Canadian Technical Report of

Fisheries and Aquatic Sciences 2001

1994

CHURCHILL RIVER DIVERSION: EFFECTS ON BENTHIC INVERTEBRATES IN LAKES ALONG THE LOWER CHURCHILL AND THE DIVERSION ROUTE

by

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This is the 66th Technical Report

from the Central and Arctic Region, Winnipeg

Cat. no. Fs 97-6/2001E ISSN 0706-6457

Correct citation for this publication:

Wiens, A.P., and D.M. Rosenberg. 1994. Churchill River diversion: effects on benthic invertebrates in lakes along the lower Churchill and the diversion route. Can. Tech. Rep. Fish. Aquat. Sci. 2001: iv + 29 p.

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Benthic invertebrates were surveyed in 12 northern Manitoba lakes in 1973, prior to Churchill River diversion, and then every two years after diversion until 1987. Severely reduced flows caused dewatering of three lakes in the lower Churchill River. A control structure on the Rat River caused water levels to rise in five lakes that comprised the new Notigi Reservoir, and substantially increased flows caused water levels to rise in two lakes downstream of the Notigi Reservoir. The water levels of two lakes used as reference systems were unaffected. Along the lower Churchill, benthic standing crops decreased by half in the remnant lakes; combined with the loss of the original littoral zone (≈46% of the lakes' areas), overall benthic standing crops declined to about 25% of preimpact values. Invertebrate standing crops increased in impounded lakes of the Notigi Reservoir; these standing crops have remained high because of nutrient additions from the new flow of the Churchill River. Qualitative changes also occurred in the benthic invertebrate community of Notigi Reservoir lakes. Invertebrate standing crops increased in lakes below the Notigi Reservoir immediately after diversion but returned to, or below, preimpact levels by 10 years after diversion. Responses of benthic invertebrates in the different parts of the system generally were accurately predicted by a preimpact environmental assessment.

Key words: Benthic invertebrates; surveys; water diversion; impoundment; flow reduction; Churchill River; northern Manitoba lakes.

RÉSUMÉ

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Les populations d'invertébrés benthiques de 12 lacs du Nord du Manitoba ont fait l'objet de dénombrements en 1973, avant le détournement de la rivière Churchill, puis à tous les deux ans jusqu'à 1987. Une forte diminution de l'écoulement des eaux a causé une baisse du niveau de trois lacs situés le long du cours inférieur de la rivière Churchill. Un ouvrage régulateur sur la rivière Rat a provoqué une hausse du niveau de l'eau dans les cinq lacs qui forment le nouveau réservoir Notigi. D'autre part, des augmentations importantes des débits ont entraîné la hausse du niveau de l'eau dans deux lacs en aval de ce réservoir. Par contre, les niveaux de l'eau dans deux lacs utilisés comme systèmes de référence n'ont pas changé. Dans les lacs partiellement asséchés situés le long du cours inférieur de la rivière Churchill, les populations benthiques sur pied ont diminué de moitié; à la suite de la perte de la zone littorale initiale (représentant 46 p. cent de la superficie des lacs), les populations benthiques sur pied ont diminué à environ 25 p. cent de ce qu'elles étaient avant le détournement. Les populations d'invertébrés sur pied ont augmenté dans les lacs qui composent le réservoir Notigi; ces populations sont demeurées florissantes grâce aux nutriments additionnels transportés par le nouveau cours de la rivière Churchill. Des changements d'ordre qualitatif se sont aussi produits dans la communauté benthique du réservoir Notigi. Juste après le détournement de la rivière, on a observé un accroissement des populations d'invertébrés sur pied dans les lacs situés en aval de ce réservoir. Cependant, dix ans plus tard, ces populations sont revenues aux niveaux d'avant le détournement, ou plus bas. Dans une évaluation environnementale effectuée avant le détournement, on avait prévu avec justesse, dans l'ensemble, les réactions qu'auraient les invertébrés benthiques dans les diverses parties du réseau.

Mots clés : Invertébrés benthiques; dénombrement de la population; détournement de l'eau; retenue; réduction du débit; rivière Churchill; lacs du Nord du Manitoba.

INTRODUCTION

The possibility of diverting the Churchill River into the Nelson catchment for hydroelectric power generation was recognized in the mid-1950s (Hecky et al. 1984). In the mid-1960s, Manitoba Hydro's commitment to focusing hydroelectric development in the lower Nelson River made the diversion a virtual certainty (Newbury et al. 1984). The first step toward making the diversion a reality was taken in 1974 when the control structure built at the outlet of Notigi Lake was closed in order to retain local runoff in the Rat River Valley (Fig. 1; Bodaly et al. 1984). In 1976, another control structure built at Missi Falls, the natural outlet of Southern Indian Lake (SIL), was closed and the lake was raised 3 m above its long-term mean level. When water levels in the lake and the new Notigi Reservoir equilibrated, water from the Churchill River was diverted through a newly constructed channel joining the southern part of SIL to the headwaters of the Rat River in the Nelson catchment. Full diversion of 760 $m^3 \cdot s^{-1}$ of Churchill River water (75% of the long-term mean flow) was completed by the summer of 1977.

The diversion caused a major loss of river flow through lakes of the lower Churchill River (LCR). In contrast, creation of the new Notigi Reservoir (NR) and diversion of Churchill River water raised the levels of a series of lakes in the Nelson River catchment. Water levels of lakes downstream of the NR were also raised, but the main impact there was dramatically increased flows. These changes, in combination with the geography of the area, produced different sets of circumstances for the study of benthic invertebrates. First, few large reservoirs located in the boreal forest zone of North America and underlain by permafrost have been studied. Second, the lakes on the diversion route and on the LCR originally both formed chains linked by only short stretches of river. Thus, when the NR was formed, the original lakes became separate basins merged within the larger reservoir. In contrast, lakes along the LCR became even more separated because of dewatering. Third, no significant drawdown occurs in either SIL or NR, so the initial effects of flooding could be studied without the complications of a drawdown regime. Our objective in this report was to describe responses of the benthic invertebrates to these sets of circumstances and to test predictions made by Hamilton and McRae (1974) in the original environmental impact assessment.

METHODS

BENTHIC SAMPLING

Benthic sampling of lakes on the diversion route and the Churchill River below SIL (Fig. 1) began in 1973 (Hamilton and McRae 1974). Three lakes downstream of the outflow of SIL were chosen: Partridge Breast, Northern Indian, and Fidler. Seven lakes were chosen on the diversion route: Karsakuwigamak, Rat, West and Central Mynarski, and Notigi were part of the NR; Wapisu and Wuskwatim lakes were downstream of the NR. Two lakes unaffected by impoundment or diversion were selected as references to examine natural fluctuations in benthic populations: Wood and East Mynarski. Pre- and postimpoundment characteristics of the study lakes are given in Table 1 (see also Brown 1974).

The sampling sites for all surveys were located in open areas of the lakes. The initial survey was done by boat and took 16 d (June 9-24, 1973); subsequent surveys were done by aircraft and took 4 d (usually June 19-22). Each lake was revisited every 2 yr after diversion, from 1977 to 1983, and in 1987.

Three to 10 sites were sampled in each lake (Table 1): one 15x15 cm Ekman grab sample was taken per site. Sediments were sieved in the field using 400 µm mesh nets, and were preserved in 10% formalin. The invertebrates were returned to the Freshwater Institute for counting and identification. Zooplankton, Nematoda, and Ostracoda were too small to be sampled quantitatively, so these taxa were not enumerated.

PHYSICAL MEASUREMENTS

Physical measurements taken during the surveys included: (i) Secchi disk readings; (2) temperature profiles through the water column to the bottom; (3) oxygen concentrations from the surface to 13 m; and (4) samples of bottom sediment for analysis of particle-size distribution.

DATA ANALYSIS

Comparisons of preimpact (1973) standing crops to those obtained from postimpact surveys were mainly qualitative because deficiencies in the design of the survey prevented the use of inferential statistics. First, the initial survey (Hamilton and McRae 1974) represented the only preimpact data obtained. This limited data base reduced the power of an analysis of variance (AOV) to detect a Type II error (i.e. the probability of accepting a null hypothesis of no effect when it is false). In biomonitoring, the cost of committing a Type II error may be as great or greater than committing a Type I error (i.e. the probability of rejecting a null hypothesis of no effect when it is true) (Cooper and Barmuta 1993; see also Trautman et al. 1982, Toft and Shea 1983, Rotenberry and Wiens 1985, and Peterman 1990).

Second, the limited preimpact baseline also precluded the use of a "Before-After-Control-Impact" (BACI) statistical design (Stewart-Oaten et al. 1986), which requires many samples from before and after the impact (Cooper and Barmuta 1993).

Third, the sampling design of the survey may have been "pseudoreplicated" in space and time (Hurlbert 1984). In other words, spatial "treatments" could not be replicated because chains of linked lakes were involved, which meant that each lake was not an independent entity. Also, year-to-year changes in abundance may not have been independent. (In reality, it is almost impossible to avoid pseudoreplication in this kind of whole-ecosystem experiment).

Fourth, low numbers of sites were sampled in each lake (Table 1). Moreover, the numbers of sites sampled in the LCR lakes varied from survey to survey because of dewatering. Only one replicate sample was collected at each site. Replicate samples are not required to test for lake-to-lake or year-to-year changes, but they are required to provide a measure of variability among habitats or depths, and to define precision of standing-crop estimates; both are essential elements of AOV (Resh and McElravy 1993).

Therefore, changes in the benthic invertebrate community after Churchill River diversion were judged by comparing total mean standing crops and taxonomic composition of collections between reference lakes and lakes affected by the diversion. Standard deviations were also calculated to indicate degree of variability around mean standing crops. Only major changes in the benthic invertebrate community could be detected using this approach.

East Mynarski Lake was chosen as the reference for the diversion-route lakes, and Wood Lake was chosen as the reference for the LCR lakes. East Mynarski Lake was representative of the diversion-route lakes before flooding, but Wood Lake was deeper and colder than the LCR lakes, and it stratified regularly. Therefore, some caution is warranted in comparing the LCR lakes to Wood Lake.

RESULTS

LOWER CHURCHILL RIVER LAKES

Physical characteristics

The lakes of the LCR lost significant surface area after diversion (Table 1): Partridge Breast and Northern Indian lakes each were reduced by about 39%, whereas Fidler Lake lost ≈70% of its surface area. This resulted in a substantial reduction in lake volume as well: Partridge Breast was reduced by 29%, Northern Indian by 49%, and Fidler by 70% (Newbury et al. 1984; table 4). Although the loss in lake elevation averaged only ≈3 m, the low geographical profile of the area resulted in the creation of new islands and the exposure of large expanses of mud flats in the former littoral zone of each lake.

Intermittent increases in discharge released through the Missi Falls control structure partially flood the former littoral zones, cause reworking of local areas of shoreline, and create increases in suspended sediment. Storm events also resuspend shoreline material. High levels of suspended sediment are particularly noticeable in Partridge Breast Lake (Newbury et al. 1984; fig. 7). However, water renewal time is short in the LCR lakes (1.3-16.4 d), so resuspended sediment is transported rapidly downstream. Sediment resuspension does not occur extensively in lacustrine areas directly on the former flow of the Churchill River;

here, shorelines are composed extensively of larger glacial till materials and are more stable.

The loss in lake elevation at Fidler Lake virtually eliminated the prediversion littoral zone, leaving a large dry area; the remainder of the lake became shallow (<1 m deep) and highly turbid because of wave action. The reduced flow of the Churchill River became restricted to a narrow channel at the northern end of the lake, and the short residence time before dewatering (1.3 d), did not change when lake elevation decreased. Benthic sampling of this lake and parts of the other two LCR lakes was suspended after 1979 when it became too hazardous to land a plane in the shallow waters.

Prior to impoundment and diversion (1973), mean temperatures of the upper 5 m of the water column showed that the LCR lakes were considerably colder than most of the other lakes studied (Table 2). Cool SIL water caused a mean temperature of 5.2°C in Partridge Breast Lake; Northern Indian and Fidler lakes also were affected by SIL water. In contrast, Karsakuwigamak Lake was 8.6°C warmer than Partridge Breast Lake. The majority of the discharge was still flowing through Missi Falls in June 1977, but ≈200 $m^3 \cdot s^{-1}$ was being diverted (Newbury et al. 1984), reducing the difference in temperature between Partridge Breast and Karsakuwigamak lakes (Table 2). By June 1979, discharge was nearly identical through Missi Falls and the diversion route (Newbury et al. 1984), and the temperatures of Partridge Breast and Karsakuwigamak were similar. From 1981 onwards, mostly cool SIL water flowed through the diversion, cooling the southern lakes and reversing the former temperature relationship.

Oxygen depletion was never observed prior to or after diversion in any of the LCR lakes because of the short water-residence times. Although oxygen profiles were measured early in the open-water season, oxygen occurred at saturation levels in all LCR lakes.

Analysis of major anions, cations, nutrient status, and algal biomass prior to diversion showed the dependence of LCR lakes on SIL water (Hecky and Harper 1974). The chemical composition of water from Partridge Breast Lake was analyzed in 1976 after the Missi Falls control structure was built and outflow from SIL was reduced, but it did not show significant changes (C. Anema, Freshwater Institute, unpubl. data). However, turbidity increased at Missi Falls after full diversion, probably because of increased shoreline erosion in SIL (Playle and Williamson 1986). Cleugh (1974) predicted changes in the chemical and nutrient composition of water in the LCR lakes when the influence of local drainage into the LCR increased from 8% prior to diversion to ≈37% after diversion. In fact, Guilbault et al. (1979) found increased calcium, phosphorus, total inorganic carbon, hardness, and colour, all of which were attributed to water from small, local rivers.

Essentially no changes were observed in water levels, temperatures, oxygen, or water chemistry in reference Wood Lake during the surveys. Unlike the other LCR lakes, Wood Lake stratified in summer; a 6.2°C difference existed between the epilimnion and hypolimnion. Wood Lake also had higher calcium and magnesium concentrations and slightly higher conductivity than the nearby LCR lakes (Cleugh 1974). However, suspended nitrogen, carbon, phosphorus, and total dissolved phosphorus concentrations were lower. Wood Lake had lower primary productivity and different species of phytoplankton than the LCR lakes (Hecky and Harper 1974).

Biological characteristics

Standing crops: Standing crops of benthic invertebrates in Partridge Breast Lake, the first lake downstream of Missi Falls, were reduced to less than half their 1973 values in the 1977-1987 surveys (Fig. 2). Initial standing crops were higher than for any other lake in the study. Standing crops in Northern Indian Lake, the second lake downstream of Missi Falls and the largest and deepest of the three LCR lakes, increased over 1973 values in the 1977, 1979, and 1981 surveys, and thereafter dropped to about half these values (Fig. 3). Standing crops in Fidler Lake, the lake furthest downstream from Missi Falls, increased over 1973 values initially (1977) and subsequently declined (1979) (Fig. 4). No further surveys were possible in Fidler Lake because of low water levels. Standing crops in Wood Lake, the reference lake, were substantially lower than in the LCR lakes (Fig. 5). Numbers increased steadily from 1973 to 1981 and then gradually decreased.

The response of benthic invertebrates in Partridge Breast Lake to water diversion appeared to be quick and drastic. The response of Northern Indian Lake took considerably longer, perhaps because it was a much larger and deeper lake than Partridge Breast (Table 1). The response of Fidler Lake was intermediate, but it could not be sampled after the 1979 survey so final conclusions could not be drawn. Temporal patterns of benthic standing crops in the three LCR lakes differed markedly from those exhibited in Wood Lake.

Individual taxa:

PARTRIDGE BREAST LAKE: Taxon abundance declined immediately after flow was reduced through Missi Falls and remained low in all subsequent surveys (Fig. 2). The high numbers of Diptera (>95% Chironomidae) in 1973 occurred at only one of the lake's four stations (unpubl. data); Diptera abundances dropped from 14940 larvae$\cdot$ m^{-2} in 1973 to 1443$\cdot$ m^{-2} in 1987. Amphipoda decreased from 3330$\cdot$ m^{-2} in 1973 to 474$\cdot$ m^{-2} in 1977, and to 0 by 1987. Pelecypoda abundances declined until 1981, and then increased; by 1987 they were more abundant than they had been in 1973. Ephemeroptera increased immediately after diversion, more than doubling their abundance, but steadily declined thereafter, and had disappeared by 1987.

NORTHERN INDIAN LAKE: Changes in the abundance of taxa differed in some respects from those in Partridge Breast Lake (Fig. 3). In general, abundances increased immediately after diversion, lasted until 1981, and then declined to near or below preimpact levels. Numbers of Diptera and Oligochaeta were higher in 1987 than in 1973; those of Amphipoda, Pelecypoda, and Ephemeroptera were lower. Ephemeroptera were abundant in 1977, but subsequently declined faster than the other taxa. Amphipoda were always abundant in Northern Indian Lake, but did not reach maximum abundance until 1981. Numbers of Diptera changed little over the years of the study.

FIDLER LAKE: Invertebrate numbers exhibited large fluctuations during the three surveys (Fig. 4). The Diptera increased from 697 larvae$\cdot$ m^{-2} to 5447$\cdot$ m^{-2} in 1977 before declining to 2045 larvae$\cdot$ m^{-2} in 1979. Responses from 1973 to 1977 by the Pelecypoda, Oligochaeta, and Ephemeroptera were similar. The Amphipoda, however, immediately declined from 4311 organisms$\cdot$ m^{-2} in 1973 to 1038$\cdot$ m^{-2} in 1977. By 1979, all of the taxa except the Diptera were below preimpoundment abundances.

In summary, the two most consistent, immediate responses to lowered water flow were exhibited by the Amphipoda and the Ephemeroptera: the Amphipoda always declined in number, whereas the Ephemeroptera always increased. For most taxa, the overall trend a decade after diversion was a decline to lower abundances than before flow manipulation. This decline reached an extreme with the disappearance of Amphipoda and Ephemeroptera from Partridge Breast Lake by 1987.

WOOD LAKE: The benthic invertebrate community was dominated by Diptera, Amphipoda, Pelecypoda, and Oligochaeta, whose abundances fluctuated throughout the survey (Fig. 5). Pelecypoda abundances increased steadily between 1973 and 1983, and then decreased slightly by 1987. Diptera abundances increased from 1973 to 1981 and declined thereafter. Amphipod abundances fluctuated throughout the study, but by 1987 were similar to preimpoundment levels. Oligochaeta numbers also fluctuated throughout the study, but were higher in 1987 than in 1973. Gastropoda occurred only sporadically throughout the study.

DIVERSION ROUTE LAKES - NOTIGI RESERVOIR

Physical characteristics

The diverted Churchill River flows directly through three of the lakes under study: Karsakuwigamak, Rat, and Notigi (Fig. 1; Table 1). West and Central Mynarski lakes are off the flow of the river, but were affected peripherally by increased water levels caused by impoundment and diversion. However, East Mynarski Lake was not flooded because of its higher elevation. Postimpoundment maximum depths of lakes of the NR are given in Table 1. The southernmost lake, Notigi, rose the most (15.2 m); Central Mynarski Lake depth increased the least (6.5 m). The average depth increase for all of the lakes forming the NR was 10.1 m.

Mean depths, volumes, and water residence times for most lakes have not been determined because the lakes were not resurveyed after impoundment and diversion; however, post-development estimates are available for Rat Lake (Cherepak 1989) and the entire NR (Newbury et al. 1984). The total flooded area of the NR was estimated as 733 km^2 (G.K. McCullough, Freshwater Institute, unpubl. data), compared to a natural surface area of 153 km^2 before impoundment and diversion.

Mean annual outflows of the Rat River system prior to impoundment and diversion ranged from 2.3 $m^3 \cdot s^{-1}$ from Karsakuwigamak Lake to 30.8 $m^3 \cdot s^{-1}$ from Notigi Lake. Wuskwatim Lake, on the Rat-Burntwood River system downstream of the NR, averaged 89.1 $m^3 \cdot s^{-1}$ (Brown 1974). Annual post-diversion outflows from SIL have averaged 860 $m^3 \cdot s^{-1}$; the annual discharge rate from the Notigi control structure has been as high as 896 $m^3 \cdot s^{-1}$ (G.K. McCullough, Freshwater Institute, unpubl. data).

Secchi disk readings taken in each year of the survey are shown in Table 3. Prior to impoundment, lakes along the diversion route had relatively low Secchi readings, which were attributed to the shallowness of the lakes and resuspension of sediments by wind (Cleugh 1974). Prior to the start of diversion flows in 1977, the NR lakes had considerably higher Secchi readings, probably as a result of sediments settling in the newly deeper basins, and protection of the shorelines by the still existent ground cover. Secchi values generally declined in following years, and reached a low in 1987. The more turbid waters of 1987 may have been caused by bank erosion, which gradually increased as the protective organic mat was broken down, exposing the glaciolacustrine shorelines to direct wave energy (Cleugh 1974; G.K. McCullough, Freshwater Institute, unpubl. data). Surveys of Rat Lake from 1987-1989 by Janusz (1990) revealed a mean Secchi value similar to what we obtained in June 1987 (0.73 m), and slightly higher values in June of 1988 (1.06 m) and 1989 (1.01 m).

Lakes of the NR were basically isothermal in midsummer; any stratification that developed was close to the bottom (Cleugh 1974). Table 2 shows that mean temperatures of the upper 5 m of the water column were similar for all of these lakes in 1973 and in 1977, except for Notigi Lake in 1977 because by then it had deepened and cooled the most. By 1979 and onward, the influx of SIL water kept the three NR lakes directly on the diversion flow cooler than those adjacent to it (the two Mynarski lakes).

The benthic surveys were done early in the summer, prior to any lake stratification. However, stratification was observed by others sampling later in summer; it first occurred after depth increased in 1975, and coincided with oxygen depletion (C. Anema, Freshwater Institute, unpubl. data).

Anoxia was not observed in any of the NR lakes during summer of 1973 (Cleugh 1974). In 1974, water in lakes of the NR began to rise because of closure of the Rat River at Notigi Lake. Oxygen measurements in Notigi Lake from 1974-1977 did not show oxygen depletion until March 1975 in the east basin, and until April 1975 in the west basin. Water below $\approx$11 m was anoxic except for short periods following seasonal overturn (C. Anema, Freshwater Institute, unpubl. data) until winter 1976 when diversion flows brought oxygenated water into Notigi Lake. Samples taken in March 1979, after full diversion, showed no further anoxia (C. Anema, Freshwater Institute, unpubl. data; see also Bodaly et al. 1984), and oxygen measurements taken down to 13 m during the later benthic surveys yielded a similar finding.

Magnesium and calcium concentrations decreased in Notigi Lake with the influx of Churchill River water. The concentration of most ions after diversion reflected those of the water in South Bay of SIL (Notigi: March 1975 - Mg = 193 $mg \cdot L^{-1}$, Ca = 427 $mg \cdot L^{-1}$; March 1978 - Mg = 132 $mg \cdot L^{-1}$, Ca = 236 $mg \cdot L^{-1}$; South Bay: March 1978 - Mg = 125 $mg \cdot L^{-1}$, Ca = 214 $mg \cdot L^{-1}$). Other major ions changed less (C. Anema, Freshwater Institute, unpubl. data).

Sites sampled in reference East Mynarski Lake were usually <6 m deep, except for a "trench" in the eastern third of the lake (Brown 1974). Stratification was not observed because of the lake's shallow nature. This lake was usually warmer than the other two Mynarski lakes (Table 2); some of the very shallow (<3 m) sites were as much as 4°C warmer than in the other lakes. Information is scanty regarding major ions and nutrient status because East Mynarski Lake was not included in the regular chemical survey. Cleugh (1974) and Hecky and Harper (1974) combined East Mynarski with the other two Mynarski lakes when discussing its nutrient status and algal biomass; in general, the Mynarski lakes had the highest algal productivity on the diversion route.

Biological characteristics

Standing crops: Standing crops of benthic invertebrates in Karsakuwigamak Lake increased steadily after impoundment and diversion (Fig. 6). They reached a peak in 1983 at 6167 organisms·m^{-2}, which was an increase of 360% from preimpoundment values. Standing crops remained at that high level in 1987. Standing crops of invertebrates in Rat Lake changed dramatically over the study period (Fig. 7). Abundances increased ≈300% in the decade following impoundment, but by 1987 had decreased to preimpoundment levels. Standing crops of invertebrates remained fairly constant in Notigi Lake over the 14 years of surveys (Fig. 8); numbers varied from 3000 organisms·m^{-2} in 1977 to 4500·m^{-2} in 1987. Mean standing crop in 1973 was 3800·m^{-2}, and over the next 10 years it fluctuated <20% from this value.

Standing crops of benthic invertebrates in West Mynarski Lake, which was affected only by inundation, changed considerably over the years of surveys (Fig. 9). The 1977 survey showed little change in total numbers from 1973 (despite two years of rising water levels), but it was followed by dramatic fluctuations in total numbers right to the last survey in 1987; standing crops increased almost linearly from 1981 to 1987. Total numbers rose from 1620·m^{-2} in 1973 to >10000·m^{-2} in 1987. Central Mynarski Lake was the last lake examined as part of the NR; like West Mynarski Lake, it was affected only by inundation. Standing crops of invertebrates in 1977 and 1979 responded similarly to West Mynarski; total benthic numbers increased substantially by 1979 (Fig. 10). However, unlike West Mynarski, the numbers of benthic invertebrates remained high after 1979.

Standing crops of benthic invertebrates in the reference lake, East Mynarski, were elevated after 1973: they increased slightly in 1977 and 1981, and peaked in 1983 (Fig. 11). Basically, all of the NR lakes, except Notigi, followed a similar pattern of relatively low standing crops in 1973 and 1977, followed by increased abundances thereafter.

Individual taxa:

KARSAKUWIGAMAK LAKE: Diptera and Gastropoda changed little over the study period, but the Amphipoda increased dramatically (Fig. 6). By 1987, the Amphipoda were the major faunal component of the lake. Pelecypod numbers also increased after diversion; they formed half of the benthic standing crops in 1979 and 1981, but decreased in later years. Oligochaeta followed the same pattern as the Pelecypoda, but with lower numbers.

RAT LAKE: All of the taxa except Pelecypoda changed significantly with manipulation of the water (Fig. 7); some of the responses occurred after inundation but before diversion (1977 survey). By 1977, the Amphipoda, Ephemeroptera, and Trichoptera (not shown in Fig. 7) had disappeared. Amphipod populations began to recover by 1979, and by 1987 had nearly returned to preimpoundment levels. The Ephemeroptera did not reappear until 1987 when several specimens were collected. The Trichoptera, rare in 1973, never reappeared. Of the Oligochaeta, Diptera, and Mollusca (Pelecypoda and Gastropoda) in 1977, only the Oligochaeta had a major increase; they formed most of the benthic population two years later. Numbers of Diptera initially decreased, and then rebounded to form the most abundant taxon in 1983; this represented an increase of ≈1200% over 1977 levels. Gastropoda numbers increased with the initial rise in water levels (1977), but they virtually disappeared after 1977.

NOTIGI LAKE: Composition of the benthic taxa changed dramatically after extensive flooding and diversion (Fig. 8). Anoxia below 11 m (see above), caused by decomposing flooded shoreline vegetation, resulted in the loss by 1977 of all of the Amphipoda and Ephemeroptera. The Amphipoda repopulated the lake when oxygenated water returned; by 1987, standing crops of 1230 individuals·m^{-2} were present. Ephemeroptera were rare in 1973, several specimens were found in 1983, but none have been found since. Abundances of Gastropoda were low in 1973 and 1977, but they were eliminated from all of the sampling sites after diversion. Numbers of Diptera decreased during the period of flooding (1977), and then fluctuated around preimpoundment values for the remainder of the study. Oligochaeta numbers increased 700% from 1973 to 1977, and decreased only slightly thereafter. Pelecypoda numbers declined initially, recovered by 1981 to preimpact population levels, but declined thereafter. Mysis relicta (not shown in Fig. 8) appeared in 1981, and abundances of this species were relatively constant ($\approx 20 \cdot m^{-2}$) since then.

WEST MYNARSKI LAKE: Major changes in numbers of individual taxa occurred almost immediately after impoundment (Fig. 9). Number of Diptera decreased from $497 \cdot m^{-2}$ in 1973 to $95 \cdot m^{-2}$ in 1977, and then rose over the following 10 years by almost 100x; by 1987, they comprised 89% of the benthic fauna. Oligochaeta were usually the second most abundant taxon in the lake after impoundment. They increased from $70 \cdot m^{-2}$ in 1973 to a high of $1597 \cdot m^{-2}$ in 1983; by 1987, they were still well above preimpoundment levels. The Amphipoda reacted differently to impoundment. They were present at an average of $600 \cdot m^{-2}$ prior to impoundment, but were eliminated from all of the sampling sites by 1977. Although they recovered slightly in later years, their overall numbers dropped to about $20 \cdot m^{-2}$, and they were once again absent from samples taken during 1987. Pelecypoda maintained moderate population numbers throughout the study. Gastropoda seldom were present in large numbers and they were only recorded twice after 1977. Ephemeroptera were never found in West Mynarski Lake.

CENTRAL MYNARSKI LAKE: In general, numerical changes in the benthic population were more important than taxonomic ones (Fig. 10). Diptera and Oligochaeta formed most of the population of benthic invertebrates prior to and following inundation. The Diptera had increased markedly from their preimpoundment abundances by 1979 and remained so for the rest of the study. Oligochaeta numbers increased following inundation and until 1981, after which time they declined, by 1987, to approximately preimpoundment values. Pelecypoda standing crops gradually increased from 1973 to 1981, and diminished slightly thereafter. The Amphipoda first appeared in 1979, and increased to 463 specimens$\cdot m^{-2}$ by 1987. Usually only one site had high numbers. Gastropoda numbers were low throughout the study (usually $<20 \cdot m^{-2}$). Ephemeroptera were never found in any of the surveys of Central Mynarski Lake.

EAST MYNARSKI LAKE: Diptera, Pelecypoda, and Oligochaeta dominated the benthic invertebrate community; the Diptera were clearly most abundant throughout the study (Fig. 11). East Mynarski Lake had a more extensive littoral zone than the other Mynarski lakes, and Diptera clearly predominated in this shallow area (APW, unpubl. data). Amphipoda, Ephemeroptera, and Gastropoda were never found at the deep sites, and these taxa were rare in the shallow areas.

DIVERSION ROUTE LAKES - BELOW NOTIGI RESERVOIR

Physical characteristics

Downstream of the Notigi Lake control structure, maximum water levels of Wapisu and Wuskwatim lakes rose ≈ 4 m (Table 1). Although water levels increased less than in the NR lakes, lakes below the NR were still subjected to the full flow of diversion waters. The flow out of Notigi Lake averaged $36 \ m^3 \cdot s^{-1}$ in 1972 and 1973, before the control structure was closed, $124 \ m^3 \cdot s^{-1}$ in 1976, $536 \ m^3 \cdot s^{-1}$ in 1977, and $819 \ m^3 \cdot s^{-1}$ from 1978-1988 (G.K. McCullough, Freshwater Institute, unpubl. data).

The surface area of Wapisu Lake increased from 45 to 66 km^2 and the surface area of Wuskwatim Lake increased from 50 to 64 km^2 (Table 1). Adjacent swampy areas that became flooded were a major contributor to the additional surface area of Wuskwatim Lake.

Secchi disk depths taken in these lakes indicated that Wapisu Lake originally was clearer than Wuskwatim Lake (Table 3). After flooding, Wuskwatim Lake became less turbid, whereas Wapisu Lake turbidities tended to remain the same. The 1987 sampling period was influenced by high wind, so turbidities increased in both lakes (Table 3). The Secchi disk readings do not indicate that a long-term increase in turbidity occurred after full diversion flows began.

Temperatures taken prior to diversion indicated that both lakes were isothermal through the summer because they were shallow and wind-exposed; maximum temperatures reached ≈20°C (Cleugh 1974). After releases from the Notigi control structure began, isothermal conditions continued through the summer because of the relatively small depth increases, continued mixing by wind, and the rapid replacement of water by the substantial diversion flows. Wapisu Lake was warmer than Wuskwatim Lake in 1973, but this relationship changed after diversion flows began (Table 2) because of colder water coming from the NR; Wapisu Lake mean temperature was nearly identical to that of Notigi Lake. Wuskwatim Lake is considerably farther downstream from the reservoir, so the water likely warmed in passing through large, shallow Threepoint Lake.

Oxygen concentrations in late June were always >7.7 ppm in Wapisu and Wuskwatim lakes, and anaerobic conditions were never detected during our surveys. However, bottom temperatures during this time were usually <11°C (APW, unpubl. data).

Chemical changes in these two lakes can be inferred from data available on Threepoint Lake on the diversion flow midway between Wapisu and Wuskwakim lakes (Ramsey et al. 1989). Concentrations of magnesium and possibly potassium were higher after diversion, but concentrations of major nutrients were lower. Both changes reflect the concentrations of ions found above the Notigi control structure, and suggest that water replacement is an important factor in the chemical budget of each lake.

Biological characteristics

Standing crops: Preimpoundment standing crops of benthic invertebrates in Wapisu Lake were 2.5x higher than in Wuskwatim Lake (Figs. 12, 13). Standing crops in Wapisu Lake increased to 12600· m^{-2} by 1979; thereafter, abundances decreased until the end of the study when they were approximately equal to preimpoundment levels.

The benthic invertebrate community of Wuskwatim Lake did not show the same magnitude of change obvious in Wapisu Lake, although total abundance doubled from 1973 to 1977 (Fig. 13); thereafter, standing crops declined at a slower rate than in Wapisu Lake and reached preimpoundment levels by 1987.

Individual taxa:

WAPISU LAKE: Amphipoda contributed most to the high standing crop of 1979, and decreased the most by 1981; however, the drop was partially offset by a doubling of Diptera standing crop (Fig. 12). The Oligochaeta responded initially (1977, 1979), but their increase was short-lived. Other taxa responded little to the altered water flow regime and changing lake conditions; no taxa disappeared from the lake during the course of the study. The 1987 benthic community was similar to that of 1973, except for fewer Diptera.

WUSKWATIM LAKE: The same taxa were represented in both lakes; however, the Ephemeroptera and Gastropoda were proportionally more important in Wuskwatim Lake (Figs. 12, 13). Standing crops of most taxa increased initially after diversion, and then declined over the following decade. Amphipoda abundances decreased slightly from 1973 to 1981, but regained their preimpact abundance by 1983. Total abundances and overall taxonomic composition by 1987 were similar to the preimpoundment survey, except for the Gastropoda, which increased in abundance from 1973 to 1977 but had disappeared from the samples by 1987.

VARIABILITY

The standard deviations calculated for mean standing crops of benthic invertebrates in the lakes of the study are presented in Table 4. Most of the data were highly variable, as was expected from pooled, single benthic invertebrate samples taken from a variety of open-water locations in a lake (see Methods section above).

DISCUSSION

Diversion of the Churchill River into the Nelson River catchment created three new water regimes: (1) reduced flow, volume, and surface area, but similar water exchange rates (LCR lakes); (2) increased depth, flow, and supplies of nutrients and particulate foods (NR lakes); and (3) moderate increase in depth, but an order of magnitude increase in water flow (lakes below NR).

LOWER CHURCHILL RIVER LAKES

Approximately half of the surface area, or almost all of the productive littoral zone, of the LCR lakes disappeared after diversion. Benthic invertebrate standing crops in the remnant lakes declined by one-half over a decade. Although the invertebrates initially may have moved into deeper water (e.g. Chironomidae during reservoir drawdown: Cowell and Hudson 1968; or during drought: Extence 1981) most of the benthic invertebrates were limited by available habitat, their small size, and their swimming ability, and probably desiccated in the dried littoral zone. Establishment of a new littoral zone has been hampered by fluctuations of water released from the Missi Falls control structure. Such fluctuations can lead to deterioration of soil composition of the exposed littoral areas, resulting in lower production of benthic organisms (Hale and Bayne 1982). Annual filling and drawdown also hampered the productivity of littoral invertebrates in Swedish lake reservoirs (Lindstrom 1973); this productivity was always lower than in natural lakes. It is unlikely that the LCR lakes will regain their overall productivity given the current water flow regime. Invertebrate populations in the lakes below the Missi Falls control structure are likely now concentrated immediately below the lowest level of drawdown, as reported for the Barrier Reservoir in Alberta (Fillion 1967), where they will maintain reduced productivity.

NOTIGI RESERVOIR LAKES

The "reservoir paradigm" of Rzoska (1966), modified by Hecky et al. (1984), may be a suitable model for discussing the NR lakes. New reservoirs are characterized by a deoxygenation of the hypolimnion, an increase of nutrients and particulate organic matter that originate from flooded shorelines, followed by increased productivity of bacteria, phytoplankton, and invertebrates that supports increased productivity of yet higher trophic levels. When the original nutrients are dissipated, productivity of the populations declines to a more stable level, sometimes lower than before the impoundment. All of the above events occurred in NR lakes within the first decade following impoundment, except for the final decline of productivity. However, this interpretation is complicated by the fact that East Mynarski Lake, the reference system, exhibited a similar pattern of response which was caused largely by the unusual predominance of Diptera in this lake.

Deoxygenation during the filling stages eliminated the Amphipoda and Ephemeroptera, but both returned when Churchill River flows began. Apparently, productivity initiated by the additional nutrients and particulate organic matter caused increases in benthic invertebrates to levels seen only in the LCR lakes before Missi Falls was dammed. Although standing crops in some lakes declined slightly in later years of the survey, the decrease anticipated by the reservoir paradigm had still not occurred by 1987, probably because the Churchill River itself was a major new source of nutrients to the reservoir. Enhancement of benthic standing crops in lakes along the flow of the Churchill River was reported by Hamilton and McRae (1974) and Wiens and Rosenberg (1984), and a similar phenomenon was observed for the Nelson River (Wiens and Rosenberg 1991). Benthic invertebrate productivity is likely to remain high in the NR, particularly with the continued input of nutrients from the diverted Churchill River, the relatively small drawdown, and the eventual development of stable benthic habitat as shoreline erosion ends.

LAKES DOWNSTREAM OF NOTIGI RESERVOIR

Wapisu Lake responded as predicted by the reservoir paradigm: an initially high benthic productivity caused by nutrients and organic matter from drowned shorelines was followed by a trophic depression when this organic material was exhausted (or rendered unavailable by siltation: Baxter 1977). The supply of nutrients by the Churchill River flow may moderate this last stage; however, the surveys ended before this effect was observed.

Invertebrate standing crops initially increased in Wuskwatim Lake, probably because of the importation of nutrients and organic matter from flooded shorelines. This productivity soon ended, however, and invertebrate standing crops returned to predevelopment levels by the 1987 survey. The response of benthic invertebrates in this lake was less dramatic than observed in Wapisu Lake probably because the greatest flooding occurred in the southwestern region of the lake, which is poorly mixed with the main body of the lake. In addition, the erodible clay shorelines and consequently increased turbidity in Wuskwatim Lake may have contributed to a dampened response.

ACCURACY OF PREDICTIONS

Predictions concerning the responses of benthic invertebrates to Churchill River diversion, made by Hamilton and McRae (1974) and reviewed in Bodaly and Rosenberg (1990), were reasonably accurate:

(1) *Total production of benthic invertebrates in the LCR lakes will decrease to less than half after completion of the Missi Falls control structure* - Present standing crops are ≈50% of preimpact levels; however, almost one-half (46%) of the most productive lake area was also lost, which means that the present total standing crops of benthic invertebrates are only ≈25% of those before the diversion. This represents a major loss of food resources for bottom-feeding fish.

(2) *Total production of benthic invertebrates in lakes along the diversion route would increase up to 4x prediversion levels* - Short-term increases of standing crops reached approximately 3x prediversion levels. Standing crops in the NR have stabilized at about 2x preimpact levels. Combined with an areal increase of 3.8x, the present water body has ≈760% more benthic invertebrates than before impoundment and diversion.

(3) *Invertebrate standing crops in NR lakes and other lakes on the diversion route will approach those formerly seen in the LCR lakes* - This occurred only for ≈4-6 years, after which numbers began decreasing to lower and more stable levels. Future invertebrate standing crops in the NR lakes will depend on a continued supply of nutrients from the Churchill River, but should remain higher than before impoundment and diversion.

ACKNOWLEDGMENTS

We thank the many people who, over the years, helped to sample the survey lakes and sort the samples collected. C. Anema and G. McCullough allowed us to use their unpublished data. D. Bodaly, D. Cobb, G. McCullough, and S. Kasian provided useful comments on early drafts of the MS. D. Laroque did the word processing required to convert the MS into a Technical Report.

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Table 1. Physical characteristics of lakes affected by the Churchill River diversion. Prediversion values are followed by postdiversion values in parentheses. Adapted from Brown (1974), Newbury et al. (1984), and G.K. McCullough (Freshwater Institute, pers. comm.).

Lakes	Water surface area (km^2)	Depth (m) Mean	Depth (m) Maximum	Residence times (days)	Initial (final) number of benthic sampling stations
Lower Churchill River					
Partridge Breast	23.8 (14.5)	6.3 (7.4)	22.5 (19.6)	1.7 (4.8)	4 (2)
Northern Indian	144.7 (87.8)	5.7 (4.7)	58.0 (55.0)	9.0 (16.4)	10 (7)
Fidler	38.8 (9.3)	3.0 (3.7)	19.0 (15.9)	1.3 (1.3)	10 (0)
Diversion Route					
Karsakuwigamak	18.8 (37.9)[a]	2.0	11.5 (21.4)	37	5
Rat	78.4 (197)[a]	3.7 (10.0)[b]	14.5 (28.5)[b]	136 (24)[b]	10
West Mynarski	6.2 (6.4)[a]	1.7	8.5 (17.5)	60	5
Central Mynarski	11.5 (12)[a]	2.7	15.0 (21.5)	213	4
Notigi	15.1 (37)[a]	5.3	12.5 (27.7)	30	6
Notigi Reservoir	153 (733)	(7.8)[c]		(62)	
Wapisu	45.1 (66)	3.3	10.0 (14.3)	42	5
Wuskwatim	50.1 (64)	6.2	12.0 (16.0)	37	3
Reference Lakes					
Wood	22.9	9.0	32.0	862	10
East Mynarski	19.0	4.2	19.5	759	5

[a] Unpublished data from satellite photographs (G.K. McCullough, Freshwater Institute, pers. comm.).

[b] Cherepak (1989).

[c] Newbury et al. (1984); new calculations of flooded shallow areas estimate mean depth in 5.8-7.3 m range (G.K. McCullough, Freshwater Institute, pers. comm.).

Table 2. Mean temperature of the upper 5 m of the water column in survey lakes on June 14, 1973 and between June 19-24 in each of the following survey years. Data for 1973 are from Cleugh (1974). N/S = not sampled.

Lake	1973	1977	1979	1981	1983	1987
Partridge Breast	5.2	11.2	8.9	12.7	13.9	16.9
Northern Indian	9.0	11.1	9.3	11.2	13.8	15.6
Fidler	8.0	11.2	10.5	N/S	N/S	N/S
Wood	9.0	13.4	7.6	9.2	8.4	13.8
Karsakuwigamak	13.8	15.0	9.4	9.5	12.7	14.2
Rat	14.0	14.6	8.8	9.8	12.4	14.3
Notigi	15.0	13.1	7.3	10.0	11.5	14.2
West Mynarski	15.0	14.9	11.1	12.3	14.9	17.6
Central Mynarski	N/S	14.4	10.9	11.6	14.6	16.2
East Mynarski	N/S	15.1	12.2	12.3	16.2	17.2
Wapisu	15.0	13.8	8.9	10.1	11.7	14.9
Wuskwatim	13.0	15.9	N/S	10.3	13.9	16.5

Table 3. Secchi disk depths (m; mean of all benthic sampling stations) in lakes on the diversion route. Data for 1973 are from Cleugh (1974). N/S = not sampled.

Lake	1973	1977	1979	1981	1983	1987
Karsakuwigamak	1.1	2.5	2.1	2.0	1.8	0.8
Rat	1.3	2.5	2.3	2.4	1.8	0.6
Notigi	1.0	3.7	1.9	2.3	1.9	0.6
West Mynarski	1.6	2.5	1.6	2.1	1.6	0.6
Central Mynarski	1.6	2.4	1.5	2.0	1.7	0.8
East Mynarski	N/S	2.0	2.7	2.7	2.8	1.8
Wapisu	1.4	1.3	1.6	1.7	1.4	0.5
Wuskwatim	0.5	0.8	N/S	1.1	1.1	0.4

Table 4. Standard deviations of benthic invertebrate mean standing crops (no. organisms·m^{-2}) in lakes along the lower Churchill River and the diversion route, 1973-1987. Values were calculated from the means shown in Figs. 2-13.

Lake	1973	1977	1979	1981	1983	1987
Lower Churchill River						
Partridge Breast	21594	5624	3168	4458	[a]	[a]
Northern Indian	3231	4039	4327	4975	799	2919
Fidler	4731	9406	3150	[a]	[a]	[a]
Wood[b]	1474	2039	3075	3940	3009	1835
Diversion Route						
Karsakuwigamak	402	1706	1741	2271	4451	5933
Rat	1794	2544	6471	3884	3962	2084
Notigi	797	3213	3548	4166	3847	2449
West Mynarski	1447	841	6855	1497	2345	7126
Central Mynarski	1087	2010	7795	2228	3575	3966
East Mynarski[b]	3839	2177	7697	8059	12473	6746
Wapisu	2677	5627	5598	7125	4020	940
Wuskwatim	480	671	[a]	329	1615	780

[a] Not sampled.

[b] Reference lake.

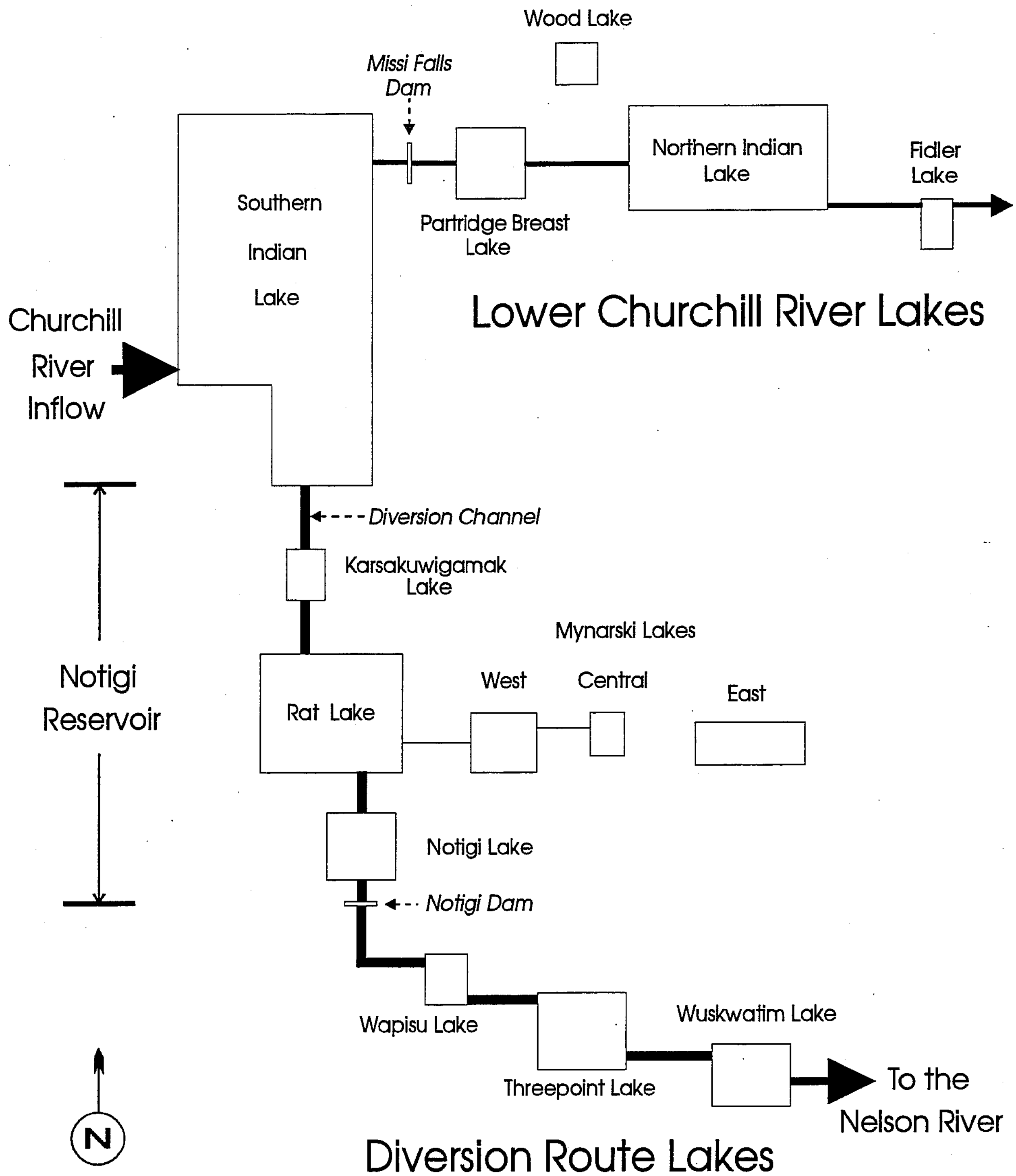

Figure 1. Schematic diagram of northern Manitoba lakes (Lat. 55°30'-57°30'N; Long. 97°-100°W) surveyed for benthic invertebrates, 1973-1987. Arrow thickness represents relative water flow. Lakes and rivers are not exactly to scale.

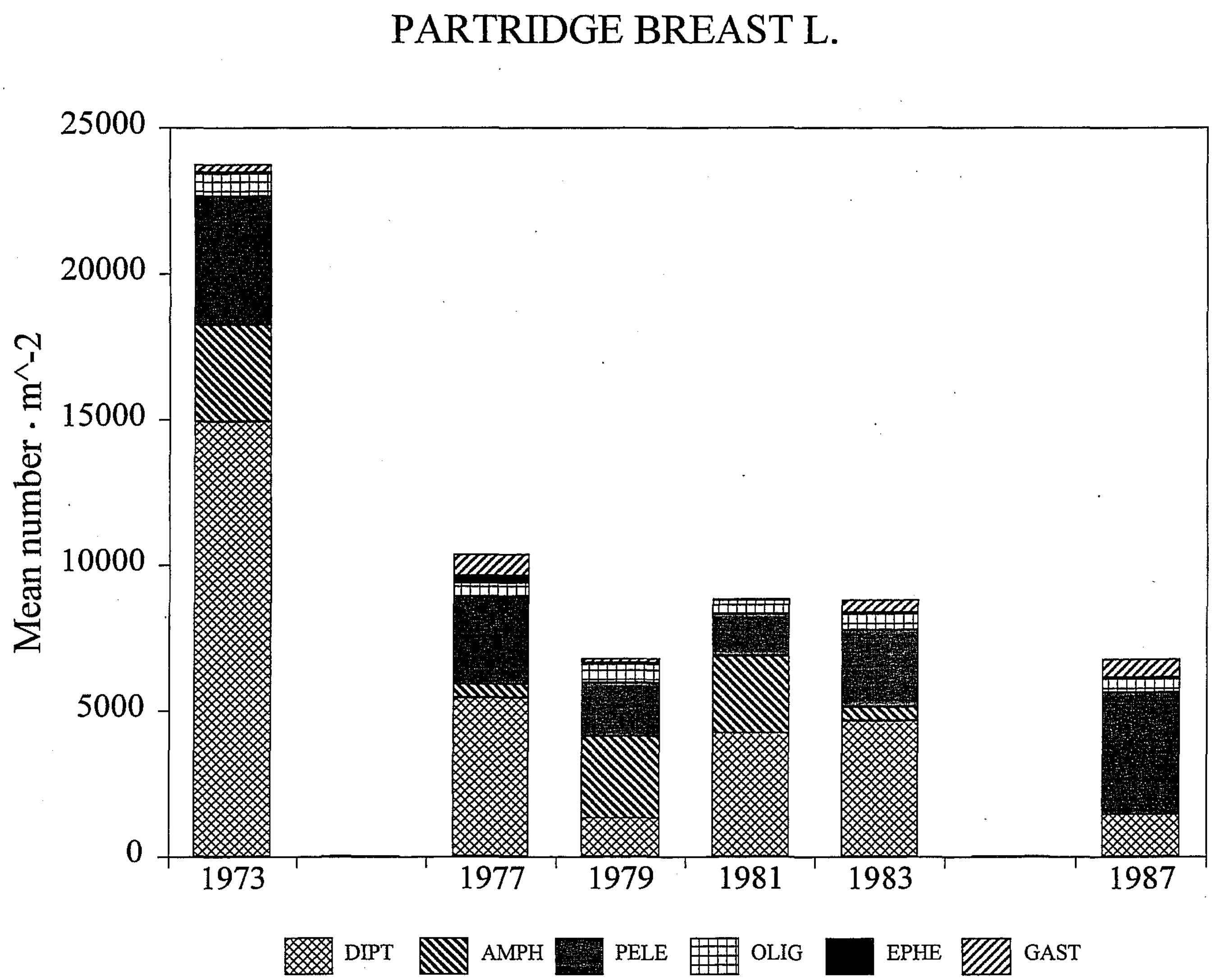

Figure 2. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Partridge Breast Lake, 1973 to 1987.

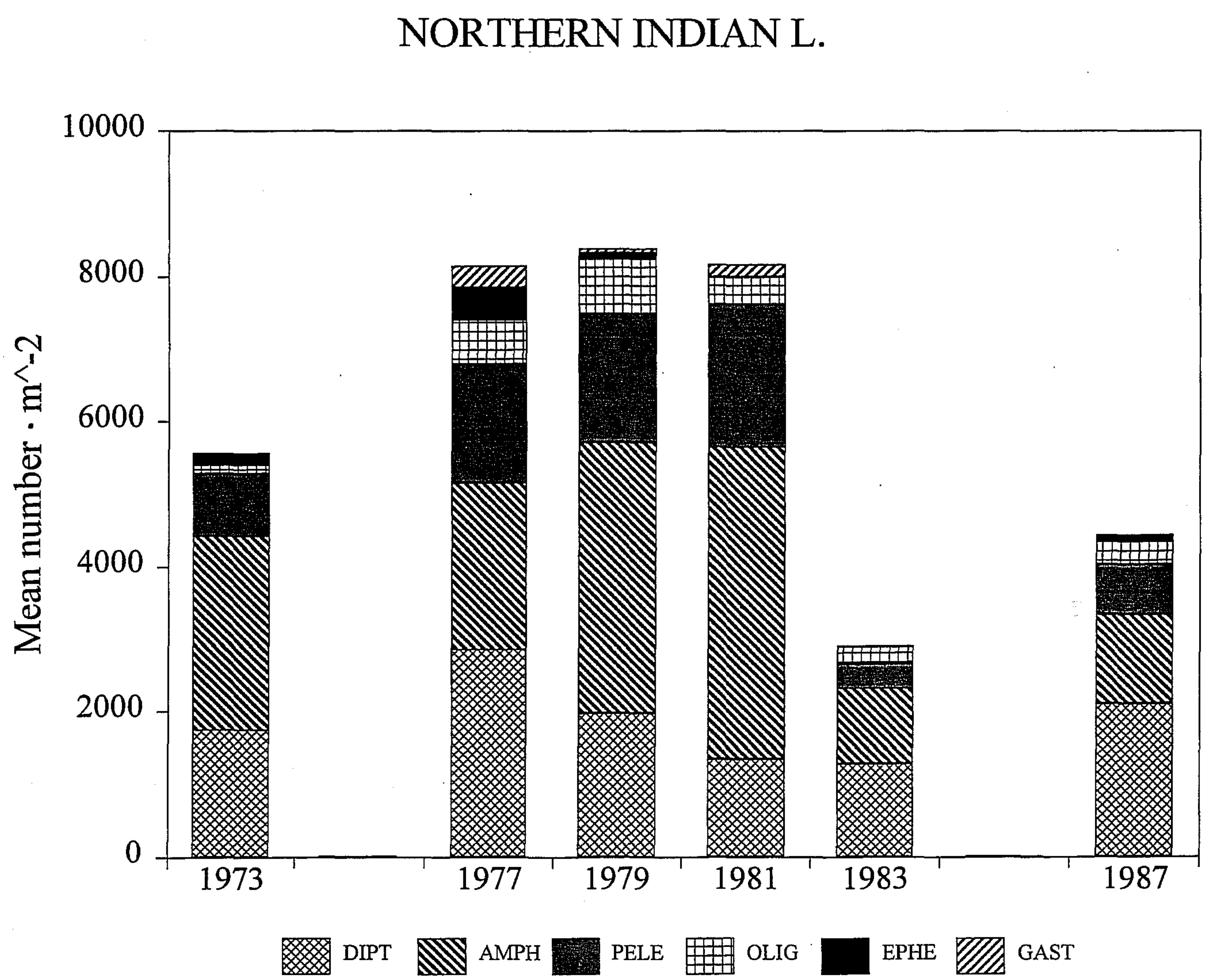

Figure 3. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Northern Indian Lake, 1973 to 1987.

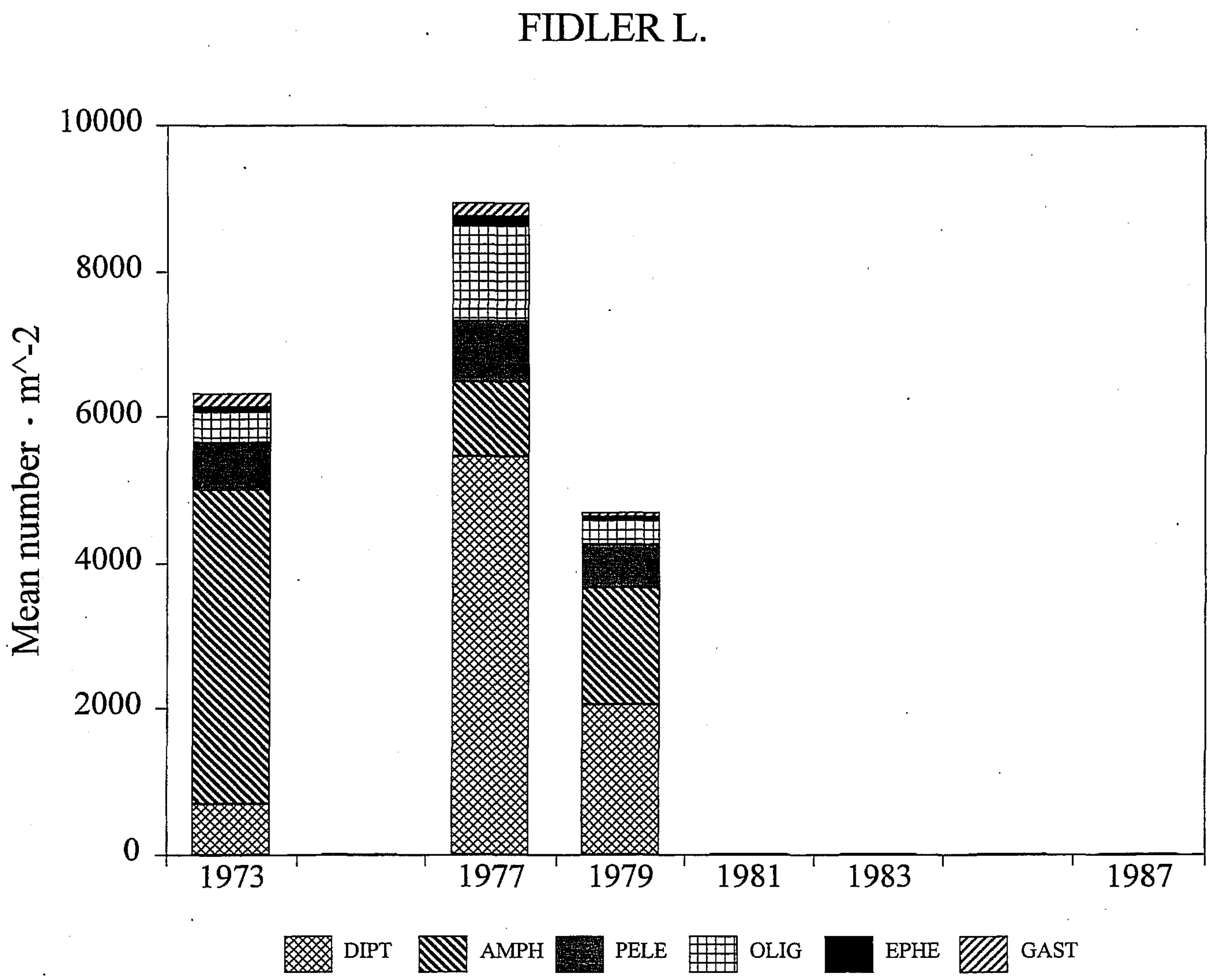

Figure 4. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Fidler Lake, 1973 to 1987.

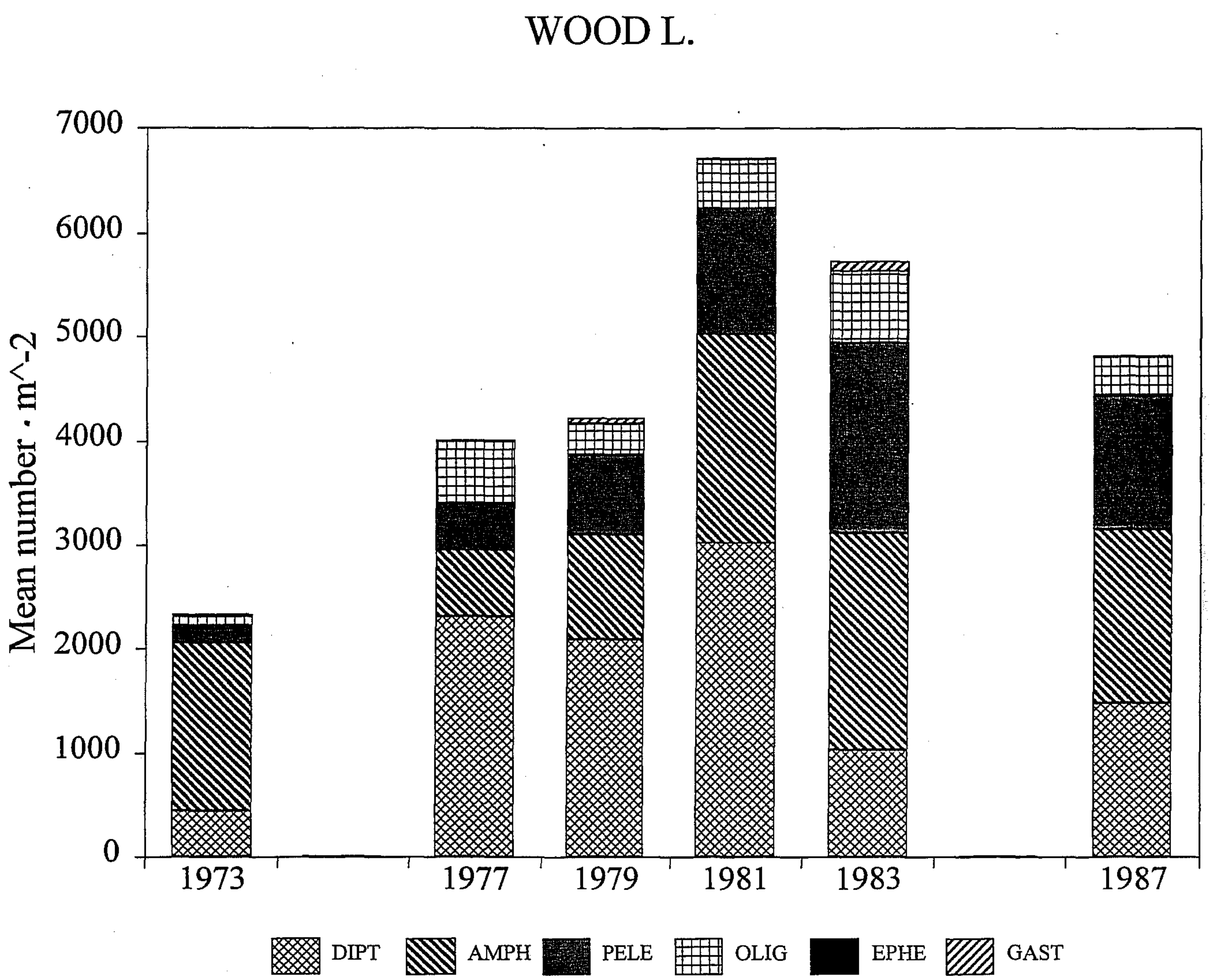

Figure 5. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Wood Lake, 1973 to 1987.

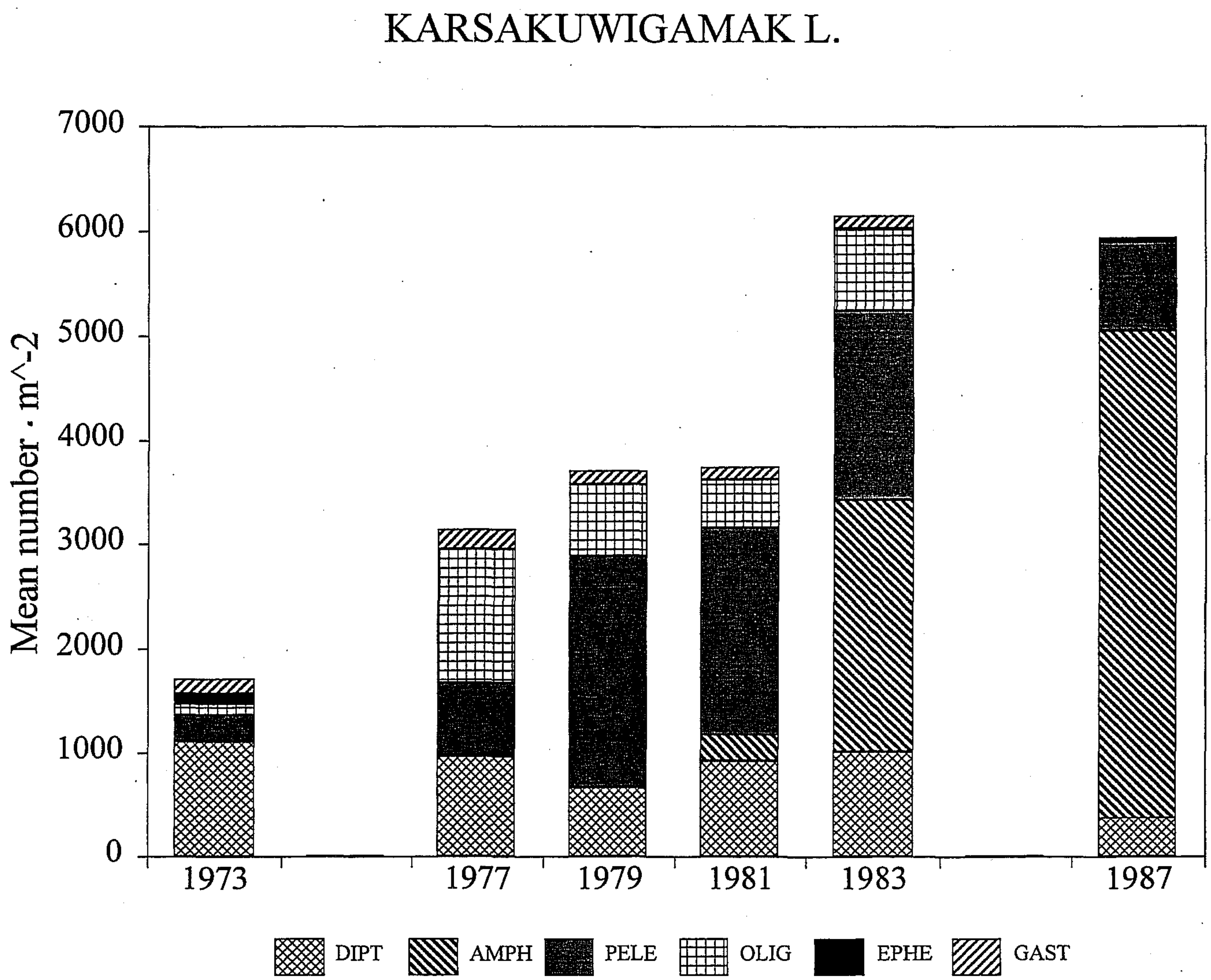

Figure 6. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Karsakuwigamak Lake, 1973 to 1987.

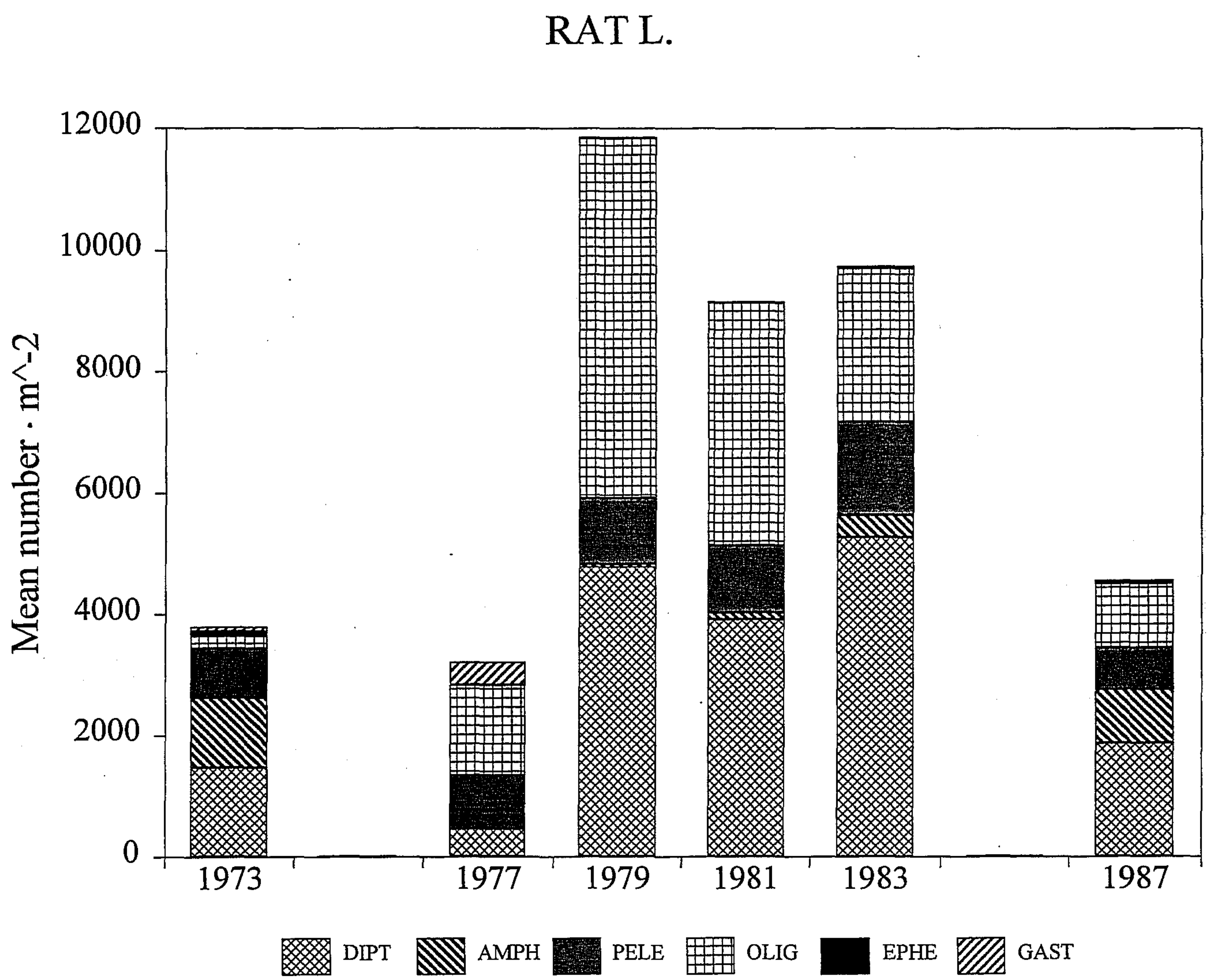

Figure 7. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Rat Lake, 1973 to 1987.

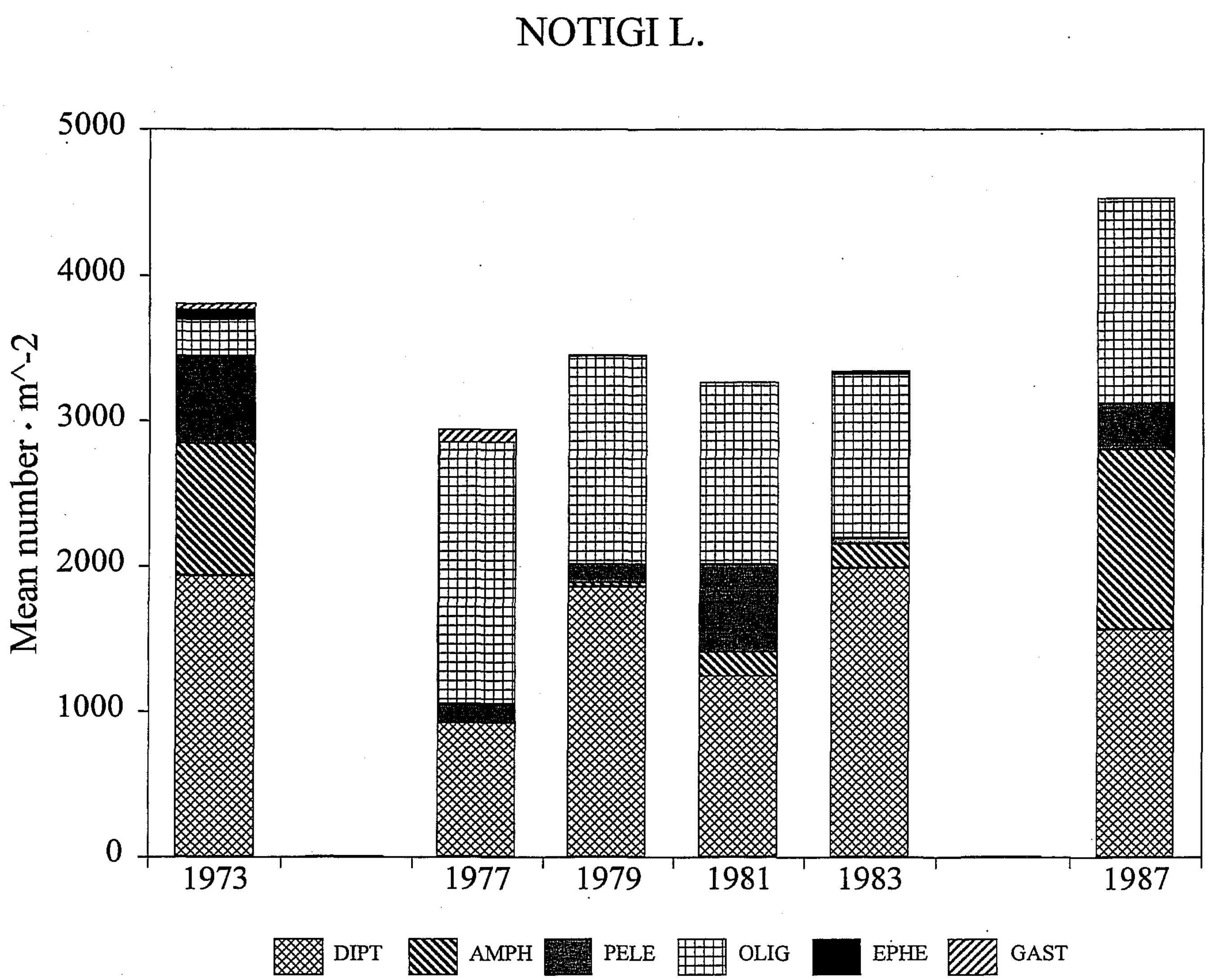

Figure 8. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Notigi Lake, 1973 to 1987.

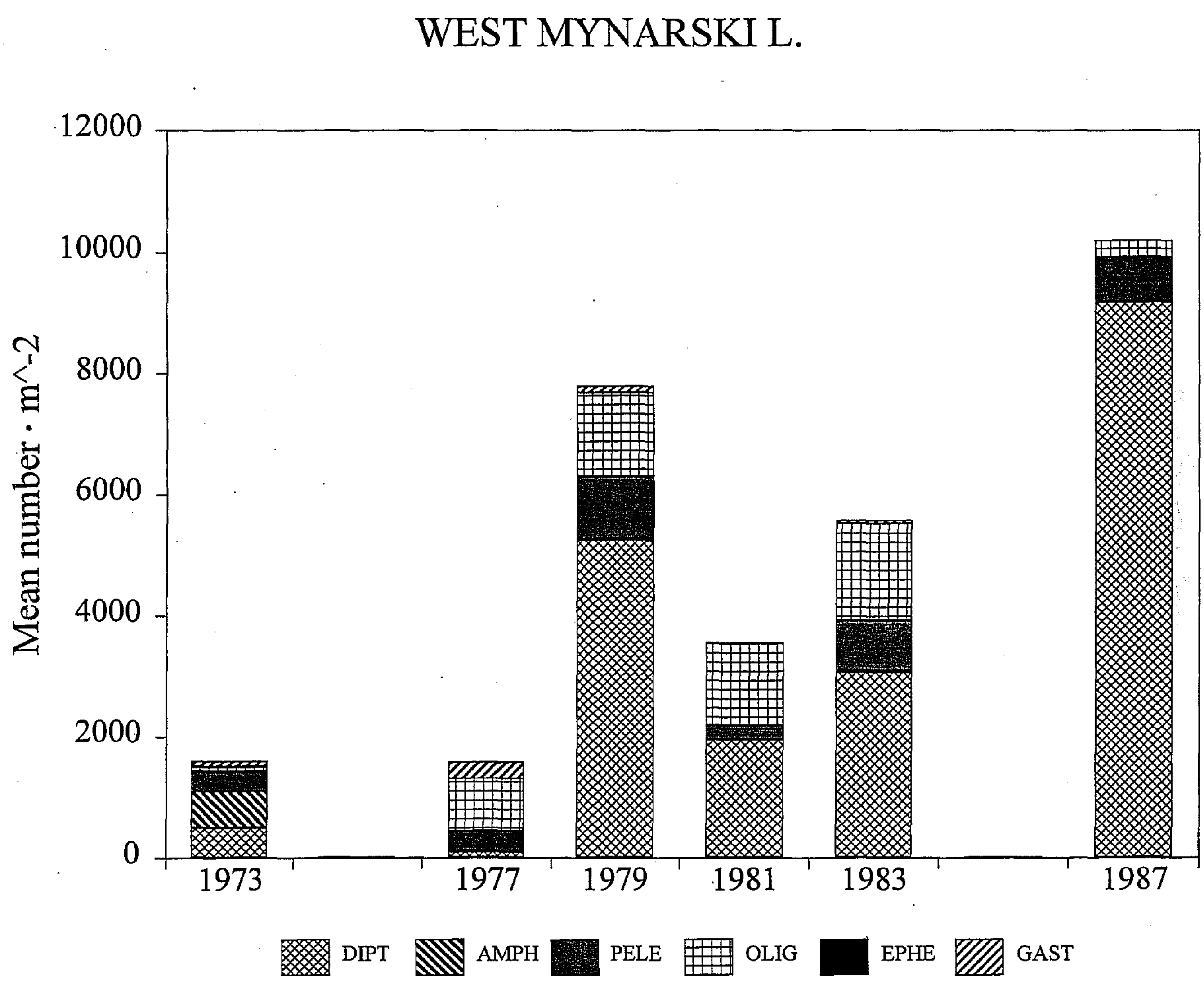

Figure 9. Standing crops of benthic invertebrates (mean no.· m^{-2}) in West Mynarski Lake, 1973 to 1987.

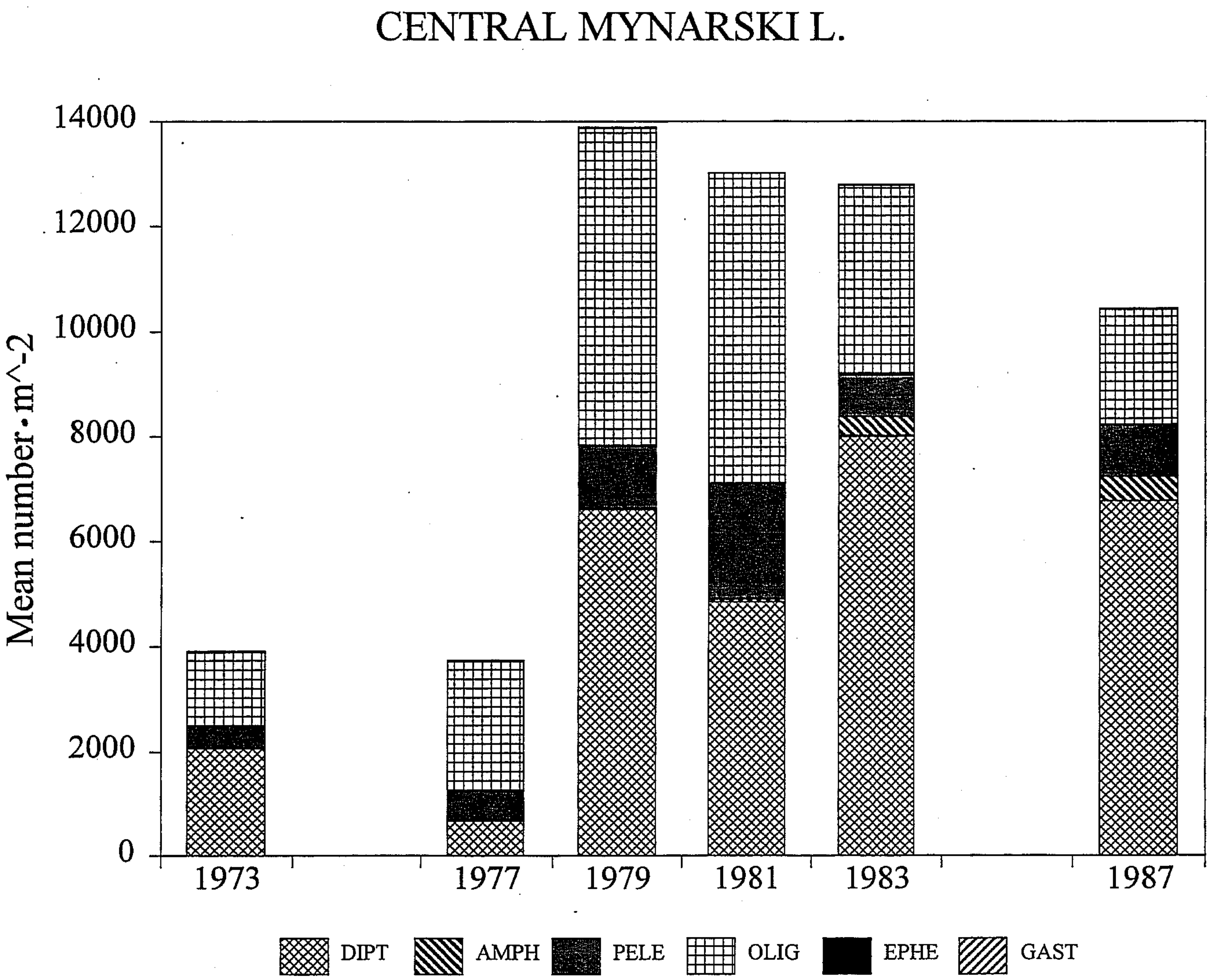

Figure 10. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Central Mynarski Lake, 1973 to 1987.

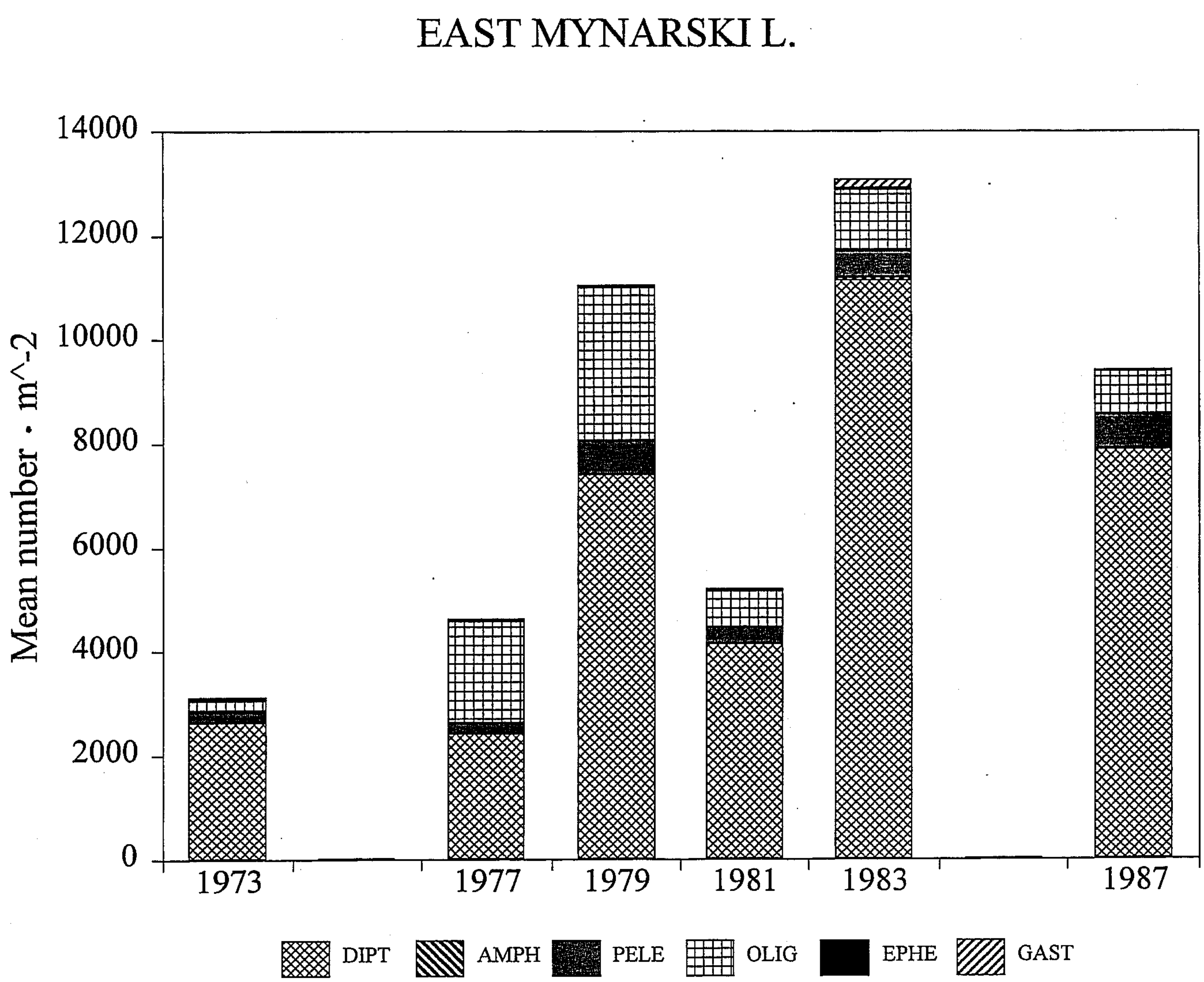

Figure 11. Standing crops of benthic invertebrates (mean no.· m^{-2}) in East Mynarski Lake, 1973 to 1987.

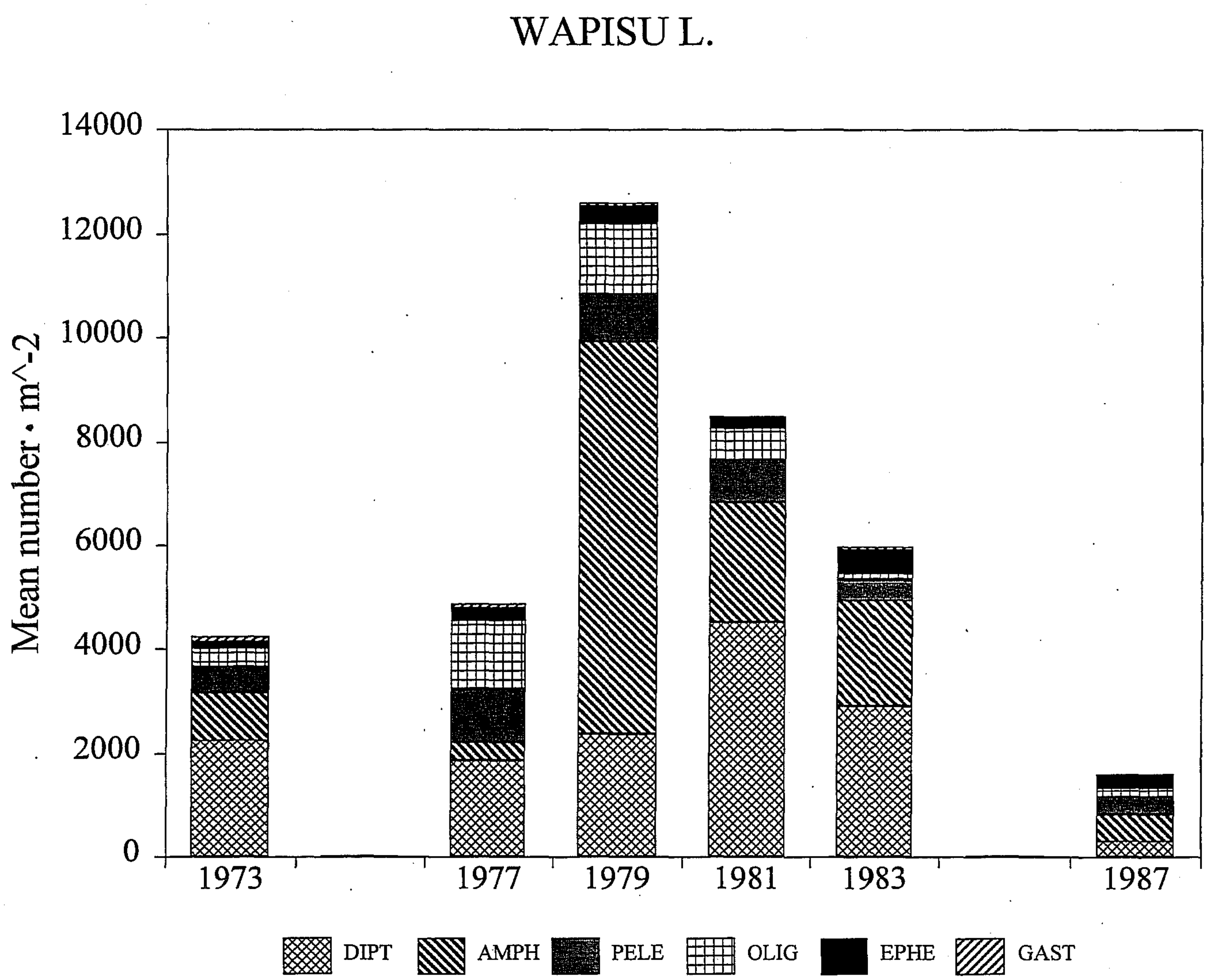

Figure 12. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Wapisu Lake, 1973 to 1987.

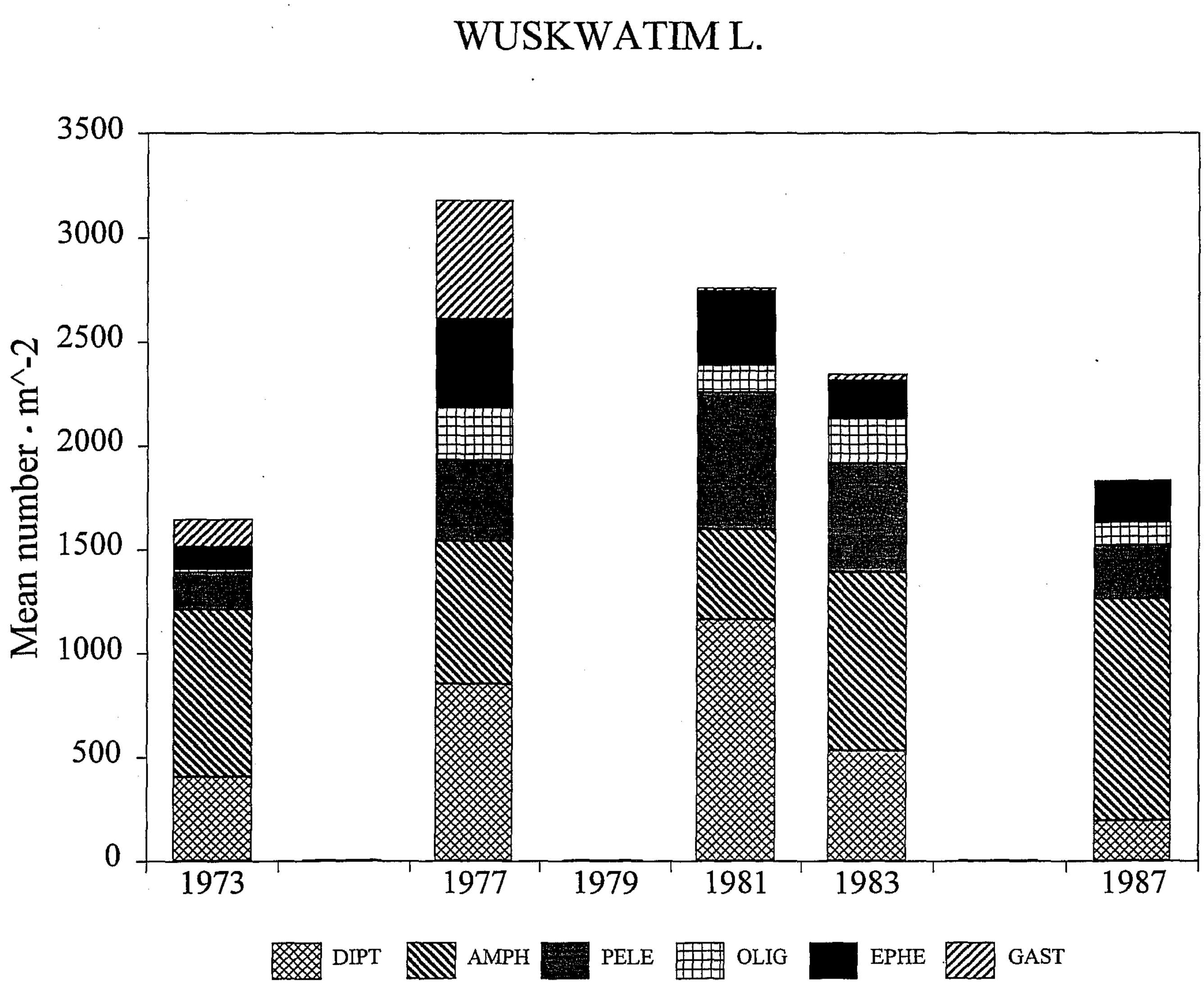

Figure 13. Standing crops of benthic invertebrates (mean no.· m^{-2}) in Wuskwatim Lake, 1973 to 1987.