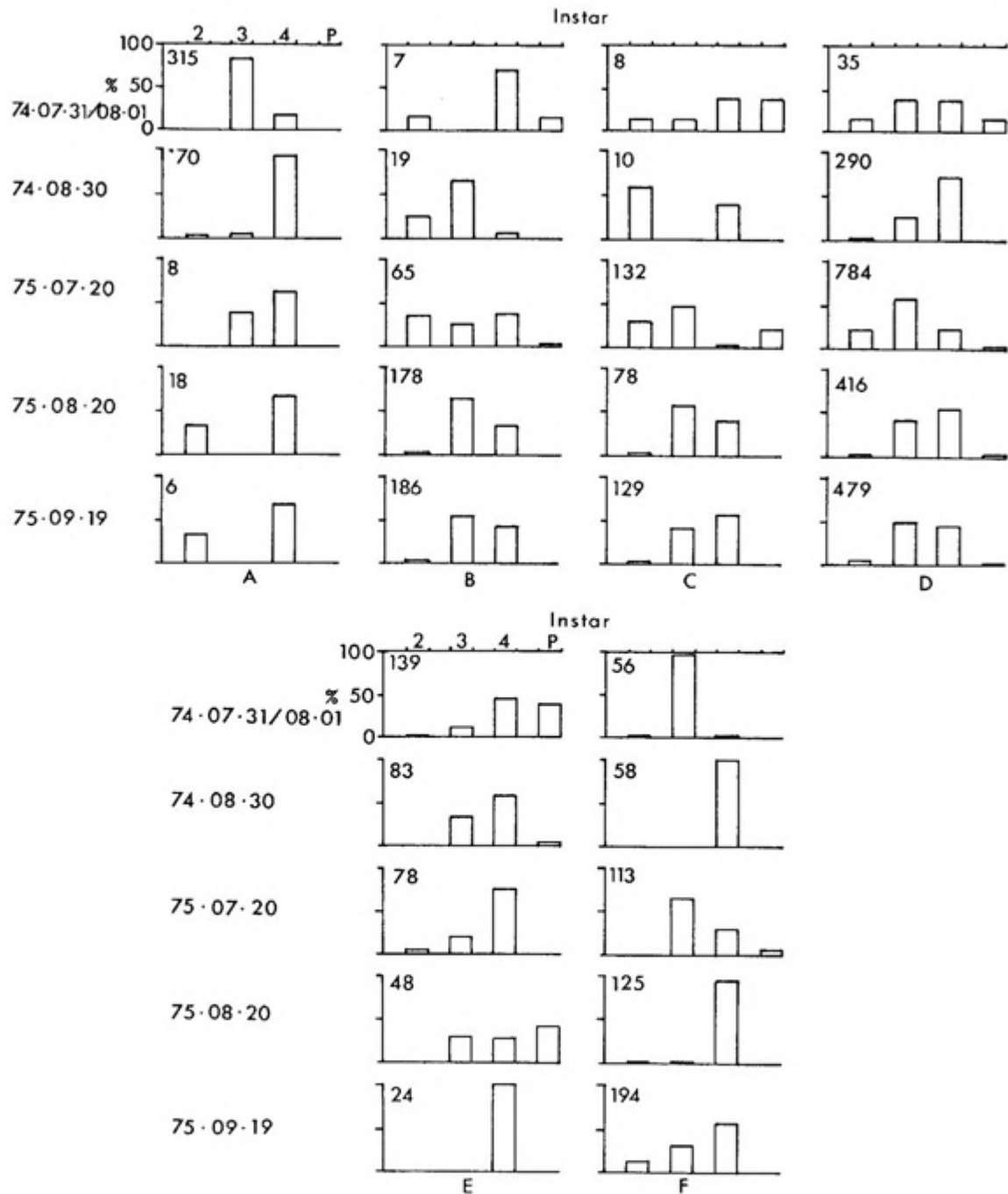


Figure 42. Instar analyses of *Phaenopsectra* (A), *Stictochironomus* (B), *Procladius* (C), *Tanytarsus* (D), *Paratanytarsus* (E), and *Micropectra* (F) in Ptarmigan Lake. Numbers examined in upper lefthand corner. Pupae and prepupae, P.

Table 21. Life cycle durations of 30 chironomid populations based on the instar analyses in Figures 35, 36 and 39 to 42.

<u>Lake</u>	<u>Genus</u>	<u>Length of Life Cycle</u>	<u>Interpretation</u>
Kingfisher	<i>Pagastiella</i>	2 yr.	One emergence per year, in spring; young from emerged adults first appear in Sept. as instar 3 larvae; previous year's young entering sampled population in May, June and July as instar 3.
	<i>Procladius</i>	?	Probably 2 spp. or more.
	<i>Tanytarsus</i>	?	Probably 2 spp. or more.
Mud	<i>Micropsectra</i>	1 yr.	One emergence per year, in spring, after which population almost disappears from samples; offspring from emerged adults appear in samples in Sept. as instars 3 and 4.
	<i>Dicrotendipes</i>	1 yr.	One prolonged emergence per year, after which the genus almost disappears from the samples; new generation begins appearing in the samples in July (instars 2 and 3), but does not become prominent until the following spring.
	<i>Tanytarsus</i>	0.5 or 1 yr.	Two emergences per year, in May and July-August; may indicate 1 sp. with 2 generation/yr., or 2 spp. with asynchronous 1-yr. cycles.
	<i>Guttipelopia</i>	at least 1 yr.	One emergence per year, in July.
Moraine	<i>Paracladius</i>	very long	Small, prolonged emergence; very little change in instar distribution over 2 yr., despite the fact that instars 2 and up should have been retained by the sieve.
	<i>Stictochironomus</i>	3 yr.	No emergence observed over 2 summers; instars 2 and 3 required about 1 year to reach instar 4; instar 4 persisted for at least 1 year and would not emerge before spring 1976.

- continued

Table 21 - cont'd.

<u>Lake</u>	<u>Genus</u>	<u>Length of Life Cycle</u>	<u>Interpretation</u>
Moraine	<i>Microseetra</i>	at least 2 yr.	One small emergence per yr., during which time many third and fourth-instar larvae <u>do not</u> emerge.
	<i>Pseudodiamesa</i>	at least 1 yr.	One small emergence per yr., data too variable and sparse to interpret with confidence.
	<i>Parakiefferiella</i>	?	Data too variable and sparse to interpret.
	<i>Heterotrissocladius</i>	?	Too few data to interpret with confidence, but life cycle is evidently very long, since instar distribution hardly changed over 2 summers.
Lower Consolation	<i>Procladius</i>	3 yr.	One emergence per yr., during which many fourth-instar larvae <u>do not</u> emerge; young derived from the emerged adults begin appearing in instar 2 by mid-Sept., reach the third instar by Aug. of following year; third and fourth-instars each last about 1 yr.
	<i>Tanytarsus</i>	2-3 yr.	One emergence per yr. in July-Aug.; young from the emerged 1974 adults reached the second instar by July 1975 and the fourth instar by Sept. 1975, over-wintering to emerge the following summer. Some 1974 third instars, already 1 yr. old, apparently would not have emerged until 1976 as well.
	<i>Psectrocladius</i>	2 yr.	One emergence per year in June-July mainly; young from 1974 adults appeared in June 1975 as third-instar larvae, reached the fourth instar by Sept. 1975 and would have emerged the following year.
Baker	<i>Procladius</i>	2 yr.	One small emergence per yr. in July; young from 1974 adults appeared in July 1975 in instars 2 and 3; these reached the fourth instar by Sept. and would have emerged the following summer.

- continued

Table 21 - cont'd.

<u>Lake</u>	<u>Genus</u>	<u>Length of Life Cycle</u>	<u>Interpretation</u>
Baker (cont'd.)	<i>Tanytarsus</i>	2 yr.	One emergence per yr. in July-Aug.; second- and third-instar larvae derived from 1974 adults dominated the July 1975 sample, reached the fourth-instar by Sept. 1975 and would have emerged the following year.
	<i>Phaenopsectra</i>	at least 2 yr.	No pupae or prepupae found, but virtual disappearance of third instar between July and Aug. 1975 suggests rapid development and emergence then; wide instar distribution and slow change in distribution in 1974 suggests the life cycle is at least 2 yrs. long.
	<i>Stictochironomus</i>	at least 2 yr. (probably 3 yr.)	One small emergence per yr. (sometimes none?); larvae apparently required at least one year to reach instar 3 (Aug. 1974-Sept. 1975); third-instar larvae took at least one year to reach instar 4 (Aug. 1974-Aug. 1975).
	<i>Microsectra</i>	at least 2 yr.	No pupae or prepupae found; Sept. 1975 third- and fourth-instar larvae might have emerged the following summer.
	<i>Paratanytarsus</i> ?	at least 2 yr.	One emergence per yr; little change in instar distribution from Aug. 1974 through August 1975 indicates at least a 2-yr life cycle.
	<i>Cricotopus</i>	at least 1 yr.	One emergence per yr. at most; data are too sparse to interpret with confidence.
	<i>Chironomus</i>	at least 1 yr.	One emergence per year, in July; too few data to interpret with confidence.
Ptarmigan	<i>Phaenopsectra</i>	?	No pupae or prepupae found; too few data to interpret confidently.
	<i>Stictochironomus</i>	at least 2 yr.	One emergence per year, in July; larvae remain in the fourth instar for at least one year (July 1975 to over the 1975-76 winter); at least one year, probably two is required to reach the fourth instar.
	<i>Procladius</i>	at least 2 yr.	One emergence per yr. in July; July 1975 second- and third-instar larvae must have been at least 1 yr. old; the third and fourth instar by Sept., and would not have emerged before July 1976.

- continued

Table 21 - cont'd.

<u>Lake</u>	<u>Genus</u>	<u>Length of Life Cycle</u>	<u>Interpretation</u>
Ptarmigan (cont'd.)	<i>Tanytarsus</i>	at least 2 yr.	One emergence per yr. in July-Aug.; July 1975 second- and third-instar larvae must have been at least one year old, reached the third and fourth instars by Sept. 1975, and would not have emerged before July 1976.
	<i>Paratanytarsus</i> ?	2 yr.	One emergence per yr. mainly in Aug.; July 1975 second-instar larvae derived from the 1974 adults reached the fourth instar by Sept. 1975 and would have emerged in summer 1976.
	<i>Micropectra</i>	2 yr.	One emergence per yr. in mid-July; third-instar larvae (July 1975) derived from the 1974 adults reached the fourth instar by Aug. 1975, and would have emerged the following spring.

populations typically had at least 2-year life cycles, and Moraine and Lower Consolation Lake populations tended to have the longest life cycles (typically 2 to 3 years). The life-cycle durations of individual genera sometimes differed among the lakes: *Tanytarsus* could have had a life cycle as short as 0.5 years in Mud Lake or as long as 3 years in Lower Consolation Lake.

Other Invertebrates. Ceratopogonids in Kingfisher Lake were of at least three species, so that no trends could be seen in the size-frequency data. In Mud Lake, *Culicoides*? evidently had a long development time in the final instar (≥ 1 year) with a possible emergence in May or June, but the data are far from conclusive (Figure 36).

Pupae appeared in the Kingfisher Lake *Oecetis* (Trichoptera) population in mid-July 1974, coincidental with the appearance of very small larvae. Small larvae only were found in mid-August. *Oecetis* pupae appeared in early July in the Mud Lake population, followed by small larvae in subsequent collections.

Caenis (Ephemeroptera) appeared with dark wingpads in mid-July in Kingfisher Lake, suggesting emergence near that time. By mid-September, *Caenis* nymphs were a little more than half their emergence length. *Caenis* nymphs with well-developed but undarkened wingpads appeared in Mud Lake in early July and had darkened wingpads in August, small nymphs appearing in the September samples.

There was insufficient material in the samples to determine life history lengths of other taxa in the six lakes.

Discussion

Amphipoda. *Hyalella azteca* has one generation per year in Kingfisher Lake, with reproduction in July when inshore (0 - 2 m) temperatures range from about 15 to 18°C (Figure 35). These results contrast with those of Cooper (1965), who found that *H. azteca* had two generations per year in Sugarloaf Lake, Michigan, when summer temperatures average about 18 to 22°C¹. The Kingfisher Lake population more closely resembles that of the same species in Marion Lake, British Columbia (Mathias 1971) and West Blue Lake, Manitoba (Biette 1969), where *H. azteca* also has one generation per year. However, in Marion Lake reproduction is continuous in shallow water from May to September, where temperatures average 15 to 20°C; and in West Blue Lake reproduction is continuous from June to September at an average temperature near 17°C. The Kingfisher Lake population thus has the shortest reproductive period of any of the four populations for which published data were available.

Although less conclusive than those for the Kingfisher Lake population, the data for *H. azteca* in Mud Lake suggest a single annual generation in Mud Lake also. This conclusion is suggested by the short periods of reproduction and recruitment into the free-living population (July and July-August, respectively), and by the summer temperatures in Mud Lake, which range from approximately 13 to 18°C in the upper two metres from June through August (Figure 9). Cooper (1965) found that *H. azteca* did not grow at 10°C, had an incubation period of 26.5 days at 15°C and a maturation period of 98 days at 15°C. At 20°C the incubation

¹ Temperature data from Cooper (1965) for the years 1963 and 1964.

and maturation periods were 12.7 and 36 days, respectively. According to Cooper's observed development times, the period when water temperatures exceed 10°C is long enough to permit only one generation per year in Mud Lake.

In Baker Lake, *Gammarus lacustris* produces one generation annually, which persists for 4 years, so that at any one time the population is made up of 4 year-classes. Growth in length is extremely slow: approximately 3, 4, 3.5 and 1 mm in the first, second, third and fourth summers, respectively, with overwinter growth (late September to early July) being approximately 1 mm.

The four-year life cycle of *G. lacustris* in Baker Lake appears to be the longest on record for this widespread species. The life cycle is typically one year in other Alberta waters (Clifford 1969, Menon 1969), Manitoba (Biette 1969), the USSR (Peckman 1954, in Winberg 1971), and Wales (Hynes 1955); although populations with a two-year cycle have been reported (Lake Sevan, USSR, by Markosyan 1948, in Winberg 1971; and *G. l. limnaeus* in southern Ontario streams, Hynes and Harper 1972).

The slow growth rate and long life cycle of *G. lacustris* in Baker Lake must be caused, at least in part, by the low water temperatures which average no more than 10°C even in mid-summer (Figure 11). Egg and embryo incubation alone takes 3 weeks at the much higher temperature of 18°C (Hynes 1955), and *G. lacustris* requires 11 months to mature in West Blue Lake, Manitoba, where temperatures average approximately 17°C from June to September (Biette 1969).

Chironomidae. Chironomids usually have 4 larval instars that are separable on the basis of head capsule dimensions (McCauley 1974,

Welch 1976), but in the present study only 3 instars were distinguishable at most. It is likely that the earlier instars, particularly of the small species such as *Corynoneura* and *Pagastiella*, were not retained efficiently by the sieve (mesh aperture 0.36 x 0.52 mm). Maitland *et al.* (1972) demonstrated that numbers of the smallest *Stictochironomus*, a large form, were seriously underestimated when a sieve having a mesh aperture of 0.5 mm was used to remove chironomids from sediment. It is also possible that young instars of certain taxa were missed because sampling was confined to the open-water period. This explanation could account for the absence of small *Psectrocladius* and *Paracladius* larvae from the Lower Consolation Lake samples. Second-instar larvae of both genera should be large enough to be retained by the sieve used, judging from the results for other species of comparable third- and fourth-instar size.

Some of the genera used in the instar analyses undoubtedly included more than one species which differed in size. In Kingfisher Lake *Procladius* prepupae were found with head capsule depths of 8 m.u., yet considerably larger non-prepupal larvae were common (Figure 38). Similarly, *Tanytarsus* prepupae in Kingfisher Lake sometimes had a head depth of 4 m.u., but non-prepupal larvae having head depths of 5 or 6 m.u. were abundant. Overlapping of instar sizes of different species in the same histogram could have obscured instar size differences of the individual species in these cases.

A more serious difficulty in working at the generic level is that including congeneric species, indistinguishable on the basis of size but having distinctly different properties, in an instar analysis could lead to an erroneous life history interpretation. However, mixed-

species populations will be of no consequence to interpretation of their life cycles if the cycles are synchronous. In cases where the data strongly suggest a one-year cycle, such as in Mud Lake *Micropectra* (Figure 36), an error in interpretation resulting from mixing species is not possible. There is only one emergence per year, so each species (if the population consists of more than one) must emerge at the same time and have a one-year life cycle. If any one of the species had a cycle longer than one year, early instars must be expected in the sample at the time of emergence. In the present example this was not the case; therefore all *Micropectra* species sampled in Mud Lake, if there were more than one, must have been univoltine.

Interpretation becomes more risky in some cases where the data suggest a life cycle of two or more years duration. It is conceivable that the genus population consists of a mixture of univoltine and hemivoltine species, for example, and that the cycle of the univoltine population could be masked by that of the hemivoltine population. It is also possible that individuals in a single-species population may take either one or two years to develop. There is no satisfactory way of distinguishing such cases in the data of this study. Considering that all but one of the populations with two- and three-year cycles were found in the rigorous environments of Moraine, Lower Consolation, Baker and Ptarmigan Lakes, and that species diversity tends to be low in rigorous environments (e.g., Ricklefs 1973:700), it was assumed that each genus population is strongly dominated by a single species, so that the life cycle interpretations apply to one species or to a group of species with synchronous life cycles.

A substantial number of studies reporting the voltinism of chironomids in a variety of habitats exist in the literature (Table 22). In general, they show that chironomids in warm or eutrophic habitats in temperate lakes have shorter life cycles than those in cooler or oligotrophic habitats, typically with those in the former group being uni- or bivoltine and those in the latter being uni- or hemivoltine. In extremely eutrophic or warm habitats such as sewage lagoons or tropical waters, chironomids may have numerous generations per year (Oliver 1971, Kimerle and Anderson 1971); in extremely cold oligotrophic arctic lakes life cycles are usually at least 2 years long, and may be as long as 3 years or more (Oliver 1968, Welch 1976). To relate the above observations to the present study, the 0.5- to 2-year life cycles interpreted for Mud and Kingfisher Lake chironomids are well within the range to be expected in low-elevation temperate lakes. The 2- and 3-year life cycles interpreted for Moraine, Lower Consolation, Baker and Ptarmigan chironomid populations are probably typical of those to be found in cold, oligotrophic arctic or alpine lakes.

Other invertebrates. The Mud Lake data suggest a life cycle of at least one year for ?*Culicoides*, with a single annual emergence in May or June. Two ceratopogonid species in Marion Lake, British Columbia, also had one emergence per year; one species emerging in May or June, the other in July and August (Hamilton 1965). Similar single annual emergence patterns have been reported for numerous ceratopogonid species in a German stream (Havelka 1976), and an annual life cycle has been reported for an Alaskan *Culicoides* species (Williams 1951). Bivoltine

Table 22. Published life cycle durations of Chironomidae (see also Table 23).

<u>Taxon</u>	<u>Habitat</u>	<u>Generation Duration (yr)</u>	<u>Source and Comments</u>
29 chironomid spp.	L.de Port-Bielh, France	1	Capblancq & Laville (1972)
2 <i>Chironomus</i> spp.	subalpine lake	2	"
several chironomid spp.	V.Finstertalersee, Austria	1	Bretschko (1974). Small part of <i>Protonypus forcipatus</i> population may have 2 gen.yr. ⁻¹
Approx. 90 chironomid spp.	alpine lake	1	Hamilton (1965), Efford (1972)
<i>Pagastiella</i> sp.	Marion L., B.C.	1 to 2	" McCauley (1974)
3 chironomid spp.	Tjeukemeer, Holland	1	Beattie <i>et al.</i> (1972)
<i>Pentapedilum uncinatum</i> G.	polder reservoir	0.5	"
<i>Stictochironomus</i> , <i>Chironomus</i>	Lock Leven, Scotland	1	Maitland <i>et al.</i> (1972)
<i>Glyptotendipes</i>	eutrophic lake	0.5 to 1	
<i>Tanytarsus</i>		0.33	
<i>Pagastiella orophila</i> (Edw.)	Kuusijarvi, Finland	1	Armitage (1971)
	mesohumic, shallow		
<i>Hydrobaenus</i> spp.	Emmaline L., Colo.	possibly 0.5	Walters and Vincent (1973)
Several chironomid spp.	alpine lake	<u>≥1</u>	
<i>Chironomus hyperboreus</i> Staeg.	L.Mývatn, Iceland	2	Lindgaard and Jónasson (1975)
<i>Tanytarsus gracilentus</i> (Holmg.)			
21 chironomid spp.}	Costello L. Ont. dystrophic	1	Miller (1941)
13 chironomid spp.}	above thermocline	0.5	
2 chironomid spp.	" below "	1	
3 chironomid spp.	" " "	2	
<i>Procladius</i>	Arctic lakes	<u>≥3</u>	Oliver (1968)

- continued

Table 22 - cont'd

<u>Taxon</u>	<u>Habitat</u>	<u>Generation Duration (yr)</u>	<u>Source and Comments</u>
Several chironomid spp.	2 eutrophic ponds, England	mostly 0.5, some 1	Learner and Potter (1974a)
<i>Glyptotendipes barbipes</i> (Staeg.)	sewage lagoon, Ore. ultra eutrophic	<<1	Kimerle and Anderson (1971)
<i>Chironomus anthracinus</i>	Esrom Sø, Denmark	1 2	above thermocline Jónasson (1972) below thermocline

emergence patterns have been found for several ceratopogonid species in another German creek by Havelka (1976), but in general a univoltine life cycle seems most likely for ceratopogonids in Mud and Kingfisher Lakes.

The caddisfly *Oecetis* evidently has a single generation per year in Mud and Kingfisher lakes, with a short emergence period in July. Univoltinism in Trichoptera has been widely reported in the literature and is held to be typical of the order (Borror and DeLong 1971, Roback 1974, Wiggins 1977). However, Wiggins (1977) suggested some limnephilids and species in other families could have a cycle two years or longer, and at least one bivoltine population is known (Anderson and Bourne 1974). Univoltine Trichoptera populations are probably the rule in Mud and Kingfisher Lakes, but the large limnephilids found in the four higher, colder lakes are likely to have generations lasting two years or longer.

The mayfly *Caenis* appears to have a univoltine life cycle in Mud and Kingfisher Lakes, with an emergence in July or August. Nearly all Ephemeroptera studied in Alberta are univoltine, a very few may be bivoltine, and none have been reported to have life cycles longer than one year (Hartland-Rowe 1964, Clifford 1969, Radford 1971, Boerger and Clifford 1975, Robinson 1976). The only Alberta location in which the life history of *Caenis* has been studied is the Bigoray River, where it had a single annual emergence, so must have had at least a one-year cycle (Boerger and Clifford 1975). Bivoltine populations have been reported from warm, productive experimental ponds, however (Hall, Cooper and Werner 1970).

PRODUCTION

Calculations

Annual production of each benthic macroinvertebrate group collected in the Ekman grab samples was estimated from the mean biomass data by multiplying mean biomass by an assumed annual $P/\bar{B}$.

Summer $\bar{B}$ was taken as a measure of annual $\bar{B}$. This assumption may not be valid, but at present there are no data on seasonal variation in benthic invertebrate biomass for Canadian Rocky Mountain lakes against which the assumption could be tested. Seasonal variations in biomass could be expected to be low when biomasses of large taxonomic groups are measured together, because overlapping generations would tend to level out biomass in time. Biomasses of individual species having discrete cohorts and life cycles of one year or less could be expected to be more variable seasonally. Seasonal variation in biomass may even be a moot consideration: sampling variability is typically so great in studies of benthos that seasonal variations in biomass may be obscured (e.g., Figures 31 to 34). Annual $P/\bar{B}$ was estimated from a knowledge of the life cycle durations to be expected in each taxonomic group, and an analysis of $P/\bar{B}$ per generation derived from a review of published data (below).

Voltinism and $P/\bar{B}$

Summary of published data. In a recent review, Waters (1977) showed that annual $P/\bar{B}$ declined as the life cycle duration of benthic macroinvertebrates increased, a phenomenon noted earlier by Mann (1967: 254) on the basis of much less evidence. Waters (1969) showed theoretically that $P/\bar{B}$ per cohort (generation) could range between about 1.5 and 8,

given a variety of reasonable assumptions about growth and mortality, and suggested that a $P/\bar{B}$ per cohort of 4.5 is probably typical of aquatic invertebrates in general.

Annual $P/\bar{B}$ divided by the number of generations per year should be approximately equal to cohort $P/\bar{B}$ (Waters 1977). The data reviewed by Waters suggest that $P/\bar{B}$ per generation so calculated may vary little regardless of voltinism or taxon, so might serve as a valuable coefficient for converting biomass data to estimates of production.

This possibility was examined by analyzing published $P/\bar{B}$ and voltinism data. The literature reviewed (Table 23) was similar to that reviewed by Waters (1977), but my analysis was restricted to freshwater invertebrates that occur or have close relatives in lakes. Some published values not considered by Waters have been included in the present analysis as have individual rather than mean estimates of $P/\bar{B}$ per generation. Some papers cited by Waters were not readily available to me, so have been omitted.

$P/\bar{B}$ per generation showed the following relationship to duration of the generation:

<u>Duration of generation(yr)</u>	<u>Mean $P/\bar{B}$ gen.⁻¹ $\pm$ SE</u>	<u>n</u>
0.33	3.76 $\pm$ 0.49	5
0.5	2.70 $\pm$ 0.32	22
1	4.25 $\pm$ 0.25	55
2	4.18 $\pm$ 0.43	13
3	4.65 $\pm$ 0.68	13

The hypothesis that there are no differences in the distribution of $P/\bar{B}$ per generation among the five life-cycle groups was rejected (Kruskal-

Table 23. Published values of $P/\bar{B}$ and voltinism, and estimates of $P/\bar{B} \text{ gen.}^{-1}$, for freshwater benthic invertebrates. Asterisks indicate values rejected from the statistical analyses.

<u>Taxon</u>	<u>Habitat</u>	<u>Generation Duration (yr)</u>	<u>$\frac{P}{\bar{B}}$</u>	<u>$\frac{P}{\bar{B}} \text{ gen.}^{-1}$</u>	<u>Comments and Source</u>
Oligochaeta	Eglwys Nunydd Res.	1	2.7	2.7	1970 Potter and Learner
<i>Tubifex tubifex</i>	Wales		1.7	1.7	1971 (1974b)
Hirudinoidea					
<i>Helobdella stagnalis</i> (L.)	Eglwys Nunydd Res.	2	3.2	1.6	1970 Learner and Potter
	Wales	2	3.0	1.5	1971 (1974b)
<i>Glossiphonia heteroclita</i> (L.)	R.Thames, England	1	5.25	5.2	Mann (1971)
<i>Erpobdella octoculata</i> (L.)	Wilfin Beck, "	2	1.67	3.3	Elliott (1973) 1966
			1.47	2.9	1967
			1.51	3.0	1968
Mollusca					
<i>Planorbis contortus</i>	R.Thames, England	1	0.32	0.32*	Mann (1971) $P/\bar{B} < 1.0$ in a univol- tine species is impossible.
<i>P.vortex</i> (L.)	R.Thames, England	1	6.47	6.5	Mann (1971)
<i>Ancylus lacustris</i> (L.)	" "	1	3.32	3.3	Mann (1971)
Crustacea					
<i>Asellus aquaticus</i> (L.)	R.Thames, England	2	3.17	6.3	Mann (1971)
" "	Eglwys Nunydd Res.	0.5	3.6	1.8	Potter and Learner yr.1
	Wales		4.4	2.2	(1974b) yr.2
" "	Pajep Maaskejaure, Sweden	2	1.96	3.9	Andersson (1969)
" "	L.Erken, Sweden	1	2.03	2.0	" "
<i>Gammarus lacustris</i>	L.Sevan, U.S.S.R.	2	2.05	4.1	Markosyan (1948) in Winberg (1971)
" "	Angara R.Lake, U.S.S.R.	1	~3	~3 *	Beckman (1954) in Winberg (1971)
<i>Pontoporeia affinis</i> Lindstr.	L.Krasnoe, U.S.S.R.	1	3.8	3.8	Kuz'menko (1969) yr.1.
			4.4	4.4	yr.2
" "	Red L. U.S.S.R.	1	4.1	4.4	Andronikova et al. (1972)

- continued

Table 23 - cont'd

<u>Taxon</u>	<u>Habitat</u>	<u>Generation Duration (yr)</u>	$\frac{P}{B}$	$\frac{P}{B_{gen}^{-1}}$	<u>Comments and Source</u>
<i>Pontoporeia affinis</i>	river, U.S.S.R.	1	3.44	3.4	Greze (1951) in Winberg (1971)
" "	northern lake, U.S.S.R.	2	1.9	3.8	
<i>Hyaella azteca</i> (Saussure)	Marion L., B.C.	1	4.18	4.2	Mathias (1971)
<i>Crangonyx richmondensis</i>	" " "	1	2.00	2.0	" "
<i>occidentalis</i> (Hubricht and Harrison)					
<i>Micruropus kluki</i>	L. Baikal, U.S.S.R.	1	2.5	2.5	Bekman (1959, 1962) in Winberg (1971)
<i>Gmelinoides fasciatus</i> Stelb.	" "	2	1.6	3.2	
" "	Possolski Sor, U.S.S.R.	1	2.9	2.9	" " "
<i>M. possolskii</i> Sow.	" " "	1	3.6	3.6	" " "
<i>Orconectes viridis</i> (Hagen)	West Lost L. Mich.	3	2.33	7.0	Momot (1967)
" "	" " "	3	0.94	2.8	Momot and Gowing (1977) yr.1
" "	" " "	3	1.33	4.0	" " yr.2
" "	" " "	3	1.32	4.0	" " yr.3
" "	North Twin L., Mich.	3	1.00	3.0	" " yr.1
" "	" " "	3	1.19	3.6	" " yr.2
" "	" " "	3	1.23	3.7	" " yr.3
" "	South Twin L., Mich.	3	1.17	3.5	" " yr.1
" "	" " "	3	1.53	4.6	" " yr.2
" "	" " "	3	1.19	3.6	" " yr.3
Ephemeroptera					
<i>Ephemerella subvaria</i> McD.	Luxemburg Cr., Minn.	1	5.93	5.9	Waters & Crawford (1973) mean of results from the 3 most reliable methods used
<i>Baetis vagans</i> McD.	Valley Cr., Minn.	0.33	9.7	3.2	Waters (1966)
<i>Choroterpes mexicanus</i> Allen	Brazos R., Texas	0.33	15.4	5.1	McClure and Stewart (1976)
<i>Ephemerella strigata</i> Eaton	Yoshino R., Japan	1	2.4	2.4	Tsuda (1972)
<i>Baetis rhodani</i> Pict.	streams, Czechoslovakia	2	8.02	4.0	Zelinka (1973)
<i>Rhithrogena semicolorata</i> Curt.	" "	1	8.84	8.8	" "
<i>Ecdyonurus</i> spp.	" "	1	8.25	8.2	" "

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Table 23 - cont'd.

<u>Taxon</u>	<u>Habitat</u>	<u>Generation Duration (yr)</u>	$\frac{P}{B}$	$\frac{P}{B} \text{ gen.}^{-1}$	<u>Comments and Source</u>
<i>Hexagenia limbata</i>	Tuttle Cr. Res. Kansas	1.02	5.39	5.5	Horst & Marzolf (1975) yr.1
" "	" "	1.02	3.67	3.8	" " yr.2
" "	" "	1.02	3.48	3.6	" " yr.3
" "	" "	1.02	4.30	4.4	" " yr.4
Odonata					
<i>Pyrrhosoma nymphula</i>	ponds, England	2	4.22	8.4	Lawton (1971) yr.1
			2.52	5.0	" yr.2
Plecoptera					
<i>Skwala curvata</i> (Hanson)	Sagehen Cr. Calif.	1	3.8	3.8	Sheldon (1972)
Megaloptera					
<i>Sialis mitsuhashii</i> Okamoto	L. Tatsu-Numa, Japan	3	3.8	11.4	Yamamoto (1972)
Trichoptera					
<i>Potamophylax cingulatus</i> Steph.	stream, S. Sweden	1	4.4	4.4	Otto (1975)
<i>Cyrmus trimaculatus</i>	R. Thames, England	1	4.63	4.6	Mann (1971)
<i>Athripsodes ancylus</i> (Vorhies)	Brashears Cr. Ky.	1	5.8	5.8	Resh (1975)
Diptera-Chironomidae					
<i>Chironomus plumosus</i>	Red L., U.S.S.R.	1	4.2	4.2	Andronikova <i>et al.</i> (1972)
<i>C. anthracinus</i>	" "	1	4.4	4.4	" "
<i>Procladius</i>	" "	0.5	5.0	2.5	" "
<i>Trissocladius</i> sp.	Char L., N.W.T.	2	1.9	3.8	Welch (1976)
<i>Pseudodiamesa arctica</i> (Mall.)	" "	2	1.5	3.0	" "
<i>Lauterbornia</i> sp.	" "	2	1.9	3.8	" "
<i>Heterotrissocladius oliveri</i>	" "	3	0.8	2.4	" "
<i>Orthocladius</i> spp. /Saeth.	" "	3	2.3	6.9	" "
<i>Phaenopsectra jucundus</i>	Sugar Loaf L. Mich.	1	4.8	4.8	Nees and Dugdale (1959)
<i>C. plumosus</i> L.	Alderfen Broad, England	0.5	1.9	1.0	Mason (1977) yr.1
"	" "	0.5	1.6	0.8	" yr.2
<i>C. tentans</i> Fabr.	Upton Broad, England	0.5	1.2	0.6	" yr.1
"	" "	0.5	1.1	0.6	" yr.2

- continued

Table 23 - cont'd.

<u>Taxon</u>	<u>Habitat</u>	<u>Generation Duration (yr)</u>	<u>P B</u>	<u>P B gen.⁻¹</u>	<u>Comments and Source</u>
<i>Tanytarsus holochlorus</i> (Edm.)	Upton Broad, England	1	8.3	8.3	Mason (1977) yr.1
"	"	1	4.5	4.5	" yr.2
<i>Procladius ruffovittatus</i>	Eglwys Nunydd Res. Wales	1	3.2	3.2	Potter and Learner (1974b)
<i>Tanytarsus lugens</i>	"	0.33	7.6	2.5	"
<i>Procladius choreus</i>	"	0.5	6.5	3.2	"
<i>C. plumosus</i>	"	0.5	6.4	3.2	"
<i>Glyptotendipes paripes</i>	"	0.5	5.9	3.0	"
<i>Limnochironomus pulsus</i>	"	0.5	6.3	3.2	"
<i>Microtendipes</i> sp.	"	0.5	5.7	2.8	"
<i>Procladius tener</i>	"	0.5	5.8	2.9	"
<i>C. manicus</i>	"	0.5	5.2	2.6	"
<i>Tanytarsus holochlorus</i>	"	0.5	6.6	3.3	"
<i>Tanytarsus inopertus</i>	"	0.5	5.2	2.6	"
<i>Limnochironomus</i>	Loch Leven, Scotland	1	3.58	3.6	Maitland & Hudspith (1974) yr.1
"	(sandy, littoral)	1	1.90	1.9	" yr.2
<i>Glyptotendipes</i>	"	1	4.98	5.0	" yr.1
"	"	1	1.85	1.8	" yr.2
<i>Stictochironomus</i>	"	1	3.06	3.1	" yr.1
"	"	1	9.80	9.8	" yr.2
<i>C. anthracinus</i>	Loch Leven, Scotland	1	3.9	3.9	Charles <i>et al.</i> (1974)
<i>Glyptotendipes</i>	(mud)	1	2.5	2.5	"
<i>Polypedilum</i>	"	1	4.5	4.5	"
<i>Limnochironomus</i>	"	1	4.0	4.0	"
<i>C. anthracinus</i> and/or	Uchinsk Res. U.S.S.R.	1	2.9	2.9	Sokolova, in Winberg (1971)
<i>Psilotanytus limnicola</i>	"	1	6.6	6.6	extremes
Chironomidae	Middle Bay of Quinte, Ont.	1	8.3	8.3	Johnson (1974)
"	Outer Bay of Quinte, Ont.	1	5.2	5.2	"
Chironomidae, profundal	Taltowisko L., Poland	1	3.1	3.1	Kajak and Rybak (1966)
"	"	1	4.3	4.3	extremes
"	Mikolajskie L.	1	3.3	3.3	"
"	"	1	5.4	5.4	"

- continued

Table 23 - cont'd.

<u>Taxon</u>	<u>Habitat</u>	<u>Generation Duration (yr)</u>	$\frac{P}{B}$	$\frac{P}{B}$ gen. ⁻¹	<u>Comments and Source</u>
<i>C. anthracinus</i>	Uchinskoye Res. U.S.S.R	1	2.9	2.9	Borutsky <i>et al.</i> (1971)
"	" "	1	4.5	4.5	" extremes
					Several other species with generations 0.5 yrs. long were omitted because Johnson (1974) claims they may have shorter durations.
<i>Procladius pectinatus</i>	Esrom Sø Denmark	1	1.68	1.7	Jónasson (1972)
<i>C. plumosus</i>	Goplo L. Poland	0.5	7.52	3.8	Wisniewski (1976)
<i>C. plumosus</i>	Tynwald L. Poland	0.33	14.2	4.7	Zytkowicz (1976)
<i>Tanytarsus gregarius</i>	" "	0.5	39.1	19.6*	"present for only a very small part of the year
<i>Procladius</i> sp.	" "	0.15	4.2	2.1*	"estimate of second generation production inaccurate
<i>Polypedilum</i>	Jeziorak L. Poland	1	2.8	2.8	Wolnomiejski <i>et al.</i> (1976)
<i>Stictochironomus</i>	sandy littoral areas	0.5	11.85	5.9	means of 3 stations
<i>Microtendipes</i>	" " "	0.5	12.88	6.4	" "
<i>Einfeldia</i>	Jeziorak L. Poland recently flooded littoral	0.33	9.83	3.3	Gizinski <i>et al.</i> (1976)

Wallis statistic $K = 11.73$, distributed as χ^2 with 4 degrees of freedom, $p < 0.025$). There is little difference in $P/\bar{B}$ per generation among taxa lasting a year or longer, so the mean $\pm$ SE for the group of 4.31 ± 0.21 might serve as a suitable estimate of $P/\bar{B}$ per generation for populations with life cycles lasting at least one year.

This possibility was examined further. $P/\bar{B}$ per generation of populations with at least one-year life cycles showed the following relationship to taxonomic group:

<u>Taxon</u>	<u>Mean $P/\bar{B}$ gen.⁻¹ $\pm$ SE</u>	<u>n</u>
Chironomidae	4.25 ± 0.33	33
Other insects ¹	5.72 ± 0.63	15
Malacostraca ²	3.76 ± 0.22	25
Other invertebrates ³	3.58 ± 0.54	8

The hypothesis that there are no differences in the distribution of $P/\bar{B}$ per generation among the four taxonomic groups was rejected ($K = 10.63$, $p < 0.025$, 3 degrees of freedom), so the means for each taxonomic group were used separately in the production calculations.

Assumed annual $P/\bar{B}$'s. To convert $P/\bar{B}$ per generation to annual $P/\bar{B}$, duration of the generations must be known. The instar analysis provided information on generation duration for many chironomids and amphipods which usually dominated biomass in the study lakes, but life cycle data on the remaining taxa were meagre. Published life-history

¹ Ephemeroptera, Megaloptera, Plecoptera, Trichoptera, Odonata

² Amphipoda, Isopoda, Decapoda

³ Hirudinoidea, Mollusca, Oligochaeta

studies, summarized below, were used to determine the probable generation durations for many taxa. The data on the duration of generations were then used with the data on mean $P/\bar{B}$ per generation to calculate annual $P/\bar{B}$ for each taxon.

Oligochaeta. A two-year life cycle was assumed for oligochaetes in Moraine, Lower Consolation, Baker and Ptarmigan Lakes. Lumbriculids, which dominated the Baker and Ptarmigan oligochaete faunas, are known to have two-year life cycles in Britain (Cook 1969). Tubificids, important in Moraine and Lower Consolation, are known to have one- or two-year life cycles elsewhere (Brinkhurst 1964, Brinkhurst and Kennedy 1965, Ladle 1971, Kennedy 1966a and b). Temperature is known to be positively correlated with annual $P/\bar{B}$ in Oligochaeta (Johnson and Brinkhurst 1971, Johnson 1974), and annual $P/\bar{B}$'s estimated by assuming a two-year life cycle would be similar to those obtained for Oligochaeta in other cold habitats (Johnson and Brinkhurst 1971, Johnson 1974).

In Mud and Kingfisher Lakes a univoltine oligochaete life cycle was assumed. One of the most common tubificids in Mud Lake was *Limnodrilus udekemianus*, which is known to have a two-year cycle elsewhere (Brinkhurst and Kennedy 1965, Kennedy 1966b). Lumbriculids, which dominate the Kingfisher oligochaete fauna, have a two-year cycle elsewhere (Cook 1969); but *Tubifex templetoni*, also found in Kingfisher Lake, can be bivoltine (Potter and Learner 1974). Much of the remaining oligochaete fauna consisted of unidentified Tubificidae, which can have more than one generation per year (Potter and Learner 1974) or high annual $P/\bar{B}$'s (Potter and Learner 1974, Mason 1977, Brinkhurst 1972, in Johnson 1974), so an assumption of one generation per year on the aver-

age seems reasonable for the entire oligochaete fauna in Kingfisher and Mud Lakes.

The mean $P/\bar{B}$ per generation for "other invertebrates" of 3.58 was used for oligochaetes, yielding estimated annual $P/\bar{B}$'s of 3.6 for oligochaetes in Mud and Kingfisher Lakes, and 1.8 for those in the remaining four lakes.

Hirudinoidea. The only leech found in Mud and Kingfisher Lakes was *Helobdella stagnalis*, a species that can be bivoltine in many temperate lakes, but is univoltine in an Alberta pond (Davies and Reynoldson 1976). Living at the maximum temperatures found in Kingfisher and Mud Lakes on each sampling date, and at 4°C through the winter, *H. stagnalis* would experience enough degree-days to be bivoltine, according to the data of Davies and Reynoldson (1976). Because it is highly unlikely that the population consistently lived at the highest temperatures available, a univoltine life cycle seems more likely for the Mud and Kingfisher Lakes populations. The mean $P/\bar{B}$ per generation for "other invertebrates" of 3.58 was therefore used to estimate *H. stagnalis* production in Mud and Kingfisher Lakes.

The leech found in Baker Lake, *Nepheleopsis obscura*, has a cohort lifespan of one to two years in two ponds near Calgary (Davies and Everett 1977). A two-year life-cycle and the mean $P/\bar{B}$ per generation for "other invertebrates" of 3.58 was assumed for *N. obscura* in Baker Lake, yielding an estimated annual $P/\bar{B}$ of 1.8.

Mollusca. The only molluscs constituting a biomass large enough to weigh separately in any of the lakes were sphaerid clams and

planorbid snails. Although published data are scarce, it appears that sphaerids have no more than one generation per year, and may frequently have fewer (Heard 1965, Mann 1971). The few published annual $P/\bar{B}$'s are consistent, ranging from 0.5 to 3.5, with most values lying between 1 and 2 (Mann 1971, Mason 1977, Johnson and Brinkhurst 1971). Johnson and Brinkhurst (1971) found sphaerid annual $P/\bar{B}$'s to be independent of mean annual temperature over the range 6 to 8°C in Lake Ontario. Sphaerid annual $P/\bar{B}$ was estimated to be 2 in all lakes based on the above considerations. The planorbids studied to date have had either univoltine or hemivoltine life cycles (Harmon 1974, Mann 1971), so a univoltine life cycle was assumed for them in Kingfisher Lake. The mean $P/\bar{B}$ per generation of 3.58 for "other invertebrates" was used to obtain an estimated annual $P/\bar{B}$ of 3.6 for planorbids.

Amphipoda. The instar analyses indicated that *Hyaletta azteca* had a univoltine life cycle in Mud and Kingfisher Lakes, and that *Gammarus lacustris* cohorts lived for four years in Baker Lake. *G. lacustris* was assumed to live for four years in Lower Consolation and Ptarmigan Lakes also. The mean $P/\bar{B}$ per generation for Malacostraca of 3.76 was used for the Amphipoda in this study, yielding estimated annual $P/\bar{B}$'s of 3.8 for *H. azteca* in Mud and Kingfisher Lakes, and 0.9 for *G. lacustris* in Baker, Ptarmigan and Lower Consolation Lakes.

Chironomidae. An average of one generation per year was assumed for Kingfisher and Mud Lake chironomids on the basis of the instar analyses. Although the analyses indicated bivoltine and hemivoltine

cycles were possible, the analyses for Mud Lake indicated univoltine cycles are more common. Furthermore, in taking an average cohort duration for the whole fauna, bivoltine and hemivoltine life cycles will average out to one generation per year. An average 2.5-year life cycle was assumed for chironomids in Moraine and Lower Consolation Lakes, and a 2-year cycle was assumed for chironomids in Baker and Ptarmigan Lakes, as suggested by the results of the instar analyses. The mean $P/\bar{B}$ per generation for chironomids of 4.25 was used to obtain an estimated annual $P/\bar{B}$ of 4.2 for chironomids in Kingfisher and Mud Lakes, 1.7 for those in Moraine and Lower Consolation Lakes, and 2.1 for those in Baker and Ptarmigan Lakes.

Other insects. A univoltine life cycle (see instar analysis) and the chironomid mean $P/\bar{B}$ per generation of 4.25 was assumed for ceratopogonids in Mud and Kingfisher Lakes, yielding an estimated annual $P/\bar{B}$ of 4.2 for the group. For *Caenis* in Kingfisher and Mud Lakes, a univoltine life cycle was assumed on the basis of the instar analysis data, and the mean $P/\bar{B}$ per generation of 5.72 for "other insects" was used to obtain an estimated annual $P/\bar{B}$ of 5.7. As was discussed in the instar analysis, Trichoptera (mainly *Oecetis*) in Mud and Kingfisher Lakes are probably univoltine, and the limnephilids in the remaining lakes probably have at least two-year cycles. The mean $P/\bar{B}$ per generation of 5.72 for "other insects" and the voltinism assumptions provided a trichopteran estimated annual $P/\bar{B}$ of 5.7 for Kingfisher and Mud Lake populations, and of 2.9 for caddisfly populations in the remaining four lakes. A two-year life cycle was assumed for Odonata in Kingfisher and Mud Lakes

(Lawton 1971), being applied to the mean $P/\bar{B}$ per generation of 5.72 for "other insects" to yield an estimated annual $P/\bar{B}$ of 2.9.

Results and Discussion

Results of the production calculations are presented in Tables 24 to 26. Estimates for predators and non-predators were tabulated separately because summing production by the two groups would in effect count predator production twice.

Only taxa considered to be predaceous mainly on other benthic macroinvertebrates were considered as predators for the purpose of production estimation. Although some chironomids are predaceous, probably very few are obligate predators (Oliver 1971), and only a few are likely to consume other macroinvertebrates as the main part of their diet. The trichopteran *Oecetis* is predaceous, but other trichopterans found in the study lakes are non-predaceous (Wiggins 1977:21). *Gammarus lacustris* can be predaceous (Anderson and Raasveldt 1974), but much of its food must be from outside the benthic macroinvertebrate community.

Production of non-predaceous macroinvertebrates in the six lakes ranged from 5.0 g m^{-2} wet weight in Mud Lake to 26.9 g m^{-2} in Baker Lake. Chironomid production constituted most of the production by non-predators in Mud, Moraine, Lower Consolation and Ptarmigan Lakes, and was the largest of any single taxon in Baker Lake. Only in Kingfisher Lake, where *Hyaletta azteca* production dominated, was chironomid production lower than that of another taxonomic group. Production by non-predaceous benthic macroinvertebrates was less than one-third that of non-predaceous crustacean plankton in Kingfisher and Mud Lakes; in the remaining four lakes it was approximately equal to almost five times that of non-preda-

Table 24. Annual production of benthic macroinvertebrates in Kingfisher and Mud Lakes.
(formalin-preserved wet weight)

Taxon	Kingfisher				Mud			
	$\bar{B}$ g m ⁻²	Assumed P/ $\bar{B}$	P g m ⁻²	% Total P	$\bar{B}$ g m ⁻²	Assumed P/ $\bar{B}$	P g m ⁻²	% Total P
Non-predators								
Chironomidae	0.3220	4.2	1.4	17.7	0.8153	4.2	3.4	68.0
<i>Hyalella azteca</i>	1.5240	3.8	5.8	73.4	0.2350	3.8	0.89	17.8
Oligochaeta	0.1582	3.6	0.57	7.2	0.0978	3.6	0.35	7.0
<i>Caenis</i>	0.0099	5.7	0.056	0.7	0.0403	5.7	0.23	4.6
<i>Pisidium</i>	0.0028	2	0.006	0.1	0.0619	2	0.1	2.0
<i>Gyraulus</i>	0.0204	3.6	0.073	0.9	0			
<i>Simocephalus vetulus</i>	0				0.0014	20	0.03	0.6
Total	2.0373		7.9	100.0	1.2517		5.0	100.0
Implied overall P/ $\bar{B}$		3.9				4.0		
Predators								
Ceratopogonidae	0.1242	4.2	0.52	19.9	0.2498	4.2	1.0	36.6
Trichoptera (mostly <i>Oecetis</i>)	0.0599	5.7	0.34	13.0	0.0417	5.7	0.24	8.8
Coenagrionidae	0.2283	2.9	0.66	25.3	0			
Libellulidae	0.0815	2.9	0.24	9.2	0.1808	2.9	0.52	19.0
Aeshnidae	0.2069	2.9	0.60	23.0	0			
Tabanidae	0.0353	5.7	0.20	7.7	0.1661	5.7	0.95	34.7
Coleoptera	0.0004	5.7	0.002	0.15	0			
<i>Helobdella stagnalis</i>	0.0116	3.6	0.042	1.6	0.0046	3.6	0.017	0.6
Turbellaria	0.0002	10	0.002	0.15	0			
Nematoda (probably parasitic)	0				0.0008	10	0.008	0.3
Total	0.7483		2.61	100.0	0.6438		2.7	100.0
Implied overall P/ $\bar{B}$		3.5				4.2		
Grand Total	2.7856				1.8955			

Table 25. Annual production of benthic macroinvertebrates in Moraine and Lower Consolation Lakes
(formalin-preserved wet weight)

Taxon	Moraine				Lower Consolation			
	$\bar{B}$ g m ⁻²	Assumed P/ $\bar{B}$	P g m ⁻²	% Total P	$\bar{B}$ g m ⁻²	Assumed P/ $\bar{B}$	P g m ⁻²	% Total P
Non-predators								
Chironomidae	4.1445	1.7	7.0	59.8	4.5943	1.7	7.8	77.2
<i>Pisidium</i>	1.8589	2.0	3.7	31.6	0.5849	2.0	1.2	11.9
Oligochaeta	0.3044	1.8	0.6	5.1	0.4246	1.8	0.8	7.9
<i>Gammarus lacustris</i>	0				0.0815	0.9	0.1	1.0
Trichoptera	0.1294	2.9	0.4	3.5	0.0716	2.9	0.2	2.0
Total	6.4372		11.7	100.0	5.7569		10.1	100.0
Implied overall P/ $\bar{B}$		1.8				1.8		

Table 26. Annual production of benthic macroinvertebrates in Baker and Ptarmigan Lakes
(formalin-preserved wet weight)

Taxon	Baker				Ptarmigan			
	$\bar{B}$ g m ⁻²	Assumed P/ $\bar{B}$	P g m ⁻²	% Total P	$\bar{B}$ g m ⁻²	Assumed P/ $\bar{B}$	P g m ⁻²	% Total P
Non-predators								
Chironomidae	5.0314	2.1	10.6	39.4	6.9944	2.1	14.7	72.8
<i>Gammarus lacustris</i>	7.5227	0.9	6.8	25.3	0.2439	0.9	0.2	1.0
<i>Pisidium</i>	2.5844	2.0	5.2	19.3	1.9016	2.0	3.8	18.8
Oligochaeta	2.1726	1.8	3.9	14.5	0.8087	1.8	1.5	7.4
Trichoptera	0.1337	2.9	0.4	1.5	0			
Total	17.4448		26.9	100.0	9.9486		20.2	100.0
Implied overall P/ $\bar{B}$		1.5				2.0		
Predators								
Hirudinoidea	0.1371	1.8	0.2	100.0				
Turbellaria	0.0102	5	~0					
Nematoda	0				0.0078	5	~0	
Total	0.1473		0.2	100.0				
Implied overall P/ $\bar{B}$		1.4						

ceous crustacean plankton. Predator production was sizeable only in Kingfisher and Mud Lakes, where it was 33 to 54% as large as production by non-predators.

The differences in production by non-predators among the lakes are attributable primarily to differences in biomass, not in estimated annual $P/\bar{B}$. Implied overall annual $P/\bar{B}$ for Kingfisher and Mud Lake macroinvertebrates were two or more times those for macroinvertebrates in the other four lakes, but biomasses of Kingfisher and Mud Lake macroinvertebrates were approximately one-third or less of those found in the four other lakes. Use of either biomass or $\bar{B}(P/\bar{B})$ as an index of macroinvertebrate production would result in the same ranking of the six lakes.

Benthic macroinvertebrate production is lowest in Kingfisher and Mud Lakes probably because the very flocculent sediments are too physically unsupportive to permit large biomasses to accumulate. Most benthic invertebrates are adapted to living on or in a substrate, but the sediments of Mud and Kingfisher Lakes are more liquid than solid.

The production estimates for the six lakes are compared to those found for other temperate-zone lakes in Table 27. Production of benthic macroinvertebrates in the Lake Louise-area lakes falls within the range of estimates published for other lakes in alpine or arctic environments, and is considerably lower than that published for lakes at more temperate elevations or latitudes. However, even the least productive of the Lake Louise-area lakes is more productive than dystrophic Lake Flosek, Poland, in terms of benthic macroinvertebrates.

Table 27. Annual production of benthic macroinvertebrates in six Lake Louise-area lakes compared to that in several other lakes. Where necessary, conversions were made by assuming dry weight = 0.1 wet weight, 1 g wet weight = 800 cal. (Cummins and Wuycheck 1971), and 1 gC = 10,980 cal (Salonen *et al.* 1976).

Lake and Habitat Notes	Non-predators						Source and Comments
	Non-pre-dators g m ⁻²	Pre-dators g m ⁻²	Total g m ⁻²	Non-pre-dators g m ⁻²	Pre-dators g m ⁻²	Implied Overall P/B	
Kingfisher	2.0313	0.7483	2.7856	7.9	2.6	3.9	This study
Mud	1.2517	0.6438	1.8955	5.0	2.7	4.0	"
Moraine	6.4372	0.0	6.4372	11.7		1.8	"
Lower Consolation	5.7539	0.0	5.7539	10.1		1.8	"
Baker	17.4448	0.1473	17.5921	26.9	0.2	1.5	"
Ptarmigan	9.9486	0.0078	9.9564	20.2	~0	2.0	"
Snowflake, Alberta alpine lake			8.7	7.4		0.85	Anderson (1975) predators & nonpredators
Teardrop, Alberta alpine pond			17.7	26.6		1.5	Anderson (1975) predators & nonpredators
Vord.Finstertalersee,Austria alpine lake			>2.5	>5.6		2.2	Pechlaner <i>et al.</i> 1972
Char, N.W.T. ultraoligotrophic arctic /lake			7.7	9.5		1.2	Rigler (1975)
Bay of Quinte,Lake Ontario							Johnson & Brinkhurst (1971) (2 different years)
Big Bay, inshore			6.8-7.6	93-97		13.7-12.8	
Glenora, inshore			37.4-37.6	291-344		7.8- 9.2	
Conway, inshore			32.1-31.9	75-82		2.3- 2.6	
Lake Ontario, open lake			48.4-34.0	63-84		1.3-2.5	
Flosek,Poland (dystrophic)				0.6			Kajak <i>et al.</i> (1972)
Mikolajskie, Poland /(eutrophic)				150			"

SECTION 5

FISH

APPROACH AND CALCULATIONS

The object of Section 5 is to determine the potential fish production of the six lakes. This was done by determining the production of fish food organisms, calculating the annual amount of food required by unit fish populations, dividing food production by food requirement to determine how many unit populations could be supported, and calculating production as the area under the curve of numbers plotted against individual weight in each age class (Allen Curve method), on the assumption that the fish populations retained constant age, growth and mortality attributes from year to year. The result was a measure of the maximum fish production sustainable over a period of years.

Basic to the approach is the principle that the fish could consume no more than the annual production of fish food organisms on a sustained basis. Fish could consume more than the annual food production in any single year, but they could not do so consistently. The consistent consumption of more than the annual food production would soon eliminate the prey populations.

The production of possible food organisms of trout was calculated in Sections 3 and 4, but not all taxa were actually eaten. The results of the stomach content analyses were used to decide which invertebrates were important as food, and only their production was used to calculate food organism production in each lake. Some food originating outside the lakes was eaten also, so the proportion of allochthonous food in the diet was used to adjust the autochthonous food production figures upward to obtain estimates of total food production.

A modification of Winberg's (1956) "balanced equation" was used with model population data to estimate the annual food requirement of trout. Two model populations, or "unit populations", were constructed having an initial number of new-born individuals of 100 and constant annual mortality of 30% and 70%, respectively (Table 28). These mortality rates were expected to bracket the true mortality rates likely to be found in trout populations of the six lakes, as suggested by the catch and age data for trout in these and other lakes near Lake Louise (Mayhood and Anderson 1976). For Mud, Lower Consolation, Baker and Ptarmigan lakes, growth of individuals in the unit populations was read from age-weight curves of trout from the respective lakes. Reliable ages could not be obtained for trout from Moraine and Kingfisher, so growth of trout in these waters was read from maximum and minimum growth curves drawn from an analysis of age-weight data for numerous Lake Louise-area trout populations. Trout were assumed to grow only in summer and to remain at constant weight throughout the winter. Fish may in fact lose some weight in winter (Chapman 1971:207), but the loss would have to be large to seriously affect the present calculations.

The food required by an individual fish over a given interval of time is described by the equation (Winberg 1956):

$$C = F + U + \Delta w + R \dots\dots\dots (1)$$

where C is the amount of food consumed,

F is the quantity of faeces

U is the quantity of excreta, mainly urine,

Δw is the change in weight (growth), and

R is the energy of metabolism,

all in units of energy.

Table 28. Structure of unit populations at two rates of annual mortality.

Age	30% mortality yr ⁻¹		70% mortality yr ⁻¹	
	N	$\bar{N}$	N	$\bar{N}$
	Unit ⁻¹	Unit ⁻¹	Unit ⁻¹	Unit ⁻¹
0	100.00		100.00	
1	70.00	85.00	30.00	65.00
2	49.00	59.50	9.00	19.50
3	34.50	41.65	2.70	5.85
4	24.01	29.16	0.81	1.76
5	16.81	20.41	0.24	0.53
6	11.76	14.29	0.07	0.16
7	8.24	10.00	0.022	0.046
8	5.76	7.00		
9	4.04	4.90		
10	2.82	3.43		

Winberg (1956:155-157) argued from a review of published data that the energy value of waste products ($F + U$) is close to 0.20C, but recently Elliott (1976a) has shown that a value of 0.28C is more appropriate for trout. Growth (Δw) can be determined from age and weight data. At constant temperature R is a function of weight, and at 20°C can be calculated from the equation¹:

$$R @ 20^{\circ}\text{C} = 9.53w^{0.761} \dots\dots\dots(2)$$

where w is the weight of the fish in grams,

0.761 and 9.53 are constants characteristic of
salmonids at 20°C (Winberg 1956:87, Elliott
1976b:942), and

R is expressed in joules per jour (J h^{-1})

R varies with temperature according to Krogh's Curve (Winberg 1956:21-26) so that if the temperatures at which the fish lives are known a coefficient (q) derived from the curve can be used to adjust $R @ 20^{\circ}\text{C}$ to R at the ambient temperatures. Summarizing the results of several Soviet authors, Winberg (1956:171) suggested that R in nature is about twice R as calculated from equation (2) (Winberg's "routine metabolism"), and more recently Mann (1965, 1967) reanalyzed other published data supporting this generalization. Taking into account all of the above considerations equation (1) can be reduced to:

$$C = 1.39 (2R + \Delta w) \dots\dots\dots(3)$$

and R and Δw being calculated as described above, and 1.39 being a coefficient to account for the assumption that $F + U = 0.28C$.

¹ Converted from $R @ 20^{\circ}\text{C}$ in $\text{ml O}_2 \text{ h}^{-1} = 0.491w^{0.761}$ (Elliott 1976b:942) assuming $4.63 \text{ cal ml O}_2^{-1}$ (Elliott and Davison 1975) and 4.19 J cal^{-1} .

Equations (2) and (3) were used to calculate the annual food requirements of individual fish in each age-class. Summer and winter R were calculated separately, the weight at each age being used to calculate winter R, and the mean of weights of adjacent age-classes being used to calculate summer R. The values of R were adjusted for temperature and converted to seasonal estimates with the season duration and temperature correction factors in Table 29. Summer temperatures at which the trout lived were taken as the mean summer lake temperatures estimated from Figures 9 to 11. Winter temperatures were estimated from the knowledge that the theoretical maximum and minimum were 4 and 0°C, respectively, supplemented with winter observations on nearby similar lakes (Anderson 1968b, 1970a). The calculated annual food requirements of individual fish in each age-class were multiplied by the mean numbers in the age-class in each unit population, the sum of the products being the estimate of the food requirement for each unit population.

To estimate potential production of trout, the annual food requirement of each unit population was divided into the estimated annual fish food production, yielding the number of unit populations that could be supported by each lake. The numbers in each age-class of the unit populations were multiplied by the number of unit populations that could be supported to determine the total number of trout in each class. Numbers in each age-class were plotted against weight at each age, and the area under the Allen Curve so obtained provided an estimate of potential production of trout populations having the growth and mortality characteristics of the model populations.

The calculation of food requirements and potential production of

Table 29. Season duration, mean ambient water temperatures experienced by trout, and temperature correction coefficient (q) obtained from Winberg's (1956) Table 1, extended to 2°C with Krogh's curve (Winberg 1956, Figure 1).

<u>Lake</u>	<u>Season Limits</u>		<u>Mean Temperature °C</u>		<u>q</u>	
	<u>Summer (hours)</u>	<u>Winter (hours)</u>	<u>Summer</u>	<u>Winter</u>	<u>Summer</u>	<u>Winter</u>
Kingfisher	May 15-Oct.15 (3672 h)	Oct.15-May 15 (5088 h)	13 (range 11-15)	3	1.94	5.88
Mud	May 15-Oct.15 (3672 h)	Oct.15-May 15 (5088 h)	11 (range 8-14)	3	2.40	5.88
Moraine	June 15-Oct.15 (2928 h)	Oct.15-June 15 (5832 h)	6 (range 4.9-6.5)	2	4.55	6.25
Lower Consolation	June 15-Oct.15 (2928 h)	Oct.15-June 15 (5832 h)	5	2	5.19	6.25
Baker	June 15-Oct.15 (2928 h)	Oct.15-June 15 (5832 h)	9 (range 7.6-9.6)	2	3.05	6.25
Ptarmigan	July 1-Oct.15 (2544 h)	Oct.15-July 1 (6216 h)	8 (range 6.4-9.2)	2	3.48	6.25

trout in Baker Lake are shown in the Results and Discussion to illustrate the details of the calculations.

RESULTS AND DISCUSSION

Species Composition and Relative Abundance

The fish species collected from the six lakes and catch-per-unit-effort data, a measure of relative abundance, are presented in Table 30. Brook trout was the most abundant species in four of the lakes and was present in the fifth. Cutthroat and rainbow trout were found in two lakes each, single specimens of lake trout were caught in two lakes, and splake and longnose dace were found in one lake each. Longnose dace found in Mud Lake was the only non-salmonid species collected.

With the possible exception of longnose dace, all of these fish species have been introduced to the lakes. All native fish would have been excluded from Ptarmigan and Baker Lakes by the falls below Baker Lake. Cutthroat trout are native to the Bow River drainage (Paetz and Nelson 1970) and may not have been excluded from Moraine or Lower Consolation Lakes because there are no impassable waterfalls on the outlet streams, but cutthroats from other watersheds have been extensively stocked in Banff Park waters, including the Bow River, Moraine and probably Lower Consolation Lakes (Parks Canada stocking records). Brook trout are native only to eastern North America, rainbow trout in Alberta are native only to the Athabaska watershed, and splake are a man-made hybrid (Paetz and Nelson 1970, Scott and Crossman 1973). Lake trout were probably introduced with other trout accidentally. Longnose dace are native to the Bow watershed (Paetz and Nelson 1970), and might conceiv-

Table 30. Catch data and evaluation of natural recruitment for fish populations in the six lakes.

<u>Lake</u>	<u>Length of Net Fished (m)</u>	<u>Hours Fished</u>	<u>Species Collected^a</u>	<u>Number Collected</u>	<u>Catch, Numbers hm⁻¹ h⁻¹</u>	<u>Natural Recruitment</u>
Kingfisher	50	39.5	rainbow trout	36	1.82	no
Mud	100	42.0	brook trout	54	1.29}	yes
			longnose dace	46	1.10} 2.39	yes
Moraine	100	42.0	splake trout	15	0.36}	?
			brook trout	7	0.17}	?
			rainbow trout	2	0.05} 0.60	?
			lake trout	1	0.02}	?
Lower Consolation	100	24.5	brook trout	44	1.80}	yes
			cutthroat trout	28	1.14} 2.94	yes
Baker	182.4	40 approx.	brook trout	65	0.89}	yes
			cutthroat trout	12	0.16} 1.05	yes
Ptarmigan	228.0	20 approx.	brook trout	93	2.04}	little
			lake trout	1	0.02} 2.06	?

^a Rainbow trout, *Salmo gairdneri* Richardson; brook trout, *Salvelinus fontinalis* (Mitchill); cutthroat trout, *Salmo clarki* Richardson; lake trout, *Salvelinus namaycush* (Walbaum); splake trout, brook trout X lake trout hybrid; longnose dace, *Rhinichthys cataractae* (Valenciennes).

ably have entered Mud Lake via the outlet, but introduction by anglers using them as live bait is also possible.

Age, Growth and Recruitment

Otoliths showed satisfactorily distinct annuli in trout populations of four of the six lakes, so that 75 to 100% of the specimens in each sample could be assigned an age. In Moraine Lake trout had otoliths with indistinct annuli at best, making it impossible to obtain a satisfactory age estimate for any Moraine Lake fish. Marks resembling annuli were usually distinct on the otoliths of Kingfisher Lake trout, but all of these fish were probably hatchery fish. Many of them were stocked after one or two years of hatchery life (Parks Canada stocking records) so it is doubtful if the marks are true annuli.

Age-weight relationships of trout in four of the lakes are illustrated in Figures 43 and 44. Baker Lake brook trout exhibited the fastest growth rate and Lower Consolation cutthroat trout the slowest. Brook trout grew much faster than cutthroat trout in both lakes in which the two species co-existed.

Growth rates of Moraine Lake trout could not be determined because the fish could not be aged. Mean wet weights $\pm$ SE of the various species were:

rainbow trout: 386.5 ± 208.5 g, $n = 2$

splake trout: 516.3 ± 69.1 g, $n = 15$

brook trout: 255.7 ± 20.3 g, $n = 7$

lake trout: 944 g, $n = 1$

Weight is plotted against number of growth checks for Kingfisher Lake trout in Figure 43, but the checks are not necessarily year marks,

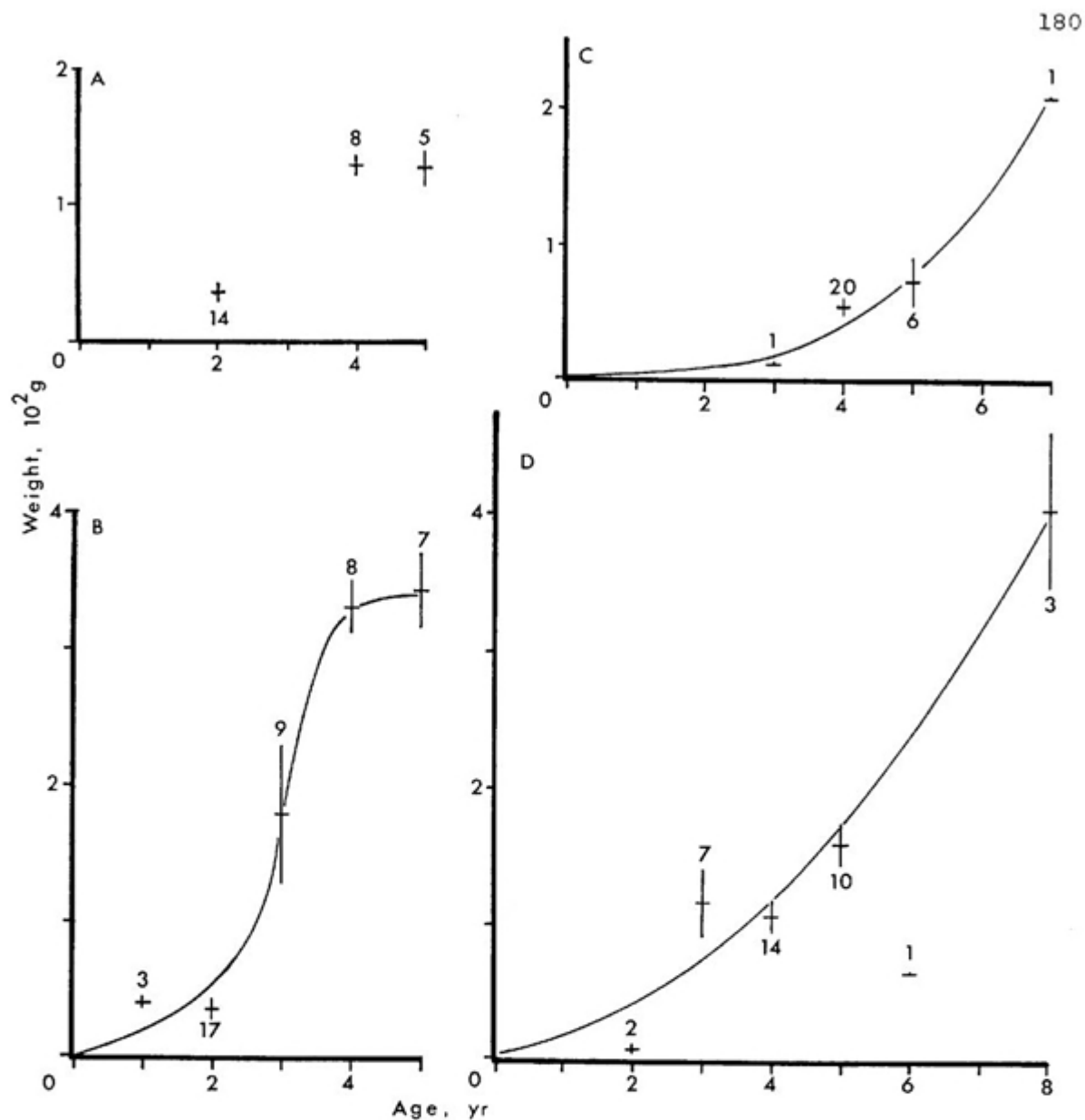


Figure 43. Age-weight relationship (mean wet weight $\pm$ SE) for Kingfisher rainbow trout (A), Mud Lake brook trout (B), Lower Consolation Lake cutthroat trout (C) and Lower Consolation Lake brook trout (D). Numbers near data points are the numbers of trout in the sample of each age-group.

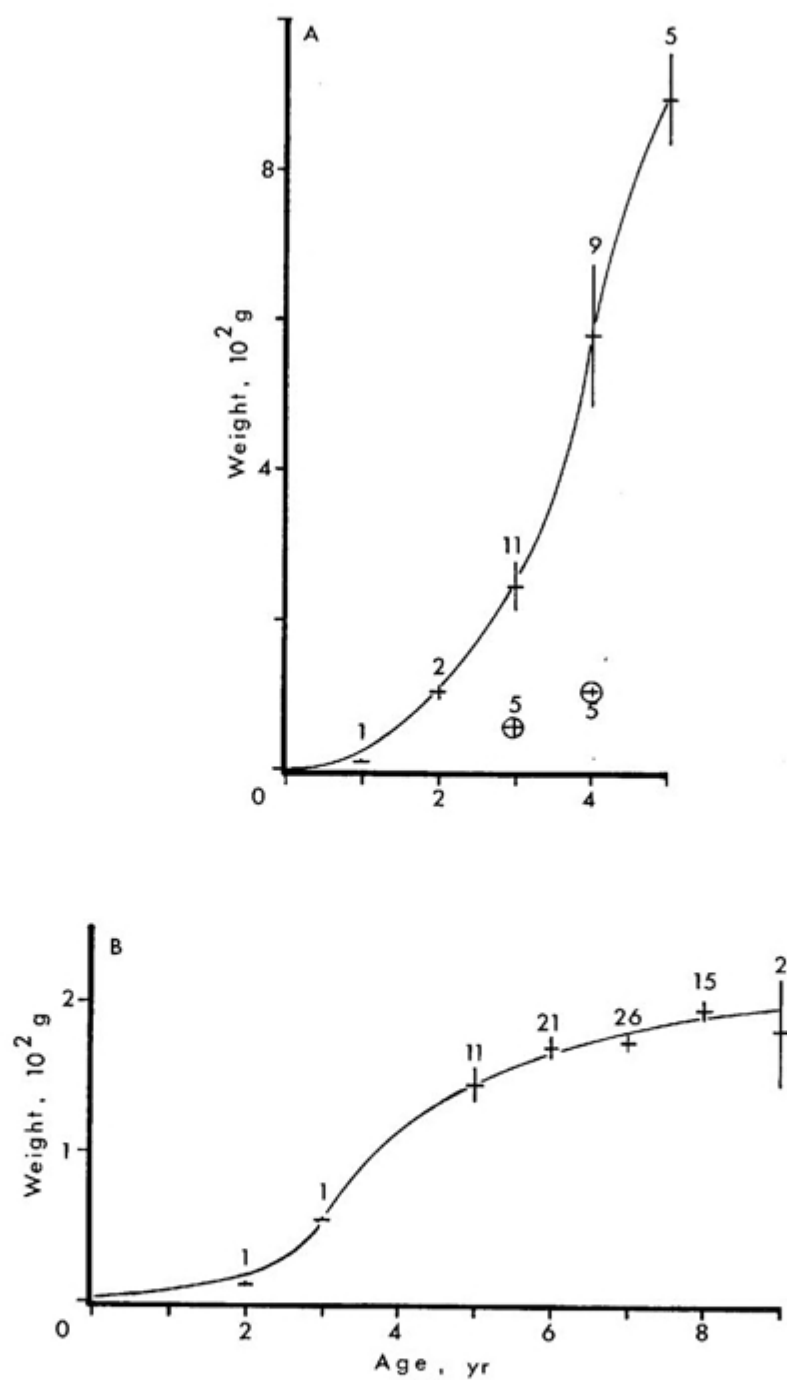


Figure 44. Age-weight relationship (mean wet weight $\pm$ SE) for Baker Lake brook trout (A; cutthroat trout circled) and Ptarmigan Lake brook trout (B). Numbers near data points are the numbers weighed in each age-group.

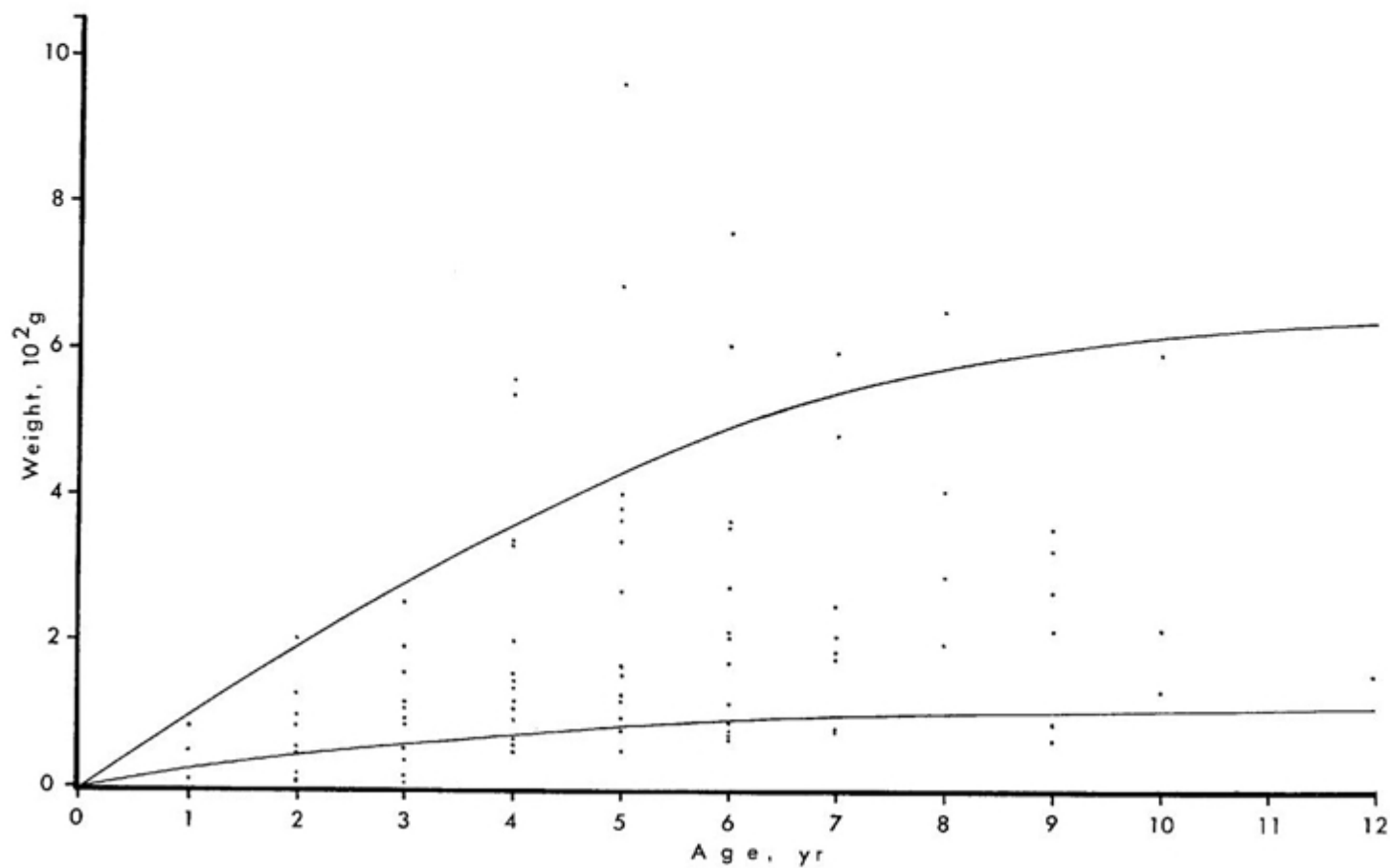
as discussed above.

Age-weight relationships for three trout species (576 individuals) from 21 populations in 17 lakes of the Lake Louise area are shown in Figure 45. The two curves illustrate high and low growth rates that would seem to be possible in lakes of the region, and were used in later calculations to estimate fish production potential in Kingfisher and Moraine Lakes. The very high weights in ages 4 to 7 are from brook trout populations in Baker and neighbouring Tilted Lakes, and are clearly exceptional for the study area.

The growth rates of trout in the Lake Louise-area lakes are low relative to those found for the same species in other North American habitats. The lowest growth rates in the Lake Louise-area lakes are among the lowest on record. Even Baker Lake brook trout, with the highest growth rate in the study area, have a growth rate little higher than the median observed for several hundred mainly North American populations (c.f. Carlander 1969).

Parks Canada had not stocked Mud, Lower Consolation, Baker or Ptarmigan Lakes for at least four years prior to the years when the fish collections were made (Parks Canada stocking records), but trout younger than four years were common in collections from all but Ptarmigan Lake, indicating that natural recruitment was adequate to maintain the population only in Mud, Lower Consolation and Baker Lakes. Natural recruitment is unlikely to be adequate to maintain the rainbow trout in Kingfisher Lake because rainbows are thought to require gravelly streams in which to spawn successfully (Carlander 1969:191), and there is no access to such streams from Kingfisher. Whether natural recruitment of trout is possible

Figure 45. Age-weight relationships in 21 trout populations in Lake Louise-area lakes (from data of Mayhood and Anderson 1976). Extreme values for single specimens not included. Curves show high and low growth rates that would appear to be possible in lakes of the study area.



in Moraine Lake is unclear because the ages of the fish could not be determined. Splake were last stocked in Moraine Lake in 1969; brook trout in 1971 (Parks Canada stocking records). The smallest splake and brook trout caught appeared to be too large to have hatched since the last recorded introductions of these species, but the sample size was small. The last recorded stocking of rainbow trout in Moraine Lake (Parks Canada stocking records) was in 1945. If the records are correct, there must have been some natural reproduction of rainbows. Natural recruitment in the various populations is summarized in Table 30.

Food

Table 31 summarizes the results of stomach content analyses of trout collected from the six lakes. Chironomids, amphipods and trichopterans were the main components of the trout diet overall, but there were some differences among the populations in the relative importance of various food items. Trout in Moraine Lake consumed few chironomids, eating mostly ephemeropteran, plecopteran and trichopteran immatures. Many in the latter two groups were stream types probably derived from Wenkchemna Creek, and the ephemeropterans were a lake-dwelling type common along the shorelines of other lakes in the study area. In Kingfisher and Baker Lakes, amphipods were quantitatively the most important items in the diet. Brook trout in Mud Lake consumed substantial quantities of odonates, especially anisopteran nymphs. In Lower Consolation Lake cutthroat trout consumed chironomids almost exclusively, in contrast to brook trout which ate large quantities of trichopteran immatures and other food items.

Only a small proportion of small trout less than 100 g in weight

Table 31. Mean percentage of total stomach contents by volume for trout collected from the six lakes. + indicates presence in trace amounts.

Lake	Kingfisher	Mud	Moraine			Lower Consolation		Baker		Ptarmigan	Weighted $\bar{x}$ all species	
Species - Stomachs examined(empty)	rainbow 36(0)	brook 50(2)	splake 15(3)	brook 7(2)	rain- bow 2(0)	lake 1(0)	brook 41(1)	cut- throat 26(0)	brook 28(4)	cut- throat 4(0)	brook 45(0)	255(12)
Chironomidae	39.4	47.8	1.6		20.0		54.0	90.4	3.2	6.3	76.5	48.7
Trichoptera	2.6	8.7	22.2	24.0		60.0	32.8	8.8	5.4	2.4	10.4	12.8
<i>Gammarus</i>							4.4	0.4	70.9	53.8	0.6	8.8
<i>Hyaletta</i>	41.7	3.0										6.8
Ceratopogonidae	0.4	1.5										0.4
Entomocstraca	+	5.7	0.9			+			8.0	37.5		2.6
Ephemeroptera	1.5	0.1	29.2	40.0	10.0	40.0	4.2					3.4
Plecoptera			37.9	2.0	35.0		1.2				2.9	2.9
Odonata	5.0	25.3										5.7
Terrestrial insects	5.4	3.4	1.6	20.0	25.0		+				6.5	3.4
Gastropoda	1.2	0.1										0.2
Hydracarina		+									+	+
Dytiscidae			6.6				1.1	0.4				0.6
Hirudinoidea									8.4			0.8
Unidentified/ other	2.8	4.4	+	14.0	10.0		2.3		4.1		3.1	2.9

consumed crustacean plankton organisms. The species eaten were the large types *Daphnia middendorffiana*, *Daphnia* (pulex group) and *Diaptomus arcticus*. *Daphnia* (pulex group) was the single most important food item volumetrically in stomachs of 10-gram brook trout in Mud Lake, but still comprised only 31% of total stomach contents by volume.

The data indicate that oligochaetes, sphaerid clams and plankton crustaceans are not a large part of the diet in the six lakes, despite their occasionally large contribution to total secondary production. Large daphnids and diaptomids could be an important food of fingerling trout, however. Allochthonous food, mostly terrestrial insects, evidently comprised less than 10% of the diet in most populations. An exception was the Moraine Lake population, which appeared to depend heavily on insects from Wenkchemna Creek.

With the exception of the Moraine Lake population, the food of the trout populations studied is typical of that for trout in lakes of the general study area. In a survey of 29 trout populations in Lake Louise-area lakes, Mayhood and Anderson (1976) found that immature Chironomidae, immature Trichoptera, and Amphipoda were the most important foods. Plankton crustaceans rarely ranked highly in the diet, and allochthonous food nearly always comprised 10% or less of total food consumed. The paucity of planktonic crustaceans in the diet seems to be typical of trout in Canadian Rocky Mountain lakes (D. Donald, pers. comm.) despite the numerous reports that daphnids are important as food for trout elsewhere (Carlander 1969).

Gerking (1962:51), among others, has suggested that soft-bodied animals such as oligochaetes are probably rapidly digested, so their im-

portance as food is likely to be underestimated by routine methods of stomach content analysis. Data on the rate of digestion of oligochaetes by rainbow trout have been provided recently by Windell *et al.* (1976). Their data indicate that, at the temperatures obtaining in the study lakes, at least 17 to 50% of oligochaete biomass should be present in stomachs of fish preserved 20 h or less after oligochaetes are consumed. In the present study, fish were analyzed or frozen within 2 to 3 h after being removed from the nets, which were usually set for less than 20 h at a time. Many fish must have fed less than 20 h prior to being preserved. If oligochaetes had been eaten in quantity, at least some should have been identifiable and the proportion of unidentifiable material should have been much greater than the 2.9% observed. The absence of oligochaetes in the stomach samples therefore is an adequate indication that these worms were unimportant in the diet of trout from the six lakes.

It is unknown whether the trout consume the same food in winter as in summer; however, the opportunity for a completely different winter diet is limited. Many planktonic Crustacea are rare in the winter plankton, or only their early instars are present (Anderson 1972, 1974a; see also discussion in Section 3). Oligochaetes and sphaerids, the two remaining potential foods, might be eaten more in winter; but trout as visual feeders are not particularly well-adapted for feeding on organisms hidden in the sediments (e.g., Efford and Hall 1975). Both taxa are consumed by trout, but they appear to be rarely important in the diet (Carlander 1969, Scott and Crossman 1973). It is unlikely that an important source of trout food has been overlooked as a result of the stomach content analyses being confined to summer collections only.

The stomach content analyses showed which invertebrates should be included in the calculations of trout food production: chironomids, amphipods, trichopterans and ephemeropterans. Although important as food for Mud Lake trout, odonates were not included in the estimates because they were expected to prey primarily on chironomids, amphipods and trichopterans. To include odonate production would have been to count their production twice, in effect. The food production estimates were increased by a factor of 1.11 to account for an assumed 10% contribution of allochthonous food to the diet. A realistic estimate of food production for trout in Moraine Lake was not possible because most food evidently came from outside the lake, but an estimate of the production of autochthonous potential food was made for comparative purposes.

The estimates of trout food production are presented in Table 32. Production by large species of crustacean plankton is provided to show the potential food supply available to very small fish.

Production of fish food was greatest in Baker Lake and least in Mud Lake, where it was one-fourth that of Baker. Chironomids were the most productive food organisms in all but Kingfisher Lake, where *Hyal-ella azteca* was the most productive. In Baker Lake, *Gammarus lacustris* was nearly as productive as the chironomids were. In the lakes having them, large planktonic Crustacea were at least as productive as the benthic food organisms.

Annual Food Requirements and Potential Production of Trout

Table 33 and Figure 46 illustrate in detail the calculations of annual food requirements of Baker Lake trout as an example of how the

Table 32. Annual production of trout food organisms in the six lakes.

Community and Taxon	Conversion ^a Factor	Kingfisher	Mud	Moraine	Lower Consolation	Baker	Ptarmigan
	<u>kJ g⁻¹</u>	<u>kJ m⁻²</u>	<u>kJ m⁻²</u>	<u>kJ m⁻²</u>	<u>kJ m⁻²</u>	<u>kJ m⁻²</u>	<u>kJ m⁻²</u>
Zooplankton							
<i>Daphnia</i> (pulex group)	21.07	39.6	26.3	3.0			
<i>D. middendorffiana</i>	21.07					51.2	
<i>Diaptomus arcticus</i>	<u>24.05</u>	<u> </u>	<u> </u>	<u>15.0</u>		<u>11.7</u>	
Total		39.6	26.3	18.0		62.9	
Benthic invertebrates							
Chironomidae	2.75	3.8	9.4	19.2	21.4	29.2	40.4
Amphipoda	3.91	22.7	3.5		0.4	26.6	0.8
Trichoptera	3.18	1.0	0.6	1.3	0.6	1.3	
Ephemeroptera	<u>4.71</u>	<u>0.5</u>	<u>0.9</u>	<u> </u>	<u> </u>	<u> </u>	<u> </u>
Total		28.0	14.4	20.5	22.4	57.1	41.2

^a Conversion factors from Cummins and Wuycheck (1971, Table 2). 1 cal = 4.19 J
zooplankton converted from dry weight, benthos from wet weight.

Table 33. Calculation of metabolism (R), food consumption (C) and population size (N) using Baker Lake data as an example.

Age (yr)	w (g)	$\bar{w}$ (g)	Summer		Winter		Summer		Winter		Annual		30% mort.		70% mort.		30% mort		70% mort.	
			R @ 20°C (J h ⁻¹)	R @ 20°C (J h ⁻¹)	R @ 20°C (J h ⁻¹)	R @ 20°C (J h ⁻¹)	R (kJ)	R (kJ)	R (kJ)	R (kJ)	Δw (kJ)	C (kJ)	$\bar{N}$ (unit ⁻¹)	$\bar{N}$ (unit ⁻¹)	N (lake ⁻¹)	N (lake ⁻¹)	N (lake ⁻¹)	N (lake ⁻¹)	N (lake ⁻¹)	N (lake ⁻¹)
0	0																3137	21,003		
		9.5	52.86				50.75													
1	19			89.58				83.59	134.34	79.61	484.12	85.00	65.00	2196	6301					
		62.0	220.34				211.53													
2	105			329.02				307.02	518.55	360.34	1942.44	59.50	19.50	1537	1890					
		177.5	490.61				470.99													
3	250			636.69				594.11	1065.10	607.55	3805.47	41.65	5.85	1076	567					
		405.0	919.11				882.35													
4	560			1176.15				1097.49	1979.84	1298.90	7309.43	29.16	1.76	753	170					
		727.5	1435.32				1377.91													
5	895			1680.47				1568.08	2945.99	1403.65	10140.93	20.41	0.53	527	51					

C = 735,342 kJ unit population⁻¹ yr⁻¹ (30% mortality yr⁻¹)

C = 109,847 kJ unit population⁻¹ yr⁻¹ (70% mortality yr⁻¹)

Annual food production = 23,070,684 kJ (whole lake) enough food for 31.37 unit populations (30% mortality yr⁻¹) or 210.03 unit populations (70% mortality yr⁻¹).

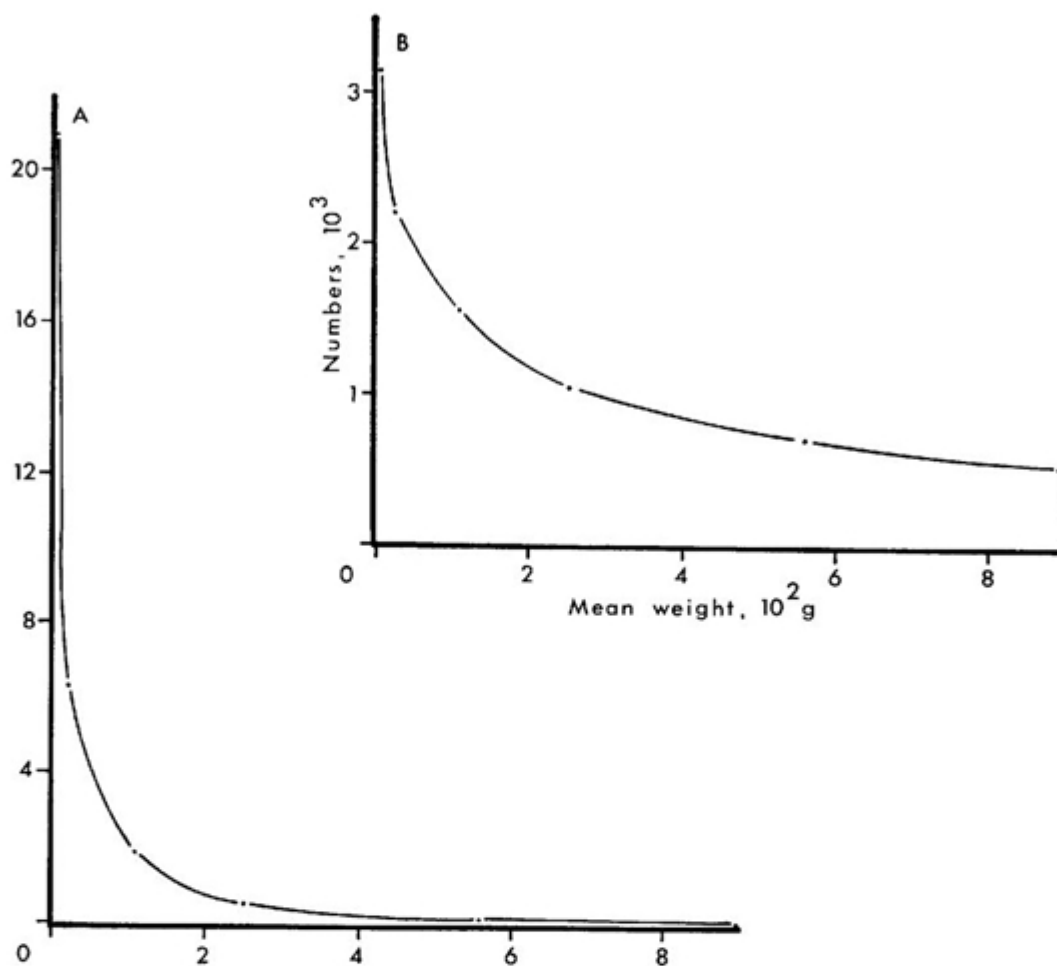


Figure 46. Allen Curves for the populations of trout in Table 33. (A), 70% annual mortality; (B), 30% annual mortality. Production in (A), 795 kg wet weight for the entire lake, and 21.8 kg ha⁻¹. Production in (B), 861 kg for the entire lake, or 23.7 kg ha⁻¹. Abcissa and ordinate have same units in both curves.

methods were applied. Table 34 summarizes the results of the calculations of annual food requirements, available food production and potential production of trout in the six lakes.

Potential production of trout showed a six-fold difference between maximum and minimum estimates, ranging from approximately 4 kg ha⁻¹ wet weight in Kingfisher to about 24 kg ha⁻¹ in Baker Lake. Nearly all estimates were less than 10 kg ha⁻¹. Despite the wide range in assumed growth and mortality, the greatest range in the estimates for any lake was 5.4 kg ha⁻¹; most estimates differed by less than 2 kg ha⁻¹. Baker Lake had clearly the highest trout production potential, but the remaining lakes differed little or not at all in their potential to produce trout.

The trout production levels summarized in Table 34 could only have been achieved if the trout consumed all of the annual food production, a highly unlikely assumption. Salmonids in Marion Lake, British Columbia, may consume as little as 4 to 23% of food production (Hall and Hyatt 1974), but this estimate appears to be unusually low, possibly because the entire benthic macrofauna was considered as the food supply, not just the species actually consumed. Most other studies have suggested that food supplies are intensively grazed by fish, and that a figure of 50 to 70% might be more typical (Mann 1967, Gerking 1962, Rigler 1975). Methodological problems encountered in estimating production of the food supply (sampler inefficiency, weight loss on preservation) would have caused underestimates of trout potential production, partially compensating for the overestimate resulting from the assumption of complete consumption of food production.

The estimates of potential production of trout in the six lakes

Table 34. Annual food requirement, annual food production and potential annual production of trout in the six lakes.

Lake	Food Required per Unit Population (kJ ⁻¹)		Whole-Lake Food Production (kJ yr ⁻¹)	Number of Unit Populations Supportable		Potential Production of Trout (kg ha ⁻¹ yr ⁻¹) ^a	
	30% mort. yr ⁻¹	70% mort. yr ⁻¹		30% mort. yr ⁻¹	70% mort. yr ⁻¹	30% mort.	70% mort.
Kingfisher high growth	1,340,112	270,511	621,600	0.46	2.30	5.3	9.2
low growth	384,883	77,992		1.62	7.97	3.8	6.2
Mud	526,396	89,443	1,166,832	2.22	13.05	4.0	4.9
Moraine high growth	853,704	189,488	8,466,500 ^b	9.92	44.68	5.5	8.3
low growth	240,383	53,185		35.22	159.11	4.0	5.8
Lower Consolation	327,397	53,066	3,605,280	11.01	67.94	7.0	8.2
Baker	735,342	109,847	23,070,684	31.37	210.03	23.7	21.8
Ptarmigan	269,165	29,656	12,759,228	47.40	430.24	9.6	12.1

^a Wet weight.

^b Benthic invertebrates only.

rank among the lowest reported for Salmonidae in the literature, but most published values are for stream populations, many of which appear to be more productive than those in lakes (c.f. Waters 1977). The estimates for the Lake Louise-area lakes are similar to those reported for entire salmonid faunas in other unproductive lake types, and are much lower than those found for entire fish faunas in more productive types of lakes (Table 35). The food chain efficiencies¹ implied by the method used to calculate potential trout production ranged from 5.1 to 17.0% (mean 11.8%, $n = 12$) depending on the assumptions of growth and mortality used, and were within the expected range of 5 to 20% (Ricklefs 1975:133). The concurrence of the food chain efficiencies with expected values and the similarity of the potential trout production estimates to published values for other unproductive lake types are additional evidence that the estimates of potential fish production made in the present study are realistic.

Application of the Findings: An Example²

The production and model population data can be used to estimate potential yield to anglers (Table 36). The potential yield estimates were made by summing the losses from the model populations for all fish of 100 g or more, considered to be the minimum size acceptable to anglers.

¹ in the sense of Ricklefs (1975:133), meaning the ratio of the production of one trophic level to that below it

² The following comments are definitely not recommendations or expressions of personal preference for managing the lakes mentioned. They are intended only to demonstrate how the results might be applied in a practical way.

Table 35. Annual production (wet weight) of entire salmonid faunas in unproductive lake types compared to estimates for the six lakes in the Lake Louise area. Estimates of production of entire fish faunas in some productive lakes are provided as examples of high fish production.

<u>Lake and Habitat Notes</u>	<u>Species</u>	<u>Annual Production kg ha⁻¹</u>	<u>Source</u>
Kingfisher, Alberta (lower subalpine)	Salmonidae	4-9	this study
Mud, Alberta (lower subalpine)	"	4-5	"
Moraine, Alberta (lower subalpine, (glacial)	"	4-8	"
Lower Consolation, Alberta (upper subalpine)	"	7-8	"
Baker, Alberta (treeline) /glacial)	"	22-24	"
Ptarmigan, Alberta (alpine)	"	10-12	"
Snowflake, Alberta (alpine)	"	3.5	Anderson (1975) long term
Teardrop, Alberta (alpine pond)	"	5.0	" " /potential
Char, N.W.T. (ultraoligotrophic, subpolar	<i>Salvelinus alpinus</i> (L.)	3.2	Rigler (1974)
Vorderer Finstertalersee, Austria (alpine)	<i>Salvelinus alpinus</i> 2 yr+	3.4	Pechlaner <i>et al.</i> (1972)
	<i>Salmo trutta</i> L. 2 yr+	1.5	
Marion, B.C. (oligotrophic, coast mtn.)	<i>Salmo gairdneri</i> }	18.7	Sandercock (1969) in Hall
	<i>Oncorhynchus nerka</i> }		and Hyatt (1974)
Bluegill, Michigan (dystrophic)	<i>Salmo gairdneri</i> age-group I	19	Johnson and Hasler (1954)
Peter and Paul, Michigan (dystrophic) }	" " "	I 30-34	" " "
Katherine, Michigan (dystrophic) }			
Narocho, U.S.S.R. (mesotrophic)	all planktivorous and	35	Winberg <i>et al.</i> (1972)
Myastro, U.S.S.R. (eutrophic)	benthivorous fish	50	
Batorin, U.S.S.R. (eutrophic)		69	
Lake Kariba, Central Africa (tropical)	all fish (20 species)	1306	Balon (1974) in Waters (1977)

Table 36. Potential annual yield of trout 100 g or more, to the nearest 100 fish, estimated from the model population and production data.

<u>Lake</u>	<u>Observed Growth</u>		<u>Estimated Growth</u>			
	<u>30% mort.</u>	<u>70% mort.</u>	high		low	
			<u>30% mort.</u>	<u>70% mort.</u>	<u>30% mort.</u>	<u>70% mort.</u>
Kingfisher			0	100	0	0
Mud	100	100				
Moraine			700	1300	300	0
Lower Consolation	400	200				
Baker	1500	1900				
Ptarmigan	1100	300				

The estimates show that Kingfisher and Mud Lakes are capable of producing few catchable-size trout. These waters may not be worth managing for sport-fishery purposes other than on a "put-and-take" basis. The other four lakes are capable of yielding substantial numbers of catchable-size trout, and might be worth managing for their sport-fisheries, depending on what other management problems they pose, and what other values the lakes might possess.

SECTION 6

GENERAL DISCUSSION AND CONCLUSION

Larkin (1974) emphasized that Canadian Cordilleran lakes are remarkably diverse because of the complex geology and geography of the mountain regions. It would be futile to attempt to describe a "typical" mountain lake for this reason; however, a group of waters could be described as representative if its lakes had a broad range of the attributes found among all lakes of the region. In this sense, the six Lake Louise-area waters studied are representative alpine and subalpine Canadian Rocky Mountain lakes with respect to several important physical, chemical and biological features, as was pointed out in Sections 2 to 5. Having a broad range of alpine and subalpine lake attributes, the waters studied are likely to exhibit a broad range in the magnitude of secondary production found in Canadian Rocky Mountain lakes in general.

Most studies of whole-lake secondary production have been done by teams of specialists working on single lakes over a period of years: examples are the Char Lake project (Rigler 1975) and the Marion Lake study (Efford and Hall 1975). A goal of the detailed projects, and of numerous other smaller studies of individual taxa, was to provide accurate data on which generalizations about secondary production could be based. In the present study, extensive use was made of the published data in detailed studies to arrive at generalizations that were used to estimate secondary production. The degree to which the estimates were adequate to meet the study objectives is considered below.

Estimates of crustacean plankton production were realistic, but

only minimum estimates of cyclopoid production were possible. Errors in abundance measurements were likely the most serious source of error in the production calculations, because errors in abundance would affect both biomass and instar development time determinations. The effects of sampling errors, counting errors, or both, were often apparent in the results. The errors probably account for the anomalies noted in the instar abundance graphs and in the Allen Curves, which too often resembled scatter plots. Abundance errors in the cladoceran instar curves would have caused errors in estimates of instar development times, but the use of smoothed curves for obtaining mean pulse-date estimates would have eliminated much of the error. Although the drawing of curved lines for Allen Curves through five scattered points might appear unjustified, any possible line through the points would have given similar results. Even in the most dubious cases, the data and calanoid biology experience suggested a descending curve with an outward concavity was the most likely shape for the Allen Curve. Because smoothed curves and summer means were used extensively, errors in individual abundance estimates would have to be unrealistically large to seriously affect the production estimates for most crustacean plankters.

Abundance estimates were least satisfactory for the Cyclopoida. The instar abundance curves strongly suggested that parts of the populations were not being sampled, because nauplii appeared when there had been few adults present to produce them. Adult cyclopoids might have been in the sediments, where they would have been unavailable to the plankton sampler, and would not have been retained by the sieve in benthic sampling. The sum of the maximum biomasses achieved by each of the

generations provided a minimum estimate of production by the plankton portion of the cyclopoid population.

There would have been a tendency for benthic macroinvertebrate biomass, and therefore production, to be underestimated; however, the production estimates are realistic in comparison to measurements made in other unproductive lake types throughout the world. Biomasses would have been underestimated because preserved weights usually underestimate live weights, some biomass would have been lost during sieving, and samplers are probably never 100% efficient. In some groups the underestimate would have been compensated for by a tendency to overestimate assumed $P/\bar{B}$'s when published data on $P/\bar{B}$ or voltinism were ambiguous. In such cases, short life cycles or high $P/\bar{B}$'s within the published ranges were deliberately assumed to compensate for expected underestimates of biomass. Even so, the production values obtained for benthic macroinvertebrates must be somewhat low in most cases.

Because the fish production estimates were based on the assumption that all of the food production would be consumed, the tendency would have been to overestimate the potential production of trout. The tendency for the food (macroinvertebrate) production to be underestimated would have compensated at least partly for the tendency toward an overestimate of food consumption. The trout production estimates implied food chain efficiencies within the expected range of 5 to 20%, were remarkably similar under a variety of assumptions about mortality and growth, and are considered to be close to the true values.

The study revealed which taxa were the most important secondary producers in the communities studied. Differences in *Daphnia* production

accounted for most of the variation in crustacean plankton production. In the plankton communities in which *Daphnia* was scarce or absent, calanoids were the most important crustacean producers. In the benthos, chironomids were the most important macroinvertebrate producers in most of the lakes. When abundant, amphipods, oligochaetes and sphaerids were also important. The relative contributions of crustacean plankton and benthic macroinvertebrate communities to secondary production varied widely among the lakes, and no generalization was possible to describe the relationship.

The most productive taxa in the lakes, usually *Daphnia*, Calanoida, Chironomidae, Amphipoda, Oligochaeta and Sphaeridae, should be emphasized in future studies of secondary production in Canadian Rocky Mountain lakes. No detailed studies of life histories or population dynamics, essential to any detailed understanding of secondary production, have been done in Canadian Rocky Mountain lakes on any of these groups, with the exception of the Calanoida (*Diaptomus tyrrelli*) studied by Anderson (1968b, 1972). Such studies on Oligochaeta and Sphaeridae are rare even in the world literature. Studies on those groups would most profitably attempt to elucidate the lengths of the life cycles, the factors affecting voltinism, to detail the relationships between P/B and voltinism, body size, temperature and other features showing promise of making production easier to estimate. Such detailed studies on the important trout food organisms would improve our ability to assess the trout carrying capacity of Canadian Rocky Mountain lakes.

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