

Life histories of burrowing mayflies (*Hexagenia limbata* and *H. rigida*, Ephemeroptera: Ephemeridae) in a northern Canadian reservoir

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SUMMARY

1. The life histories and population dynamics of the burrowing mayflies *Hexagenia limbata* and *H. rigida* were examined from 1986 to 1988 in four regions of an impounded lake in northern Manitoba, Canada.
2. Bottom temperatures reached 15–20°C, but ice-free periods of 4–6 months resulted in annual degree day (dd > 10°C) accumulations of only 210–650 in various regions and years.
3. The life cycles (egg to adult) of both *Hexagenia* species required 3 yr in the three warmest regions studied and 4 yr in the coolest area; total dd accumulations to complete the life cycle ranged from 1222 to 1468 dd > 10°C.
4. Fecundity (no. of eggs/♀) was strongly correlated to body size of subimagos, and subimago size was strongly correlated to length of nymphal exuviae, so field collection of nymphal exuviae could be used to determine both the size and fecundity of the emerging females.
5. Degree day accumulation in the final year before emergence was a better predictor of emergence timing than overall dd accumulations for the life cycle.

Introduction

Southern Indian Lake is a large (2391 km²) lake located on the Churchill River in northern Manitoba, Canada (57°N, 99°W). Following impoundment, water level was raised 3 m in 1976, and in 1977 most of the water of the Churchill River was diverted southward through the lake into the Nelson River catchment to augment flows for hydropower generation in the lower Nelson River (Newbury, McCullough & Hecky, 1984). Southern Indian Lake became the focus of several studies on the environmental impacts of hydroelectric development in northern Canada, including impacts on fish, zoobenthos, zooplankton, primary productivity and hydrology (summarized in Hecky *et al.*, 1984). The major physical impacts of the development involved increased turbidity from extensive shoreline erosion and altered lake water temperatures (Newbury *et al.*, 1984).

The abundances of burrowing mayflies [*Hexagenia limbata* (Serville) and *H. rigida* McDunnough] declined dramatically following impoundment and diversion (Wiens & Rosenberg, 1984), although subsequent study suggested that the population decline may have been related to a cold period rather than to the hydroelectric development itself (Giberson, Rosenberg & Wiens, 1992). This observation prompted a study on the population dynamics of the burrowing mayflies in the lake, to determine whether the observed decline was, in fact, weather related and how weather variables affected populations. Both field and laboratory study is required to elucidate life history information in mayflies (Brittain, 1982); the field data are presented here while the results of the laboratory study on growth and development of *Hexagenia* from the lake are given in Giberson & Rosenberg (1992a, b).

Growth and development of *H. limbata* and *H. rigida*

are related to temperature. The life cycle of *H. rigida* is not well documented, but in Lake Winnipeg, Canada, where the populations overlap, *H. rigida* showed a similar life cycle pattern to *H. limbata* (Neave, 1932; Flannagan, 1979). Development from oviposition to adult may be completed in ≤ 1 yr in the southern U.S. by *H. limbata* (e.g. Edmunds, Jensen & Berner, 1976; Welch & Vodopich, 1989), although the life cycle may take ≥ 2 yr in the northern part of the range (e.g. Neave, 1932; Mozely & Ladronka, 1988). Mixed life cycle populations are also common; in these, individuals within a single location may require either 1 or 2 yr to complete development, depending upon water temperature and the timing of emergence and oviposition (e.g. Hudson & Swanson, 1972; Flannagan, 1979; Heise, Flannagan & Galloway, 1987). Temperature effects on growth and development may be quantified by using a degree day (dd) model, in which accumulated dd required to complete the life cycle are calculated; these data can then be compared with other populations or locations (Southwood, 1978; Higley, Pedigo & Ostlie, 1986). The objectives of this study were to investigate *Hexagenia* population dynamics temporally in four regions of Southern Indian Lake that varied with respect to temperature regimes, and to determine the mechanisms by which temperature and other weather variables could affect abundance.

Study site

The region is one of discontinuous permafrost, and much of the lake's shoreline consists of a mix of layered silty clays and ice. Lake impoundment resulted in contact between warm lake water and frozen shoreline sediments, melting the ice and causing high erosion rates and turbidity (Newbury & McCullough, 1984). Because of the flooding and continued erosion, the near-shore zone now consists mainly of flooded and dead black spruce [*Picea mariana* (Mill.) B.S.P.] forest and peatland, whereas the off-shore zone is primarily clay aggregate. Thermal stratification in the lake is rare because the basin is shallow and narrow, and wind and river flow keep it well mixed; therefore, there is a strong correlation between air temperature during the open-water period and water temperature (Hecky, 1984; Giberson *et al.*, 1992). The duration of the ice-free period for the lake is variable and depends on local weather conditions; between 1972 and 1987

the open-water period ranged from ~ 4.0 to 6.2 months (Giberson *et al.*, 1992). Details of geology, vegetation and climate for the region may be found in Newbury *et al.* (1984).

Materials and methods

Sampling locations

Four study regions (Fig. 1) were chosen that provided a gradient in dd accumulations and yielded sufficient *Hexagenia* for life-history analysis. The warmest region, Opachuanau, was located at the inflow of the Churchill River. The next warmest region investigated was Wupaw Bay, located just south of the main flow through the lake, followed by South Bay East, a series of small and shallow bays in the south-eastern part of the lake. South Bay West, the new outlet for most of the Churchill River flow, was the coldest region. Four sites were chosen within 100 m of shore in each region to avoid the nearshore area of flooded vegetation (Fig. 1). Sediments in these sites consisted mainly of clay aggregates; water depths ranged from 6 to 12 m in Opachuanau, 5 to 6 m in Wupaw Bay and South Bay East, and 7 to 10 m in South Bay West.

Sampling of nymphs

Eight to 10 samples were collected from each site with a 15×15 cm weighted Ekman grab (Burton & Flannagan, 1973) approximately monthly throughout the open-water season. Samples were washed through a $200 \mu\text{m}$ mesh net and preserved in 10% formalin in the field; after 1 month they were washed and transferred to 70% ethyl alcohol for sorting and identification. Samples were sorted under a dissecting microscope, and burrowing mayflies were identified to species using the characters given by McCafferty (1975) and J.F. Flannagan (personal communication). Species could be identified at *c.* 7–8 mm in length (*c.* one-quarter of final size); relative proportions of each species for smaller, unidentifiable nymphs found on given sampling dates were assumed to be the same as those on later sampling dates when species could be determined. Sexes were separated for each species based on the presence or absence of the developing penes in the males. The rudiments of the penes and forceps could be seen under $\times 50$ magnification when nymphs were ≥ 6 mm in length.

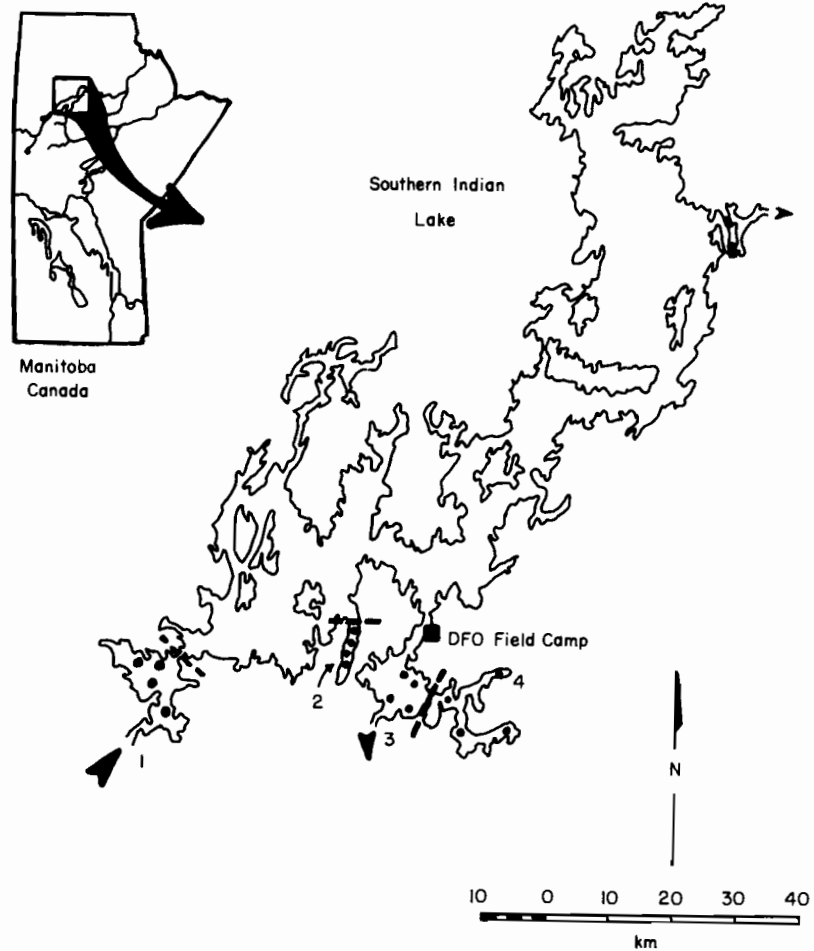


Fig. 1 Sampling sites on Southern Indian Lake (dots), and location of Department of Fisheries and Oceans (DFO) field camp (square). Study Regions are numbered: (1) Opachuanau, (2) Wupaw Bay, (3) South Bay West, (4) South Bay East. Arrows refer to major inflow (Churchill River at Opachuanau), diversion outflow (South Bay West) and former, natural outlet.

Life-history analysis

Cohorts (year classes, based upon oviposition time) were separated for life-history analysis by examining the size-frequency distributions of nymphal morphological features. Cohorts could not be adequately separated using any one feature; sizes overlapped between cohorts because of variable growth rates and sexual dimorphism in the later stages. Therefore, three features were measured using an ocular micrometer lens in a dissecting microscope: (i) body length: distance (mm) between the tip of the frontal process and the end of the abdomen, excluding the caudal filaments; (ii) head width: width (mm) just in front of the eyes; and (iii) wing-pad length: length (mm) of the developing wing bud on the mesothorax. Body length and head width provided the best measures for separation of young nymphs; wing-pad length was most useful for older nymphs.

Mortality estimates

We attempted to calculate year-to-year mortality for each species and each location to compare mortality rates with thermal regime. After cohorts were identified, the mean density for each cohort was plotted against time for each species in each study area. Within-summer densities were generally stable in each year-class, except for the cohort that was emerging as adults or just hatching from eggs; however, densities declined dramatically between summers. Therefore, densities were averaged for each summer and compared with the average density for the succeeding summer to obtain an estimate of between-year mortality. Mortality was calculated as the percentage difference between the mean annual abundance from one year to the next (i.e. 1-year-old minus 2-year-old nymphs, and 2-year-old minus 3-year-old nymphs).

Quantification of mortality during other life-cycle

stages was not possible. A direct estimate of emergence mortality could not be obtained because standard floating emergence traps proved unsuitable for the rough water conditions encountered in Southern Indian Lake and because the mayflies avoided submerged traps (A.P. Wiens, personal communication). Evaluation of oviposition success was hindered by high sedimentation rates in the lake. However, qualitative observations were made during the emergence periods to evaluate the effects of different weather conditions on emergence and oviposition success.

Adult collections

Adults were collected in a light trap located near the field camp at the north end of South Bay West (Fig. 1), in 'pan traps' (see below) along shorelines in each sampling region, and by sweeping and hand-picking shoreline vegetation. The light trap was installed in the first week of June in all years, usually when there was still some ice on the lake, and shorelines and vegetation were checked on each sample day. Five replicate plastic dish pans (33 cm L × 23 cm W × 14 cm H) were filled with 3–4 cm of ethylene glycol (car antifreeze) and set into the peat near one of the sampling sites in each region; adults that fell into the pans were unable to escape and were captured. The antifreeze acted as a preservative and as a surfactant even when diluted with rainwater, but evaporated only slowly during dry periods. These pan traps, which could be left in isolated and inaccessible sites for up to 2 weeks, provided information on the duration of the emergence period and relative inter-site abundances of emerging adults. *Hexagenia* were removed and the antifreeze was renewed weekly, weather permitting, from the beginning of July to the end of September. Shoreline vegetation was checked visually and swept with a collecting net during visits to service pan traps, to obtain adults for determination of adult size and fecundity for each location. Last-stage nymphal exuviae floating along the shorelines during emergence periods were also collected during site visits; these served as a check on the timing of the emergence period, because exuviae were present even when adult densities were too low to be adequately sampled by the pan traps. The exuviae were also measured to provide an estimate of the size of mature nymphs in each region.

Fecundity

Fecundity estimates were determined for each region from the relationship between female body size and the number of eggs carried. Eggs were dissected and counted from twenty-two premeasured female subimagos (both species combined, because adult females cannot be assigned to species) collected from all four regions. The relationship between subimago body size and fecundity was determined by regression analysis, so that fecundity could be estimated by measuring subimagos from each region. However, subimagos were usually only captured on a single day during the emergence period, so last-instar nymphal exuviae from each location were also collected to increase the sample size from each region (for better statistical analysis) and to obtain a sample that was spread over the entire emergence period. Fecundity was then determined indirectly from the relationship between nymphal size and subimago size. To establish this relationship, large, nearly mature nymphs were collected from Wupaw Bay and reared in a screened aquarium at room temperature. The aquarium was checked several times daily for emergence, and any newly emerged subimagos and floating exuviae were associated and measured. The relationship between exuvial lengths and subimago lengths was determined by regression analysis. Lengths of field-collected exuviae were converted to subimago lengths using the regression relationship, and an overall mean female subimago size was estimated for the entire emergence period at each study location. The mean fecundity for mayflies from each location was then estimated from the regression equation for the relationship between female subimago body size and number of eggs.

Temperature and dd analysis

Temperature profiles (1-m depth intervals) and bottom temperatures were taken with a YSI telethermometer at each site on each sampling date, and in at least two of the four sites whenever the regions were visited. This resulted in approximately biweekly temperature profiles in 1986, and approximately weekly temperature data for 1987 and 1988. Bottom temperatures (temperatures recorded when the temperature probe was resting on the sediment surface) were plotted for each year, and dd were calculated by summing the

total Celsius degrees above the threshold temperature for development for each period (from Southwood, 1978):

$$dd = \Sigma(T - T_o)d \quad (1)$$

where T = temperature, T_o = threshold temperature for development and d = days above threshold temperature.

The analyses of regional dd accumulations were carried out using two assumed threshold temperatures: (i) 10°C—the threshold temperature derived using empirical data from the lake; and (ii) 8°C—the experimentally determined developmental threshold (Giberson & Rosenberg, 1992a, b). In order to compare annual and cohort accumulations for each region, dd were summed for three periods in each area:

1 annual—the period each year from ice-out to freeze-up, calculated as $dd > 10^\circ\text{C}$ for comparison with literature values;

2 emergence—the period each year from ice-out to first week of occurrence of adults in pan traps;

3 one life cycle—the period from oviposition to emergence.

Degree-day accumulations for 1 and 2 were calculated directly from the temperature plots for each year, whereas those for 3 were determined from a combination of direct measurements (1986–88) and estimated values for the periods not covered by regular temperature measurements (1985 and 1989; Giberson, 1991). The oviposition periods for 1985 and 1989 were inferred from the relationship between emergence date and accumulated dd in the summer of emergence. Accumulated dd from ice-out to emergence were calculated for each region and each year, then averaged to estimate the dd required for emergence in the final year of growth. Water temperatures for 1985 and 1989 were estimated from the relationship between air temperature and water temperature for each study area (Giberson *et al.*,

1992). Total accumulated dd for the 1985 cohort was determined by summing the dd from the estimated date of oviposition in 1985 until emergence in 1988 (3-yr life cycle) or 1989 (4-yr cycle).

Results

Temperature patterns and degree day accumulations (1986–88)

Annual. The coolest of the three study years was 1986. In that year, maximum summer temperatures were lowest, and each region warmed later in the spring and cooled earlier in the autumn than in succeeding years (Fig. 2). Temperature patterns for 1987 and 1988 were similar at the beginning of the year within each study area, although high temperatures persisted for longer in 1988 than 1987 (Fig. 2); this resulted in greater total annual dd accumulation in 1988 (Table 1). Among regions and years, Opachuanau was warmest, followed by Wupaw Bay, South Bay East and South Bay West, although annual dd ($>10^\circ\text{C}$) accumulations were highly variable, both among years and among sites. These ranged from 210 (South Bay West, 1986) to 650 (Opachuanau and Wupaw Bay, 1988). Total 3-yr dd accumulations in each area varied from 990 to 1605 (Table 1).

Hexagenia development times in the different study areas were predicted from a comparison of the observed temperature data and the expected requirement of *c.* 2000 dd $> 10^\circ\text{C}$ to complete development (based upon Heise *et al.*, 1987). The predicted life cycle lengths in the four regions ranged from 3.75 to 6 yr, compared with observed life cycle lengths of 3–4 yr (Table 1; see below for life cycle determination).

Emergence. Degree day accumulations from ice-out to emergence ranged from 168 to 218 dd $> 10^\circ\text{C}$ or 257 to 302 dd $> 8^\circ\text{C}$ (Table 2a) in the four regions between

Table 1 Total accumulated degree days (dd) $> 10^\circ\text{C}$ for the four study areas in Southern Indian Lake, 1986, 1987 and 1988. The predicted life-cycle duration is based on an assumed requirement of 2000 dd $> 10^\circ\text{C}$ to complete development and the mean dd for each region. Actual durations were determined from Figs 4 and 5

| Location | Degree days $> 10^\circ\text{C}$ | | | | Life-cycle duration (yr) | |
|----------------|----------------------------------|------|------|-------|--------------------------|--------|
| | 1986 | 1987 | 1988 | Total | Predicted | Actual |
| Opachuanau | 380 | 575 | 650 | 1605 | 3.74 | 3 |
| Wupaw Bay | 300 | 525 | 650 | 1475 | 4.07 | 3 |
| South Bay East | 280 | 500 | 600 | 1380 | 4.35 | 3 |
| South Bay West | 210 | 380 | 400 | 990 | 6.06 | 4 |

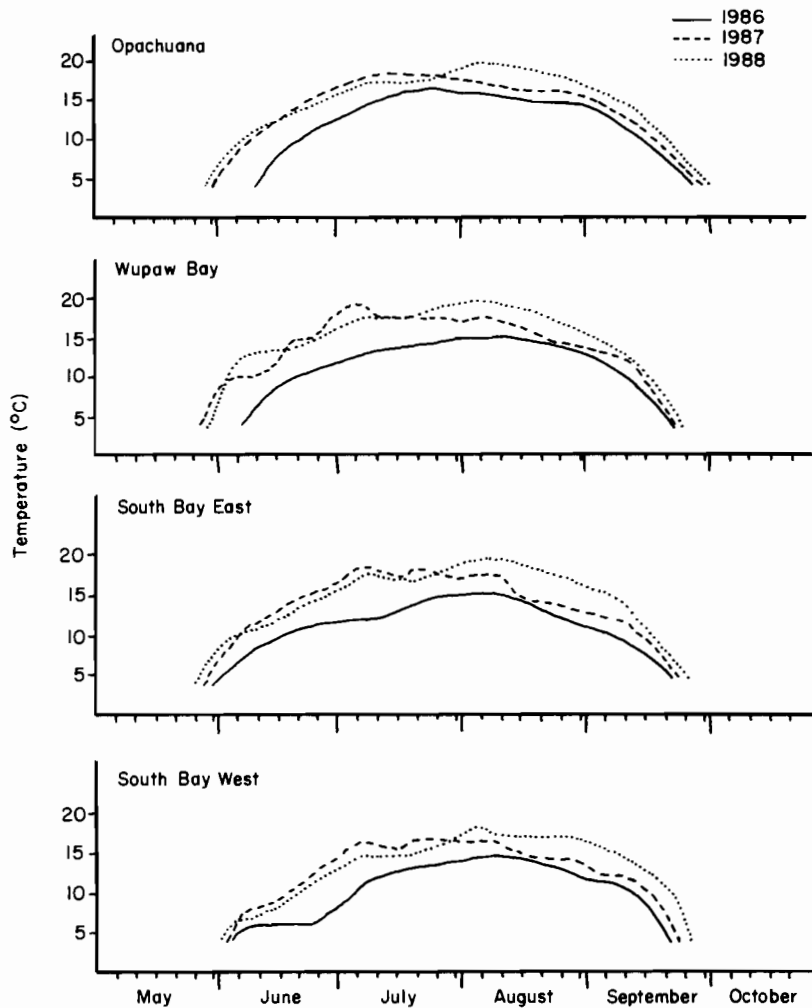


Fig. 2 Summer bottom-water temperatures ($^{\circ}\text{C}$) for the four study regions in Southern Indian Lake, 1986–88.

1986 and 1988, with an average of 191 dd $> 10^{\circ}\text{C}$ or 279.3 dd $> 8^{\circ}\text{C}$. Probable oviposition dates in each region in 1985 and 1989 were taken as the dates that corresponded with the accumulations of 191 dd $> 10^{\circ}\text{C}$ (or 279 dd $> 8^{\circ}\text{C}$). The estimated 1985 and 1989 dd accumulations are shown in Table 2b.

The reliability of using dd to first emergence as a predictor of emergence timing may be checked by rewriting eqn (1) as:

$$d = \text{dd} \div \Sigma(T - T_0) \quad (2)$$

Equation (2) allows us to express the range in dd accumulation as a range of days at a given temperature value. At the time of emergence in the four study sites, bottom temperatures ranged from 13 to 18 $^{\circ}\text{C}$ (Table 2a). At these temperatures, the difference in emergence timing among sites was 6–17 days, at an

assumed threshold of 10 $^{\circ}\text{C}$, or 4–6 days at an assumed threshold of 8 $^{\circ}\text{C}$.

Life cycle. Degree day requirements (oviposition to adult) ranged from 1222 to 1468 dd $> 10^{\circ}\text{C}$ or 1798 to 2059 dd $> 8^{\circ}\text{C}$ in the different study regions (Table 2b). The highest accumulations were recorded in Opachuanau, the warmest study area, followed by Wupaw Bay, South Bay West and South Bay East (Table 2b).

Life history

Individuals of both species were found in most samples, although *H. limbata* predominated in Opachuanau and *H. rigida* was most common at the three other study sites (3-yr average; Table 3). Cohort

Table 2 Accumulated degree days (dd) for *Hexagenia* development calculated assuming developmental thresholds of 8 and 10°C. (a) Degree days to emergence in the final year of development (all cohorts), and dates and bottom temperatures at first emergence; (b) total dd from egg to adult (1985 cohort)

| (a) Emergence | | | | | |
|------------------------------|-------|--------------------|--------------------------------|----------------|----------------|
| Location | Year | Date 1st emergence | Bottom temp. (°) 1st emergence | dd > 8°C | dd > 10°C |
| Opachuanau | 1986 | 20 Jul. | 16 | 272 | 188 |
| | 1987 | 16 Jul. | 18 | 286 | 206 |
| | 1988 | 17 Jul. | 17 | 275 | 189 |
| Wupaw Bay | 1986 | 1 Aug. | 14 | 269 | 175 |
| | 1987 | 17 Jul. | 17 | 302 | 218 |
| | 1988 | 24 Jul. | 18 | 282 | 200 |
| South Bay East | 1986 | 5 Aug. | 15 | 276 | 175 |
| | 1987 | 17 Jul. | 18 | 296 | 210 |
| | 1988 | 29 Jul. | 18 | 293 | 198 |
| South Bay West | 1986 | 23 Aug. | 13 | 257 | 168 |
| | 1987 | 28 Jul. | 17 | 268 | 180 |
| | 1988 | 28 Jul. | 17 | 275 | 185 |
| (b) Life cycle (1985 cohort) | | | | | |
| Threshold | Year | Degree days | | | |
| | | Opachuanau | Wupaw Bay | South Bay East | South Bay West |
| 8°C | 1985 | 358 | 309 | 273 | 195 |
| | 1986 | 560 | 470 | 438 | 360 |
| | 1987 | 782 | 729 | 696 | 373 |
| | 1988 | 359 | 383 | 393 | 590 |
| | 1989 | | | | 280 |
| | Total | 2059 | 1891 | 1800 | 1798 |
| 10°C | 1985 | 259 | 214 | 171 | 123 |
| | 1986 | 380 | 300 | 278 | 210 |
| | 1987 | 575 | 524 | 496 | 388 |
| | 1988 | 254 | 278 | 277 | 400 |
| | 1989 | | | | 193 |
| | Total | 1468 | 1316 | 1222 | 1314 |

Table 3 Total and summer mean *Hexagenia* abundances (no. m⁻², all cohorts; $\bar{x} \pm SE$) for the study regions in Southern Indian Lake, 1986–1988

| Location | Species | Mean abundance ($\bar{x} \pm SE$) | | | |
|----------------|-------------------|-------------------------------------|-------------|--------------|--------------|
| | | 1986 | 1987 | 1988 | Average |
| Opachuanau | <i>H. limbata</i> | 146.3 ± 12.5 | 59.8 ± 19.1 | 172.3 ± 80 | 121.9 ± 25.3 |
| | <i>H. rigida</i> | 98.5 ± 12.4 | 49.5 ± 9.5 | 174.3 ± 83.6 | 101.4 ± 25.5 |
| Wupaw Bay | <i>H. limbata</i> | 117.3 ± 9.1 | 61.0 ± 8.0 | 57.3 ± 22.1 | 80.5 ± 11.0 |
| | <i>H. rigida</i> | 137.3 ± 12.9 | 88.3 ± 12.1 | 59.3 ± 19.0 | 98.2 ± 12.4 |
| South Bay East | <i>H. limbata</i> | | 16.8 ± 4.6 | 27.3 ± 12.5 | 21.3 ± 5.7 |
| | <i>H. rigida</i> | | 39.0 ± 18.3 | 31.7 ± 15.5 | 35.9 ± 11.5 |
| South Bay West | <i>H. limbata</i> | 10.3 ± 3.8 | 30.3 ± 4.8 | 19.0 ± 9.5 | 20.1 ± 4.0 |
| | <i>H. rigida</i> | 39.5 ± 13.1 | 29.0 ± 4.8 | 18.7 ± 2.3 | 30.0 ± 5.3 |

separation was facilitated by examining the frequency distributions of all three body measurements. For example, as shown in Fig. 3, it would have been difficult in July and August to separate nymphs of the emerging cohort (3-yr old) from 2-yr old nymphs, based on body length or head width. However, nymphs that were in later developmental stages showed much greater wing development than similar-sized, but younger nymphs. Wing-pad length could therefore be used as a developmental stage indicator allowing the cohort about to emerge to be identified. Once the cohorts were separated (Fig. 3), they were superimposed upon length-frequency distributions for the whole study period to follow the life cycles through time (Figs 4 and 5).

The life cycles of the two species appear to be nearly identical (Figs 4 and 5). Three cohorts were identified on each sampling date in the three warmer

locations, and four cohorts were noted in South Bay West, suggesting life-cycle durations of 3 and 4 yr, respectively. Within the 3-yr study period, no cohorts were followed entirely from oviposition to adult emergence; however, the patterns observed from 1986 to 1988 confirmed the 3-4-yr duration. The cohort present as very small nymphs in June of 1986 in all regions probably began as eggs in the summer of 1985 and overwintered as eggs or very small nymphs (Figs 4 and 5). In Opachuanau and Wupaw Bay, nymphs of that cohort grew through 1986 and 1987 (Figs 4a,b and 5a,b), and emerged as adults in 1988, yielding a 3-yr life cycle. South Bay East (Figs 4c and 5c) was not sampled in 1986, but the pattern was similar to Opachuanau and Wupaw Bay in 1987 and 1988, suggesting a 3-yr life cycle there as well. However, in South Bay West (Figs 4d and 5d) the cohort that began as eggs in the summer of 1985 did

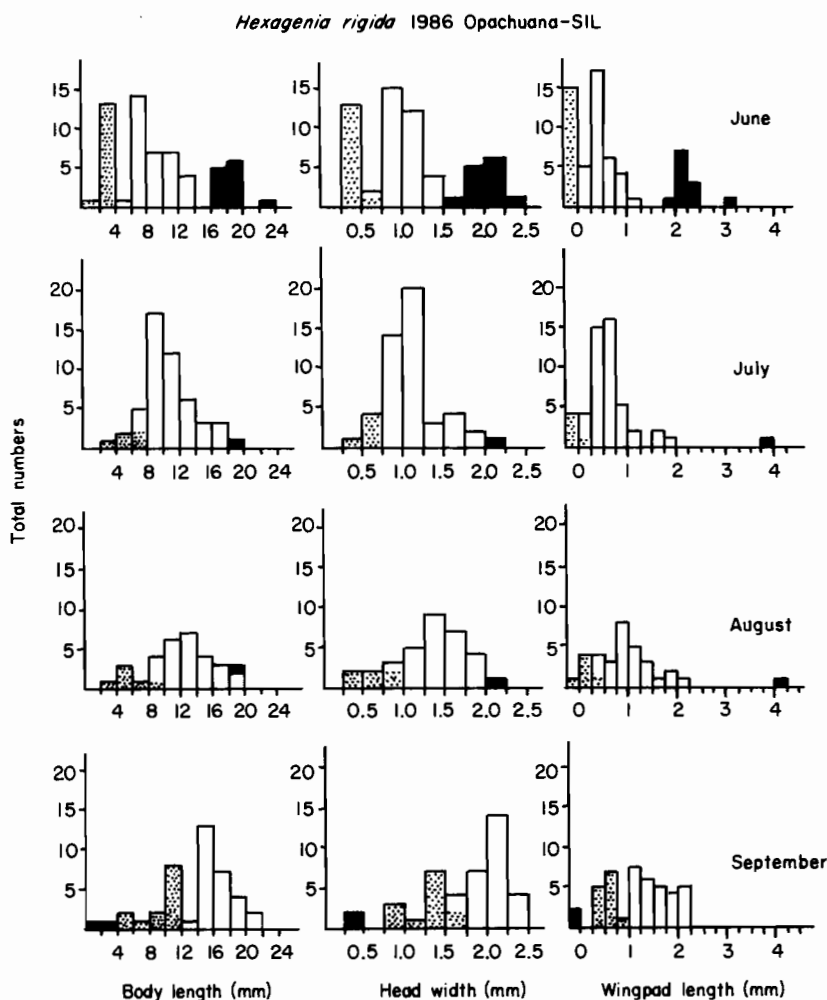


Fig. 3 Frequency distributions for body length, head width and wing-pad length (mm) for *Hexagenia rigida* in Opachuanau, Southern Indian Lake, 1986. Different stippling patterns represent different cohorts.

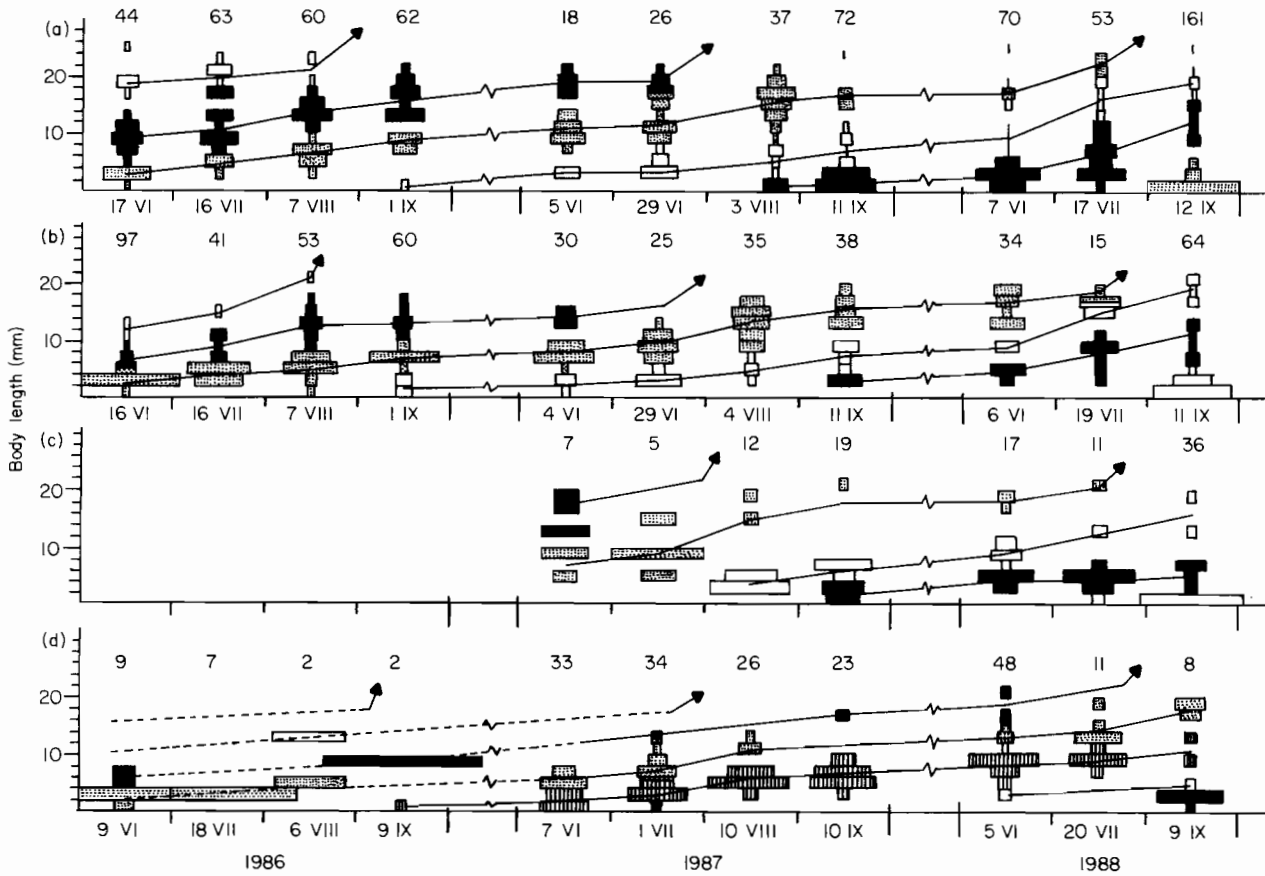


Fig. 4 Length-frequency distributions for *Hexagenia limbata* with cohorts superimposed; different shading represents separate cohorts. Lines bisect the midpoints of each cohort as a guide for following the cohorts through time. Bars represent % frequency of each size class, and numbers at the top of each distribution refer to the total numbers collected. (a) Opachuanau, (b) Wupaw Bay, (c) South Bay East, (d) South Bay West.

not complete development in 1988; they probably emerged in 1989, requiring a total of 4 yr.

Eggs generally began hatching within a few weeks of the oviposition period each summer in the three warmer locations; new recruits were first observed in the September sample (Figs 4 and 5). Some eggs must also have overwintered, however, since newly hatched nymphs (body length *c.* 1 mm) were also noted in samples in early spring (early June), when ice still covered part of the lake, and long before any adults were seen. Nymphs grew so slowly during their first year that by mid-summer, those that had hatched the previous summer and overwintered were indistinguishable from those that hatched that summer. Most or all eggs apparently overwintered in South Bay West, since small nymphs were rarely observed there until the following spring (Figs 4 and 5).

Mortality. Densities of individual cohorts within regions varied annually and with respect to nymphal size (Table 4). Cohort densities showed a greater percentage decline following 1986, the coldest study year, than after 1987. Between-year mortality was higher for mid-sized (2-yr old) nymphs than for the smaller (1-yr old) nymphs, except in South Bay sites.

Although no quantitative emergence estimates were obtained, observations during emergence suggested that *Hexagenia* are highly susceptible to adverse weather. Individuals emerging in windy conditions were swamped repeatedly by waves, and most or all emerging mayflies drowned when attempting to emerge when waves exceeded *c.* 1 m in height. Stormy weather that coincided with emergence periods left shorelines littered with dead subimagos, and attempts to collect adults on the mornings after storms were generally unsuccessful. In addition, no mating flights were observed on windy nights.

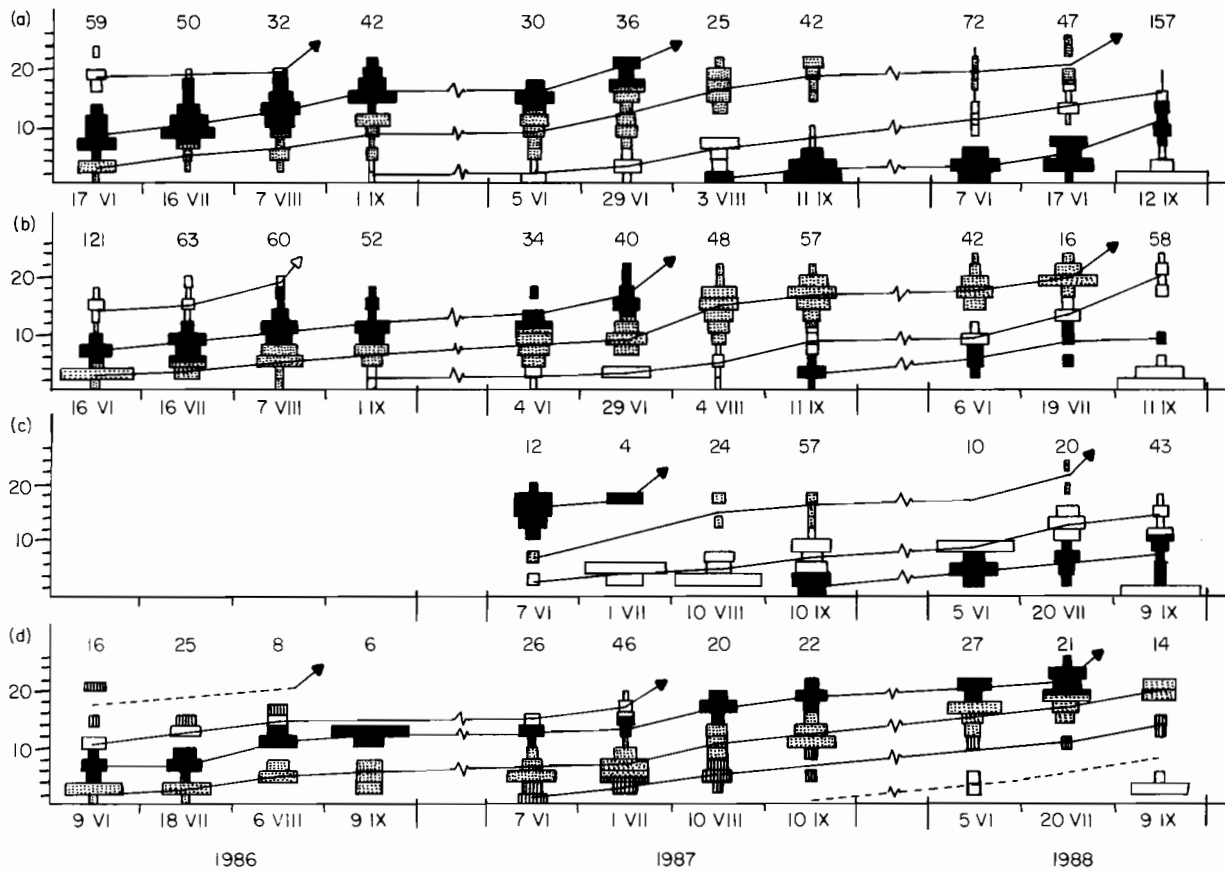


Fig. 5 Length-frequency distributions for *Hexagenia rigida* with cohorts superimposed; different shading represents separate cohorts. Lines bisect the midpoints of each cohort as a guide for following the cohorts through time. Bars represent % frequency of each size class, and numbers at the top of each distribution refer to the total numbers collected. (a) Opachuanau, (b) Wupaw Bay, (c) South Bay East, (d) South Bay West.

Size, fecundity and abundance. Body size (length) of the mature nymphs was based upon the size of final-stage exuviae collected in each area during emergence periods because too few mature nymphs were captured in bottom samples to assess regional size differences adequately, and because body size in mayflies may decline during the emergence period (Brittain, 1982). Individuals of both species tended to be larger in Opachuanau and South Bay West than Wupaw Bay and South Bay East (Table 5), and size differences were most pronounced for female nymphs. For female *H. limbata*, large nymphs were found in both Opachuanau and South Bay West, whereas large *H. rigida* were only found in Opachuanau. Since individuals in Opachuanau, Wupaw Bay and South Bay East are believed to have a 3-yr life cycle, there appears to be a trend for body size to decline with thermal accumulation within the populations having

the 3-yr cycle. Size of mature nymphs increased again in South Bay West when the life-cycle duration increased to 4 yr.

Length of last-stage nymphal exuviae was strongly correlated ($r^2 = 0.93$) with subimago size (Fig. 6), which in turn was strongly correlated ($r^2 = 0.85$) with fecundity (Fig. 7); therefore, fecundity of *Hexagenia* for each area could be estimated from exuvial length. The effects of varying dd accumulations on fecundity were similar to the effects on nymphal size because of the relationship between size and fecundity. In regions with 3-yr life cycles, fecundity was highest for adults from Opachuanau, and was lower in South Bay East and Wupaw Bay (Table 5). Fecundity of adults emerging from South Bay West, after a 4-yr life cycle, was higher than either Wupaw Bay or South Bay East.

Mean *Hexagenia* densities for the study period

Table 4 Year to year mortality (%) of *Hexagenia* nymphs from the four study regions in Southern Indian Lake, 1986–88. Mean summer abundance was calculated for each year class (e.g. 1-yr old, 2-yr old, etc.), and mortality was estimated as the % difference from one year to the next. NS = no sample; * density too low to estimate mortality

| Species | Location | Year | 1st–2nd year | 2nd–3rd year |
|-------------------|--------------|---------|--------------|--------------|
| <i>H. limbata</i> | Opachuanau | 1986–87 | 53.7 | 87.9 |
| | | 1987–88 | * | 54.3 |
| | Wupaw Bay | 1986–87 | 53.6 | 80.7 |
| | | 1987–88 | 33.6 | 61.8 |
| | South Bay E. | 1986–87 | NS | NS |
| | | 1987–88 | 53.5 | 31.3 |
| South Bay W. | 1986–87 | * | 57.9 | |
| | 1987–88 | 42.6 | * | |
| <i>H. rigida</i> | Opachuanau | 1986–87 | * | 74.2 |
| | | 1987–88 | * | 38.5 |
| | Wupaw Bay | 1986–87 | 22.9 | 70.8 |
| | | 1987–88 | 20.5 | 46.1 |
| | South Bay E. | 1986–87 | NS | NS |
| | | 1987–88 | 53.5 | 31.3 |
| South Bay W. | 1986–87 | * | 52.1 | |
| | 1987–88 | 72.4 | 44.0 | |

were also related to regional dd accumulations (Tables 1 and 3). Highest total mean abundance (3-yr average) was found in Opachuanau, followed by Wupaw Bay, South Bay East and South Bay West; however, mean *Hexagenia* density in Wupaw Bay exceeded that in Opachuanau in 1986 and 1987 (Table 3). The seasonal abundance pattern reflected the life histories of the two species: lowest numbers occurred in mid-summer when one cohort was emerging and new recruits had not yet entered the population (Figs 4 and 5).

Adult emergence. Adult emergence data were combined for the two species because it was not possible to identify the adult females to species. Therefore,

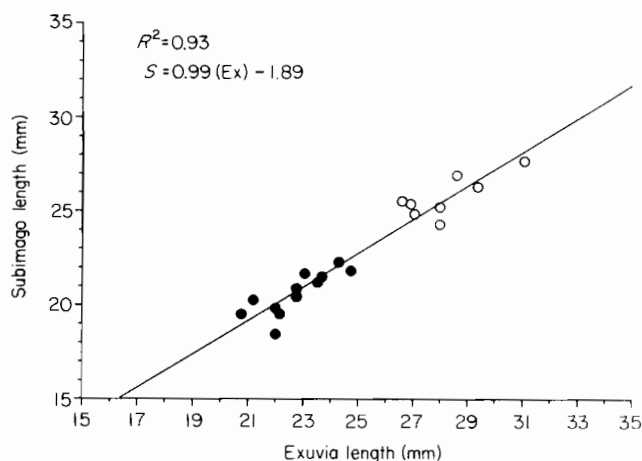


Fig. 6 Relationship between length of last stage exuviae and length of subimago for *Hexagenia* from Southern Indian Lake. Ex = nymphal (exuviae) body length; S = subimago body length (● = ♂; ○ = ♀).

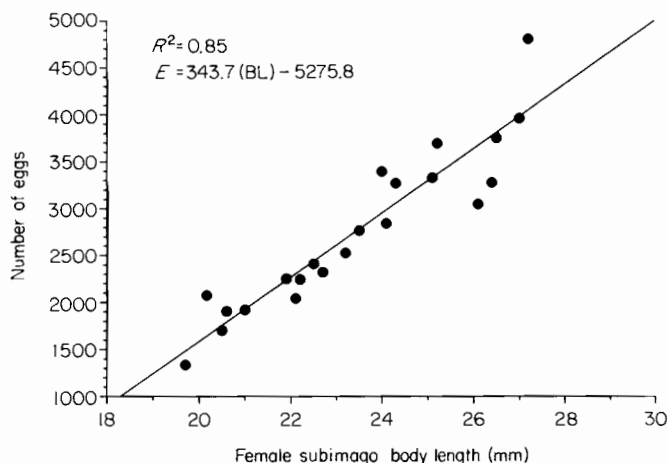


Fig. 7 Relationship between female subimago body length of *Hexagenia* (both species combined) and fecundity (no. eggs/♀). E = no. of eggs; BL = body length.

Table 5 Mean lengths (mm) of exuviae of emerging *Hexagenia limbata* and *H. rigida* nymphs collected from each study area in Southern Indian Lake during 1986, 1987 and 1988, and estimated mean fecundity (no. eggs/♀; $\bar{x} \pm 95\%$ CI) for each region

| Location | <i>Hexagenia limbata</i> | | | <i>Hexagenia rigida</i> | | |
|----------------|--------------------------|------------|--------------------|-------------------------|------------|--------------------|
| | Length (mm) | | Fecundity (eggs/♀) | Length (mm) | | Fecundity (eggs/♀) |
| | ♂ | ♀ | | ♂ | ♀ | |
| Opachuanau | 24.8 ± 1.2 | 28.0 ± 2.5 | 3574 ± 319 | 23.3 ± 0.6 | 27.4 ± 1.5 | 3385 ± 516 |
| Wupaw Bay | 21.7 ± 1.5 | 24.3 ± 2.1 | 2319 ± 200 | 20.3 ± 0.6 | 23.3 ± 1.5 | 1976 ± 516 |
| South Bay East | 22.0 ± 0.6 | 25.7 ± 1.5 | 2794 ± 163 | 20.2 ± 0.7 | 23.8 ± 2.3 | 2148 ± 791 |
| South Bay West | 23.2 ± 0.8 | 28.5 ± 1.0 | 3757 ± 132 | 21.9 ± 0.7 | 24.2 ± 0.8 | 2279 ± 275 |

possible species-specific differences in emergence phenologies could not be determined for the populations as a whole. Among emerging males, however, *H. limbata* generally emerged first followed within a few days by *H. rigida*, although males of the two species overlapped for most of the emergence period. Emergence of both species occurred throughout the day, but was most common during mid-morning. On sunny, calm mornings, newly emerged subimagos rose from the water within minutes and flew to trees and bushes on shore. On windy days, emergence was hindered by wave action.

There was no apparent relationship between emergence and a specific threshold water or air temperature. *Hexagenia* emerged at water temperatures ranging from 8 to 20°C, although the annual onset of emergence within each region occurred when bottom water temperatures were between 13 and 18°C (Table 2a). In some locations, the first emergence was observed as temperatures were still rising in early summer (e.g. Opachuanau, Wupaw Bay and South Bay East in 1988; Figs 2 and 8); in other areas, first emergence occurred when temperatures were declining at the end of the summer (e.g. South Bay West, 1986; Figs 2 and 8). Air temperatures during emergence periods ranged from 0°C (in snow) to 30°C; however, no *Hexagenia* subimagos rose successfully from the water during late-season snow flurries. A few individuals that were collected from the water surface and held in cages in protected locations at 0°C all died before transforming to the imago.

Once on shore, the subimagos rested in trees and bushes until transforming into the final imaginal stage. Individuals picked from the surface of the water and placed in mesh cages on the trees required from 24 to 48 h to complete the final moult at air temperatures between 10°C (night) and 25°C (day); longer subimaginal periods were noted on cool and cloudy days (daytime temperatures $\leq 15^\circ\text{C}$). Mortality within the cages was low (one out of twenty-five), but predation by birds and dragonflies may be significant for the winged stages; large numbers of both predators were seen feeding on *Hexagenia* during swarming. Mating swarms occurred at dusk (22.30–00.30 h in mid-July to c. 20.00–21.00 h later in the season). After copulation, fertilized females flew directly to the water near shore and expelled their eggs.

No adult *Hexagenia* were noted before July in any

year. Emergence periods were fairly synchronous within a region, although differences were noted among regions and among years. Ninety per cent of all the adults collected within each region were caught within a 2–3-week period each year, but emergence periods occurred successively later in the cooler study regions within years, and also in cooler years within study regions (Fig. 8). The years 1987 and 1988 had similar dd accumulations during the early part of the season (Fig. 2) so emergence timing is also similar (Fig. 8). The year 1986 was considerably cooler than 1987 and 1988, so emergence was delayed in comparison with the other two years, particularly in South Bay West.

Discussion

Life cycles

Brittain (1982) wrote 'In the same way as taxonomy presents an obstacle to further progress in biology, so the lack of accurate life history information hinders progress in explaining community processes and in monitoring and assessing man's impact on aquatic ecosystem.' Life cycle information provides a basis for predicting the amount of time required for a population to recover after an episodic stress event. Neave (1932) and Flannagan (1979) reported maximum life cycle durations of 2 yr for *Hexagenia* species in the northern basin of Lake Winnipeg, located just south of the present study location, and Hunt (1953)

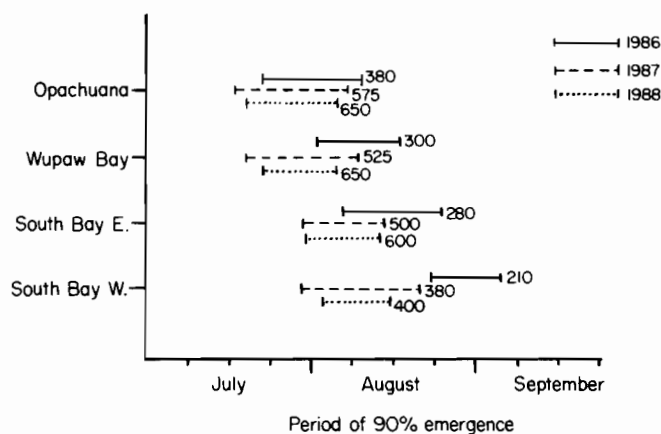


Fig. 8 Periods of 90% emergence for *Hexagenia* in the four study areas, 1986–88. Numbers beside each bar refer to total accumulated water dd > 10°C for each summer.

suggested that the maximum duration was <3 yr. Therefore, if we assume a 2-yr life cycle for *Hexagenia* in Southern Indian Lake, recovery of the population following weather stress (a cold period, for example) should have been seen within one or two life cycles, or 2–4 yr. In fact, densities declined drastically throughout the lake immediately following impoundment and remained low for *c.* 6 yr, resulting initially in the hydroelectric development being implicated in the decline (Giberson *et al.*, 1992). The 3–4 yr life cycle identified here provides an explanation for the long recovery period.

The life cycles of the two species were nearly identical, as was observed by Neave (1932) and Flannagan (1979) for *Hexagenia* in Lake Winnipeg. Adults emerged and deposited their eggs some time after the middle of July, and recruitment began within *c.* 4–6 weeks, depending on water temperature and the date of oviposition. In South Bay West, the coldest area investigated, emergence and oviposition usually occurred late in the season and young nymphs were rarely seen that summer; most or all of the eggs presumably overwintered. Prolonged egg development at low temperatures was also found in laboratory trials (Giberson & Rosenberg, 1992b). In the warmer regions of the lake (Opachuanau, Wupaw Bay and South Bay East), eggs regularly hatched in the summer of oviposition, although little nymphal growth was observed prior to winter. In those locations, newly hatched nymphs were also observed early the next summer, before any adults emerged and oviposited. Therefore, some of that cohort must have overwintered as eggs, despite suitable conditions for hatching in the previous year. In the laboratory, only *c.* 50% of *H. limbata* eggs from the Southern Indian Lake hatched immediately at 20°C; the remainder hatched only after exposure to a period of cold (4°C) temperatures (Giberson & Rosenberg, 1992b). The occurrence of a bimodal hatching pattern in the field may be due to a combination of egg diapause (at least for *H. limbata*) and low temperature quiescence.

The 3–4-yr life cycle observed is longer than previously reported for *Hexagenia*, although not as long as was predicted from dd estimates and temperature accumulations in the lake. Life cycles were generally believed to range from ≤ 1 yr in southern North America to a maximum of 2 yr in northern North America (Hunt, 1953; Carlander *et al.*, 1967; Flannagan, 1979; Heise *et al.*, 1987). Three-year life cycles have

been postulated for *Hexagenia*, although they had not been previously demonstrated (McCafferty, 1975; Mozley & Ladronka, 1988). The life cycle of *Hexagenia* in Southern Indian Lake is more flexible than previously believed, but the limits to this flexibility will depend upon the interaction between temperature, fecundity and mortality.

Degree day requirements

Quantification of dd required for growth allows comparison of development responses between widely separated populations, and also provides a basis for prediction of life cycle duration and emergence timing if temperature data are available (Tokeshi, 1985). For *Hexagenia*, a threshold temperature of 10°C has become widely accepted for calculating dd requirements for the life cycle because of generally good agreement in dd accumulation among widely separated populations, primarily in lower latitude zones in North America (calculated from Hunt, 1953; Hudson & Swanson, 1972; McCafferty & Pereira, 1984). However, dd requirements reported for *Hexagenia* development appear to decline with latitude, casting doubt on the suitability of this method for predicting life-cycle length. For example, southern populations of *H. limbata* require *c.* 2300–2500 dd > 10°C to complete development (calculated from Hunt, 1953; Hudson & Swanson, 1972; Welch & Vodopich, 1989; latitudes 31°35' to 45°51'N), compared with *c.* 1800–2000 dd > 10°C in Dauphin Lake, Manitoba (Heise *et al.*, 1987; latitude 51°14'N), and only *c.* 1200–1500 for the population in Southern Indian Lake (latitude 57°N). The discrepancy in dd accumulation led us wrongly to predict 4–6-year life cycles in the lake, based upon temperature data and dd requirements from the literature (see Table 1).

The apparent decline in calculated dd requirements may be caused by a decline in the developmental threshold temperature with increasing latitude. Northern populations of many insect species have lower thresholds than southern ones (Danks, 1987). Initially, analysis of data on *Hexagenia* developmental dynamics supported this hypothesis, because the actual threshold for development of *H. limbata* from the lake is near 8°C (Giberson & Rosenberg, 1992a), 2°C lower than that commonly cited for the species (Hunt, 1953; Heise *et al.*, 1987). Further, when dd accumulations were determined using an 8°C threshold, the

values ranged from *c.* 1800 to 2050, which were similar to values determined for more southern populations. However, the threshold temperatures reported from southern populations were based only on field data and they had not been determined experimentally for either *H. limbata* or *H. rigida*. In addition, dd requirements calculated using the linear dd model (Southwood, 1978) are based on an *estimated* threshold temperature, which is often higher than the actual threshold because the total development/temperature response follows a logistic (sigmoidal) curve, and is only linear in the middle of the temperature range (Pruess, 1983; Higley *et al.*, 1986; see also discussion in Giberson & Rosenberg, 1992a). Although the actual threshold for the Southern Indian Lake population of *H. limbata* is near 8°C, the estimated, or derived, threshold was near the 10°C usually cited for *H. limbata* (Giberson & Rosenberg, 1992a, b). Therefore, there is no evidence for geographic differences in the derived threshold or in responses to temperatures in the linear part of the temperature/response curve. Until it is possible to compare experimentally derived thresholds among populations, it cannot be assumed that differences in dd accumulation are caused by lower thresholds in northern populations.

An alternative explanation for the decline in dd requirements with increasing latitude may, however, relate to the large amount of time spent by northern populations at temperatures near the lower threshold for development. Bodies of water in which *Hexagenia* are found typically warm quickly in spring and cool rapidly in the autumn (e.g. Heise *et al.*, 1987). The majority of the growth period, therefore, is spent at temperatures in the middle (linear) portion of the temperature response curve, so a linear dd model adequately predicts development. However, because the temperature/development curve is sigmoidal in shape, development is faster than predicted from the linear model at temperatures near the lower threshold, and slower than predicted near the upper threshold (Pruess, 1983; Higley *et al.*, 1986). In many parts of Southern Indian Lake, considerable time may be spent in spring and autumn at temperatures between about 8 and 10°C, resulting in faster development than predicted from the dd model, and lower apparent dd requirements. Therefore, the linear dd model may not be appropriate for predicting life-cycle durations at extreme geographic ranges.

Another explanation that has been given for vari-

ations in dd accumulations between populations is the presence of a threshold temperature for emergence (Heise *et al.*, 1987), because some *Hexagenia* do not emerge when water temperatures are below *c.* 14°C (Fremling, 1973; McCafferty & Pereira, 1984). However, emergence timing did not appear to be related to a specific threshold temperature, since water temperatures at the start of emergence varied between 13 and 18°C, and emergence occurred when water temperatures were 8–20°C, into air temperatures of 0–30°C. Instead, temperature in spring may serve as a cue to synchronize a population which has achieved a certain body size, as has been reported in studies of other burrowing mayflies (Britt, 1962: *Ephemera simulans* Walker; Takemon, 1990: *E. strigata* Eaton). In our population, the timing of emergence showed close agreement with dd accumulation in the final summer. Individuals beyond a certain size or stage of development apparently responded to a temperature cue (such as warming in spring) to begin the final stages of development before emergence; subsequent development, however, was still temperature dependent. This would explain the differences in emergence timing between years and study regions, and it would also explain why *Hexagenia* emerged late in the season in some localities, despite the catastrophic effects that resulted.

Body size and fecundity

Adult body size is an important ecological variable because of its relationship to fecundity and potential recruitment success (Hunt, 1953; Clifford & Boerger, 1974; Brittain, 1982; Sweeney, 1984). Factors that affect size, therefore, may also ultimately affect abundance. Sweeney & Vannote (1978) predicted that size of hemimetabolous aquatic insects would be maximized in areas where temperature conditions were optimum, and that it would decrease at temperatures above and below the optimum. However, this 'thermal equilibrium hypothesis' was developed for north-temperate species with fixed life-cycle lengths which are exposed to the entire range of thermal conditions in one year; it does not necessarily hold for species with more flexible life cycles (Stanley & Short, 1988). For multivoltine species in warm-water habitats, a single location can provide several different successive thermal regimes, some of which might be optimal and others suboptimal for development.

Similarly, for semivoltine species with flexible life cycles, populations in the same geographical area may be exposed to widely different thermal regimes simply by changing voltinism. Adult body size would be expected to decline with increasing latitude, or distance from the optimum habitat, to the point where the voltinism changed. Body size should then increase in response to the longer period spent in growth.

Hexagenia limbata vary widely in body size throughout their range, but a pattern can be seen over a latitudinal gradient from *c.* 31°N to 57°N (Table 6). The maximum reported size of *c.* 35 mm was observed both at 42°36'N in Michigan, where a 1-yr life cycle was reported (Hunt, 1953), and at 51°14'N in Dauphin Lake, Manitoba, where most nymphs had a 2-yr life cycle (Heise *et al.*, 1987); sizes declined on both sides of these peaks (Table 6). In Southern Indian Lake, the largest nymphs of both species were found in Opachuanau and South Bay West. Opachuanau was the warmest study area investigated for populations with 3-yr life cycles and in South Bay West the life cycle was believed to be 4 yr.

Body size also varied between species. *Hexagenia limbata* tended to be larger than *H. rigida* in all locations, and size differences between regions were more pronounced for *H. limbata* than for *H. rigida*. *Hexagenia limbata* increased its fecundity by a greater amount in the change from a 3-yr to a 4-yr life cycle, suggesting that it may be better adapted to cold

environments than *H. rigida*. This pattern is consistent with the distribution of the two species, since *H. limbata* has been reported further north than *H. rigida* (Rawson, 1953; Oliver, 1960; Harper & Harper, 1981).

Fecundity in *Hexagenia* was related to female body size, and so it varied with temperature in the same way that body size did. The highest fecundities, and therefore highest potential abundance, were noted in Opachuanau (the warmest location) and in South Bay West, where life cycles were longest.

The relationship between fecundity and body size appears to be constant over a wide geographic range. The relationship reported by Hunt (1951) for *H. limbata* adults from Michigan, when corrected for the difference in size between subimagos and adults (Giberson, 1991), was virtually identical to that found in Southern Indian Lake. Although the size/fecundity relationship should be further evaluated before it becomes a general model, the relationship determined in this study and in the study by Hunt (1951) may be useful for quickly estimating fecundity of *H. limbata* from a variety of habitats.

Mortality

Individual *Hexagenia* cohorts in Southern Indian Lake experienced their greatest population declines while in larger size classes and following a cold summer and long winter. Although *Hexagenia* are not the

Table 6 Maximum reported sizes for *Hexagenia limbata* nymphs in populations from Texas to northern Manitoba, and requiring from 1 to 4 yr to develop

| Location | Latitude (°N) | Life cycle | Max. size (mm) | Source |
|----------------------------------|---------------|------------|----------------|--------------------------------|
| Lake Waco, Texas | 31°35' | 1 yr | 30 | Welch & Vodopich (1989) |
| Brandenberg Pond, Ohio | 39°30' | 1–2 yr | >30 | Rutter (1972) |
| Pool 19, Mississippi River, Iowa | 40°30' | 1 yr | >32 | Carlander <i>et al.</i> (1967) |
| Gun Lake, Pine Lake, Michigan | 42°36' | 1 yr | 35 | Hunt (1953) |
| Straits of Mackinac, Michigan | 45°49' | 2–3 yr? | 28 | Mozley & Ladronka (1988) |
| Lewis & Clark Lake, South Dakota | 45°51' | 1–2 yr | 33 | Hudson & Swanson (1972) |
| St. Mary's River, Ontario | 46°20' | 2 yr | >30 | Schloesser & Hiltunen (1984) |
| Savanne Lake, Ontario | 48°50' | 2 yr | >32 | Riklik & Momot (1982) |
| Dauphin Lake, Manitoba | 51°14' | 1–2 yr | 35 | Heise <i>et al.</i> (1987) |
| Lake Winnipeg, Manitoba | 50–54° | 2 yr | 30 | Neave (1932) |
| Southern Indian Lake, Manitoba | 57° | 3–4 yr | 30 | This study |

major food source for most of the fish species in the lake (e.g. lake whitefish [*Coregonus clupeaformis* (Mitchill)], northern pike [*Esox lucius* (Linn.)], yellow walleye [*Stizostedion vitreum vitreum* (Mitchill)]), they are selectively eaten by the whitefish (Hamilton, 1974), which are visual predators and may select for larger size classes. The weather pattern is consistent with the observed population decline following impoundment and diversion, which initially prompted the study into *Hexagenia* life cycles (Giberson *et al.*, 1991). Below-normal temperatures affected the survival of newly hatched nymphs (Giberson & Rosenberg, 1992a), emergence and mating success (this study; see also Lyman, 1944; Hunt, 1953; Whelan, 1980), and egg-hatching success (Giberson & Rosenberg, 1992b). Higher between-year mortality following 1986 (cold year) compared with 1987 (warm year) may simply have been due to insufficient food reserves for some to survive the unusually long winter.

A combination of long-term monitoring and intensive laboratory- and field-based life-history study was required to identify the mechanisms controlling *Hexagenia* abundance in Southern Indian Lake. Both approaches should be considered when attempting to interpret population fluctuations following anthropogenic stress.

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References

- Britt N.W. (1962) Biology of two species of Lake Erie mayflies, *Ephoron album* (Say) and *Ephemera simulans* Walker. *Bulletin of the Ohio Biological Survey*, **1**, 1–70.
- Brittain J.E. (1982) Biology of Mayflies. *Annual Review of Entomology*, **27**, 19–47.
- Burton W. & Flannagan J.F. (1973) An improved Ekman-type grab. *Journal of the Fisheries Research Board of Canada*, **30**, 287–290.
- Carlander K.D., Carlson C.A., Gooch V. & Wenke T.L. (1967) Populations of *Hexagenia* naiads in pool 19, Mississippi River, 1959–1963. *Ecology*, **48**, 873–878.
- Clifford H.F. & Boerger H. (1974) Fecundity of mayflies, with special reference to mayflies of a brown-water stream on Alberta, Canada. *Canadian Entomologist*, **106**, 1111–1119.
- Danks H.V. (1987) *Insect Dormancy: An Ecological Perspective*. Biological Survey of Canada Monograph Series No. 1, 439 pp.
- Edmunds G.F., Jensen S.L. & Berner L. (1976) *The Mayflies of North and Central America*. University of Minnesota Press, Minneapolis, 330 pp.
- Flannagan J.F. (1979) The burrowing mayflies of Lake Winnipeg, Manitoba, Canada. *Proceedings of the 2nd International Conference on Ephemeroptera* (Eds K. Pasternak and R. Sowa), pp. 103–114. Polish Academy Navk, Krakow.
- Fremling C.R. (1973) Factors influencing the distribution of burrowing mayflies along the Mississippi River. *Proceedings of the 1st International Conference on Ephemeroptera* (Eds W.L. Peters and J.G. Peters), pp. 12–25. E.J. Brill, Leiden.
- Giberson D.J. (1991) *Fluctuations in abundance of burrowing mayflies in Southern Indian Lake, Manitoba: Mechanisms and implications for environmental monitoring*. PhD Thesis, University of Manitoba, Winnipeg, Manitoba, Canada.
- Giberson D.J. & Rosenberg D.M. (1992a) Effects of temperature, food quantity, and nymphal rearing density on life-history traits of a northern population of *Hexagenia* (Ephemeroptera: Ephemeridae). *Journal of the North American Benthological Society*, **11**, 181–193.
- Giberson D.J. & Rosenberg D.M. (1992b) Egg development in *Hexagenia limbata* (Ephemeroptera: Ephemeridae) from Southern Indian Lake, Manitoba: temperature effects and diapause. *Journal of the North American Benthological Society*, **11**, 194–203.
- Giberson D.J., Rosenberg D.M. & Wiens A.P. (1991) Changes in abundance of burrowing mayflies in Southern Indian Lake: Lessons for environmental monitoring. *Ambio*, **20**, 139–142.
- Giberson D.J., Rosenberg D.M. & Wiens A.P. (1992) *Long-term abundance patterns of Hexagenia (Insecta: Ephemeroptera: Ephemeridae) in Southern Indian Lake, Manitoba: responses to weather and hydroelectric development*. Canadian Technical Report of Fisheries and Aquatic Sciences 1837, 16 pp.
- Hamilton A.L. (1974) *Zoobenthos survey of Southern Indian Lake, Lake Winnipeg, Churchill and Nelson Rivers Study Board, 1971–1975*. Technical Report, Appendix 5,

- Fisheries and Limnological Studies 1G, 32 pp.
- Harper F. & Harper P.P. (1981) Northern Canadian mayflies (Insecta: Ephemeroptera), records and descriptions. *Canadian Journal of Zoology*, **59**, 1784–1789.
- Hecky R.E. (1984) Thermal and optical characteristics of Southern Indian Lake before, during, and after impoundment and Churchill River diversion. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 579–590.
- Hecky R.E., Newbury R.W., Bodaly R.A., Patalas K. & Rosenberg D.M. (1984) Environmental impact prediction and assessment: The Southern Indian Lake experience. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 720–732.
- Heise B.A., Flannagan J.F. & Galloway T.D. (1987) Life histories of *Hexagenia limbata* and *Ephemera simulans* (Ephemeroptera) in Dauphin Lake, Manitoba. *Journal of the North American Benthological Society*, **6**, 230–240.
- Higley L.G., Pedigo L.F. & Ostlie K.R. (1986) DEGDAY: a program for calculating degree days, and assumptions behind the degree day approach. *Environmental Entomology*, **15**, 999–1016.
- Hudson P.L. & Swanson G.A. (1972) Production and standing crop of *Hexagenia* (Ephemeroptera) in a large reservoir. Studies in Natural Sciences, Eastern New Mexico University, Portales, Vol. 1, pp. 1–36.
- Hunt B.P. (1951) Reproduction of the burrowing mayfly *Hexagenia limbata* (Serville) in Michigan. *Florida Entomologist*, **34**, 59–70.
- Hunt B.P. (1953) The life history and economic importance of a burrowing mayfly *Hexagenia limbata* in southern Michigan Lakes. Michigan Department of Conservation, Bulletin of the Institute for Fisheries Research, No. 4, 151 pp.
- Lyman F.E. (1944) Notes on emergence, swarming and mating of *Hexagenia* (Ephemeroptera). *Entomological News*, **55**, 207–210.
- McCafferty W.P. (1975) The burrowing mayflies of the United States (Ephemeroptera: Ephemeroidea). *Transactions of the Entomological Society of America*, **101**, 447–504.
- McCafferty W.P. & Pereira C. (1984) Effects of developmental thermal regimes on two mayfly species and their taxonomic interpretation. *Annals of the Entomological Society of America*, **77**, 69–87.
- Mozley S.C. & Ladronka R.M. (1988) *Ephemera* and *Hexagenia* in the straits of Mackinac 1955–56. *Journal of Great Lakes Research*, **14**, 171–177.
- Neave F. (1932) A study of the may flies (*Hexagenia*) of Lake Winnipeg. *Contributions to Canadian Biology and Fisheries*, **7**, 177–201.
- Newbury R.W. & McCullough G.K. (1984) Shoreline erosion and restabilization in the Southern Indian Lake reservoir. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 558–565.
- Newbury R.W., McCullough G.K. & Hecky R.E. (1984) The Southern Indian Lake Impoundment and Churchill River Diversion. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 548–557.
- Oliver D. (1960) The macroscopic bottom fauna of Lac La Ronge, Saskatchewan. *Journal of the Fisheries Research Board of Canada*, **17**, 607–624.
- Pruess K.P. (1983) Day-degree methods for pest management. *Environmental Entomology*, **12**, 613–619.
- Rawson D.S. (1953) The bottom fauna of Great Slave Lake. *Journal of the Fisheries Research Board of Canada*, **10**, 486–420.
- Riklik L. & Momot W.T. (1982) Production ecology of *Hexagenia limbata* in Savanne Lake, Ontario. *Canadian Journal of Zoology*, **60**, 2317–2323.
- Rutter R.P. (1972) Distribution, abundance, and rates of respiration and food turnover of the burrowing mayfly, *Hexagenia limbata*, in a pond ecosystem. MA Thesis, Miami University, Oxford, OH.
- Schloesser D.W. & Hiltunen J.K. (1984) Life cycle of a mayfly *Hexagenia limbata* in the St. Mary's River between Lakes Superior and Huron. *Journal of Great Lakes Research*, **10**, 435–439.
- Southwood T.R.E. (1978) *Ecological Methods, with Particular Reference to the Study of Insect Populations*, 2nd edn. Chapman and Hall, London, 524 pp.
- Stanley E.H. & Short R.A. (1988) Temperature effects on warmwater stream insects—a test of the thermal equilibrium hypothesis. *Oikos*, **51**, 313–320.
- Sweeney B.W. (1984) Factors influencing life history patterns of aquatic insects. *The Ecology of Aquatic Insects* (Eds V.H. Resh and D.M. Rosenberg), pp. 56–100. Praeger Publishers, New York.
- Sweeney B.W. & Vannote R.L. (1978) Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science*, **200**, 444–446.
- Takemon Y. (1990) Timing and synchronicity of the emergence of *Ephemera strigata*. *Mayflies and Stoneflies* (Ed. I.C. Campbell), pp. 61–70. Kluwer Academic Publishers, Norwell, MA.
- Tokeshi M. (1985) Life-cycle and production of the burrowing mayfly, *Ephemera danica*: a new method for estimating degree days required for growth. *Journal of Animal Ecology*, **54**, 919–930.
- Welch C.L. & Vodopich D.S. (1989) Production by *Hexagenia limbata* in a warm-water reservoir and its association with chlorophyll content of the water column. *Hydrobiologia*, **185**, 183–193.
- Whelan K.F. (1980) Some aspects of the biology of *Ephemera danica* Müller (Ephemeroidea, Ephemeroptera) in Irish waters. *Advances in Ephemeroptera Biology*

(Eds J.F. Flannagan and E. Marshall), pp. 187–199. Proceedings of the 3rd International Conference on Ephemeroptera, Winnipeg, 1979. Plenum Press, New York.

Wiens A.P. & Rosenberg D.M. (1984) Effects of impoundment and river diversion on profundal macrobenthos

of Southern Indian Lake, Manitoba. *Canadian Journal of Fisheries and Aquatic Sciences*, **41**, 638–648.

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