Report

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Changes in Abundance of Burrowing Mayflies in Southern Indian Lake: Lessons for Environmental Monitoring

Surveys of benthic invertebrates in subarctic Southern Indian Lake, Manitoba, before and after manipulation of the lake for hydroelectric development, revealed that *Hexagenia* (Insecta: Ephemeroptera) populations collapsed following the diversion phase. Initial conclusions attributed the collapse to lake manipulation, but intensive life-history studies indicated that the cause was a series of cold years immediately following diversion. A simple model relating air temperature during the open-water season to *Hexagenia* abundance was successful in predicting burrowing mayfly abundance in the lake. This indicated the significance of temperature in regulating these populations, which are near their northern limits of distribution in Manitoba. The difficulty in discriminating between natural ecosystem variability and anthropogenic effects during the course of an environmental monitoring program is illustrated by this study.

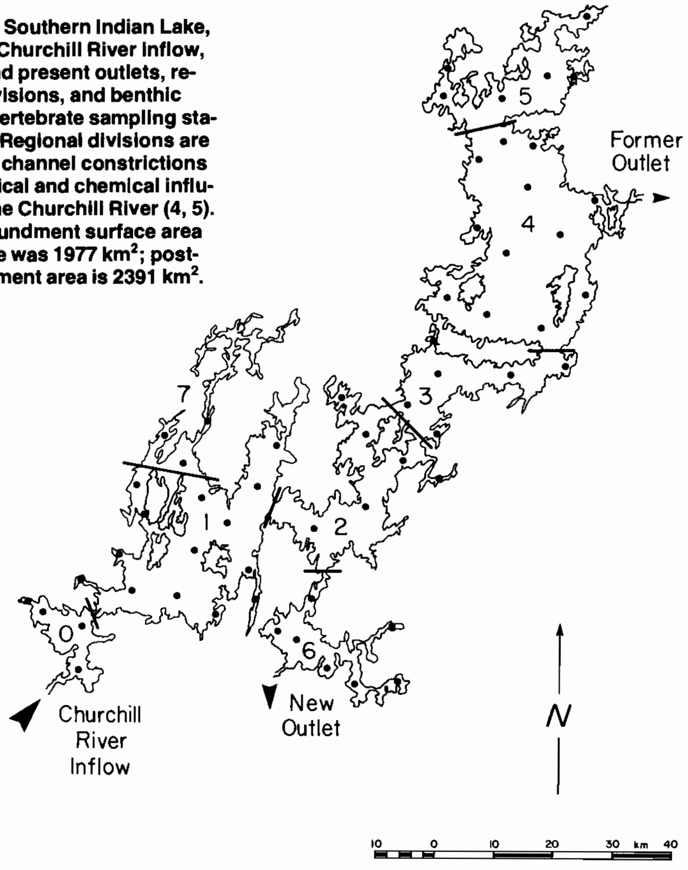

Figure 1. Southern Indian Lake, showing Churchill River inflow, former and present outlets, regional divisions, and benthic macroinvertebrate sampling stations (•). Regional divisions are based on channel constrictions and physical and chemical influence of the Churchill River (4, 5). Pre-impoundment surface area of the lake was 1977 km^2; post-impoundment area is 2391 km^2.

INTRODUCTION

A basic problem in monitoring industrial developments is discriminating between natural ecosystem variability and anthropogenic effects. Although good examples of the possible confusion of these factors exist for marine habitats (1–3), few are available for fresh waters. Surveys of populations of burrowing mayflies (*Hexagenia limbata* and *H. rigida*; Insecta: Ephemeroptera) in Southern Indian Lake (SIL), northern Manitoba, provided an example of how the causes of dramatic changes in standing stocks of biota can be misinterpreted.

SIL (lat. 57°N, long. 99°W) is a major lake on the Churchill River in central Canada. The lake lies on the western arm of the Precambrian Shield within a zone of widespread discontinuous permafrost. Glacio-lacustrine sediments overlie much of the bedrock, and boreal forest with peat deposits up to 5 m deep surround the lake. Mean annual temperature is -5°C, mean daily temperatures range from -26°C in January to +16°C in July. The average ice free period lasts from June to late October.

Manitoba Hydro's long-term plan to develop the 10 000 MW hydroelectric potential of the nearby lower Nelson River called for diversion of about 850 m$^3 \cdot$ sec^{-1} of water, or 75% of the flow, from the Churchill River into the Nelson catchment at SIL (4). The Churchill flows into SIL from the southwest and, prior to diversion, exited from the northeast on its way to Hudson Bay (Fig. 1). In 1976, the natural outlet of SIL was dammed and water levels in the lake rose 3 m. By fall 1977, the diversion was operating at full capacity through a newly excavated channel in the southeastern part of the lake that led into the Nelson catchment.

Long-term (1912–1967) pre-impoundment mean water level of SIL was 254.93 m (MSL) (max.: 256.79 m, min.: 253.82 m), whereas licensed operating range of the lake is 257.25 m–258.17 m (MSL) (4). Levels generally have been maintained from 257–258 m (MSL) since reservoir forma-

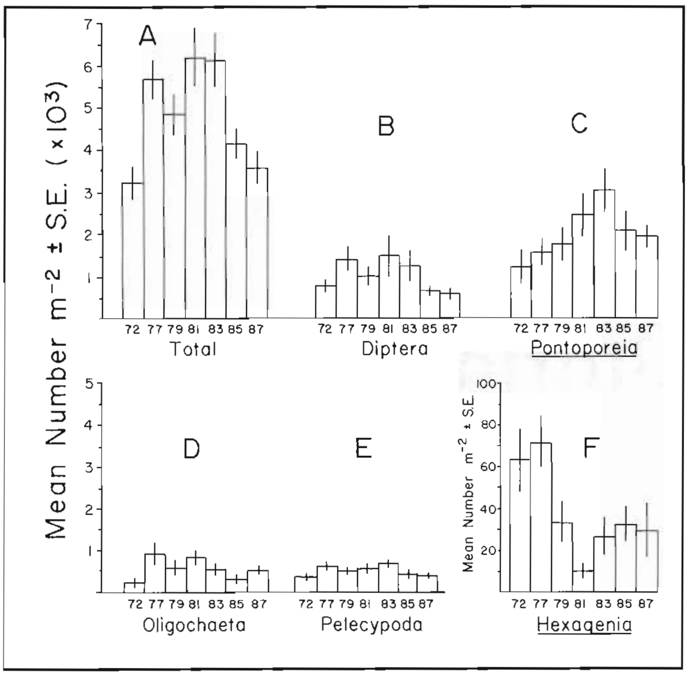

Figure 2. Standing stocks of benthic macroinvertebrates from surveys of Southern Indian Lake; A) total macroinvertebrates, B) immature flies (Diptera), C) freshwater shrimp (*Pontoporeia brevicornis* grp.), D) aquatic worms (Oligochaeta), E) freshwater clams (Pelecypoda), F) burrowing mayflies (*Hexagenia limbata* and *H. rigida*; note difference in scale).

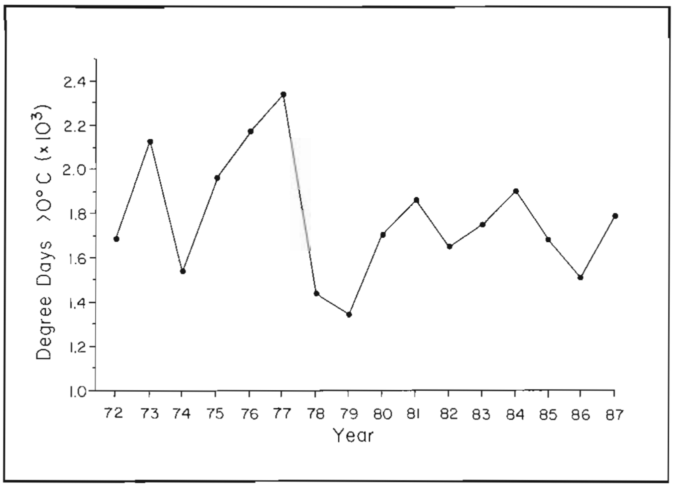

Figure 3. Atmospheric degree days > 0°C for the open-water season at SIL. Full diversion was completed in fall 1977.

An adult male burrowing mayfly (*Hexagenia limbata*) resting on black spruce (*Picea mariana*) in the northern part of Southern Indian Lake, Manitoba. Nymphal development takes at least three years, and is closely tied to air and water temperatures. Successful emergence and mating depend on calm, warm weather. Burrowing mayflies in the lake are near their northern limits of distribution in Manitoba, and are very sensitive to environmental disruptions involving temperature. Photo: D. J. Giberson.

tion (G.K. McCullough, Freshwater Institute, Winnipeg, pers. comm.).

METHODS

Benthic macroinvertebrates in SIL were surveyed before impoundment (1972) as part of a multidisciplinary environmental impact assessment (5, 6). Surveys were continued after impoundment but before diversion was complete (1977), after full diversion (1979), and every 2 yrs thereafter until 1987. Replicate benthic samples were collected with a 15 x 15 x 23 cm weighted, modified Ekman grab, along with physical and chemical data, at 58 stations spread throughout the lake (Fig. 1). The surveys usually were done during the first 10 days of July.

Samples were sieved in the field using 400-µm mesh nets, and were preserved in 10% formalin. Invertebrates were sorted under a stereomicroscope, identified, enumerated, and stored in 70% ethanol.

Weather data were based on daily air temperatures taken from the Canada Department of Environment, Atmospheric Environment Service Record of Meteorological Observations for Western Canada. Ice-free days were calculated as described in (7).

RESULTS AND DISCUSSION

Standing stocks of the benthic macroinvertebrate community as a whole responded to impoundment by initially increasing and then by decreasing to near or

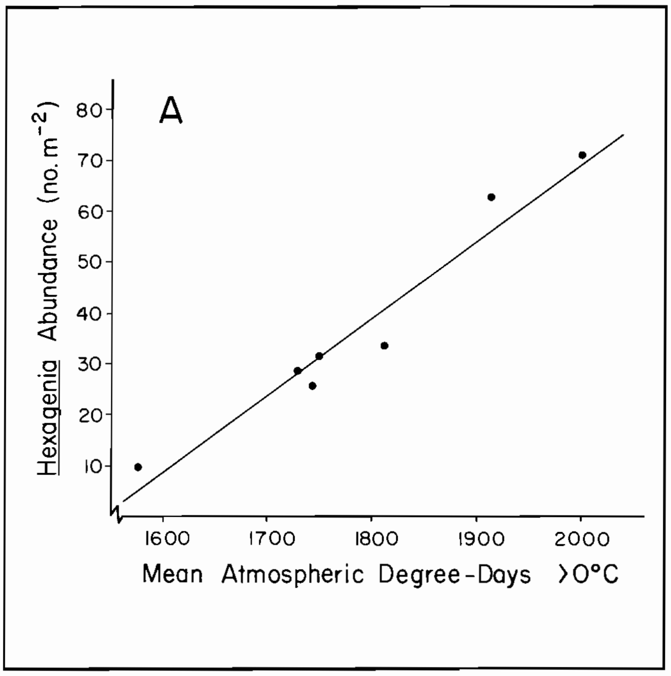

Figure 4A. Relationship between air temperature during the life cycle and mean standing stocks of *Hexagenia* in Southern Indian Lake. Air temperature is expressed as annual atmospheric degree days (> 0°C) averaged over the 3 yrs of the life cycle. $Y = 0.152 (X) - 235$ ($R^2 = 0.951$, $p = 0.0006$).

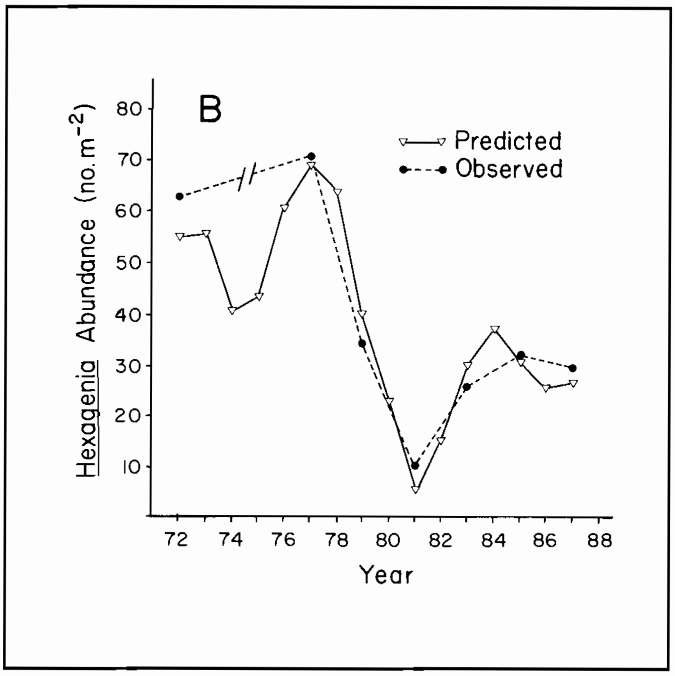

Figure 4B. Predicted vs observed *Hexagenia* abundances based on relationship shown in Fig. 4A. Samples were not collected in Southern Indian Lake between 1972 and 1977, but they were collected every 2 years after 1977.

below pre-impoundment levels (Fig. 2A). A post-impoundment "trophic upsurge" is typical of new reservoirs. It results from an initial input and then subsequent depletion of nutrients and organic matter originating from newly flooded land. In SIL, benthic macroinvertebrates were the only biotic group to show this pattern of response (6, 8).

The four most abundant benthic groups, the immature flies (Diptera, mainly Chironomidae), the freshwater shrimp (Amphipoda: *Pontoporeia brevicornis* grp.), the aquatic worms (Oligochaeta), and the freshwater clams (Pelecypoda), all responded similarly, thus creating the overall pattern (Figs 2B–2E). However, an opposite pattern was observed for burrowing mayflies (Fig. 2F). Lakewide standing stocks increased slightly following impoundment (1977 survey), but fell dramatically following full diversion to about 15% of the pre-development level by 1981. Following the 1983 survey, we attributed the reduction in *Hexagenia* standing stocks to an inability by *Hexagenia* to maintain their burrows because of severe shoreline erosion and altered substrate composition, and to a decrease in water temperatures in the northern part of the lake because of river diversion and incipient thermal stratification (9). Had no further surveys been done, we would have claimed, erroneously, that burrowing mayflies in SIL were adversely affected solely by manipulations of the lake for hydroelectric development. However, the surveys were continued, and although standing stocks never returned to the pre-development level during the 10 yrs of post-development monitoring, populations increased substantially after 1981 and stabilized at about 50% of the 1972 level, despite the fact that impoundment and diversion still affected the lake.

In 1986, an experimentally based program of autecological research was initiated. Its intent was to describe the life history of *Hexagenia* populations in SIL, with a view to interpreting the long-term survey data.

We believe that the observed collapse of *Hexagenia* populations in SIL was caused by unusually cold temperatures that immediately followed lake diversion (Fig. 3). Growth and development of *Hexagenia* species in more southerly locations is intimately tied to degree-day (dd) accumulation; most reseachers indicate that 2000–2500 water dd above a threshold of 10°C are required to complete a 1–2 yr life cycle (e.g. 10–12). *Hexagenia* mayflies in SIL are near their northern limits of distribution in Manitoba and require at least 3 yrs to accumulate the necessary dd for development (13). Moreover, the threshold of development for the SIL population was experimentally determined to be near 8°C (14), rather than the 10°C reported for southern populations.

Weather conditions affect *Hexagenia* abundance in three major ways in SIL. First, cooler water temperatures extend duration of the nymphal life cycle, which results in a higher probability of natural mortality, fewer emerging adults, and lower reproduction (15). Second, water temperatures affect egg-hatching success, i.e. fewer eggs hatch at lower temperatures (16). Third, windy or stormy weather during emergence periods results in high mortality and low mating success, again limiting recruitment (17).

One weather variable, air temperature (expressed as atmospheric dd > 0°C during the open-water season), correlates well with the factors that affect *Hexagenia* abundance in SIL. Most areas of the lake do not thermally stratify, so bottom-water temperatures are directly related to air temperatures during the open-water season. Also, during the 10-yr period of weather records for SIL, windy and stormy conditions during emergence were associated with cool mean summer air temperatures, whereas calm and clear summers were usually warm (G.K. McCullough, Freshwater Institute, Winnipeg, pers. comm.). Moreover, air temperatures > 0°C are biologically important because they contribute to heating the water mass up to the 8°C developmental threshold for *Hexagenia* in SIL. Thus, air temperatures were used in the following predictive manner: when atmospheric dd > 0°C (from July–July) were averaged over the 3 yrs of the life cycle and regressed against mean abundance of *Hexagenia* (numbers · m^{-2}) in SIL, > 95% of the variability in *Hexagenia* standing stocks during the study period could be explained (Fig. 4A). The resulting relationship was then used to predict *Hexagenia* abundance based upon air temperatures alone. The close relationship between predicted abundances and those observed on each lake survey (Fig. 4B) indi-

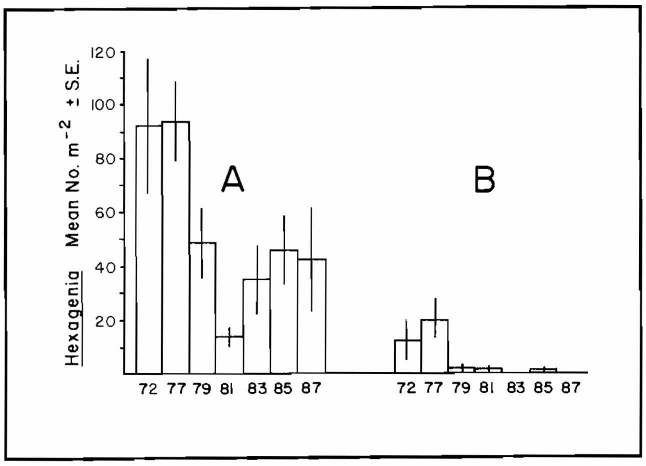

Figure 5. Standing stocks of *Hexagenia* in regions of Southern Indian Lake; A) regions 0, 1, 2, 5, 6 and 7 where water temperatures did not decline as a result of river diversion, and B) regions 3 and 4 where water temperatures declined as a result of river diversion. See Figure 1 for location of regions.

cates the importance of temperature in regulating populations of *Hexagenia* in SIL.

Effects of lake manipulation, however, were not entirely blameless in changing standing stocks of *Hexagenia* in SIL. After impoundment and diversion, water temperatures decreased in the large northern areas of the lake (regions 3 and 4) because warm Churchill River water was diverted away from these regions. This resulted in delayed ice break-up in the spring, reduction in length of the heating season, and lowered maximum water temperatures relative to regions upstream of the diversion (6, 18). *Hexagenia* was never very abundant in regions 3 and 4 (because of their deep, cool nature even before diversion), so changes of standing stock in these regions had little effect on total lake response. However, the period of below-average temperatures combined with cooling due to water diversion produced a different pattern of abundance for regions 3 and 4 than for the rest of the lake (Fig. 5). Although *Hexagenia* appears to be recovering in most regions of SIL, these mayflies have disappeared from all but the warmest, most sheltered areas of regions 3 and 4.

CONCLUSION

The challenge in environmental monitoring is to discriminate between natural variability and anthropogenic effects. This problem is especially critical when dealing with populations at or near their limits of distribution, because such populations can be extremely sensitive to environmental change.

Although survey data alone are usually inadequate for establishing cause and effect, they are valuable for indicating areas that need attention in the course of a monitoring program. The results of post-development monitoring at SIL indicated a need to examine factors other than those relating to hydroelectric development in order to explain patterns of abundance of burrowing mayflies. A combination of survey and experimental approaches helped distinguish between effects of lake manipulation and natural variability in SIL, and should be essential ingredients in most environmental monitoring programs.

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13. *Hexagenia* populations were studied intensively in four areas of Southern Indian Lake, chosen to cover a range of temperature regimes, from 1986–1988 (D.J. Giberson, unpublished data). Cohort analysis (based on examination of a combination of length-frequency measures and developmental-stage indicators over the entire study period) indicated a 3-yr life cycle in the warmer parts of the lake (where average annual water degree days > 8°C for the study period ranged from 650-750) and a 4-yr cycle for the coldest location studied (where average annual water dd were approx. 500). A 3-yr life cycle was characteristic of about 80% of the lake.
14. *Hexagenia* were reared in the laboratory at 4, 8, 10, 12.5, 15, and 20°C (D.J. Giberson, unpublished data). No larval growth was detected at 4°C for any size class, but later stage *Hexagenia* showed some growth at 8°C, and all stages showed detectable growth at temperatures above 10°C. An 8°C development threshold was further indicated by egg development and some egg hatch at this temperature.
15. Within a life cycle, effects of stage-specific mortality are cumulative with time, so increasing time spent within a stage will increase mortality over the entire length of the stage, even if the number of deaths per unit time is unaffected; see discussion in Rempel, R.S. and Carter, J.C.H. 1987. Modelling the effects of accelerated development and reduced fecundity on the population dynamics of aquatic Diptera. *Can. J. Fish. Aquat. Sci. 44*, 1737–1742.
16. Both artificially and naturally inseminated *H. limbata* eggs from Southern Indian Lake were held in the laboratory to determine hatching variables at different temperatures (D.J. Giberson, unpublished data). Approximately 80% of eggs hatched (in 5–14 d) at 20°C, compared to only 33% at 15°C (in 9–30 d) and <10% at 8°C (in >75 d).
17. Field observations at Southern Indian Lake indicated that *Hexagenia* subimagos attempting to emerge when waves exceeded approx. 1 m height were unsuccessful. After prolonged periods of stormy weather (particularly in 1986), shorelines were littered with dead subimagos that had drowned while attempting to emerge, and few young larvae were subsequently collected from those regions. A similar phenomenon was reported by Whelan, K.F. 1980. Some aspects of the biology of *Ephemera danica* Müll. (Ephemeridae: Ephemeroptera) in Irish waters. In *Advances in Ephemeroptera Biology*, Flannagan, J.F. and Marshall, K.E. (eds.) *Proc. 3rd Int. Conf. on Ephemeroptera*, 1979, July 4–10, Winnipeg. Plenum Press, New York, p. 187–199 for the burrowing mayfly *Ephemera danica*, and Hunt, B.P. (1953; see note 10) recorded high mortality of mating *H. limbata* during a storm.
18. Hecky, R.E. 1984. Thermal and optical characteristics of Southern Indian Lake before, during, and after impoundment and Churchill River diversion. *Can. J. Fish. Aquat. Sci. 41*, 579–590. Region 5, the one furthest north, was never affected by the flow of the Churchill River; local inflows were important in determining ice break-up in the spring.
19. Research was supported by the Canadian Department of Fisheries and Oceans, and a University of Manitoba Graduate Fellowship to D.J.G. D. Bodaly, M. Friesen, T. Galloway, R. Hecky, J. Mathias, G. McCullough, and K. Patalas provided helpful reviews of earlier drafts of the manuscript. D. Laroque did the word processing.
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