FLUCTUATIONS IN ABUNDANCE OF BURROWING MAYFLIES IN SOUTHERN INDIAN LAKE, MANITOBA: MECHANISMS AND IMPLICATIONS FOR ENVIRONMENTAL MONITORING

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Donna J. Giberson

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ERRATUM

Note that the page numbers 29, 84, and 161 are missing, although the text is intact. Those page numbers were inadvertently left out during typing.

ABSTRACT

In the mid-1970's, Manitoba Hydro impounded Southern Indian Lake (SIL) and diverted much of the flow of the Churchill River into the Nelson river catchment for hydroelectric power generation. A subsequent dramatic decline in burrowing mayfly (*Hexagenia*) populations was originally attributed to the manipulation, until recovery of the population was observed despite ongoing physical impacts from impoundment and diversion. In 1986, an intensive study on *Hexagenia* in SIL was implemented to determine the actual mechanisms controlling population abundance in the lake to aid in the interpretation of the long-term monitoring data.

The major factors affecting the population dynamics of *Hexagenia* in SIL during the study period were related to weather variables, primarily water temperature during development (and its relationship to air temperature during the open water period) and weather conditions (wind, air temperature) during the emergence period. The two species in the lake, *H. limbata* and *H. rigida*, approach their northern range limit at or near SIL. Their life cycles were similar in the study regions and closely related to thermal regime; requiring 3-yr in warmer areas of SIL and 4-yr in the coldest study region. Subimago emergence occurred from mid-July to mid-August in warm years and warm locations, but not until September in colder years or regions. September weather at SIL was often stormy and cold, and these conditions hindered emergence success. After emergence, transformation to the adult (imago) stage was dependent on air temperatures; the final moult required ≈24-48 h at 10-25°C and was unsuccessful at very low temperatures (near 0°C).

Size of nymphs at maturity was related to thermal regime and the length of the life cycle. Mean body length of mature nymphs declined with decreasing thermal regime in the lake regions where 3-yr life cycles predominated. In

the coldest region investigated, where the life cycle length increased from 3-yr to 4-yr, body size was similar to that from the warmest location. Body size in the female was strongly correlated to fecundity (number of eggs/female); therefore, mean fecundity showed the same relationship to temperature as body size.

The link between nymphal development and temperature was confirmed in laboratory studies. Growth was noted at all temperatures evaluated (8°, 10°, 12.5°, 15°, and 20°C), and growth rates increased with increasing temperature for both species. Variations in growth rate affected both the time required for development and the size at maturity. Total development times (from egg hatch to first emergence) were 380 d at 15°C compared to only 183 d at 20°C, and individuals reared at 15°C were smaller and less fecund than those reared at 20°C. Growth and development was also affected by food availability: nymphs reared under limiting food conditions took longer to develop and adults were smaller and less fecund than those reared under non-limiting food conditions. Nymphal rearing density, at levels ranging from 215 to 1290 nymphs/m^2, had no significant effect on growth.

Egg hatch was related to temperature. Eggs hatched at temperatures from 8°C to 20°C (the highest temperature evaluated), but not at 4°C. Fewer eggs hatched and the time required for hatch was extended at the lower temperatures. Egg hatching success was improved by subjecting eggs to cold temperatures (4°C) during development. In addition, experiments indicated a bimodal hatching response in the eggs: some eggs hatched immediately if conditions were favourable, and the remainder apparently required exposure to cold to initiate hatch.

Abundance and distribution of nymphs in the lake was related to thermal regime. The greatest abundance was noted in the warmest locations, and

numbers declined with decreasing temperature. Temperature affected abundance through its effects on life history parameters: lower relative temperatures resulted in longer life cycles and higher accumulated mortality, fewer eggs hatching, and delayed emergence with a higher probability of temperature- or storm-related impacts on emergence and mating.

Between-year weather differences should result in similar weather-related fluctuations in abundance as were noted between regions, and two consecutive very cold years (1978 and 1979) coincided with the inception of hydroelectric development. Over the 15-yr monitoring period, ≈95% of the variation in whole-lake abundance of burrowing mayflies (R^2=.947) could be explained by air temperature. Therefore, the overall decline in *Hexagenia* numbers, originally thought to be anthropogenic, was more likely a response to weather.

Regionally, however, the *Hexagenia* response to air temperature was not uniform throughout the lake. In part of the lake, temperature variations resulting from the hydroelectric development were minor, so population responses due to temperature were primarily related to weather. However, other regions (e.g. the large northern basins) experienced diversion-related declines in water temperature as well as the weather effects. Abundance declined in all areas following the cold years of 1978 and 1979, but subsequent recovery in the latter regions was delayed or arrested because of a permanent diversion-related lowering of water temperature.

In this study, a combination of long-term monitoring, intensive field study and experimental hypothesis testing was required to identify population responses to natural factors (e.g. weather) and separate them from those due to anthropogenic effects.

TABLE OF CONTENTS

LIST OF FIGURES

FIGURE

FIGURE

FIGURE

FIGURE

LIST OF TABLES

TABLE

TABLE

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My committee members, Dr. D. M. Rosenberg (supervisor), Dr. T.D. Galloway, Dr. R. Hecky, and Dr. J. Mathias, contributed greatly to the study, providing input and direction at all stages of the project, and I would like to thank them collectively as well as individually. My external examiner, Dr. B.W. Sweeney, also provided many very helpful comments on improving the thesis.

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Finally, I'd like to acknowledge the constant support and encouragement of my husband, Patrick Crawford, who cheerfully endured my long absences while collecting field data, and my many moods during the collection, analysis, and writing up of the data.

FOREWORD

This thesis is presented in "paper-style" format. Four journal papers have, or are expected to result from the thesis project, although only three are presented in manuscript form in the thesis. One paper currently in press in AMBIO, is a summary of the project and includes parts of the introduction and the summary chapters from this thesis (Chapters I and VI). The other papers have been or will be submitted in essentially the form in which they appear in the thesis. Chapter VI will appear as a Canadian Fisheries and Marine Services Technical Report from the Freshwater Institute.

CHAPTER I

INTRODUCTION

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 (Bowman 1978, Cullinane and Whelan 1983), few are available for freshwaters. Between 1972 and 1987, results from benthic surveys of 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, a large lake on the Churchill River, is part of a major hydroelectric development in northern Manitoba. Manitoba Hydro's long-term plan to develop the 10,000-MW hydroelectric potential of the nearby lower Nelson River called for diversion of ≈850 $m^3.sec^{-1}$ of water (≈75% of total flow) from the Churchill River into the Nelson catchment at SIL (Newbury *et al.* 1984). The Churchill flows into SIL from the southwest and, prior to diversion, exited from the northeast on its way to Hudson Bay (Fig. I-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 leading from the southeastern part of the lake into the Nelson catchment (Fig. I-1).

Standing stocks of the benthic macroinvertebrate community as a whole responded to impoundment by initially increasing, then decreasing to near pre-impoundment levels (Giberson *et al.* 1991). A post-impoundment "trophic upsurge", typical of new reservoirs, results from an initial input and then subsequent depletion of nutrients and organic matter originating from newly flooded land. However, an opposite pattern to the apparent trophic upsurge was observed for burrowing mayflies (*Hexagenia*): lakewide standing stocks increased slightly following impoundment (1977 survey), but declined after

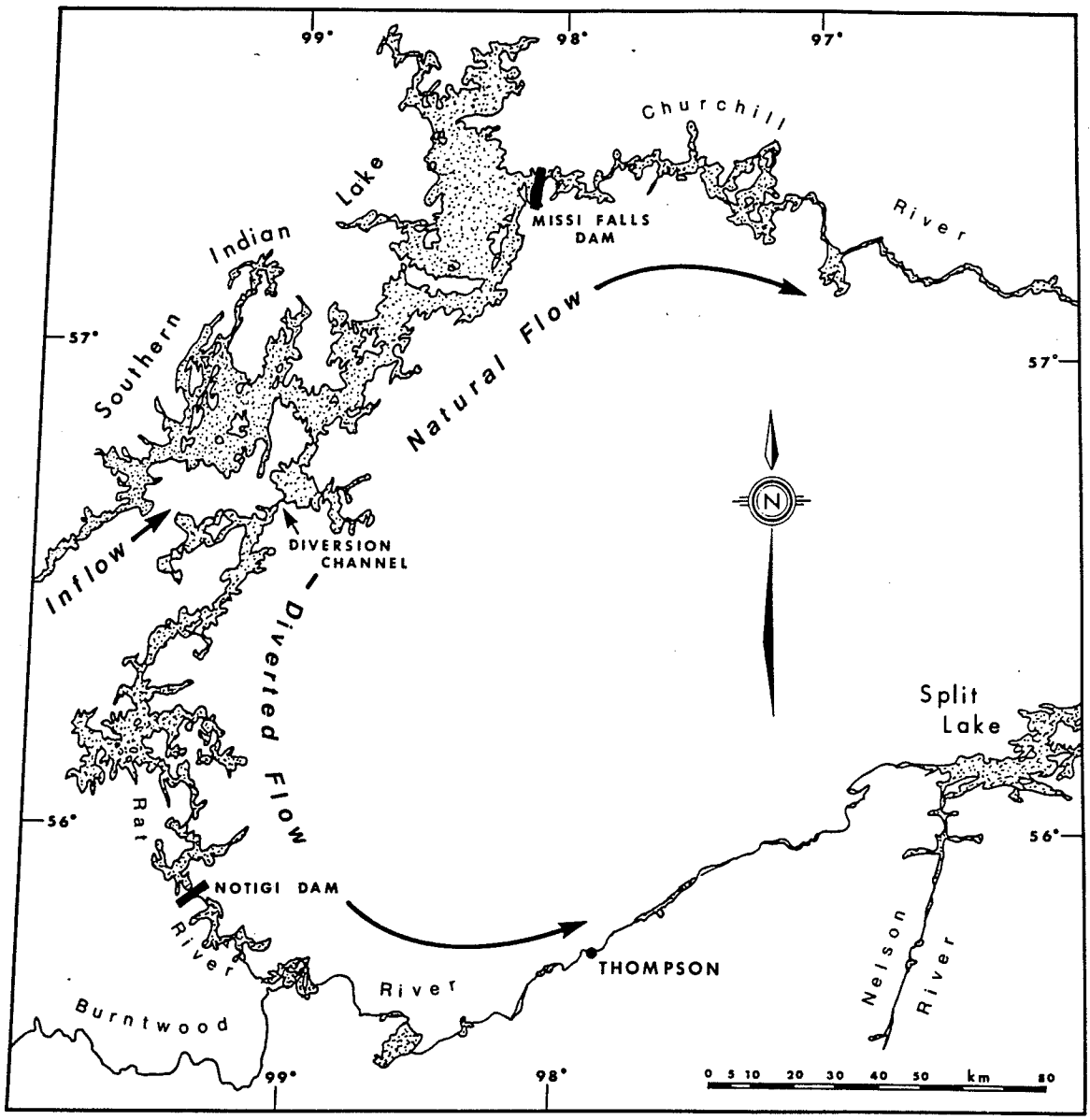

Fig. I-1. Natural and diversion flows of the Churchill River in northern Manitoba (latitude in °N, longitude in °W).

full diversion to ≈15% of the pre-development level (1981 survey; Giberson *et al.* 1991). Following the 1983 survey, the reduction in *Hexagenia* standing stocks was attributed to an inability by *Hexagenia* to maintain their burrows in the sediment because of severe shoreline erosion and altered substrate composition, and to a decrease in water temperature in the northern part of the lake because of river diversion (Rosenberg and Wiens 1985). However, sampling of the lake continued through 1987 and a partial recovery of the population was observed, despite the fact that impoundment and diversion still affected the lake.

It seemed likely that some other factor or factors besides those relating to the hydroelectric development were responsible for the observed decline in *Hexagenia* numbers. Because those factor(s) coincided with the development, interpretation of the monitoring data was confused, and the development was blamed. Factors that were considered as potentially important in controlling *Hexagenia* abundance were predation, food availability, and weather. Responses to predation were thought to have little effect on the observed pattern because the major predator of *Hexagenia* in SIL, lake whitefish (*Coregonus clupeaformis* DeKay), also declined following impoundment and diversion (Bodaly *et al.* 1984). If *Hexagenia* was responding to predation, numbers should have increased, rather than decreased, following the release of predation pressure. Similarly, if *Hexagenia* was responding primarily to food availability in the lake, abundance should have also increased after the development, due to increased nutrient and organic matter inputs from flooded shorelines. However, there was a strong correlation between air temperatures and lake-wide abundance of *Hexagenia* over the 15-yr monitoring period, suggesting that weather variables had an important influence on *Hexagenia* population dynamics (Giberson *et al.* 1991).

In 1986, an experimentally based autecological study was initiated to describe the life histories of *Hexagenia* spp. in SIL in relation to weather variables, in order to interpret the long-term survey data. The project consisted of two parts: 1) an intensive study of the population dynamics of *Hexagenia* in SIL under different weather conditions and thermal regimes and in the laboratory at different temperature, food and density levels, and 2) an application of this information to the interpretation of the survey data. Both *Hexagenia* species in the lake, *H. limbata* and *H. rigida*, were monitored in the lake and in preliminary experiments in the laboratory. However, an incubator failure during the study resulted in the deaths of laboratory cultures of *H. rigida*, so most of the laboratory experiments were conducted on *H. limbata*. The objective of the project was to determine the mechanisms of population control in SIL, in order to separate responses to natural factors from those relating to the development.

CHAPTER II.

REVIEW OF THE PERTINENT LITERATURE

1. ENVIRONMENTAL IMPACT ASSESSMENT AND MONITORING IN AQUATIC SYSTEMS

Aquatic ecosystems are valuable as sources of food, fresh water, faunal habitat, and recreation. Natural stresses that act on these systems include climate-related factors like temperature, wind-induced turbulence and mixing, and water availability. Anthropogenic stresses relate to industrial development or resource harvesting. "Stress" is defined as "any environmental factor that restricts growth and reproduction of an organism or population; any factor acting to disturb the equilibrium of a system" (Lincoln *et al.* 1982, p. 236). In practice, increasing public awareness of the deterioration of aquatic ecosystems has led to the perception that "stress" refers only to anthropogenic stress. This perception effectively prevents the separation of anthropogenic stresses from natural ones, since any changes (e.g. in population abundance or distribution) that are observed in a study of environmental impacts are assumed to stem from the industrial development being evaluated (Green 1984, Nichols 1985). If such were the case, detection of man-induced stresses would be a relatively simple matter, because all that would be required would be a description of spatial or temporal changes (Green 1984). However, mechanisms that influence population abundance are poorly understood in all but a few species, and population fluctuations relating to natural factors (e.g. weather, predation, competition) can dwarf or obscure potential anthropogenic ones (Nichols 1985). Our ability to detect man-induced ecosystem stresses must necessarily stem from the ability to characterize ecosystem responses to all types of stresses.

When evaluating ecosystem stresses, researchers are, in effect, looking at cause-and-effect relationships between the stress(es) and the ecosystem response. The most common way of doing this is to test a null hypothesis of "no change" against an implicit alternate hypothesis of "detectable change" in

the presence of the stress (assumed to be a change for the worse unless proved otherwise; Green 1984). The parameters of interest, e.g. abundance or biomass, are assumed to remain stable or vary predictably with time (e.g. seasonally; Nichols 1985).

However, both biotic and abiotic factors vary temporally and spatially in response to a variety of natural factors, many of which (e.g. climatic anomalies) cannot be predicted (Bakun 1986, Iker 1983; see Buchanan *et al.* 1978, Macan 1977, Northcote 1952, Oliver 1960, Schneider 1965, Stahl 1986, and Wright 1978 for examples). In many cases it is difficult, if not impossible, to exactly determine the mechanisms of population regulation in ecosystems, due to a complex interaction of events, all operating at different temporal and spatial scales and on different levels of organization (Hengevold 1987, Resh and Rosenberg 1989).

To illustrate this complexity, Carpenter *et al.* (1985) considered a hypothetical example in which a fluctuation in an abiotic parameter, such as abnormally low temperatures or water levels, might cause a recruitment failure of the dominant predator in a lake, a large piscivorous fish. This could lead to a temporary but significant decline in predation pressure on zooplanktivorous fish and, due to selective feeding on large zooplankton by zooplanktivorous fish, change the size structure of the zooplankton community. This in turn could result in pronounced differences in grazing and recycling rates, eventually affecting primary production (Carpenter *et al.* 1985, Scavia *et al.* 1986). In natural systems, sequences of cascading trophic interactions as described above will propagate from stochastic fluctuations, with lag effects occurring since generation times differ, and because trophic levels do not always remain constant (Carpenter *et al.* 1985). Concurrently, fluctuations in biotic and abiotic parameters may act directly on each level

of organization, creating new sets of interactions and dampening others. Because of this, clear cause and effect relationships rarely emerge from analysis of lake ecosystems.

Cause and effect, however, can be inferred from the results of long-term or broad-scale monitoring, as long as lagged responses are taken into effect, and as long as inferrences are tested experimentally to determine their validity. Both long-term and broad-scale monitoring provide a large enough data base for correlations to be made between biotic and abiotic variables (Schindler 1987, Strayer *et al.* 1986), thereby allowing separation of responses due to natural factors and those due to anthropogenic ones (Callahan 1984, Keegan 1986, Likens 1983, Nichols 1985, Schindler 1987, Strayer *et al.* 1986). Long-term monitoring is particularly suited to answering questions about slow processes (e.g. biotic succession, wood decomposition), rare events (e.g. major floods or fires), subtle processes (where year-to-year variation is large compared to the magnitude of the trend), and complex phenomena (where there are a large number of biotic and abiotic variables; Strayer *et al.* 1986).

However, because of a natural bias to associate any dramatic change occurring concurrently with a development to that development, changes relating to natural factors may be overlooked or ignored. In one case, an oil spill off the coast of Scotland in 1976 coincided with a decline in abundances of intertidal biota that was consistent with predictions from lab and synoptic monitoring studies relating to oil spill clean-up (Bowman 1978). However, the species response was far more widespread than the "impact" and was in fact a weather-related anomaly. In another example, a "drastic" change in abundance in intertidal organisms off the coast of Ireland actually led to a search for the anthropogenic stress that caused it; the changes eventually were

attributed to natural factors (Cullinane and Whelan 1983). Similarly, in Southern Indian Lake, the decline in *Hexagenia* coincident with hydroelectric development was attributed to flooding and diversion (Rosenberg and Wiens 1985) until after several years of monitoring, when weather variables were thought to be the primary cause (Giberson *et al.* 1991).

Misinterpretations of monitoring data, such as shown above, are most frequently associated with short-term studies where insufficient baseline data or inadequate controls are available to characterize natural fluctuations. Long-term monitoring like that by Bowman (1978) and in the SIL study provides the basis for identifying these errors in interpretation, but may not allow identification of the factors actually responsible. Correlations may be made between environmental variables and population responses, but the most appropriate use of such correlations is to generate and test hypotheses, rather than assume cause and effect (Coull 1985, 1986, Herman and Heip 1986, Schindler 1987). Experimental hypothesis testing has occurred at the laboratory level for many years, in the testing of potential pollutants against single species (Cairns 1984). These very simple tests have been used to set levels of toxicants in nature, even though their design bore little resemblance to natural systems (Cairns 1984, Schindler 1987). Currently, more emphasis is being put on larger scale experimental studies (e.g. field enclosures, whole system studies) that more closely approximate natural systems (Schindler 1987). All levels of experimental design (i.e. lab and field testing) can yield important ecological information, particularly when used in conjunction with each other, to test hypotheses arising from synoptic monitoring studies (Cairns 1984, Schindler 1987).

2. THE CHURCHILL-NELSON HYDROELECTRIC DEVELOPMENT AND SOUTHERN INDIAN LAKE

Hydroelectric development in northern Manitoba was begun in the late 1950's to supply power to a nickel mine and refinery in Thompson, Manitoba. In 1964, federal and provincial agencies examined the feasibility of additional generating stations to supply markets in southern Canada and the U.S.A. In 1966, nine dam sites on the lower Nelson River were identified, but development of the Churchill River was not recommended. Instead, consideration was given to diverting the waters of the Churchill into the Nelson to increase flows through Nelson River dams. The decision to proceed with full Nelson River development, announced in 1966, included the diversion of the Churchill River into the Nelson at Southern Indian Lake (SIL) (Newbury *et al.* 1984).

The Churchill River basin drains an area of ≈242,000 km² extending over the northern half of Alberta, Saskatchewan, and Manitoba (Fig. II-1). The much larger Nelson River catchment drains an area of ≈1,200,000 km² and extends into the northern U.S.A. The two basins together drain much of the interior plains of western North America (Fig. II-1). Between Lake Winnipeg and Hudson Bay, the Nelson River falls 218 m, dissipating 5406 MW of hydraulic power over 680 km of channel with a mean discharge of 2480 $m^3.sec^{-1}$.. The Churchill River falls 255 m between SIL and Hudson Bay, and before diversion, dissipated 2702 MW of power over 460 km of channel with a mean discharge of 1011 $m^3.sec^{-1}$ (LWCNR 1975, Newbury *et al.* 1984).

In 1976, the natural outlet of the lake (Missi Falls) was dammed, and the water level rose by 3 m over its long-term mean. By July 1977, water levels were high enough to spill into a newly dug diversion channel between the southeast portion of SIL and the Rat River, a tributary of the Nelson (Fig. I-1), and by fall 1977, diversion flows were near design capacity.

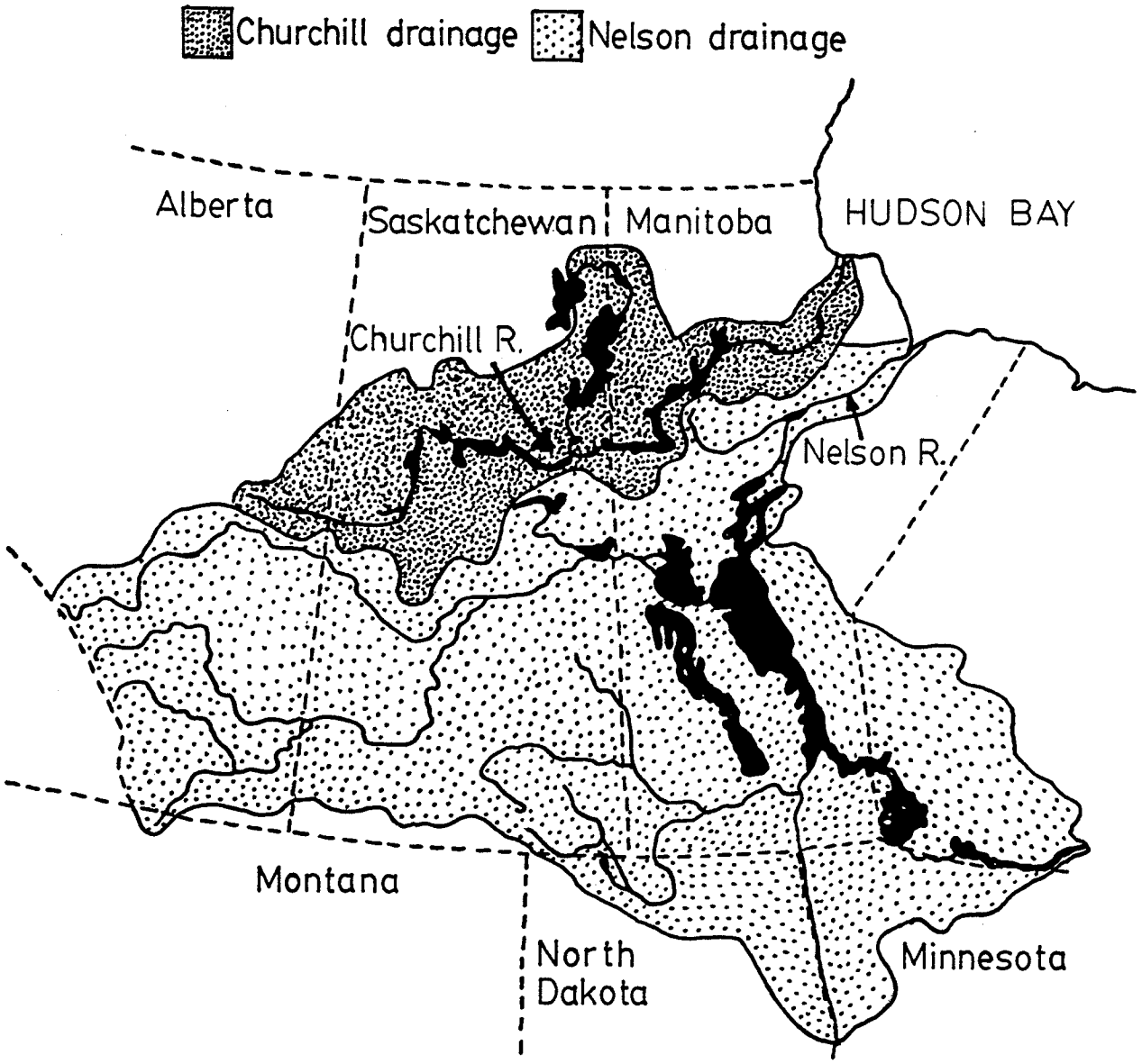

Fig. II-1. Drainage basins of the Churchill and Nelson Rivers in western North America (LWCNR 1975).

Currently, ≈75% of the flow of the Churchill River (as an annual average) is routed into the lower Nelson River valley (Newbury *et al.* 1984).

Southern Indian Lake is located in a region of discontinuous permafrost, overlying Precambrian Shield. The retreat of the glaciers between 8000 and 10,000 years ago left extensive areas of glacio-fluvial sands and gravels on the uplands surrounding the far northern one third of the lake. Uplands around the southern portions consist of varved silty clays up to 20 m thick that were deposited under an arm of glacial Lake Agassiz. Since deglaciation, forests primarily composed of black spruce (*Picea mariana* (Mill.) B.S.P.) have developed and Sphagnum peat moss has accumulated to depths of up to 3 m (Newbury *et al.* 1984).

The rising lake level resulted in the flooding of large areas of this forest and peatland; it was estimated that 200,000 t of carbon, 2,490 t of nitrogen, and 295 t of phosphorus were added to the lake from breakdown of spruce needles alone (Crawford and Rosenberg 1984). Flooding above the pre-impoundment wave-washed zone effectively reversed the natural state of shorelines: before flooding, 88% of shorelines were bedrock-controlled and stable; after flooding, 86% of shorelines were dominated by highly erodable clays and silts (Newbury *et al.* 1984). Rates of shoreline erosion varied depending upon exposure to wave action and composition of backshore materials (Newbury and McCullough 1984), but erosion added ≈4,000,000 t of sediment per year to the lake in the first three years of impoundment (Hecky and McCullough 1984). Increased sediment loads to the lake reduced light penetration, and affected primary productivity and visibilty for predators (Hecky 1984); however, the effect on primary productivity was somewhat offset by an increase in nutrients from the flooded shorelines (Hecky and Guildford 1984).

Flooding and diversion also affected thermal properties of the lake

(Hecky 1984). A well developed thermocline was not present before or after flooding, although temperatures generally declined with depth. However, the increased depth due to impoundment and backscatter of light from high suspended solids concentrations resulted in decreased heat penetration and slightly lower temperatures in all regions. Diversion of Churchill River flows had a much more noticeable effect on temperature, however, particularly in the northern part of the lake, which was essentially cut off from the Churchill River. In these areas, break-up now occurs much later in spring resulting in lower maximum and mean temperatures and reduced degree days (Hecky 1984).

Benthic macroinvertebrates in the lake were surveyed before impoundment (1972) as part of a multidisciplinary environmental impact assessment (Hamilton 1974, Hecky *et al.* 1984). Surveys were continued after impoundment but before diversion was complete (1977), after the diversion was fully operational (1979), and every 2 yr thereafter until 1987 (Giberson *et al.* 1991). Standing stocks of the benthic macroinvertebrate community increased following impoundment, probably in response to an initial addition of nutrients and organic matter from flooded shorelines, and then gradually declined to pre-impoundment levels by 1987 (Giberson *et al.* 1991). Total macroinvertebrate standing stocks responded positively to the impoundment/diversion, so the apparent negative effect on the abundance of burrowing mayflies following the diversion was especially noteworthy (Rosenberg and Wiens 1985). Subsequent recovery of the population, despite the continuation of the physical impacts originally believed responsible for their decline, prompted the current research.

III. *HEXAGENIA* (EPHEMEROPTERA: EPHEMERIDAE)

Hexagenia species are burrowing mayflies in the family Ephemeridae. Nymphs (Fig. II-2) construct U-shaped burrows in the bottom mud of lakes and rivers over much of North America (Edmunds *et al.* 1976). Respiration is by diffusion through the body surfaces; as oxygen in the water in the burrow is depleted, fresh water is pumped through the burrows by beating the abdominal gills (Eriksen 1963). Food is primarily detritus with some algal material, and is apparently collected by a combination of filter feeding from respiratory currents and grazing around the openings to the burrows (Zimmerman and Wissing 1980).

Five *Hexagenia* (Walsh) species are recognized from Mexico to Canada by Edmunds *et al.* (1976) and McCafferty (1975). Several subspecies have also been described, particularly within *H. limbata* (Serville) and *H. munda* Eaton. However, McCafferty and Pereira (1984) indicated that colour variations associated with different *H. limbata* subspecies were probably temperature related rather than genetic, and both McCafferty (1984) and Berner and Pescador (1988) have included most subspecies of *H. munda* in *H. limbata*.

Only two species, *H. limbata* (Serville) and *H. rigida* McDunnough, are found in SIL. *Hexagenia limbata* is widespread throughout North America, from the Atlantic to the Pacific coasts and from Mexico to Great Slave Lake, NWT (Edmunds *et al.* 1976, Rawson 1953). *Hexagenia rigida* has a more central and eastern distribution (Edmunds *et al.* 1976, McCafferty 1975), and has been reported as far north as northern Manitoba (Rosenberg and Wiens 1985). *Hexagenia* species in SIL are near the northern limits of their distribution in Manitoba.

Hexagenia species are important in many freshwater ecosystems and have been widely studied. Nymphs grow to a maximum size of about 35 mm (Hunt 1953)

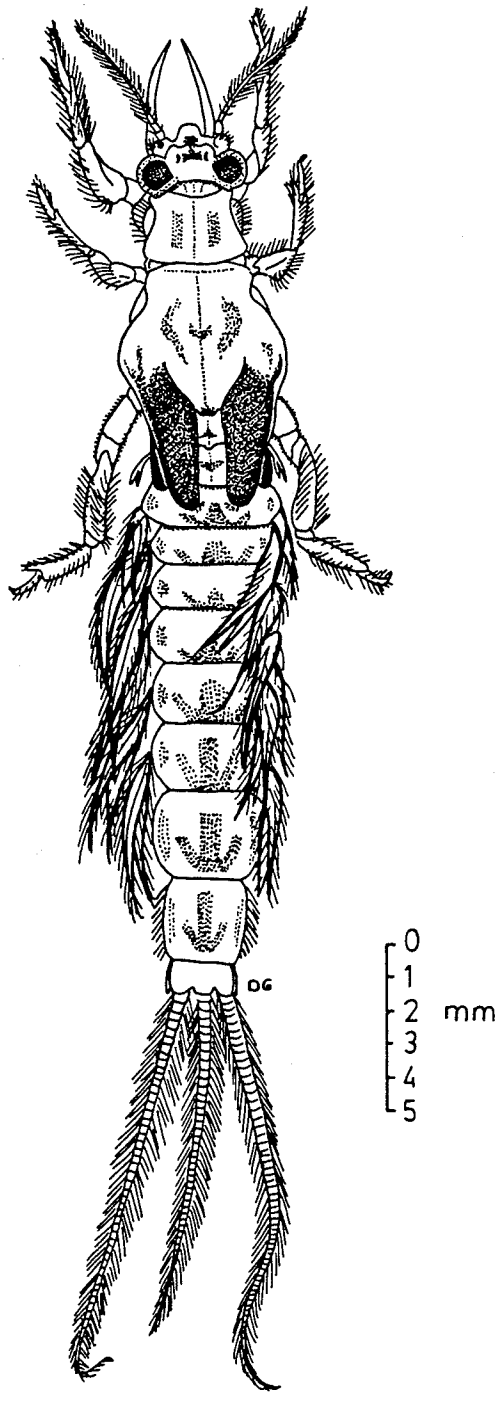

Fig. II-2. Mature male Hexagenia limbata nymph from Southern Indian Lake.

and they are a major component in the diets of fish over most of their range (Hunt 1953, Neave 1932). Their size and habitat requirements also make them a useful organism for toxicological studies, because they inhabit the sediments where contaminants accumulate (Fremling and Johnson 1990) and they are large enough to handle and analyze easily.

Development of *H. limbata* and *H. rigida* is related to temperature. *Hexagenia limbata* development from egg to adult may be completed in ≤1 yr in the southern U.S. (Carlander *et al.* 1967, Craven and Brown 1969, Edmunds *et al.* 1976, Fremling and Johnson 1990, Horst and Marzolf 1975, Welch and Vodopich 1989), although the life cycle may take ≥2 yr in the northern part of the range (McCafferty 1975, Mozley and Ladronka 1988, Neave 1932, Riklik and Momot 1982, Schloesser and Hiltunen 1984). Mixed 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. Flannagan 1979, Heise *et al.* 1987, Hudson and Swanson 1972, Rutter 1972). Temperature effects on growth and development may be quantified by using a degree day model, in which the accumulated degree days (dd) required to complete the life cycle are calculated; these data then can be compared with those for other populations or locations (Southwood 1978). *Hexagenia limbata* need ≈1900–2600 dd above a developmental threshold of 10°C to complete development over most of their range (Heise *et al.* 1987, McCafferty and Pereira 1984; and calculated from Hudson and Swanson 1972, Hunt 1953, Rutter 1972, Welch and Vodopich 1989), although Heise *et al.* (1987) noted a decline in degree day requirements with increasing latitude. Degree day requirements have not been calculated for *H. rigida*, but Friesen *et al.* (1979) determined that the threshold temperature for *H. rigida* was similar to *H. limbata* (near 10°C), and Neave (1932) noted that the life cycles of the two

species were virtually identical in Lake Winnipeg.

Hexagenia distribution within a habitat is known to be affected by substrate composition and dissolved oxygen concentration. Nymphs cannot tolerate oxygen concentrations below ≈1.2 ppm (Eriksen 1968), and so they will not be found in hypolimnetic areas that are anoxic during summer or winter (Rutter 1972). Depth alone apparently does not limit their distribution (Hunt 1953 recorded nymphs to depths of 21 m in lakes in Michigan), unless those depths are also associated with thermal stratification and hypolimnetic oxygen deficits. If oxygen conditions are suitable, *Hexagenia* is most common in substrates containing a substantial fraction of silt or mud, and they appear to avoid substrates composed predominately of sand or gravel (Heise *et al.* 1987, Hunt 1953, Neave 1932).

CHAPTER III

POPULATION DYNAMICS OF *HEXAGENIA LIMBATA* (SERVILLE) AND *H. RIGIDA* MCDUNNOUGH (EPHEMEROPTERA: EPHEMERIDAE) IN SOUTHERN INDIAN LAKE, MANITOBA, CANADA: THE INFLUENCE OF TEMPERATURE

ABSTRACT

The life history and population dyanamics of *Hexagenia limbata* and *H. rigida* were examined from 1986 to 1988 in four regions of Southern Indian Lake (SIL), Manitoba, as part of a study into impacts of hydroelectric development in the area. Maximum summer bottom-water temperatures during the study period ranged from 15° to 20°C in the study regions, although the open water season lasted only about 4-6 mo. The life cycles for both species were similar, requiring 3 yr from egg to adult in the three warmest areas and ≥4 yr in the coolest site. Degree day (dd) requirements for development ranged from 1222 to 1468 dd>10°C, but in general, dd accumulations over the entire life cycle were not a good predictor of the timing of emergence. However, there was a good relationship between emergence timing and accumulated dd in the final summer before emergence. Adult emergence generally occurred between mid-July and late August. Emergence periods were fairly synchronous within study regions (~3 wk), but varied among regions, depending upon thermal regime. In most regions, eggs apparently hatched in two groups, the first within 3-6 wk if conditions were favourable, and the second after overwintering. In the coldest region, all eggs probably overwintered in most years and hatched the next spring.

Mean body lengths of mature nymphs collected in different years and from different study sites ranged from 21.7 - 24.8 mm (males) and 24.3 - 28.5 mm (females) for *H. limbata* and from 20.2 - 23.3 mm (males) and 23.3 - 27.4 mm (females) for *H. rigida*. Mean body length decreased with declining thermal regime in the three locations where the life cycle was 3 yr long, then increased again where the life cycle took 4 yr to complete. Fecundity (number of eggs/female) was strongly correlated to body size, so regional differences in thermal regime also resulted in differences in fecundity. Mean fecundity

for the four study areas ranged from 2319 - 3757 eggs/female for *H. limbata* and 1976 - 3385 eggs/female for *H. rigida*.

Weather affected abundance of *Hexagenia* in SIL directly through its effects on emergence and mating success, and indirectly through its relationship with water temperature during the open-water season. Most emerging adults drowned when wind produced waves ≥1 m in height, and strong winds also hindered mating flights. Air temperature during the emergence period affected the duration of the winged stages and the length of time they were susceptible to predation by terrestrial predators. Water temperature was related to air temperature during the ice-free season at SIL, and water temperature influenced life cycle duration and accumulated mortality, emergence timing, and egg hatching success.

INTRODUCTION

The benthic invertebrates of Southern Indian Lake (SIL) in northern Manitoba have been investigated since the early 1970's as part of a study into impacts of hydroelectric development on lakes and rivers in the area. In 1976, SIL was impounded and the water level raised ≈3 m. In 1977, most of the water of its major inflow, the Churchill River, was diverted southward through the lake into the Nelson River catchment to augment the hydroelectric potential of the lower Nelson River (Newbury *et al.* 1984).

The burrowing mayflies in SIL (*Hexagenia limbata* and *H. rigida*) declined dramatically following manipulation of the lake. *Hexagenia* are important in the diets of many freshwater commercial fish populations; e.g. lake whitefish and young walleye in Lake Winnipeg and Dauphin Lake, Manitoba (Neave 1932, Heise *et al.* 1987). Although the *Hexagenia* decline was originally attributed to the hydroelectric development, further study suggested that weather factors rather than anthropogenic ones were mainly responsible (Giberson *et al.* 1991, Chapter VI).

The initial attribution of responses to hydroelectric development resulted partly from an underestimate of the duration of the life cycles for the two species in the lake. In other locations, *Hexagenia limbata* has been reported to take from 17 wk (Edmunds *et al.* 1976) to 2 yr (Heise *et al.* 1987, Flannagan 1979, Neave 1932) and to require ≈1900–2600 degree days (dd) above a threshold temperature of 10°C to complete development (Heise *et al.* 1987, McCafferty and Pereira 1984, and calculated from Hudson and Swanson 1972, Hunt 1953, Welch and Vodopich 1989). Life cycle information for *H. rigida* is rare, but Neave (1932) indicated that its life cycle was almost identical to *H. limbata*, and Friesen *et al.* (1979) determined that the threshold temperature for egg development was also similar to *H. limbata*.

Information on life cycle duration is important when examining anthropogenic impacts because it provides a basis for predicting the amount of time required for a population to recover after a stress. The *Hexagenia* numbers in SIL declined following manipulation of the lake in 1976 and 1977, and *Hexagenia* had virtually disappeared from the lake by 1981, 5 yr later (Giberson *et al.* 1991, Chapter VI). If *Hexagenia* had a life cycle of 2-yr duration, and was responding to a single point-in-time weather stress, then some recovery of the population would have been expected in that period. In contrast, the flooding and diversion related to hydroelectric development at SIL are ongoing, so development-related effects should still be occurring, strengthening the argument during the early stages of the study that the *Hexagenia* decline was an anthropogenic response. By 1983, however, 7 yr after lake manipulation, the population had begun to recover, despite the ongoing physical impacts. Thus, the initial population decline was likely related to factors other than hydroelectric development, and there were other reasons for the long delay in the recovery. In 1986, an intensive study was implemented on the population dynamics of *Hexagenia* in SIL to determine the factor(s) affecting abundance and the reasons for the long recovery period.

STUDY SITES

Southern Indian Lake is located in a shallow bedrock basin on the Churchill River, in northern Manitoba (57°N, 99°W; Fig. III-1). The lake is located in a region of discontinuous permafrost, and shoreline sediments around much of the lake consist of a mix of silty clays and ice. Flooding resulted in contact between warm lake water and frozen shoreline sediments, melting the ice and causing high erosion rates and turbidity (Newbury and McCullough 1984). Beyond the flooded zone, substrates consisted of fairly

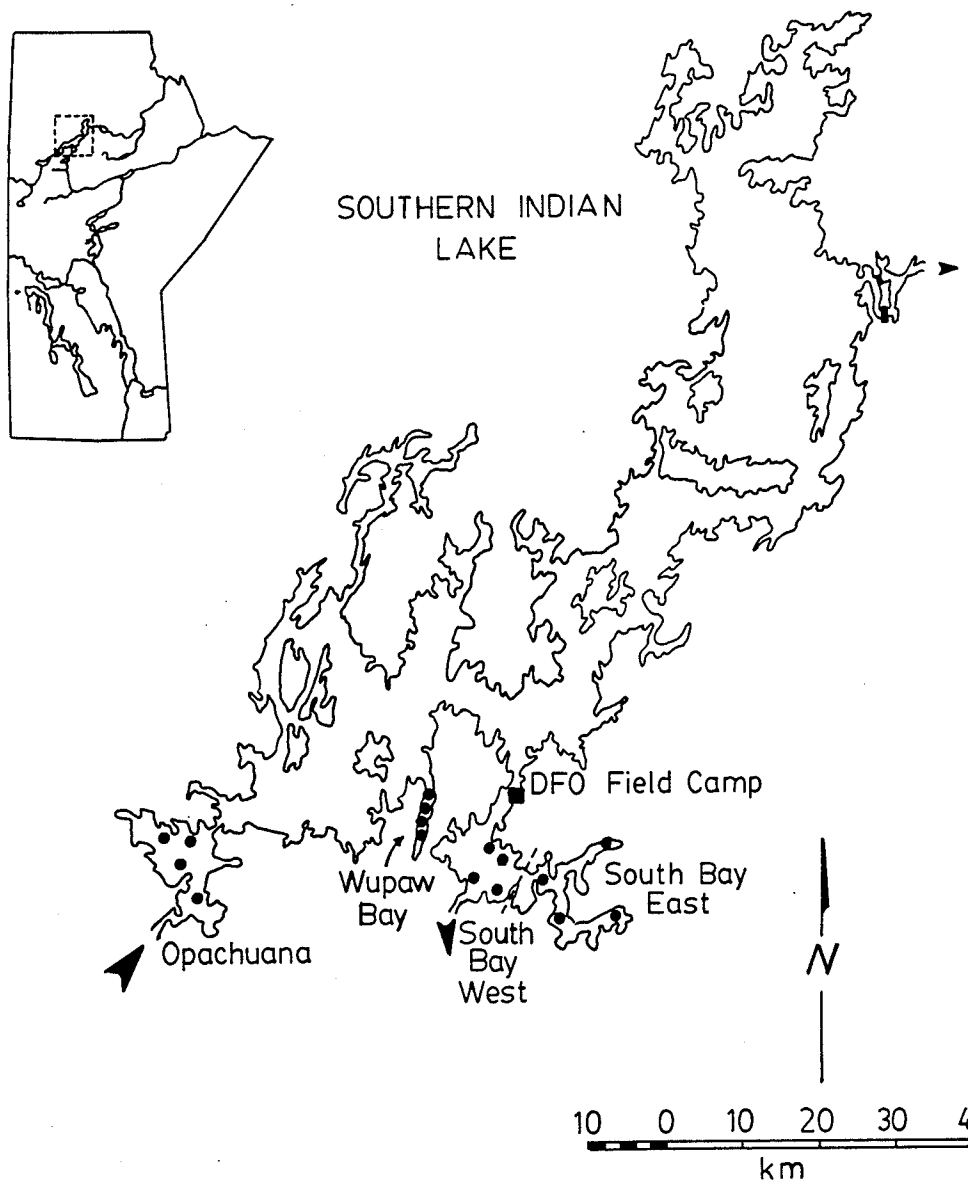

Fig. III-1. Sampling sites on Southern Indian Lake (dots), and location of Fisheries and Oceans (DFO) field camp (square). Arrows refer to major inflow and outflows.

uniform clay aggregates over most of the lake, except in the far northern region in which sand predominated (Hecky and McCullough 1984). Because of the flooding and continued erosion, the near-shore zone now consists mainly of flooded black spruce forest and peatland. The lake did not usually stratify thermally due to the shallow nature of the basin and the effects of river flow (Hecky 1984). The ice-free season was variable, depending on local weather conditions, but ranged from ≈4.5-6.2 mo between 1972 and 1979 (McCullough 1981). Details of geology, vegetation, and climate for the region may be found in Newbury *et al.* (1984).

Preliminary study indicated that air temperature during the growth period was strongly correlated to lake-wide *Hexagenia* abundance (Giberson *et al.* 1991, Chapter VI). Because air temperature was directly related to water temperature during the open-water period (Hecky *et al.* 1984) and water temperature was widely reported to affect *Hexagenia* growth and development, water temperature was believed to have a major influence on *Hexagenia* population dynamics in SIL. To test this hypothesis, four study areas (Fig. III-1) were chosen to provide a gradient in degree day accumulations, while still yielding sufficient *Hexagenia* for life-history analysis. Maximum summer temperatures were similar in the study areas, ranging from 15-20°C between 1986-1988, but there were large differences in degree day accumulations due to regional and annual differences in the length of the open-water season. The warmest area investigated was Opachuanau basin, located at the inflow of the Churchill River (Fig. III-1). Next warmest was Wupaw Bay, located just south of the main flow in the next major basin, followed by South Bay East, a series of small bays in the southeastern part of the lake, and South Bay West, the new outlet for most of the Churchill River flow (Fig. III-1). Degree day accumulations for 1986-1988 for each area are shown in Table III-1.

Table III-1. Total accumulated degree days (dd) >10°C for the four study areas in 1986, 1987, and 1988. The predicted life cycle duration is based on an assumed requirement of 2000 dd>10°C to complete development and the mean dd for each region.

Location	Degree days >10°C 1986	1987	1988	Total	Predicted Life-cycle duration (yr)
Opachuanau	380	575	650	1605	3.74
Wupaw Bay	300	525	650	1475	4.07
South Bay East	280	500	600	1380	4.35
South Bay West	210	380	400	990	6.06

Four profundal sites were sampled in each area for *Hexagenia* nymphs (Fig. III-1). Each site was located within 100 m of shore; water depths ranged from 6-12 m in Opachuanau, 5-6 m in Wupaw Bay and South Bay East, and 7-10 m in South Bay West. Adults were collected on protected shorelines near the sampling sites.

METHODS

Sampling - nymphs

Eight to ten samples were collected from each site with a 15 x 15 cm modified Ekman grab (Burton and Flannagan 1973) approximately monthly throughout the open-water season. Samples were washed through a 200-µm mesh net and preserved in 10% formalin in the field; within 1 mo they were washed and transferred to 70% ethyl alcohol for sorting and identification. Samples were sorted under a dissecting microscope, and the burrowing mayflies were identified to species using the characters given by McCafferty (1975) and J.F. Flannagan (Freshwater Institute, Winnipeg, personal communication). Species could be identified at ≈7 or 8 mm in length; relative proportions of each species for smaller nymphs found on given sampling dates were assumed to be the same as that 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 50X magnification when nymphs were at least 6 mm in length.

Life history analysis

Cohorts were separated for life history analysis by measuring morphological features of the nymphs with an ocular micrometer in a dissecting microscope, and examining the size-frequency distributions of those features.

Separation of cohorts using the frequency distribution of a single feature was difficult because sizes tended to overlap between cohorts due to differential growth rates and the presence of sexual dimorphism in later stages. Therefore, three measures were used to separate the cohorts: 1) body length - the distance between the frontal process and the end of the abdomen, excluding the caudal filaments; 2) head width - width just in front of the eyes, and 3) wing-pad length - length 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. (An example of the frequency distributions with separated cohorts is shown in Fig. III-2, see Appendix A for complete cohort analysis).

Mortality

Year-to-year mortality was calculated for each species and each location in order to compare mortality rates with thermal regime. Cohorts were separated using the methods given above, and mean density for each cohort was plotted against time, for each species in each study area (Appendix B). Changes in density during the summer months were generally small or not statistically significant ($p<.05$), although large decreases were seen between summers. Therefore densities were averaged for each summer, then compared to the average density for the succeeding summer to obtain an estimate of between-year mortality. Mortality was the per cent difference between the mean annual abundance from one year to the next, and was expressed as the mortality between 1-yr old nymphs and 2-yr old nymphs, 2-yr old and 3-yr old nymphs, and where applicable, 3-yr old and 4-yr old nymphs.

Mortality estimates were also made for the period between the emergence of one cohort and the recruitment of the next. It was not possible to obtain

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a direct estimate of emergence mortality because floating emergence traps were unsuitable for the rough water conditions encountered at SIL, and because the mayflies avoid submerged traps (A.P. Wiens, Freshwater Institute, personal communication). Nor was it possible to obtain an estimate of adult mortality caused by predation or weather. Therefore, a combined estimate was calculated for the period just prior to adult emergence to the appearance of the new recruits. Combined mortality was calculated for each species and each location as follows:

1)	$N_1 \div 2 = F$	N_1 = mean density of final cohort just before emergence
		F = number of females (based on ≈1:1 sex ratio)
2)	F x Fec. = E	Fec.= mean fecundity (# eggs/female)
		E = potential number of eggs deposited if no mortality
3)	$E - N_2 = D$	N_2= mean density of new recruits
		D = difference between potential recruitment and actual recruitment
4)	$M = (D \div E)100$	M = % Mortality

This estimate, expressed as mortality between 3-yr old nymphs and 1-yr old nymphs (or 4-yr old and 1-yr old nymphs where applicable) included nymphal emergence mortality, subimago emergence mortality, mortality of winged stages (e.g. from predation), egg mortality, and mortality of newly hatched nymphs.

Adult collections

Adults were collected in a light trap located near the SIL field camp at the north end of South Bay West, in pan traps in each sampling area, and by sweeping and hand-picking shoreline vegetation. Pan traps were used instead

of light traps or sticky traps for most sampling locations because they can be left in isolated and inaccessible sites for up to 2 wk. Five replicate pans (33 cm long x 23 cm wide x 14 cm high) were set into the peat near one of the sampling sites in each area, so that the edges were flush with the ground. Each pan was filled with 3-4 cm of ethylene glycol (antifreeze), which acts both as a preservative and as a surfactant. Insects fall into the pans and drown, so the pans provide a qualitative measure of presence or absence of adults. *Hexagenia* were removed and the antifreeze was renewed weekly, weather permitting, from the beginning of July to the end of the season, to provide information on the duration of the emergence period and relative abundances of emerging adults.

While the pans were being serviced, the shoreline vegetation was also checked visually and swept with a collecting net to obtain adults for determination of adult size and fecundity for each location. Last-stage nymphal exuviae could be seen floating along the shorelines during the emergence periods, and were collected when the pans were serviced and whenever other data were collected within a study location. The presence of exuviae was noted as an independent check on the timing of the emergence period, and exuviae were measured to provide an estimate of the size of mature nymphs.

Fecundity

Regional fecundity estimates were determined from the relationship between female body size and the number of eggs. Eggs were dissected and counted from 22 pre-measured female subimagos (both species together) collected from all four sampling areas. The relationship between subimago body size and fecundity (# eggs/female) was then determined by regression analysis, so that fecundity could be estimated by measuring subimagos from

each region. Subsequently, to increase the sample size to improve statistical analysis, and to obtain a sample that was spread over the entire emergence period, fecundity was also estimated from measured exuviae from each location. Large, nearly mature nymphs were collected from Wupaw Bay, and reared in a screened aquarium at room temperature (see Chapter V for rearing methods). The aquarium was checked several times daily for emergence, and any newly emerged subimagos and floating exuviae were associated and measured. Only those that could be reliably associated were considered; if ≥2 subimagos emerged together and could not be positively associated with their exuviae, they were discarded. The relationship between exuvial lengths and subimago lengths was determined by regression analysis. Exuvial lengths were then converted to subimago lengths using the regression relationship, and then an overall mean subimago size (males and females separated) was estimated for the entire emergence period in 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 degree day analysis

Temperature profiles (1-m depth intervals) and sediment 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 areas were visited. This resulted in approximately bi-weekly temperature profiles in 1986, and approximately weekly temperature data for 1987 and 1988. Sediment temperatures were plotted for each year, and degree days (dd) were calculated by summing the total Celsius degrees above the threshold temperature for each summer (from Southwood 1978):

$dd = \Sigma (T - T_0) d$ T = temperature

T_0 = threshold temperature

d = days above threshold temperature

The derived temperature threshold (from the above relationship) for calculating dd accumulations for *Hexagenia* is near 10°C, but the actual threshold is ≈8°C (Chapters IV & V), so dd accumulations were calculated using both values. Degree days were calculated for three periods in each area: 1) annually, from ice-out to freeze-up, 2) for the duration of one entire life cycle, and 3) annually, from ice-out to first emergence of adults. Annual dd accumulations, both for the whole season and for the period to the first emergence, were calculated directly from the temperature plots for each year. Accumulated dd for 1986-1988 were measured directly, as detailed above. Total accumulated dd for the 1985 cohort were determined by summing the dd from the point when eggs were deposited in 1985 until emergence in 1988 (3 yr life cycle) or 1989 (4 yr cycle). The oviposition periods for 1985 and 1989 were inferred from weather data and accumulated dd for the remainder of 1985 and beginning of 1989 were estimated from the relationship between air temperature and water temperature for each study area (A.P. Wiens, Freshwater Institute, unpublished data).

RESULTS

Temperature

The seasonal bottom-temperature pattern for each study region for 1986-1988 is shown in Fig. III-3. 1986 was the coolest of the three study years. Water temperatures in each area warmed later in the spring and cooled earlier in the fall in 1986 than in succeeding years, and maximum summer temperatures were also lowest in 1986. 1987 and 1988 had similar temperature patterns at the beginning of the year within each study area, although warm temperatures persisted for a longer period in 1988 than 1987 (Fig. III-3); this resulted in greater annual dd accumulation in 1988 (Table III-1). Annual dd accumulations (>10°C) were highly variable, both among years and among sites, ranging from as low as 210 in South Bay West in 1986 to 650 in Opachuanau and Wupaw Bay in 1988. Total dd accumulations >10°C in each area for the 3-yr study period varied from 990 - 1605 (Table III-1). Duration of *Hexagenia* life-cycles was predicted from SIL temperatures and an assumed minimum requirement (from the literature) for at least 2000 dd>10°C to complete development; these ranged from ≈4 yr in Opachuanau, Wupaw Bay, and South Bay East, to 6 yr in South Bay West.

Life history

Individuals of both species were found in most samples, often in similar numbers, although *H. limbata* predominated in Opachuanau, and *H. rigida* was most common in Wupaw Bay, South Bay East and South Bay West when data was averaged over the 3-yr period (Table III-2). The cohorts were separated by looking at the frequency distributions for length, head width, and wing-pad length simultaneously for each species, year, and sample area (Fig. III-2). For example, for *H. rigida* in Opachuanau (Fig. III-2), it would have been

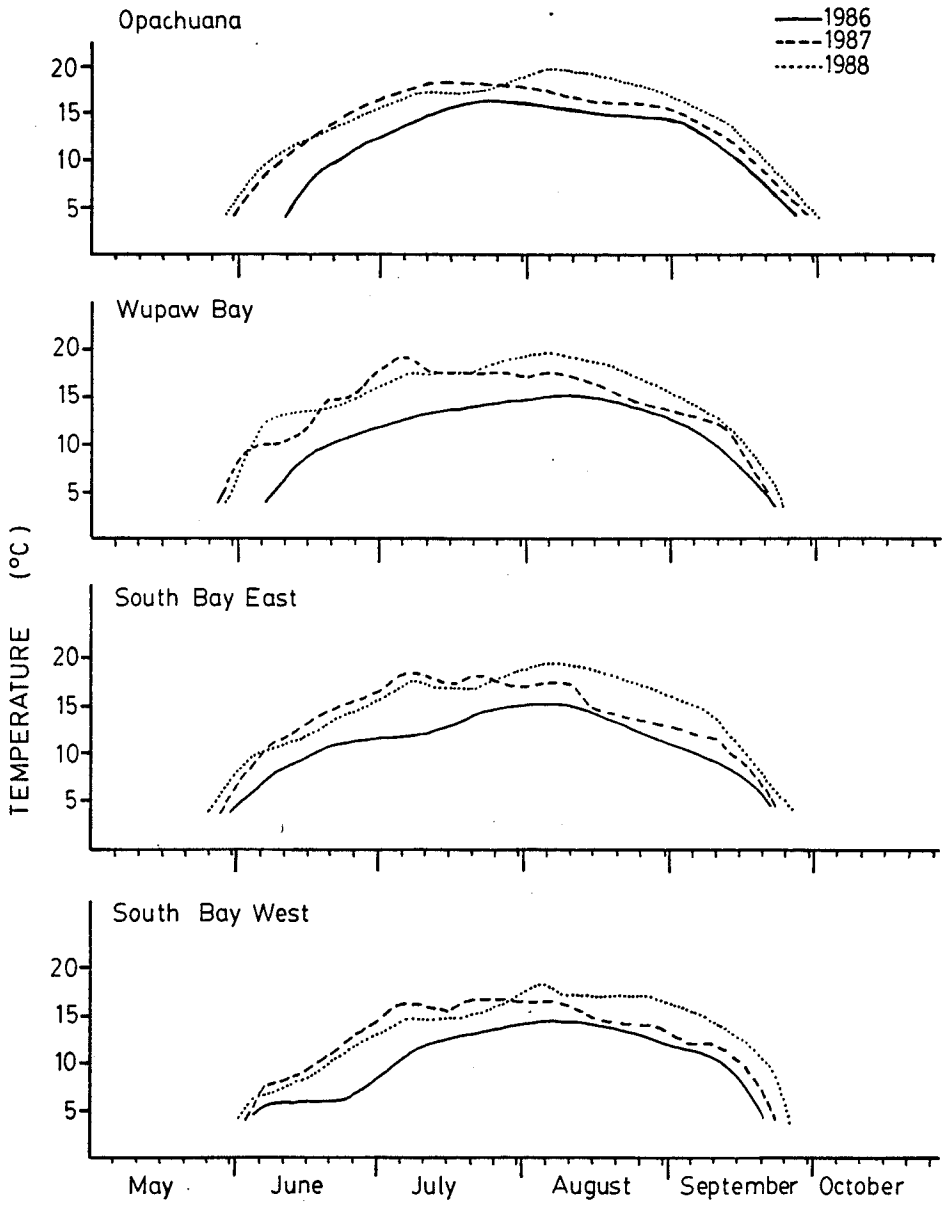

Fig. III-3. Summer bottom water temperatures (°C) in the four study areas in Southern Indian Lake, 1986-1988.

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

Location	Species	Mean Abundance ($\bar{x}$ ± SE) 1986	1987	1988	Total
Opachuanau	*H.limbata*	146.3 ± 12.5	59.8 ± 19.2	172.3 ± 80	121.9 ± 25.3
	H.rigida	98.5 ± 12.4	49.5 ± 9.5	174.3 ± 83.6	101.4 ± 25.5
Wupaw Bay	*H.limbata*	117.3 ± 9.1	61.0 ± 8.0	57.3 ± 22.1	80.5 ± 11.0
	H.rigida	137.3 ± 12.9	88.3 ± 12.1	59.3 ± 19.0	98.2 ± 12.4
South Bay East	*H.limbata*		16.8 ± 4.6	27.3 ± 12.5	21.3 ± 5.7
	H.rigida		39.0 ± 18.3	31.7 ± 15.5	35.9 ± 11.5
South Bay West	*H.limbata*	10.3 ± 3.8	30.3 ± 4.8	19.0 ± 9.5	20.1 ± 4.0
	H.rigida	39.5 ± 13.1	29.0 ± 4.8	18.7 ± 2.3	30.0 ± 5.3

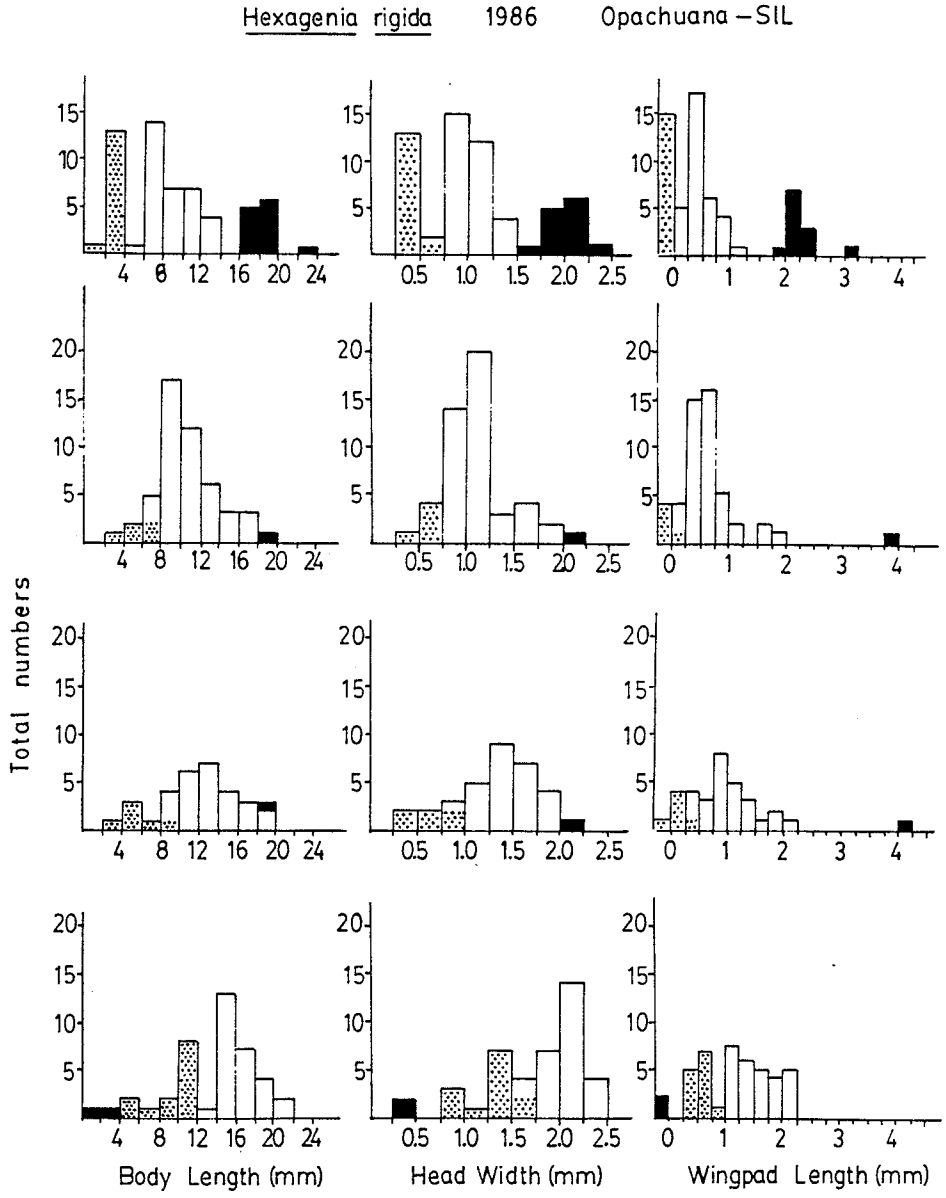

Fig. III-2. Frequency distributions for body length, head width, and wing-pad length (mm) for *Hexagenia rigida* in Opachuanau, Southern Indian Lake, Manitoba (1986). Cohort separation: different stippling patterns represent different cohorts.

difficult in the July and August samples to distinguish the larger cohorts based on body length or head width, since no clear separation was evident. By using wing-pad length as a developmental stage indicator, the cohort that was developmentally ready to emerge was easily distinguished. Once the cohorts were separated (Appendix A), they could be superimposed upon length-frequency distributions for the whole study period, to follow the life cycles through time (Figs. III-4, III-5).

The life cycles of the two species appear to be virtually identical. For both species, three cohorts were present on each sampling day in the three warmer locations, and four cohorts were identified in South Bay West (Figs. III-4, III-5). Within the 3-yr study period, it was not possible to follow any cohorts from oviposition to adult emergence, but life cycles can be inferred. The cohort present as very small nymphs in June of 1986 likely began as eggs in the summer of 1985. In Opachuanau and Wupaw Bay, the cohort grew through 1986 and 1987, and emerged as adults in 1988, resulting in a 3-yr life cycle. South Bay East 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, the cohort that began in the summer of 1985 did not complete development in 1988, but presumably emerged in the succeeding year, for a 4-yr life cycle.

Eggs generally began hatching within a few weeks of the oviposition period each summer in the three warmer locations, with new recruits usually noted in the September sample (Figs. III-4, III-5). Some eggs must also have overwintered, however, since newly-hatched nymphs were also noted in samples in early summer. Most or all eggs usually overwintered in South Bay West, since small nymphs were rarely observed there until the following spring (Figs. III-4, III-5).

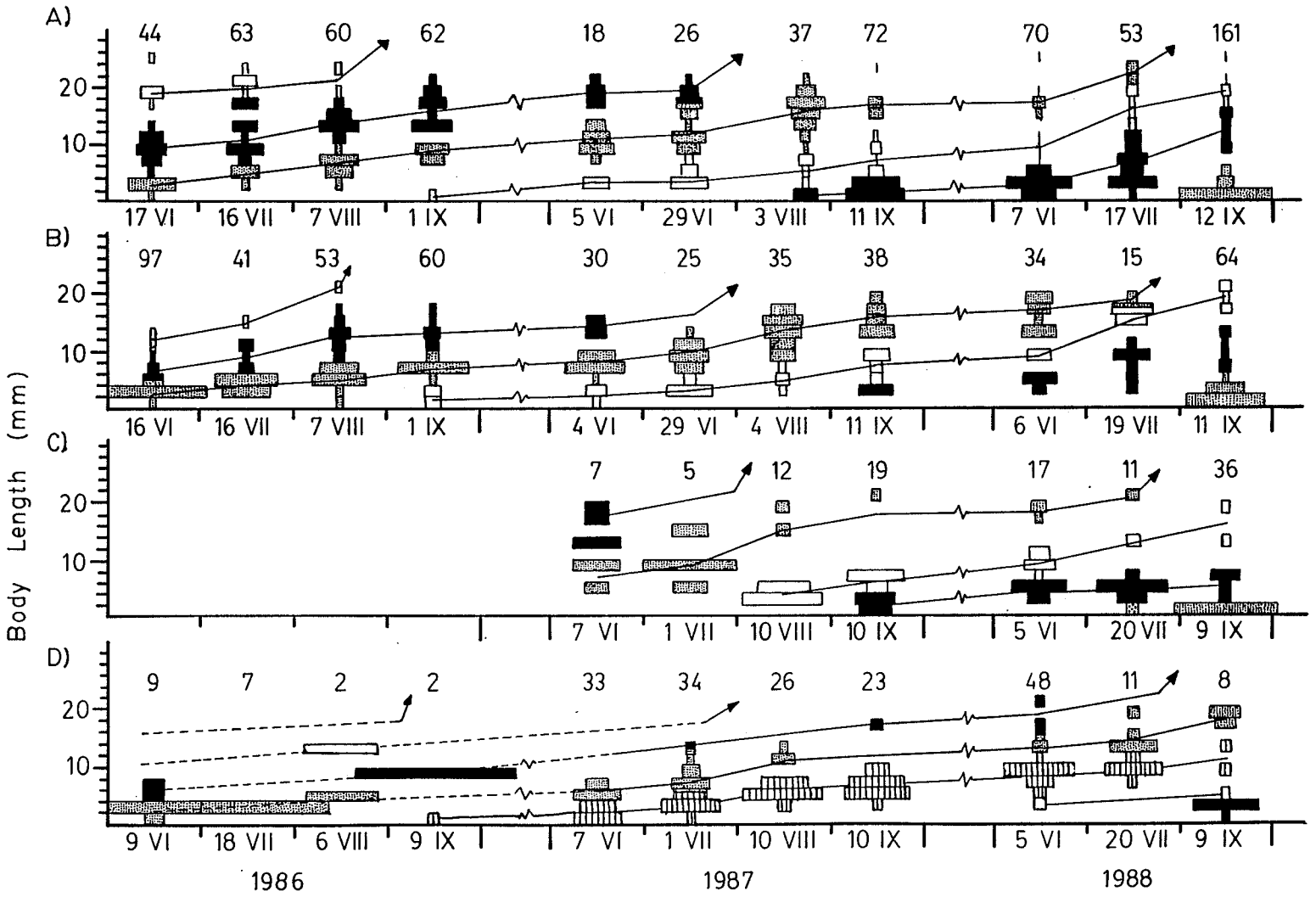

Fig. III-4. Length-frequency distributions for *Hexagenia limbata* with cohorts superimposed. Lines bisect the midpoints of each cohort as a guide for following cohorts through time (different stippling patterns represent different cohorts). Numbers at the top of each distribution refer to the total numbers collected. A) Opachuanau B) Wupaw Bay C) South Bay East D) South Bay West.

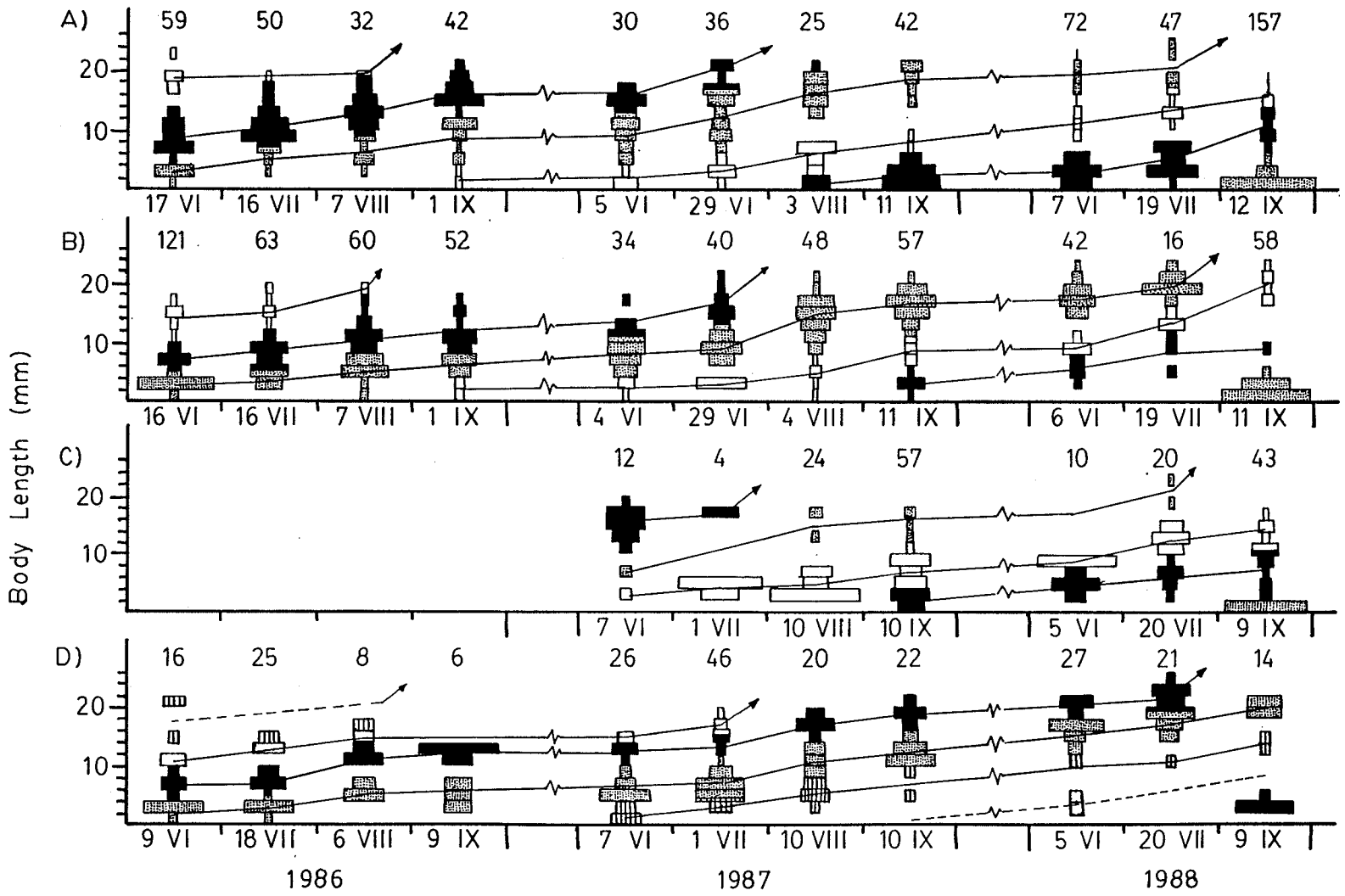

Fig. III-5. Length-frequency distributions for *Hexagenia rigida* with cohorts superimposed. Lines bisect the midpoints of each cohort as a guide for following cohorts through time (different stippling patterns represent different cohorts). Numbers at the top of each distribution refer to the total numbers collected. A) Opachuanau B) Wupaw Bay C) South Bay East D) South Bay West.

Mortality

When *Hexagenia* abundances were high enough to estimate year-to-year cohort mortality, certain patterns were noted (Table III-3; see Appendix B for actual cohort survivorship curves and mortality calculations). The highest mortality rates were seen in the period between the last nymphal stages of one generation and the first stages of the next. Based on nymphal density estimates just prior to emergence and the potential number of recruits if all nymphs had emerged and oviposited, >99% mortality occurred during this period. Mortality was usually also higher between 1986 and 1987 than between 1987 and 1988, and for mid-sized, (2-yr old) nymphs than for smaller (1-yr old) nymphs.

Size and abundance

Both abundance and size of mature nymphs appeared to be related to thermal regime. Body size of mature nymphs was determined from final-stage exuviae collected in each area during emergence because too few mature nymphs were captured in bottom samples to assess size differences adequately. Size at maturity declined for both species with decreasing dd accumulations in those areas where life cycles were of 3 yr duration, and then increased in South Bay West where the life cycle extended to 4 yr (Tables III-1 and III-4). Nymphs from Opachuanau were largest at ≈23 and ≈27 mm in length for male and female *H. rigida*, and ≈25 and ≈28 mm for *H. limbata*. Nymphs from Wupaw Bay and South Bay East were similar to each other in size, at ≈20 (male) and ≈23 mm (female) for *H. rigida* and ≈22 (male) and ≈25 mm (female) for *H. limbata*. Mature *H. limbata* nymphs from South Bay West were about the same size as those from Opachuanau, but *H. rigida* nymphs from South Bay West were smaller than those from Opachuanau.

Mean *Hexagenia* densities for the whole study period were also related to

Table III-3. Year to year mortality (%) of *Hexagenia* nymphs from the four study regions in Southern Indian Lake for 1986-1988 (See Appendix B for calculations). 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. Mortality between 3rd-1st yr, and between 4th-1st yr, refers to the total mortality between the last stage nymphs of one generation and the potential number of 1st stage nymphs of the new one. NS=no sample, *density too low to estimate mortality.

Species	Location	Year	1st-2nd year	2nd-3rd year	3rd-1st (4th) year	4th-1st year
H. limbata	Opachuanau	86-87	53.7	87.9	99.9	
		87-88	*	54.3	99.5	
	Wupaw Bay	86-87	53.6	80.7	99.7	
		87-88	33.6	61.8	99.8	
	South Bay E.	86-87	NS	NS	NS	
		87-88	53.5	31.3	99.9	
	South Bay W.	86-87	*	57.9	99.8	*
		87-88	42.6	*	*	*
H. rigida	Opachuanau	86-87	*	74.2	99.9	
		87-88	*	38.5	99.8	
	Wupaw Bay	86-87	22.9	70.8	99.8	
		87-88	20.5	46.1	99.9	
	South Bay E.	86-87	NS	NS	NS	
		87-88	53.5	31.3	99.9	
	South Bay W.	86-87	*	52.1	46.1	99.9
		87-88	72.4	44.0	12.5	99.8

Table III-4. Mean lengths (mm) of exuviae of emerging *Hexagenia limbata* and *H. rigida* nymphs collected from each study area in SIL during 1986, 1987, and 1988, and estimated mean fecundity (# eggs/female; $\bar{x}$ ± 95% C.I.) for each region.

Location	*Hexagenia limbata*			*Hexagenia rigida*		
	Length (mm)		Eggs/♀	Length (mm)		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

regional thermal regime (Tables III-1 and III-2). Highest total mean abundance (3-yr) was found in Opachuanau, followed by Wupaw Bay, South Bay East, and South Bay West. However, within years, the pattern was not as clear, since the mean *Hexagenia* density in Wupaw Bay usually exceeded that in Opachuanau in 1986 and 1987 (Table III-2). The seasonal abundance pattern reflected the life history of the two species: lowest numbers occurred in mid-summer when one cohort was emerging and the new recruits had not yet entered the population.

Adult emergence

Adult emergence data were generally combined for the two species because it is not possible to identify the adult females to species. However, among emerging males, *H. limbata* generally emerged first, followed within a few days by *H. rigida*, although for most of the emergence period, males of the two species overlapped. Emergence of both species was observed throughout the day, but most commonly during mid-morning. On sunny, calm mornings, the wings of newly emerged subimagos dried and hardened enough for flight within minutes, after which they flew to trees and bushes on shore. On windy days, emergence was hindered by wave action; the newly emerged subimagos were often swamped repeatedly by waves. Subimagos could apparently withstand considerable buffeting by waves, although wave action delayed their flight to shore, but most or all emerging mayflies were drowned when there were high winds and waves exceeding ≈1 m in height.

There was no apparent relationship between emergence and a specific water or air temperature threshold. *Hexagenia* emerged from water ranging from 8°C to 20°C. 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. III-3 and III-6), while in other areas, first emergence occurred when temperatures were declining at the end of the summer (e.g. South Bay West, 1986; Figs. III-3 and III-6). Air temperatures during emergence periods ranged from 0°C (in snow) to 30°C; however, no *Hexagenia* subimagos were seen to rise successfully from the water during snow flurries. Also, 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 in the trees required from 24-48 hours to complete the final moult at air temperatures of 10 - 25°C; longer subimaginal periods were noted on cool and cloudy days. Mortality within the cages was very low, but mortality due to predation could be significant during this period because many mayflies were captured and eaten by birds and dragonflies. Mating swarms occurred at dusk, 2200-2300 h in mid-July to ≈2100 h later in the season. After copulation, fertilized females plunged directly to the water near shore and expelled their eggs.

Emergence periods were fairly synchyronous within a region, although differences were noted among regions and among years. 90% of all the adults within each area were caught within a 2-3 wk period each year, but emergence periods occurred successively later in the cooler study locations within years, and also in cooler years within study areas (Fig. III-6). 1987 and 1988 had similar annual dd accumulations (Table III-1) and emergence timing was also similar. 1986 was considerably cooler than 1987 and 1988, resulting in delayed emergence when compared to the other two years, particularly in the cooler locations.

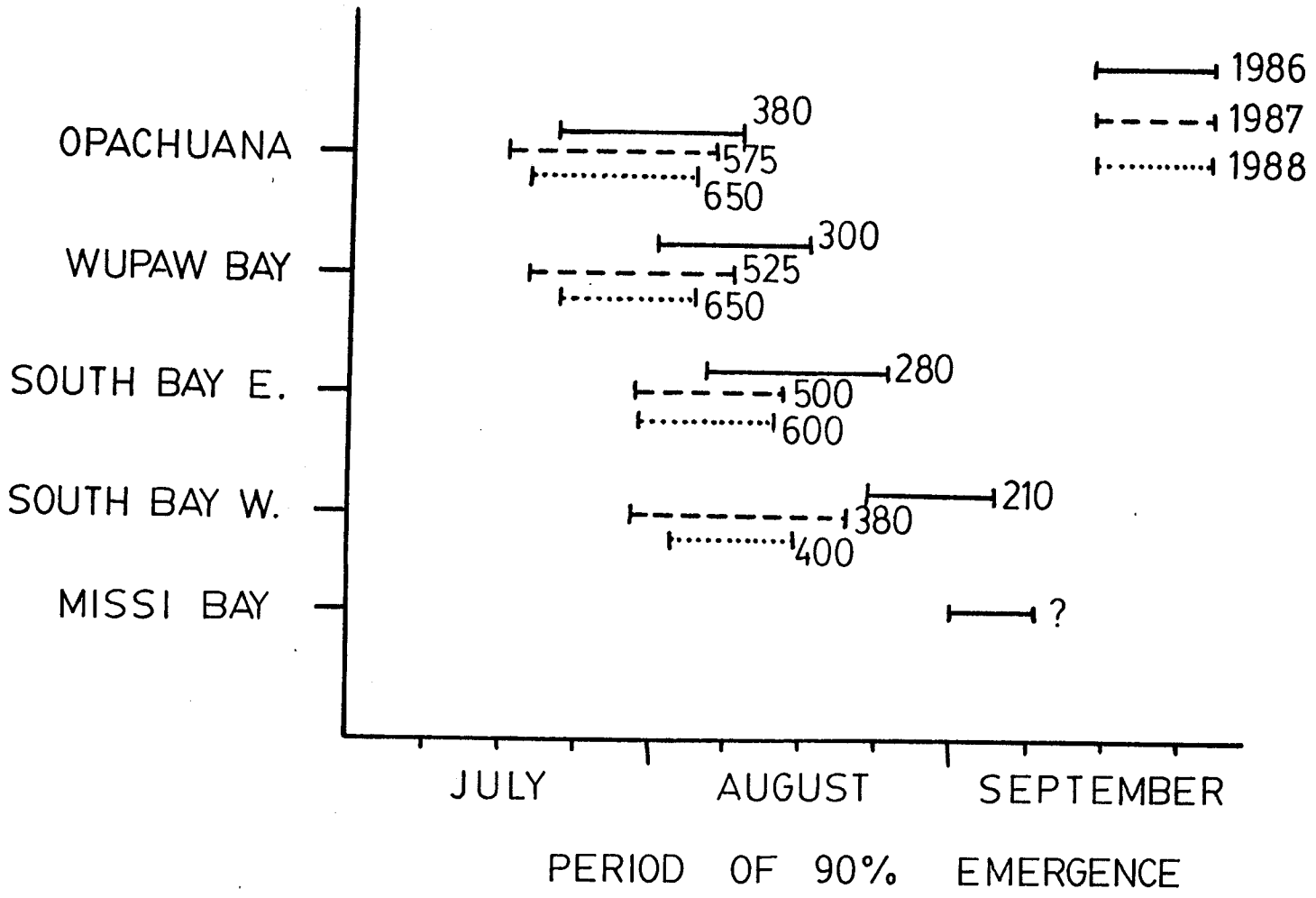

Fig. III-6. Periods of 90% emergence for *Hexagenia* in the four study areas and for Missi Bay, a small bay near the natural outlet of the lake, 1986-1988. Numbers beside each bar refer to total accumulated water dd>10°C for each summer.

Usefulness of a degree day (dd) model to predict Hexagenia development

Accumulated dd requirements for total development (egg to adult) were not consistent among regions, ranging from 1222-1468 dd>10°C (or 1800-2086 dd>8°C) in the different study areas (Table III-5a). This lack of consistency suggests that the standard dd model (Southwood 1978) is not a good predictor of *Hexagenia* emergence in SIL. For example, differences of 246 dd>10°C and 286 dd>8°C were seen between the four areas, or a maximum deviation of 123 dd>10° and 143 dd>8° from the average. For purposes of comparison, if a constant bottom water temperature of 15°C around the time of emergence is assumed, 123 dd is equivalent to ≈25 days above a threshold temperature of 10°C [since $dd \div (T-T_m)=d$, where T=temperature, T_m=threshold temperature, d=days; $123 \div (15-10)=25$] and 143 dd is equivalent to ≈20 d >8°C. In other words, if an emergence date was predicted from the mean dd accumulation for the four study areas, at 15°C, observed emergence in all study areas would have varied from the predicted date by several weeks.

However, if dd accumulation was summed for just the final summer prior to emergence (Table III-5b), the predictive capability of the dd model was considerably improved. Degree days to onset of emergence in each year and each area ranged from 168-218 dd>10°C or 257-302 dd>8°C (Table III-5b), or a difference in predictive capability at 15°C of only 3.5 to 5 d.

Fecundity

Fecundity (number of eggs/female) was strongly correlated to female subimago body size (Fig. III-7), so this relationship could be used to determine fecundity by measuring subimagos from each area. However, adults and subimagos were collected only on one or two occasions through any emergence period. Exuviae from last-stage nymphs were collected throughout

Table III-5. Accumulated degree days (dd) for *Hexagenia* development calculated assuming developmental thresholds of 8°C and 10°C. a) Total dd from egg to adult (1985 cohort), b) dd to emergence in the final year of development (all cohorts).

a) Total Development (1985 cohort)

		Degree Days			
Threshold	Year	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				368
	Total	2059	1891	1800	2086
10°C	1985	259	214	171	123
	1986	380	300	278	210
	1987	575	524	496	388
	1988	254	278	277	400
	1989				268
	Total	1468	1316	1222	1389

b) Accumulated dd from thaw to start of emergence in each year

Location	Year	Date of 1st Emergence	Bottom temp: 1st emergence	dd>8°C	dd>10°C
Opachuanau	1986	20 July	16°C	272	188
	1987	16 July	18°C	286	206
	1988	17 July	17°C	275	189
Wupaw Bay	1986	1 August	14°C	269	175
	1987	17 July	17°C	302	218
	1988	24 July	18°C	282	200
South Bay East	1986	5 August	15°C	276	175
	1987	17 July	18°C	296	210
	1988	29 July	18°C	293	198
South Bay West	1986	23 August	13°C	257	168
	1987	28 July	17°C	268	180
	1988	28 July	17°C	275	185

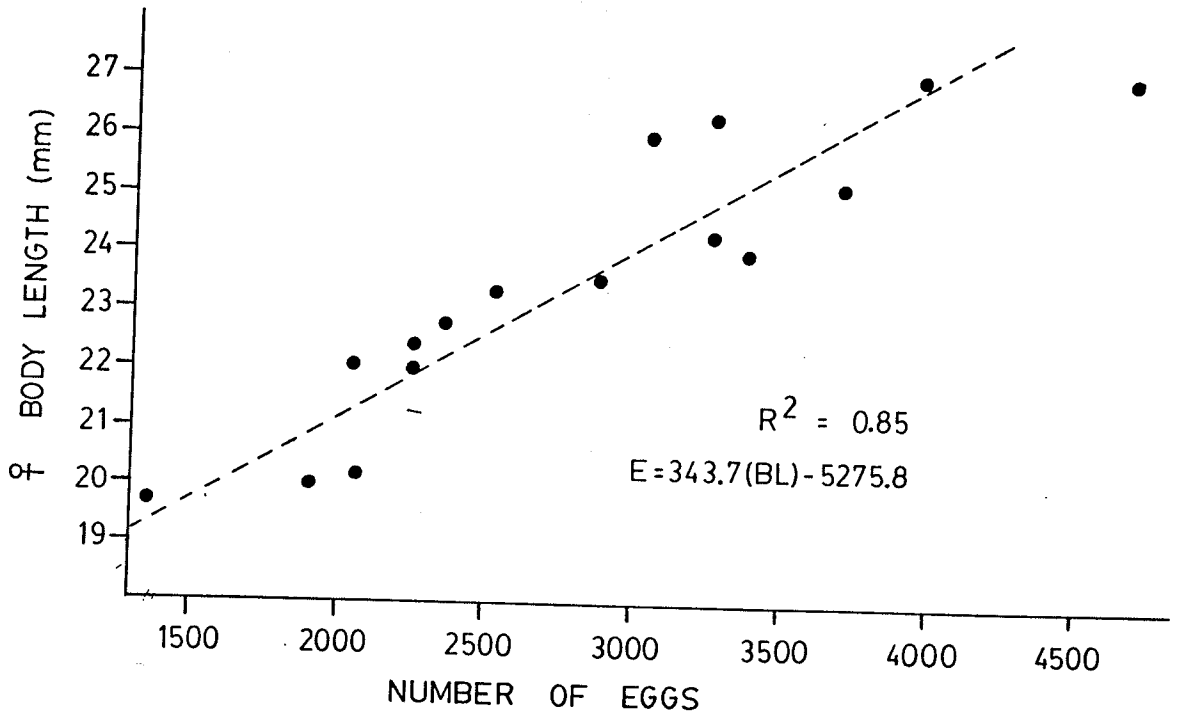

Fig. III-7. Relationship between female subimago body length (both species combined) and fecundity (no. eggs/female). E=no. of eggs; BL=body length

the emergence periods, and therefore, gave a better indication of overall mean size from a given area. Furthermore, size of exuviae was strongly correlated with subimago size (Fig. III-8), so fecundity of *Hexagenia* for each area could be determined indirectly from exuvial length.

The effects of thermal regime on fecundity were similar to the effects on nymphal size because of the relationship between size and fecundity. In the areas with 3-yr life cycles, fecundity was highest for adults from Opachuanau, averaging nearly 3400 eggs/female for *H. rigida* and 3600 eggs/female for *H. limbata* (Table III-4), compared to only ≈2300-2800 (*H. limbata*) and ≈2000-2150 (*H. rigida*) eggs/female from Wupaw Bay and South Bay East. Adults emerging from South Bay West, after a 4-yr life cycle, had higher fecundities than either Wupaw Bay or South Bay East, at >3750 eggs/female for *H. limbata* and nearly 2300 eggs/female for *H. rigida* (Table III-4).

DISCUSSION

I. LIFE HISTORY

Life cycles

Life cycles of the two species were nearly identical, ranging from 3 yr in the warmer locations of Opachuanau, Wupaw Bay, and South Bay East, to 4 yr in South Bay West. Adults emerged and deposited their eggs sometime after the middle of July; recruitment began about 4-6 wk after oviposition, depending on water temperature and the date of oviposition. In South Bay West, the coldest area investigated, oviposition generally occurred too late in the season for egg hatch to occur that summer, and most or all of the eggs presumably overwintered. Even in the warmer areas, where egg hatching occurred in the summer of oviposition, newly hatched nymphs were also observed early in the

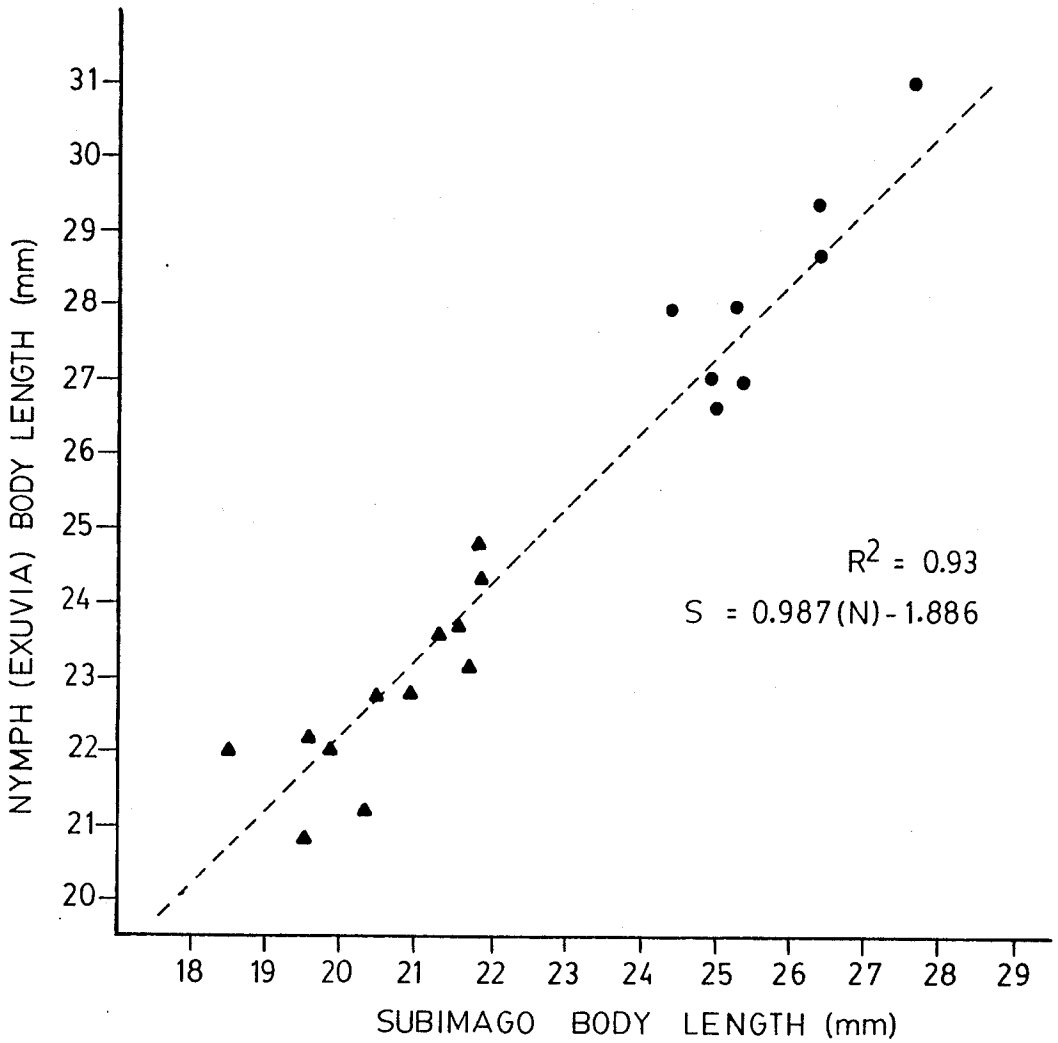

Fig. III-8. Relationship between exuvia (N) and subimago (S) body length for *Hexagenia* from Southern Indian Lake. ▲ = ♂ ● = ♀

next summer, before any further emergence. Some eggs must have overwintered in these locations. In the laboratory, only ≈50% of eggs of *H. limbata* from SIL hatched immediately under suitable temperature conditions; the remainder hatched after exposure to a period of cold (4°Cd) temperatures (Chapter IV). The occurrence of a similar bimodal hatching pattern in the field would explain the presence of small nymphs early in summer, before the adult emergence period.

In this study, determination of cohorts was facilitated by evaluating frequency distributions for mesothoracic wing-pad length, a developmental stage indicator, as well as for two growth measurements (body length and head width). Life history analysis is based on the assumption that members of a cohort grow at the same rate, so that when a growth measure is plotted as a frequency distribution, the cohorts are assumed to correspond to the peaks in the distribution (Butler 1984). However, determination of *Hexagenia* life cycles is frequently confused by the overlapping of frequency distributions for successive cohorts, due to differential growth rates between sexes and individuals, and to delayed hatching responses (Heise *et al.* 1987). By superimposing a developmental stage indicator onto the growth responses, the cohorts are easier to separate. For example, Heise *et al.* (1987) were able to separate a complex of several life-cycle types of *H. limbata* in Dauphin Lake, Manitoba by looking at subjectively determined wing-pad stages to estimate the approximate developmental stage.

The 3-4 yr life cycle observed in the study areas in SIL is considerably longer than previously reported for *Hexagenia*. Life cycles are related to thermal regime, but were generally believed to range from about a year in the south to a maximum of 2 yr in the north (Carlander *et al.* 1967, Flannagan 1979, Heise *et al.* 1987, Horst and Marzolf 1975, Hudson and Swanson 1972, Hunt

1953, Riklik and Momot 1982, Rutter 1972). McCafferty (1975) briefly mentioned a possible 3-yr life cycle for *H. limbata*, but did not note the location. Mozley and Ladronka (1988) suggested that a deep water population of *H. limbata* in the Straits of Mackinac, between Lakes Michigan and Huron, may also require 3-yr to complete development. The life cycle of *Hexagenia* is obviously more flexible than previously believed; the question arises: how long can *Hexagenia* extend its life cycle to accumulate the necessary dd for growth.

Degree day requirements

Degree day (dd) requirements, at least for *H. limbata*, appear to decline with latitude. In southern populations, *H. limbata* require ≈2500 dd >10°C to complete development (calculated from Hudson and Swanson 1972, Hunt 1953, Welch and Vodopich 1989), compared to 1700-2000 dd>10°C in Dauphin Lake, Manitoba (Heise *et al.* 1987), and only 1200-1500 for the SIL population. It is tempting to postulate that the apparent decline in dd requirements is caused by a decline in the threshold temperature for growth and development with increasing latitude; northern populations of many insect species have lower developmental thresholds than southern ones (Danks 1987). Preliminary analysis of the data supported this hypothesis because the actual threshold for development for *H. limbata* from SIL is near 8°C (Chapters IV & V), which is lower than that commonly cited for the species (Heise *et al.* 1987, Hunt 1953). However, it is not possible to make comparisons with southern populations, because the reported threshold temperatures cited for these populations are based on field data, and have not previously been determined experimentally for either *H. limbata* or *H. rigida.* In addition, dd requirements calculated using the linear dd model are based on an estimated

threshold temperature, which may be higher than the actual threshold because the actual development/temperature response follows a logistic, rather than a linear curve (Higley *et al.* 1986, Pruess 1983, see also discussion in Chapter IV). Although the actual threshold for the SIL population of *H. limbata* is probably near 8°C (Chapter IV), the estimated, or derived, threshold was determined to be near the 10°C usually cited for *H. limbata* (Chapter IV). Therefore, no geographic differences were seen in the responses in the middle part of the temperature range or in the derived threshold. Although it is not possible to compare experimental thresholds among studies since these were not determined for southern populations, there is no evidence that differences in dd accumulation are caused by lower thresholds in northern populations.

Another, more likely, explanation for the decline in dd requirements with increasing latitude is the increased amount of time spent by northern populations at temperatures near the lower threshold. Because the relationship between developmental time and temperature follows a logistic (sigmoidal) curve, it can only be represented by a linear model for temperatures in the middle ranges of the curve (Higley *et al.* 1986, Pruess 1983). Consequently, development will be faster than predicted from the dd model at temperatures near the lower threshold, and slower than predicted near the upper threshold. In more northerly habitats, considerable time may be spent in spring and fall at temperatures between about 8°C and 10°C, resulting in faster development than predicted from the dd model, and lower apparent dd requirements.

Other researchers have indicated that *Hexagenia* may not be able to emerge at temperatures below about 14°C (Fremling 1973, McCafferty and Pereira 1984), and have hypothesized that an emergence threshold temperature could result in variations in dd requirments between populations (Heise *et al.*

1987). However, *Hexagenia* in SIL began emerging when water temperatures varied between 13°-18°C in the different study locations, and the emergence occurred over a water temperature range of 8°-20°C into air temperatures of 0°-30°C. Therefore, it is unlikely that an emergence threshold temperature plays a role in emergence timing of the SIL population. In contrast to a temperature threshold, Neave (1932) suggested that *Hexagenia* in Lake Manitoba needed to reach a certain threshold size before emergence. In the SIL population, closer agreement was found between emergence timing and dd accumulation in the final summer than between emergence timing and total dd accumulation over the whole life cycle. It is possible that individuals beyond a certain developmental stage may respond to a temperature cue (such as warming in spring) to progress through the final developmental stages before emergence; development to the final stage, however, would still be temperature dependent. This would result in the differences in emergence timing between study areas with different thermal regimes, and it would also explain why *Hexagenia* were observed emerging late in the season in some localities, despite the catastrophic effects associated with such a late emergence.

Body Size

Adult body size is an important ecological parameter because of its relationship to fecundity, and potential recruitment success (Clifford and Boerger 1974, Sweeney 1984). Sweeney and Vannote (1978) predicted that size of hemimetabolous aquatic insects would be maximized in areas where temperature conditions were optimum, and that body size would decrease at temperatures above and below the optimum. Food conditions also play a role in determining body size (Söderström 1988, Sweeney et al. 1986a, b, see also Chapter V), but in general, body size is expected to decrease with distance of

the population away from the optimum habitat. However, Stanley and Short (1988) pointed out that this "thermal equilibrium hypothesis" was developed for north-temperate univoltine species which were exposed to the entire range of thermal conditions in a year, and that it did not necessarily hold for species that were not univoltine. For multivoltine species in warm-water habitats, a single location could provide several different successive thermal regimes, some of which might be optimal, whereas others would be sub-optimal. Similarly, for species whose life cycles vary in length depending on temperature, populations located near to each other geographically may be exposed to different thermal regimes simply by changing voltinism. Adult body size would be expected to decline with increasing latitude to the point where voltinism changed, then increase in response to the longer period spent in growth. This is the pattern seen in *H. limbata* over the latitudinal gradient from ≈31°N to 57°N (Table III-6). The maximum reported size of ≈35 mm was observed both at 42°36'N in Michigan (Hunt 1953), and at 51°14'N in Manitoba (Heise *et al.* 1987); sizes declined on both sides of these peaks (Table III-6). In SIL, the effects of 3- and 4-yr life cycles and different thermal regimes on body size are clear. Average size of mature nymphs declined with decreasing temperature within the locations where nymphs had a 3-yr life cycle, then increased dramatically when the life-cycle jumped to 4-yr. The pattern was more pronounced for *H. limbata* than for *H. rigida*, however, suggesting that *H. limbata* is better adapted to cold environments than *H. rigida*.

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

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

Fecundity

Fecundity in a population is an important life history parameter that influences its overall success through its effects on the number of potential recruits to the population. Fecundity was related to female body size, and so it was expected to vary with the factors that affect body size (e.g. temperature). Consequently, there was higher fecundity, and therefore higher potential abundance, in the warmest location (Opachuanau), and also in South Bay West, where the life cycle was 4-yr in length rather than 3-yr.

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

Mortality

A number of mortality factors may be acting on the SIL population: 1) predation in the nymphal stage, 2) overwintering mortality, perhaps related to insufficient food reserves to survive the very long SIL winter, 3) emergence mortality from weather or predation, 4) predation while in the winged stages, and 5) temperature-related egg mortality (low hatching success) (Fig. III-9). Although *Hexagenia* are not the major food source for most of the commercially important fish species in SIL (Lake Whitefish, Northern Pike, Yellow Walleye), they are apparently selectively eaten, at least by Whitefish (Hamilton 1974).

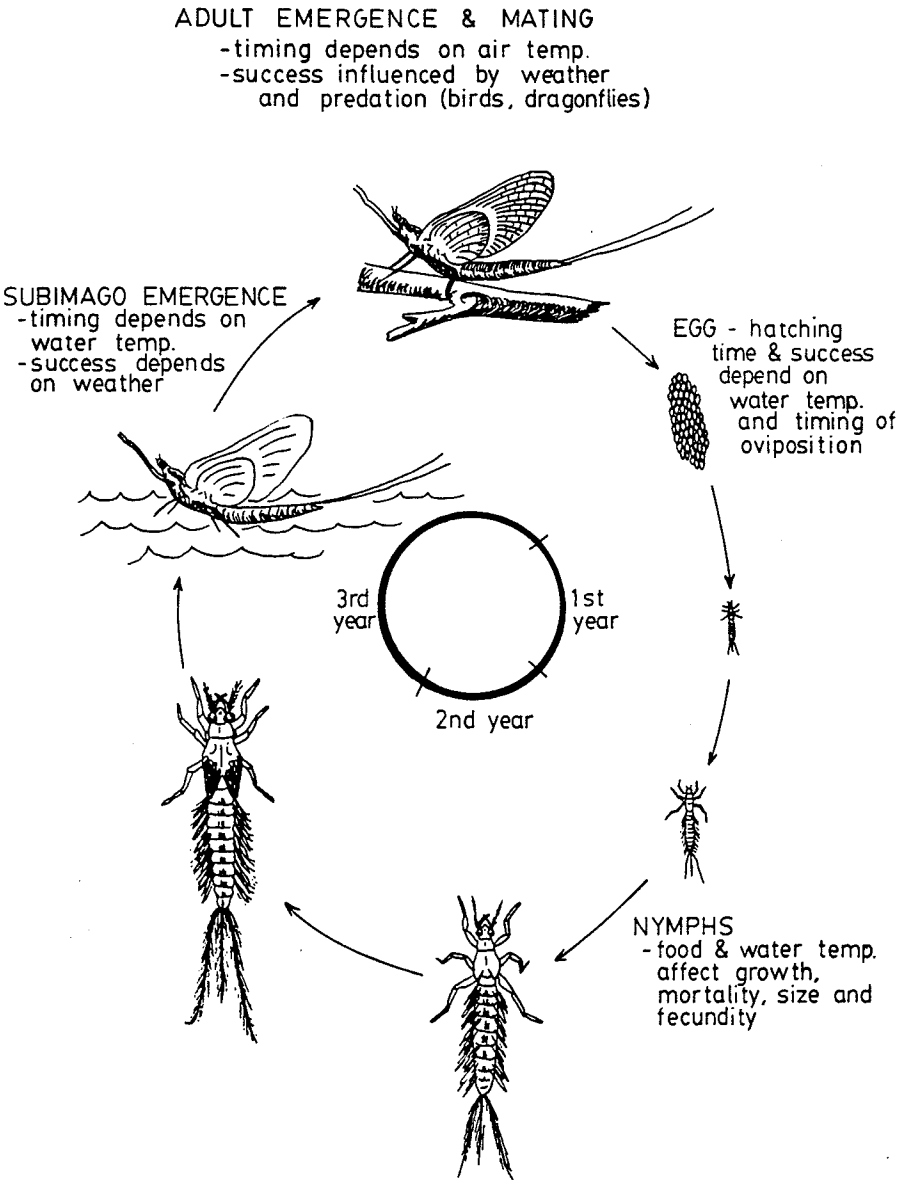

Fig. III-9. Summary of 3-yr *Hexagenia* life cycle and the factors influencing abundance in Southern Indian Lake.

In addition, large numbers of subimagos and adults are eaten by birds and dragonflies during emergence and swarming, so predation is probably also a factor during the winged stages. Laboratory experiments on an SIL population of *H. limbata* indicated that the very young nymphs cannot survive at low temperatures for more than a few months (Chapter V), so for this age-group at least, overwintering mortality may be very high. Finally, hatching success of the eggs was low at low temperatures (Chapter IV), indicating that fewer of the potential recruits may enter the population in colder years or colder areas.

In SIL, the greatest mortality was seen in the period between the late-stage nymphs of one generation and the first-stage nymphs of the next, so that <1% of potential recruits to the population (calculated from estimated density and fecundity for each area) actually survive. Of the <1% that do survive, mortality through the nymphal life cycle reduces the population by a further 40-95%, with the greatest nymphal mortality occurring between the 2nd and 3rd year of growth. Nymphs range from about 10-20 mm in length at that stage, and so may be more susceptible to predation by Whitefish due to their relatively large size and visibility. Mortality was also higher after the cold year of 1986 than after 1987, suggesting that periods of extended cold may influence mortality.

II. TEMPERATURE EFFECTS ON ABUNDANCE OF *HEXAGENIA* IN SIL

One of the major objectives of this research was to determine the factor or factors controlling *Hexagenia* abundance in SIL. Because *Hexagenia* abundance was strongly correlated to a weather variable (air temperature), over the 15-yr monitoring period (Giberson *et al.* 1991, Chapter VI), weather effects on population dynamics were evaluated.

Weather affected *Hexagenia* over the whole life cycle, through its effects on nymphal and adult mortality, size and fecundity, and egg hatching success (Fig. III-9). Because the lake does not stratify thermally, water temperature in SIL was directly related to air temperature during the open-water season, although the relationship was different for each lake region. Relatively cool water temperatures in SIL, compared to more southerly locations, resulted in very long *Hexagenia* life cycles, which in turn, should result in higher accumulated mortality (Rempel and Carter 1987). Therefore, low temperatures would result in higher overall nymphal mortality, and fewer emerging adults in colder regions, or in colder years within regions. Fewer emerging adults would result in lower potential recruitment, and subsequently, lower potential abundance.

Weather during the emergence period affected emergence and mating success, and consequently may also have influenced potential recruitment. Whelan (1980) reported that populations of *Ephemera danica* were nearly eliminated in Ireland by cold weather and high winds during an emergence period, and Hunt (1953) and Lyman (1944) noted that cold, windy weather hindered both emergence and swarming of *H. limbata* in Michigan lakes and in Lake Erie. In SIL, *Hexagenia* did not successfully emerge in waves of >1 m, and emergence was hindered at wave heights of much less than that. Cool air temperatures also delayed moulting to the imaginal stage, increasing the risk

of predation; in extreme cold (near freezing), the final moult did not occur. Cooler water temperatures delayed emergence, both among years and among regions within a year. At SIL, cooler years were generally windier than warm years (Appendix C), and even in warm years, storms were more likely later in the season than during mid-summer. Consequently, storm-related emergence mortality was a factor in cool years in all regions, and especially in the coolest regions where the emergence periods extended as late as September.

The temperature regime during nymphal development also influenced growth and size at maturity, which in turn affected fecundity. Food also affected size at maturity of *Hexagenia* nymphs (Chapter V), but food was probably not limiting in SIL during the study period due to continued inputs of nutrients and organic matter from flooded shorelines (Crawford and Rosenberg 1984, Wiens and Rosenberg 1984). Size and fecundity declined with decreasing temperature within a voltinism type (3-yr or 4-yr), resulting in lower potential recruitment and abundance in the cold regions or colder years within regions. The larger size and higher fecundity observed in South Bay West compared to the warmer Wupaw Bay and South Bay East was at least partially offset by the higher accumulated mortality associated with the longer life-cycle.

Finally, weather affected egg hatching and initial mortality of young nymphs, through temperature effects on hatching success and timing. Fewer eggs hatched in the laboratory at lower temperatures (Chapter IV), suggesting that recruitment would be lower in colder regions or colder years. In addition, cooler temperatures delayed egg-hatch (Chapter IV). In SIL, eggs in cool areas would not hatch until very late in the oviposition season, resulting in newly-hatched nymphs entering winter without the nutritional reserves required to overwinter successfully. In these locations, bimodal egg hatching due to diapause (Chapter IV) probably ensured that at least some of

the new cohort would overwinter in the egg stage, even if most of those that hatched in the fall did not successfully overwinter. Ironically, cool summer weather was probably beneficial to populations in South Bay West, the coldest area studied, since all eggs (diapausing and non-diapausing) would be expected to overwinter, giving higher overall survivorship. In contrast, the warm year of 1988 resulted in an autumn hatch of non-diapausing eggs in South Bay West, and a high probability of overwintering mortality of the newly hatched nymphs.

Air temperature accounted for ≈95% of the variation in whole-lake *Hexagenia* abundance during the period from 1972 to 1987 (Giberson *et al.* 1991, Chapter VI). Therefore, factors such as predation or competition may not be as important to this northern population, possibly because of relatively low densities compared to southern populations (Chapter V). Temperature, on the other hand, is important because of the increased impact of small weather changes on a population living near the extreme edge of its distribution.

Despite the strong correlation, it is evident from this study that the relationship between air temperature and abundance of burrowing mayflies is not a simple one. The strong relationship stems from the correlation between air temperature and those factors that actually do influence *Hexagenia* abundance. Air temperature was related to conditions during emergence, which affected mortality and mating success, and to water temperature during the life cycle, which affected nymphal mortality, egg-hatch and timing, and emergence timing and fecundity. The length of the life-cycle, which was considerably longer than previously believed, resulted in a very long recovery period after the population decline in the late 1970's, and confused the interpretation of the monitoring data. Life history information is crucial to the understanding of impacts due to industrial development, and should be an integral part of monitoring and impact studies.

CHAPTER IV

EGG HATCHING IN *HEXAGENIA LIMBATA* (SERVILLE) (EPHEMEROPTERA: EPHEMERIDAE) FROM SOUTHERN INDIAN LAKE MANITOBA: TEMPERATURE EFFECTS AND DIAPAUSE

ABSTRACT

Egg hatching was investigated for *Hexagenia limbata* (Serville) from Southern Indian Lake (SIL) in northern Manitoba, Canada. In the SIL population, located near their northern range extent in Manitoba, some important differences in hatching dynamics from southern populations were observed. Hatching success and egg development time were related to temperature, as reported in the south, but the developmental threshold temperature for the SIL population was near 8°C, 2° lower than previously reported. Therefore, storage of the eggs at 8°C resulted in slow but measurable development rather than low-temperature quiescence as expected, and subsequently, inconsistent degree day estimation among temperature treatments. Following storage at 8°C, eggs took longer to hatch and hatching success was lower at 8°C and 15°C than at 20°C. Hatching success improved with increasing time in storage, ranging from only 50% hatch in unstored eggs to >90% hatch in eggs that had been stored at 8°C for ≈6 mo. In addition, a bimodal hatching response was seen in the eggs, with about half of the eggs deposited by individual females hatching immediately under favourable conditions, and the remainder hatching after exposure to cold. A lower threshold than previously reported and a previously undescribed egg diapause may enable *H. limbata* to persist near the northern extent of its distribution.

INTRODUCTION

Hexagenia limbata (Serville) is a burrowing mayfly found in lakes and rivers over much of North America (Edmunds *et al.* 1976, McCafferty 1975). Development of eggs and nymphs is temperature dependent, and the life cycle ranges from <6 mo in Utah irrigation canals (Edmunds *et al.* 1976) to >4 yr at the extreme northern edge of their distribution (Chapter III). The egg stage may be completed in as little as 2-3 wk under summer conditions (>20°C: Flattum 1963, Hunt 1953, Neave 1932), or it may extend over weeks or months at cooler temperatures (Flattum 1963, Hudson and Swanson 1972). The developmental threshold temperature, or the temperature below which no development occurs, has been reported to be around 10°C for all stages (Hunt 1953, Flattum 1963, Hudson and Swanson 1972, Heise *et al.* 1987).

Developmental variability in *Hexagenia* often results in life cycles that are complex and difficult to interpret. Cohorts frequently overlap, which makes them difficult to distinguish using standard frequency analysis. There may also be mixed life cycles, in which some individuals complete development in a year or less, while others in the same population lag behind by several months (e.g. Flannagan 1979, Heise *et al.* 1987, Horst and Marzolf 1975). Overlapping cohorts and mixed cycles result from the year-year differences in emergence timing of adults, which in turn relate to the developmental variability of the immatures. Previous workers have concentrated on nymphal development when interpreting the life cycle, but large variations in voltinism can be attributed to timing of egg development as well. Eggs deposited early in the season, when temperatures are warm, hatch quickly, enabling substantial nymphal growth in the first season. Eggs deposited later in the season, however, may not hatch before winter; several months may pass

before hatching and the start of nymphal growth. The alternating 14/24 mo cycles found for *H. limbata* in Lakes Winnipeg and Dauphin in Manitoba (Flannagan 1979, Heise *et al.* 1987), for example, are a result. An understanding of the dynamics of egg development, therefore, is crucial to the understanding of the life cycle of *Hexagenia*.

In this paper, temperature affects on hatching parameters of *H. limbata* were examined on eggs collected from Southern Indian Lake, Manitoba, a large reservoir located near the northern limits of distribution of *H. limbata* in Manitoba. The implications of these effects, including a previously undescribed egg diapause, on life-cycle strategies will also be discussed.

MATERIALS AND METHODS

Site description and collection of adults

Southern Indian Lake (SIL) is located in northern Manitoba, Canada (lat. 56°38' to 57°40' N; long. 99°45' to 98°10' W; Fig. IV-1). The lake, a newly impounded reservoir, lies in a region of discontinuous permafrost, and has an annual ice-free period of about 5 mo (Newbury *et al.* 1984). *Hexagenia* adults were collected from two sites: Opachuana basin, at the inflow of the Churchill River into SIL (56°42'N, 99°34'W) and Wupaw Bay, a shallow bay just south of the main flow through the lake (56°47'N, 99°6'W; Fig. IV-1).

Adults were collected by hand-picking and sweeping shoreline vegetation with a net at each site during the peak of the emergence period in 1987. Specimens were returned to the lab for identification, and eggs for the study were fertilized by artificial insemination.

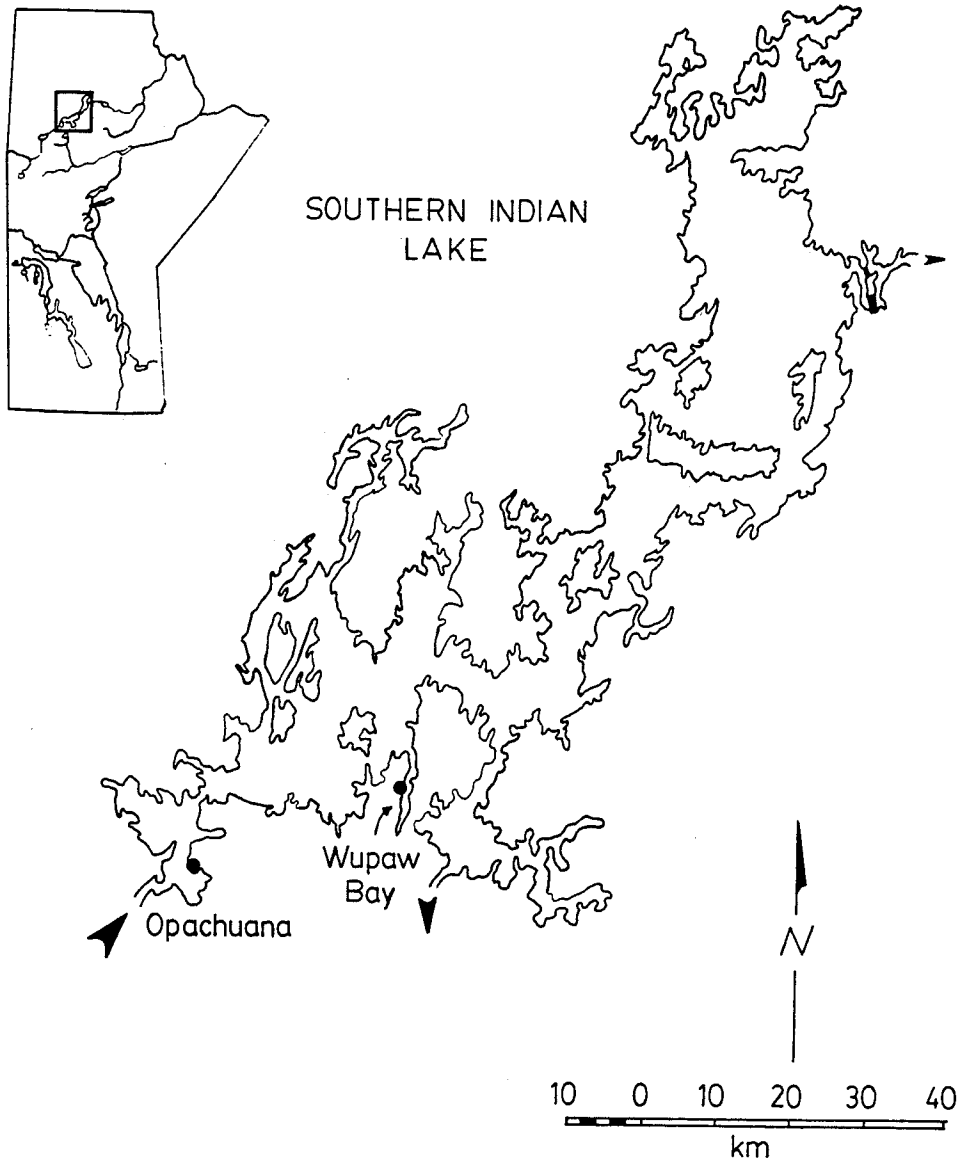

Fig. IV-1. Southern Indian Lake, Manitoba, with locations of adult collections (solid dots) and major lake inflow and outlets (arrows).

Artificial insemination technique

Two *Hexagenia* species occur in SIL: *H. limbata* and *H. rigida*. Males are easily separated by the shape of the penes, but females cannot be distinguished (McCafferty 1975). Therefore, the method of Friesen (1981) was used to ensure that fertilized eggs of *H. limbata* were obtained for the experiments. Two thousand to four thousand eggs (depending on female size, see Chapter III) were stripped from each of 15 female *Hexagenia* subimagos at 20°C, and the eggs from each female were separated into three groups in separate Petri dishes containing a few drops of Yaeger's solution (formula given in Friesen 1981). Mating does not occur until the imaginal stage, but eggs from subimagos are viable, so subimagos were used to ensure that the females had not previously mated (Friesen 1981, Hunt 1951). Terminal abdominal segments of individual male *H. limbata* were then added to one Petri dish in each group, those from male *H. rigida* were added to a second set of dishes, and the third set was left without fertilization. The terminal segments were macerated and mixed with the eggs in the Yaeger's solution. The mixtures were allowed to stand for 10 min, then dishes were filled with filtered lake water.

Development in the eggs is obvious within a few days. On the fifth day after insemination (5 d into the experimental period), eggs were examined under a dissecting microscope. Dishes with <5% of eggs showing development at this time were assumed to have been unsuccessfully inseminated or to have resulted from accidental crosses between the *H. limbata* males and *H. rigida* females, and were discarded. Successful insemination was noted in four dishes, with little or no apparent development in the remaining 11 dishes. Eggs from the four successful crosses were separated into groups of 50 (for each cross), and were added to 50 dram vials containing filtered lake water

for storage and later treatment at different temperature combinations. Each treatment consisted of three replicate vials containing 50 eggs each from each of the four successful male:female pairings.

Storage procedure

Friesen (1981) determined that *H. rigida* eggs could be stored at 8°C, 2°C below the reported developmental threshold, for up to a year with little or no change in hatching parameters. *Hexagenia limbata* eggs have also been reported to stop development below 10°C (Flattum 1963), so eggs were cooled in 4 C° increments (4 d each) to 8°C (Friesen 1981), and stored at 8°C until the start of treatments. Storage was necessary because eggs were collected from SIL during the summer, but treatments could not begin in the Winnipeg laboratory until winter.

Treatments

Eggs were incubated in controlled environment chambers (temperature fluctuations <0.5°C), and in constant light. Vials were examined under a dissecting microscope, and newly hatched nymphs were counted and discarded.

Treatment 1 (Fig. IV-2) was originally designed as a control treatment. Eggs were maintained at 20°C at SIL, and were checked daily for 45 d to record hatching success and time to hatch for comparison with stored eggs. After 45 d, remaining unhatched eggs from the control treatment were inadvertently transported with the eggs stored at 8°C to the Winnipeg lab. After about a month, these were re-warmed to 20°C, and checked again.

Treatment 2 was the "storage" control, established to ensure that 8°C was below the developmental threshold. Eggs were held at 8°C throughout the study period and checked approximately weekly.

In treatments 3-6, eggs were stored at 8°C for at least 90 d before

being placed at the various study temperatures (note that 8°C was believed to be below the developmental threshold, so development was expected to be arrested during the storage period). Temperature treatments following storage (Fig. IV-2) were chosen to simulate conditions observed at different times or locations at SIL:

- -Treatment 3: overwintering at 4°C - eggs were cooled to 4°C for a further 90 d (after storage) to mimic winter conditions, and then warmed to 8° (Treatment 3a), 15° (3b), and 20°C (3c). Spring temperatures in SIL were ≈8°, mid-summer temperatures in cool areas were ≈15°, and those in warm areas were ≈20°C.
- -Treatment 4: SIL summer temperatures - eggs were warmed immediately to 15° (Treatment 4a) and 20°C (4b) following storage.
- -Treatments 5 & 6: warm summer temperatures but varying time in storage - eggs were maintained at the storage temperature for 120 d and 190 d, respectively, before warming to 20°C.

In all treatments, eggs were examined daily after warming to the final treatment temperature. Treatment differences were analyzed by comparing hatching success (mean % hatch ± S.E.) and developmental periods (total days required for hatch, days above the threshold temperature, and degree days above the threshold) at the various temperature combinations. Degree days (dd) were calculated using a linear model (Southwood 1978):

$$dd=(T-T_0)d$$

where T=study temperature

T_0=threshold temperature

d=days>threshold

5. Diapause trials

Although no diapause stage had previously been reported for *Hexagenia*, preliminary results from the egg hatching experiments suggested that some *H. limbata* eggs from SIL required exposure to cool temperatures to hatch. Eggs from Treatment 1 were accidentally cooled to 8°C for 30 d after being held at 20°C for more than a month after the last observed hatch. After subsequent re-warming to 20°C, a further 1-19% of these eggs hatched. The un-hatched eggs were viable, but apparently needed cold stimulation to hatch.

To test for diapause, fertilized eggs were obtained as above from a previously unmated pair of adults (both parents had been reared in the lab from SIL eggs). Fifty eggs were placed in each of twelve vials, and allowed to develop and hatch at 20°C. Vials were checked daily, and newly hatched nymphs were removed from vials and discarded. Hatching success and time to initial hatch were recorded as in Treatment 1 (egg-hatching experiments). Thirty days after the last recorded hatch, the groups of vials containing the remaining eggs were then separated into four diapause treatments (Fig IV-3), each with three replicates. Vials from the first treatment in the diapause series were held at 20°C for an additional 60 d to determine whether further hatching would occur during that period without exposure to cold. Eggs in the remaining three treatment series were cooled in 4 C° stages (of 4 d each) to 4°C for 30 or 60 d, or to 8°C for 30 d before re-warming to 20°C (Fig. IV-3). After re-warming, eggs were again checked daily for hatch, and treatments were analyzed by comparing overall hatching success and time to hatch at each temperature combination.

RESULTS

Hatching Success

Eggs from individual parent crosses were initially kept separate to determine whether there were differences in hatching responses among egg masses. No differences were seen in the hatching success from the different crosses for most temperature temperature treatments (Tukey's multiple comparison test, alpha=.05). Significant differences were seen in temperature treatments 3b and 3c, but the differences were not consistent between crosses; therefore hatching results using eggs from different parents were combined and summarized in Fig. IV-2 and Table IV-1.

Only about half of the eggs held at 20°C (Treatment 1; Fig. IV-2) hatched within the initial hatching period, although 77-92% of eggs from the same egg masses hatched at that temperature following storage (Treatments 3c,4b,5, and 6; Fig. IV-2). However, after unhatched eggs in Treatment 1 were cooled and subsequently re-warmed, a further 1-19% hatched, resulting in a total mean hatch in the control treatment of about 60%. Hatching success of eggs warmed to 20°C generally improved with increasing time spent at the 8°C storage temperature; 92% of eggs hatched following storage for 190 d compared to 84-86% after 90 and 120 d of storage (Treatments 4b,5, and 6; Fig. IV-2).

Egg hatch occurred at all temperatures evaluated except 4°C, although at 8° C (Treatment 2), only about 5% hatched over 202-272 d (including 12 d cooling to storage temperature; Fig. IV-2). Hatching in this treatment and in Treatment 3a may have been incomplete, however, since the 8°C trials were terminated following an incubator failure on day 272. Cooling to 4°C before warming (Treatment 3) resulted in improved hatch at 8° and 15° C when compared to similar treatment after storage at 8°C (Treatments 2 and 4a).

Hatching occurred at 8°C, although at that temperature the hatching

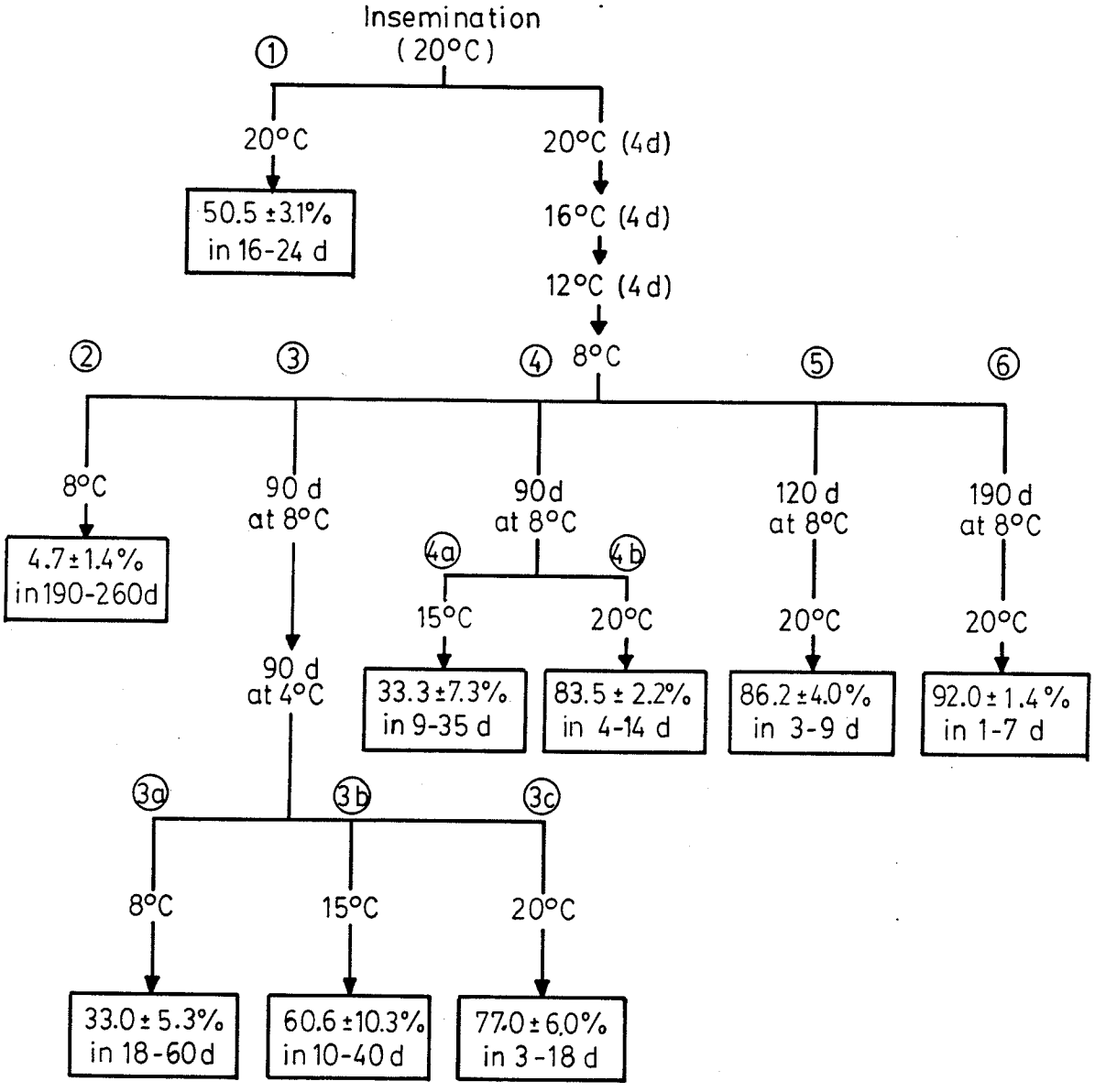

Fig. IV-2. Egg hatching treatments and results for *Hexagenia limbata*. Hatching success is expressed as mean % hatch (±S.E.), and development time is the number of days (d) required for hatch after warming to final treatment temperature.

success was low and hatching was extensively delayed. Therefore, the assumption of a 10° C developmental threshold for the SIL population is incorrect; the threshold is likely near 8°C. Consequently, degree day estimations for development of *H. limbata* eggs were calculated using both 10°C (literature threshold) and 8°C (experimental threshold).

Development time

The minimum egg development period (days to first hatch) at constant temperatures ranged from 16 d at 20°C to 202 d at 8° C (Treatments 1 and 2; Fig. IV-2, Table IV-1). Eggs in the storage treatments (Treatments 3-6) started to hatch in 106 - 210 d (including 12 d of cooling to storage temperature; Table IV-1), depending upon the amount of time spent in storage. If the storage temperature had been below the developmental threshold temperature for *H. limbata*, no development should have occurred during storage, and consequently, hatching times after warming should have been consistent for given temperatures. Therefore, if 8°C was below the threshold, time to onset of hatch (excluding storage time) should have been similar for Treatments 4b, 5, and 6, the treatments that were essentially identical except for the amount of time in storage. However, eggs hatched at 8°C, and although egg development slowed, it did not cease during storage at 8°C. Not surprisingly then, the number of days to initial hatch (following warming) decreased with increasing time in storage in treatments 4b, 5, and 6 (Table IV-1, Fig. IV-2).

There were conflicting results in treatments in which eggs were exposed for a period to 4°C. Eggs that were held at 8°C for 90 d and then warmed to 15° and 20°C (Treatments 4a and 4b) had similar post-warming hatching times as eggs that were held for 90 d at 8°C, and then for a further 90 d at 4°C

Table IV-1. Total number of days, number of days above 8°C, and degree days (dd) >8° and >10°C required for initial hatch of *Hexagenia limbata* eggs exposed to different temperature treatments. Treatment numbers correspond to Fig. IV-2. Twelve-day period of cooling to storage temperature and dd accumulated during cooling to storage temperature is included in counts for all except Treatment 1.

Final Treatment Temperature	Treatment #	Total Days	Days>8°C	dd>8°C	dd>10°C
20°C	1	16	16	190	160
	4b	106	16	144	112
	5	135	15	132	102
	6	203	13	108	82
	3c	195	15	132	102
15°C	4a	111	21	159	117
	3b	202	22	166	122
8°C	2	202	0	96	72
	3a	210	0	96	72

(Treatments 3b and 3c; Table IV-1). Therefore, there was no evidence for egg development at 4°C. However, in the cases where the final treatment temperature was 8°C (Treatments 2 and 3a), eggs began hatching after 200-210 d whether the time was spent at a constant 8°C or a combination of 8° and 4°C. If 4°C was below the developmental threshold temperature, the time to initial hatch should have been extended by a period equal to that spent at 4°C; since it was not, some development might, in fact, have occurred at 4°C.

Development could not be predicted using the ordinary degree day (dd) accumulation model, because the storage temperature was not below the developmental threshold. Since development occurred at 8°C, the number of dd>10° and dd>8°C decreased with time in storage. Degree days to first hatch ranged from 72-160 >10°C, and from 96-190 >8°C (Table IV-1).

Egg diapause

As in Treatment 1, ≈50% of eggs in the diapause trial hatched within 2-4 wk at 20°C, (Fig. IV-3). No additional hatch was recorded at 20°C, at least within the 13-wk period following the end of the initial hatch period. However, in all cases where eggs were cooled subsequently and re-warmed, further hatch occurred. Hatching success following cold treatment was highest after storage at 4°C for 60 d: >27% of the original total number of eggs, for a total hatch of 79%. Storage at 4°C for 30 d resulted in a further 23% hatch (total 75%), but exposure to 8°C for 60 d only resulted in a further hatch of 10% (total 62%).

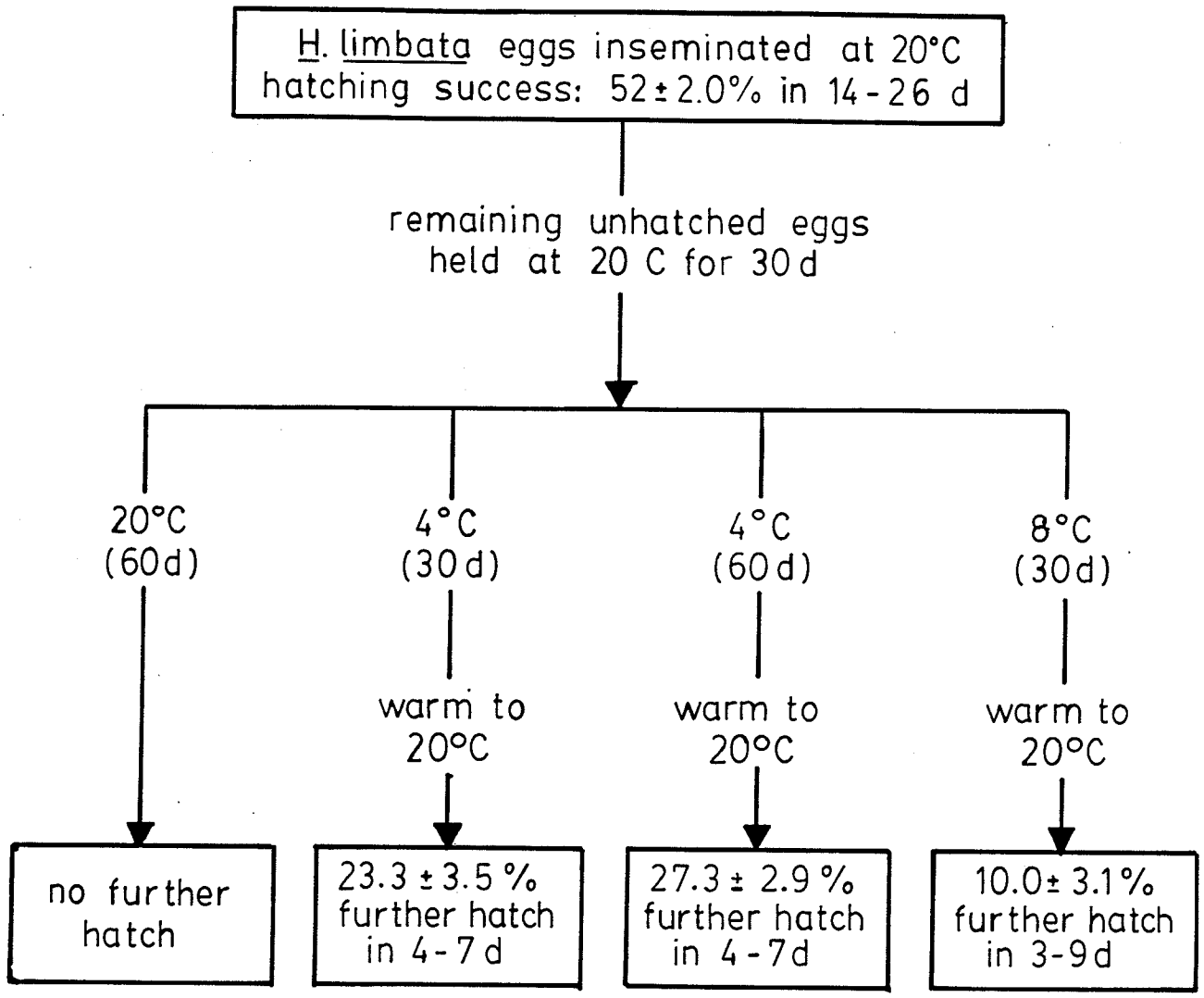

Fig. IV-3. Summary of *Hexagenia limbata* diapause trials. Eggs were allowed to hatch at 20°C, then the remaining unhatched eggs were cooled to mimic overwintering, and then rewarmed to 20°C. Mean % hatch (±S.E.) and time to hatch after warming (d) are given for each treatment.

DISCUSSION

In most species of mayflies, egg hatching success and incubation period are related to temperature (Brittain 1990, Elliott and Humpesch 1980, Suter and Bishop 1990). Hatching success is generally highest at some optimum temperature, and decreases at temperatures on either side of the optimum (Brittain 1990, Elliott and Humpesch 1980). Incubation period decreases as temperature increases. The relationship between temperature (T) and incubation time (t) usually follows a power law:

$$t=aT^{-b}$$

where a and b are empirically derived constants (Brittain 1990, Elliott and Humpesch 1980, Suter and Bishop 1990). Prediction of egg hatching times using this relationship requires constant temperatures, which are rarely encountered in field situations. However, egg hatching time may also be described in terms of development rate (1/t) with temperature (T), in the form of a logistic curve (Davidson 1944, e.g. Fig. IV-4). The advantage of this latter relationship is that for temperatures in the middle region of the curve, a linear relationship between temperature and development rate exists, and incubation time can be predicted using thermal summation (degree days, dd) even under changing temperature conditions (Davidson 1944, Rosillon 1988, Suter and Bishop 1990). In the middle temperature range:

$$1/t=a+bT$$

where a and b are empirically derived constants, dd>threshold required for development will equal 1/b, and the derived threshold for predictive purposes will be the temperature at which development rate = 0. However, due to the non-linearity of the development/temperature response over the entire temperature range, the actual threshold will be lower than that derived from extrapolation from the linear model (Fig. IV-4). Also, development will be

faster than predicted by the dd model at temperatures near the lower developmental threshold and slower than predicted near the upper threshold. Deviations from this response will occur when egg development depends upon an obligatory diapause state (Elliott and Humpesch 1980, Suter and Bishop 1990).

The response of *Hexagenia* egg development time to temperature has been well documented. A linear response in development rate has been observed with temperature above a 10°C threshold for the species studied (Flattum 1963, Friesen *et al.* 1979, Hunt 1953, Wright *et al.* 1982). In this study, rather than simply record incubation times at a variety of temperatures, an effort was made to approximate conditions at SIL. Although the general pattern of decreased development time with increased temperature was confirmed, specific details of the development/temperature response were quite different from southern populations.

Based on egg development studies by Flattum (1963) and Friesen *et al.* (1979), storage below the reported threshold of 10°C was expected to result in low temperature quiescence, with no further development until eggs were subsequently warmed. Egg hatch could then be predicted as a function of the accumulated dd>10°C. However, the threshold temperature for egg development in the SIL population is below, but probably near 8°C. Consequently, development at that temperature was faster than predicted by the linear dd model (Fig. IV-4), resulting in lower apparent dd requirements following storage of the eggs at 8°C.

Eggs in the 20°C control treatment were not stored, so their hatching times could be compared to results from other studies reporting dd accumulation. Eggs in the present study required 160-240 dd>10°C for completion of the initial hatch, compared to 170-190 dd in Lake Winnipeg and 200-260 dd in Michigan (calculated from Neave 1932 and Hunt 1953).

Differences in dd for hatching were minor, but appeared to follow a pattern of decreased dd requirements with increasing latitude, possibly due to the presence of a lower developmental threshold for the northern populations. Lower developmental thresholds with increasing latitude have been reported in the literature for other insects (see review in Danks 1987), although the degree to which this phenomenon applies to *Hexagenia* is not known. The assumption of a 10°C threshold for *H. limbata* is primarily based on field data from Hunt (1953), in which growth of nymphs ceased at temperatures below about 48°F (generally taken as 10° C although 48°F = 8.9°C). In subsequent studies, there was good agreement between nymphal development and dd accumulation >10°C (Craven and Brown 1969, McCafferty and Pereira 1984, Hudson and Swanson 1972, Heise *et al.* 1987), so 10°C has become widely accepted as the developmental threshold temperature for *H. limbata*.

In fact, calculation by linear regression of the derived threshold (one based on the linear dd model) for egg development for *H. limbata* using data from several sources, including the present study (Fig. IV-4), yields a value of 9.8°C. For temperatures in the middle of the temperature range then, calculation of dd >10°C should be generally valid for prediction of egg hatch over the entire range, including SIL. Geographic comparisons of an experimentally determined lower threshold cannot be made because it has not been determined for southern populations. However, the response to temperature among populations (for the temperatures in the middle temperature ranges) is consistent, suggesting that geographic trends, if they occur, are minor. Therefore, the hypothesis of a lower threshold for the northern population has not been validated.

One apparent anomaly in hatching responses among eggs in the different treatments was seen in the treatment that mimicked overwintering conditions at

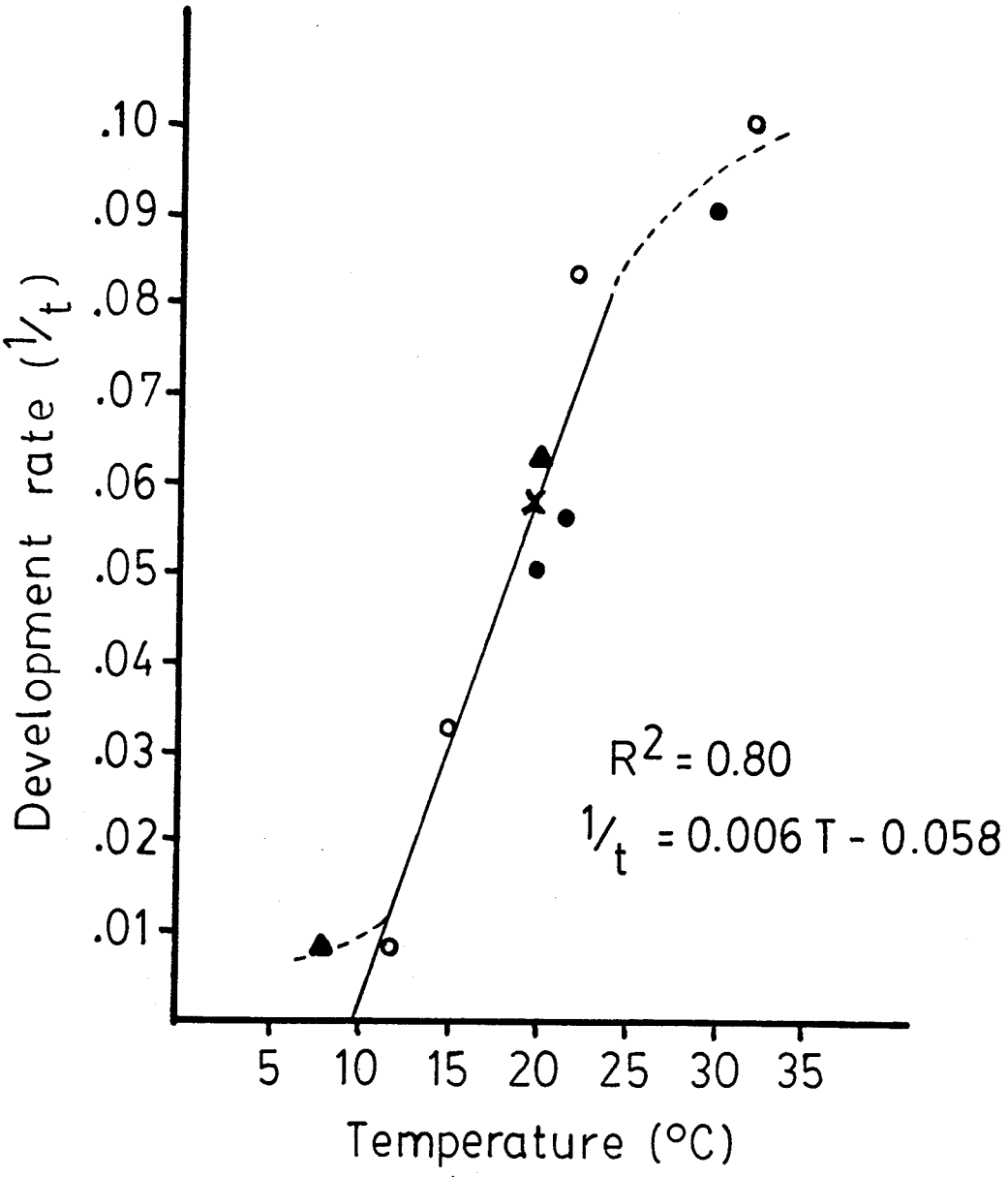

Fig. IV-4. Relationship between development rate (1/t) and incubation temperature for *Hexagenia limbata* eggs. (data from Hunt 1953 (●); Flattum 1963 (o); Neave 1932 (x); and this study (▲))

SIL (Treatment 3). The onset of hatch in eggs held at a constant 8°C (Treatment 2) began at about the same time as those that spent nearly half of the storage period at 4°C (Treatment 3a). Since 4°C is several degrees below the proposed developmental threshold of 8°C, no development was expected at that temperature, and the incubation period should have been extended by a period equal to that spent at 4°C. Development was extended by the period spent at 4°C in "overwintering" eggs warmed to 15° or 20°C, but not in those warmed to 8°C. It is possible that a sudden rise in temperature in spring may serve as a cue to speed development at 8°C, particularly since hatching success of eggs exposed to 4°C was also improved at 8°C.

Temperature effects on hatching success have not been well documented for *Hexagenia*, although Hunt (1953) reported that >90% of naturally inseminated *H. limbata* eggs would hatch at ≈20°C, without exposure to a cold period. In this study, hatching success continued to improve with increasing temperature within the range of study temperatures investigated. Therefore, the optimum temperature for hatch is 20°C or greater. At 20°C, hatching success also improved with increased amount of time in storage, ranging from ≈50% hatch for no storage (Treatment 1) to >90% hatch after more than 190 d in storage (Treatment 6). The poor initial hatch in Treatment 1 was originally attributed to the artificial insemination technique. However, there was a high hatching success of eggs from the same egg masses following low temperature storage. Eggs were viable, but apparently required an environmental cue to stimulate hatch.

A second set of experiments confirmed that the unhatched eggs entered a true diapause, rather than a low temperature quiescence, since they did not hatch until after exposure to a temperature stimulus. Under natural conditions, this would result in a bimodal egg hatching pattern, in which some

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eggs in an egg mass hatch immediately if conditions are favourable, and the remainder would enter diapause. Generally, although both diapause and non-diapause eggs may be produced in the same species, or even the same population of insect, individual females usually lay batches containing either one kind or another (Walker 1980). In SIL *Hexagenia limbata*, individual females produced both diapausing and nondiapausing eggs in the same egg mass, but bimodal hatching in the field would only be expected to occur when conditions in the summer of oviposition were favourable for hatching. The presence of a bimodal hatching response in a population, when it occurs, is generally associated with environmental unpredictability (Danks 1987, Tauber *et al.* 1986).

The egg diapause observed in the SIL population of *H. limbata* appears to be limited geographically. Hunt (1953) recorded >90% hatching success of naturally fertilized eggs in Michigan without cold-treatment. However, there is anecdotal information in the literature to suggest that diapause occurs in other northern populations. Neave (1932) recorded only 50% hatch of *H. limbata* eggs from Lake Winnipeg, Manitoba, and Heise et al. (1987) could not relate the presence of small nymphs of *H. limbata* early in the spring in Dauphin Lake, Manitoba, to an emergence period during the previous season.

The adaptive significance of this type of diapause is obvious. It presents a "bet-hedging" strategy in the unpredictable conditions that may occur at the limits of distribution of a species. Weather conditions at SIL are highly variable, resulting in some years that provide favourable conditions for *Hexagenia* and other years that are unfavourable (Giberson *et al.* 1991). Emergence timing and success are strongly associated with weather conditions at SIL, and may vary by several weeks from one year to the next (Chapter III). Conditions that result in two widely separated egg hatching

periods can effectively split the cohort. In years of early emergence (mid-summer), nymphs hatch early and develop to a sufficient degree for successful overwintering. However, a late emergence and hatching would result in few survivors in the following spring, because newly hatched nymphs show poor overwintering success (Chapter V). In the latter situation, an egg diapause with subsequent spring hatching ensures that at least some members of a cohort will have a good chance of survival.

Bimodal egg hatching responses, whether they result from diapause as in the SIL population or from low temperature quiescence, may have a significant effect on interpretation of *H. limbata* life cycles in other locations. In SIL, the presence of diapausing eggs ensured survivorship of a cohort, but had little obvious effect on subsequent growth patterns of the nymphs. Because nymphs grow slowly in SIL, those hatching in August were still tiny by the autumn and subsequent spring, when the remainder of the cohort hatched. Therefore, the two parts of the cohort were virtually indistinguishable by the end of the second year (Chapter III). However, in warmer locations, two egg-hatching periods could result in a splitting of the cohort into two distinguishable groups, if nymphs from early hatching eggs can grow significantly before their first winter. The resultant bimodal nymphal size-frequency distribution could be related to development in the egg stage, rather than the often-cited temperature responses of nymphs (e.g. Heise *et al.* 1987, Pritchard 1978, Svensson 1977).

In conclusion, eggs of *H. limbata* from SIL show the same pattern of increasing development rate and hatching success with increasing temperature as has been reported in other populations, but there were also some important differences. Eggs from SIL *H. limbata* appear especially adapted to overwintering, with higher hatching success in eggs stored at winter

temperatures, and higher success after increasing time at cool temperature. In addition, this northern population has a previously undescribed egg-diapause, resulting in the potential for two hatching periods for the same egg cohort. This appears to be a "bet-hedging" response, that allows them to persist in the unpredictable environment at the northern edge of their distribution.

CHAPTER V

EFFECTS OF TEMPERATURE, FOOD QUANTITY, AND NYMPHAL REARING DENSITY ON LIFE-HISTORY TRAITS OF *HEXAGENIA* (EPHEMEROPTERA:EPHEMERIDAE) FROM SOUTHERN INDIAN LAKE, MANITOBA, CANADA

ABSTRACT

Hexagenia limbata (Serville) and *H. rigida* McDunnough from Southern Indian Lake, Manitoba were reared at 10°, 15°, and 20°C to assess temperature effects on growth. *Hexagenia limbata* nymphs were also reared at a range of temperatures, food quantities, and rearing densities to determine whether these factors affected life history features such as growth, development, fecundity and mortality. Nymphs of both species grew at 8°C, 2° below the published developmental temperature threshold. At limited and unlimited food levels, growth and development rates increased with increasing temperature, but food limitation slowed both growth and development within a temperature treatment and resulted in increased degree day (dd) requirements. Nymphs reared at 20°C at a non-limiting food level grew into significantly larger and more fecund adults than those reared at 20°C at a limiting food level, or at 15°C under non-limiting food conditions. Growth and development rates were not affected by rearing density. The observed dd requirements in the laboratory were near the lower end of those observed in nature, and are probably a reflection of the effect of temperature on development under near optimal conditions. The higher dd requirements observed in some field studies may have been related to food limitation, although the possiblity of geographical differences in dd requirements cannot be ruled out. Growth responses to temperature were similar for the two species.

INTRODUCTION

Temperature and food are the factors most frequently reported to affect life-history traits in aquatic insects (see review by Sweeney 1984). Many researchers have shown a strong relationship between growth or development rate and temperature (e.g. Britt 1962, Brittain 1976, Elliott 1984, Humpesch 1979, 1981, Vannote and Sweeney 1980). Others, however, have shown that growth may depend on the quality and quantity of food (Anderson and Cummins 1979, Anderson and Cargill 1987, Fuller and Mackay 1981, Webb and Merritt 1987). In most studies on aquatic insect growth and development, workers have concentrated on one of these factors at a time, varying food quality while holding temperature constant (e.g. Bird and Kaushik 1984, Fuller and Mackay 1981, Golladay *et al.* 1983, Webb and Merritt 1987), or varying the rearing temperature while maintaining a constant food level (e.g. Elliott 1987, Humpesch 1981, Leggott and Pritchard 1985, Park 1988). The relative influences of each factor are difficult to separate, because temperature and food interact in nature. Temperature directly affects growth by influencing metabolic rates (Robinson *et al.* 1983, Ward and Stanford 1982) and feeding rates (Wallace and Merritt 1980, Zimmerman and Wissing 1978); it also affects food quantity and quality by influencing algal production and microbial growth rates on detritus (Anderson and Cummins 1979, Anderson and Sedell 1979, Rempel and Carter 1986, Ward and Stanford 1982).

In spite of difficulties associated with separating temperature and food effects, several researchers (e.g. Baker and Feltmate 1987, Rosillon 1988, Söderström 1988, Sweeney *et al.* 1986a, b, and Sweeney and Vannote 1984) have shown the importance of considering both of these factors simultaneously when evaluating growth and development of aquatic insects. Temperature appears to be the most important variable affecting the growth/development response, as

long as there is no environmental cue controlling phenology (e.g. photoperiod). However, food can modify the response, resulting in changes in body weight, fecundity, and developmental timing.

A third factor, rearing density, is rarely considered when evaluating growth and development. At high densities, competitive interactions between organisms may affect feeding rates and growth. For example, Rosillon (1988) found that individually reared *Ephemerella ignita* nymphs were larger and more fecund as adults than those reared in groups.

In this paper, I focus on the relative importance of temperature, food quantity, and nymphal rearing density on some life-history traits of two species of burrowing mayfly, *Hexagenia limbata* and *H. rigida*, from Southern Indian Lake (SIL), Manitoba (lat. 56°38' to 57°40'N, long. 98°10' to 99°45'W). *Hexagenia limbata* is widespread throughout much of North America, although *H. rigida* is more restricted to the eastern part of the continent (McCafferty 1975). Both approach their northern range limits at SIL. *Hexagenia* development is known to be strongly temperature dependent, with life cycles ranging from <1 yr in the south (Carlander *et al.* 1967, Craven and Brown 1969) to 2 yr in mid-lattitude locations (Flannagan 1979, Riklik and Momot 1982), to several years in the extreme northern part of the range (Chapter III). The reported developmental threshold temperatures (temperatures below which no development occurs) are ≈10°C for both species (Hunt 1953, Friesen *et al.* 1979), with an apparent requirement for ≈1900-2500 degree days (dd) above 10°C to complete development (Heise *et al.* 1987, McCafferty and Pereira 1984). *Hexagenia* are collector/ filterers, feeding primarily on detritus (Zimmerman and Wissing 1980, Zimmerman et al. 1975), but little is known about the effect of food on their growth, fecundity, and development. Although reported to occur in very high densities in some locations (>1000/m^2: Carlander *et al.*

1967, Heise *et al.* 1988, Hudson and Swanson 1972), it is not known whether density influences their life histories.

MATERIALS AND METHODS

Study animals

Rearing trials were conducted on mid-sized (17.1 ± 1.4mm, $\bar{x}$ ± SD) *H. limbata* and *H. rigida* nymphs collected from Wupaw Bay, SIL (see Chapter IV, Fig. IV-1) in September 1987, and on *H. limbata* nymphs reared from artificially inseminated eggs obtained from SIL adults in July 1987. Nymphs were collected by gently washing the contents of an Ekman grab through 400-µm mesh nets. Adults for insemination were captured with sweep nets and by hand-picking from vegetation along shorelines in Opachuana and Wupaw Bay, SIL (Fig. IV-1). The eggs from 20 females were combined and mixed with the macerated terminal segments of 20 adult males, and then were cooled to 8°C for storage (Friesen 1981, see also Chapter IV). Subsequent hatching success for eggs treated in this fashion was 85-95%.

Experimental trials

All nymphs were maintained in continuously aerated 3-L plexiglass aquaria (7 cm wide X 30 cm long X 15 cm high) containing ≈5 cm of sterilized SIL sediment and deionized tap water. The top 6 or 7 cm of water were decanted from each aquarium monthly during the experimental period, and replaced with deionized water. Trials were run in constant light in controlled environment chambers (temperature fluctuations <0.5°C of required study temperature).

Nymphs were fed a diet of ground Tetramin-B®. However, food requirements varied between temperature treatments due to the effect of temperature on metabolic rates, and they also varied with time, as nymphs grew

larger. Therefore, aquaria in the preliminary temperature experiments were examined twice weekly, and additional food added when necessary to maintain a barely visible layer of food on the surface of the mud, to provide a "non-limiting" level of food. In experiments where food availability and rearing density were evaluated as well as temperature, non-limiting food requirements were determined twice weekly as above for the aquaria containing the highest nymphal density at each study temperature. Food amounts for the remaining aquaria in each temperature treatment were then calculated based on comparative nymphal densities and desired food treatment. For example, if the highest nymphal density in a treatment was 30 nymphs/aquarium, food levels for aquaria containing 20 nymphs was calculated as 2/3 of that needed for 30 nymphs, and the amount for aquaria containing 10 nymphs was 1/3. "Limiting food" was calculated as half the amount given in the non-limiting treatments.

Experiment 1 was a 3-way factorial experiment, in which field-collected mid-sized nymphs (see Table V-1 for sizes) of both sexes and both species were reared under non-limiting food conditions at 10°, 15°, and 20°C. Species were identified using characters given in McCafferty (1975) and J.F. Flannagan (Freshwater Institute, Winnipeg, personal communication). Sexes were separated (based on the presence or absense of the developing penes in the male) and individual body lengths were measured (using an ocular micrometer in a dissecting microscope) before being added to the aquaria. Each treatment consisted of two replicate aquaria, each containing 8 individuals of each sex and each species; these were established and monitored at 10°, 15°, and 20°C (total of 8 aquaria at each temperature, or 24 aquaria). Growth (mm) was calculated as the difference between initial size and size at the end of the trial (120 d at 10°C, 80 d at 15°C, and 50 d at 20°C). Because growth is usually exponential, instantaneous growth rates (G, %length/d) were determined

Table V-1. Growth and mortality of mid-sized *Hexagenia limbata* and *H. rigida* nymphs reared in the lab at 10°, 15°, and 20°C ($\bar{x}$ ± SD, n=16; Experiment 1).

			Initial Size (mm)	Final size (mm)	days	Mortality total (%)	%/d
H.limbata	♀	10°C	15.83 ± 0.62	21.15 ± 0.71	120	17	0.14
		15°C	17.29 ± 0.28	22.71 ± 1.2	80	26	0.33
		20°C	16.50 ± 0.77	22.00 ± 0.2	50	30	0.60
	♂	10°C	17.51 ± 0.42	20.97 ± 0.26	120	17	0.14
		15°C	16.15 ± 0.80	20.64 ± 0.9	80	17	0.21
		20°C	13.78 ± 0.77	19.00 ± 1.3	50	17	0.34
H.rigida	♀	10°C	18.73 ± 0.59	22.84 ± 1.1	120	6	0.05
		15°C	17.29 ± 0.32	22.35 ± 0.4	80	0	0
		20°C	17.45 ± 0.40	22.00 ± 0.37	50	68	1.36
	♂	10°C	17.81 ± 0.80	21.21 ± 1.28	120	6	0.05
		15°C	17.47 ± 0.59	20.75 ± 0.12	80	12	0.15
		20°C	16.28 ± 0.51	19.80 ± 0.39	50	12	0.24

using an exponential relationship between body length (L,mm) and time (t,days):

$$L=ae^{bt}$$

$$G=100b$$

where a and b are empirically derived constants (Rosillon 1988). Growth rates (after arcsine transformation) were compared for each sex and each species at each temperature using a 3-way ANOVA.

In Experiment 2, *H. limbata* nymphs were reared from eggs to determine the shape of the growth curve and the time required for development at 8° and 15°C (nonlimiting food level), and at 20°C (non-limiting and limiting food levels). Fifty-five eggs were added to each of eight aquaria in each treatment at 20°C; eggs were used at this stage because there was less mortality handling eggs compared to small nymphs. In order to estimate the timing and success of egg hatch, three additional dishes of 55 eggs each from the same egg mass were set up and checked daily. After 7 d, all eggs had hatched in the dishes. Aquaria in the 8° and 15°C treatments were held at 20°C for an additional four days, and then they were transferred to a 15°C incubator. Aquaria in the 8°C treatment were transferred to the 8°C incubator four days later. Newly hatched nymphs were 1.01±0.02 mm in length ($\bar{x}$±SD; n=50). Body length of the nymphs following placement at 8° and 15°C was estimated to be 2.05 mm from growth in the dishes. The numbers of eggs hatching in the dishes ranged from 49-51 ($\bar{x}$=50, or 91%).

One aquarium in each treatment was sacrificed at ≈45-d intervals, and nymphs were gently washed from the mud through a 200-µm screen and measured. Sex ratios were near 1:1 in all aquaria. Survivorship was calculated on each sampling date as the % remaining from the original number of eggs hatched, and mortality was expressed as %/d. Screens were placed on each aquarium to

prevent emerging adults from escaping, and the size and fecundity of the emerging adults were determined. Adult (subimago) body size was measured as body length (mm) between the tip of the frontal process and the end of the abdomen, excluding the caudal filaments. Fecundity was determined by dissecting female subimagos and counting the eggs. Development time was expressed as number of days from egg hatch to emergence, and also as dd to first emergence (Davidson 1944):

$dd = (T-T_0)d$ where: T=study temperature

T_0=threshold temperature

d=number of days above threshold

The relationship between development rate and temperature is generally logistic, but for temperatures in the middle range of the development/ temperature curve, the relationship is approximately linear and can be described by:

$1/t=a+bT$ where: t=days required for development

T=temperature

a and b are empirically derived constants.

The threshold temperature is calculated by extrapolating the line to the point where the development rate (1/t) approaches zero; and dd = 1/b (Davidson 1944, Pruess 1983, Rosillon 1988).

Experiment 3 was designed to evaluate the relative importance of temperature, food, and nymphal density on specific growth rates of *H. limbata*, again designed in a 3-way factorial configuration. Since growth rates were

dependent upon body size, two size classes were used: 1) small nymphs that were reared directly from eggs as described above (initial size, $\bar{x} \pm SD$: 1.01±.02 mm; determined by measuring 50 freshly killed hatchlings; Table V-2), and 2) large nymphs, which developed for 90 d at 20°C prior to treatment (Initial size, $\bar{x}\pm SD$: 20.0±0.58 mm; determined by direct measurement before placement into aquaria; Table V-3). Each treatment consisted of two replicate aquaria containing 10, 20, or 30 small nymphs (430, 860, and 1290/m^2) or 5 or 10 large nymphs (215 and 430/m^2) at each of two food levels (non-limiting and limiting, as above) and five constant temperature regimes (8°, 10°, 12.5°, 15°, and 20°C). Therefore, there were 12 aquaria (6-limiting food, 6-nonlimiting food) containing small nymphs and 8 containing large nymphs (4 and 4) at each of the five temperatures. The amount of food/nymph was kept constant in each food treatment, regardless of density, in order to separate the potential effects of competition for food and competition for space. Each trial lasted 90 d or until all adults had emerged, and specific growth rates were calculated as above. Growth rates at the different treatments (G, %length/d, arcsine transformed) were compared using ANOVA.

RESULTS

Growth Rates

Temperature was the most important variable evaluated with respect to nymphal growth and development in all experiments. Temperature alone accounted for >80% of the variability in growth for both species (Table V-4, Figs. V-1, V-2), and differences in rearing temperature also caused large differences in emergence timing in *H. limbata* (Fig.V-3). Growth of large nymphs was observed at all temperatures evaluated, although growth rates were

Table V-2. Growth and mortality of small *Hexagenia limbata* nymphs reared in the laboratory at two food levels and a range of temperatures and nymphal densities for 90 d ($\bar{x}$±SD); initial size for all treatments: 1.01 ± 0.02mm (Experiment 3).

		LIMITING FOOD			NON-LIMITING FOOD		
Temp. (°C)	Density (#/aquarium)	Final size (mm)	Mortality total (%)	%/d	Final size (mm)	Mortality total (%)	%/d
8	10	0.99±.06	68	0.76	1.21±.05	70	0.78
	20	1.10±.05	66	0.73	1.07±.06	74	0.82
	30	1.00±.04	77	0.85	1.12±.05	80	0.89
10	10	-	100	1.11	5.01±.30	66	0.73
	20	3.21±.47	70	0.78	4.04±.95	65	0.72
	30	3.56±.78	68	0.76	4.06±.65	67	0.74
12.5	10	5.92±.86	45	0.50	5.85±.01	25	0.28
	20	5.10±.02	35	0.39	6.02±.87	32	0.36
	30	4.11±.21	13	0.14	5.95±0	3	0.03
15	10	10.48±.18	47	0.53	12.25±.25	50	0.56
	20	9.55±0	50	0.56	12.00±.7	27	0.30
	30	9.62±1.8	40	0.45	12.72±1.8	40	0.45
20	10	10.05±.77	40	0.45	20.13±.67	55	0.61
	20	14.80±6.8	55	0.61	21.64±0	60	0.67
	30	17.05±4.5	57	0.63	20.21±.25	51	0.57

Table V-3. Growth and mortality of large *Hexagenia limbata* nymphs reared in the lab at two food and nymphal density levels and a range of temperatures. Growth was measured after 120 d at 8°, 10°, and 12.5°, after 90 d at 15°C, and at first emergence at 20°C (35-70 d after start of experiment; $\bar{x}$ ± SD; Experiment 3).

		LIMITING FOOD				NON-LIMITING FOOD			
Temp. (°C)	Density (number/ aquarium)	Initial size (mm)	Final size (mm)	Mortality Total(%)	%/d	Initial size (mm)	Final size (mm)	Mortality total(%)	%/d
8	5	19.80±2.2	22.44±2.5	13	0.11	19.71±2.3	22.48±1.7	0	0
	10	20.01±1.8	22.89±2.6	7	0.06	20.32±1.9	23.20±1.8	13	0.11
10	5	19.59±1.9	23.40±3.0	26	0.22	19.32±2.4	22.39±1.4	0	0
	10	19.01±1.8	22.45±2.8	13	0.11	20.64±2.1	24.37±.35	0	0
12.5	5	20.88±2.2	24.96±3.8	0	0	19.78±2.0	24.13±1.8	13	0.11
	10	20.01±1.9	25.73±3.4	13	0.11	20.21±2.4	26.02±3.4	26	0.22
15	5	20.13±1.8	26.31±3.6	5	0.06	20.63±2.3	28.20±1.7	10	0.11
	10	20.03±1.7	27.31±2.9	5	0.06	20.04±2.1	29.01±4.2	20	0.22
20	5	20.63±2.2	24.64±2.6	40	0.44	19.45±2.2	26.35±3.6	11	0.22
	10	21.24±1.6	25.55±6.4	12	0.22	19.15±2.2	25.79±2.6	29	0.78

Table V-4. ANOVA and Regression statistics used to test for temperature, food, and density effects on growth of *Hexagenia* reared in the laboratory. For each experiment, temperature was evaluated separately (regression analysis) and in conjunction with other factors (ANOVA); P=probability level, R^2=correlation coefficient.

Experiment	Size-class	Treatment	df	F	P	R^2
1	Mid-sized (both species)	Temperature	2,20	42.5	<0.001	0.81
		Temperature	2,11	55.6	<0.001	0.92
		Species (Sp)	1,11	4.6	0.055	
		Sex	1,11	5.8	0.035	
		Temp X Sp	2,11	1.3	0.307	
		Temp X Sex	2,11	0.3	0.879	
		Sp X Sex	1,11	0.04	0.830	
		Temp X Sp X Sex	2,11	0.7	0.519	
3	Small (*H.limbata*)	Temperature	4,41	240.6	<0.001	0.85
		Temperature	4,16	147.8	<0.001	0.94
		Food	1,16	27.8	<0.001	
		Density (D)	2,16	0.12	0.85	
		Temp X Food	4,16	1.09	0.36	
		Temp X D	8,16	1.28	0.30	
		Food X D	2,16	1.31	0.27	
		Temp X Food X D	8,16	1.64	0.17	
3	Large (*H.limbata*)	Temperature	4,35	175.2	<0.001	0.82
		Temperature	4,20	93.3	<0.001	0.98
		Food	1,20	7.6	0.01	
		Density (D)	1,20	0.01	0.93	
		Temp X Food	4,20	4.8	0.007	
		Temp X D	4,20	0.25	0.91	
		Food X D	1,20	0.72	0.41	
		Temp X Food X D	4,20	0.61	0.66	

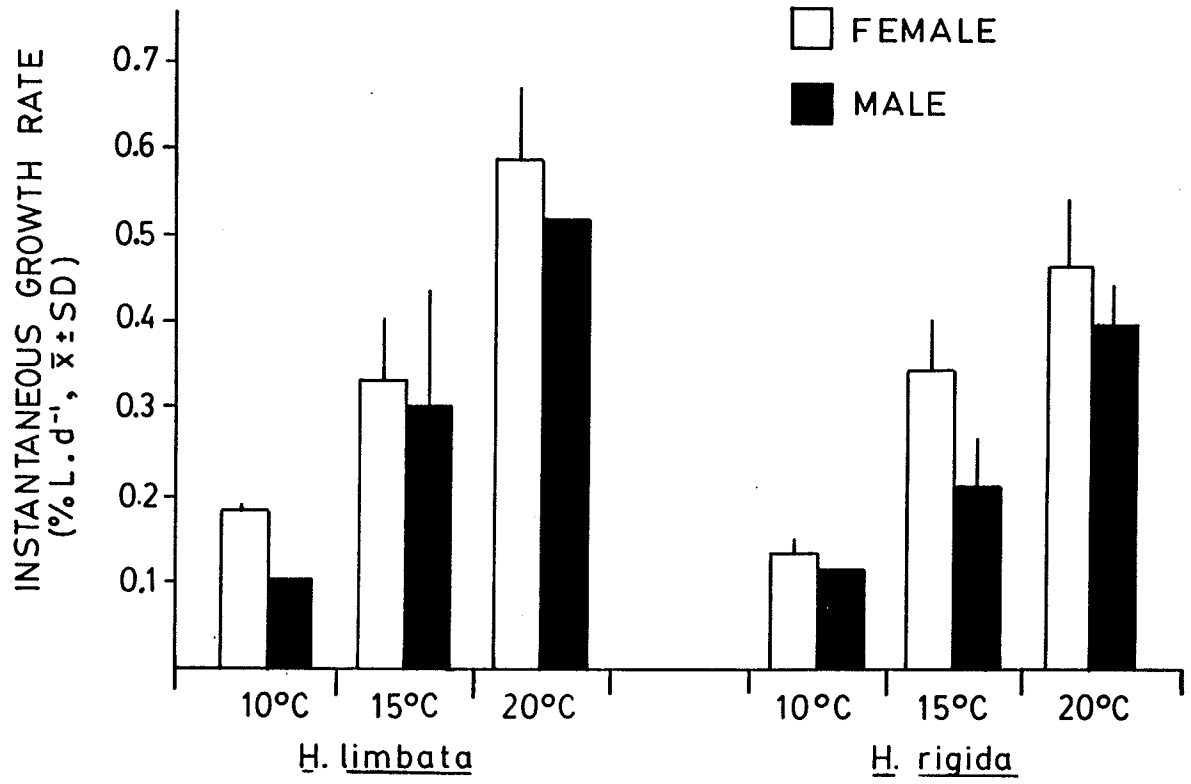

Fig. V-1. Instantaneous growth rates (%length/d) of mid-sized field-collected *Hexagenia* nymphs at a range of temperatures in the laboratory (Experiment 1).

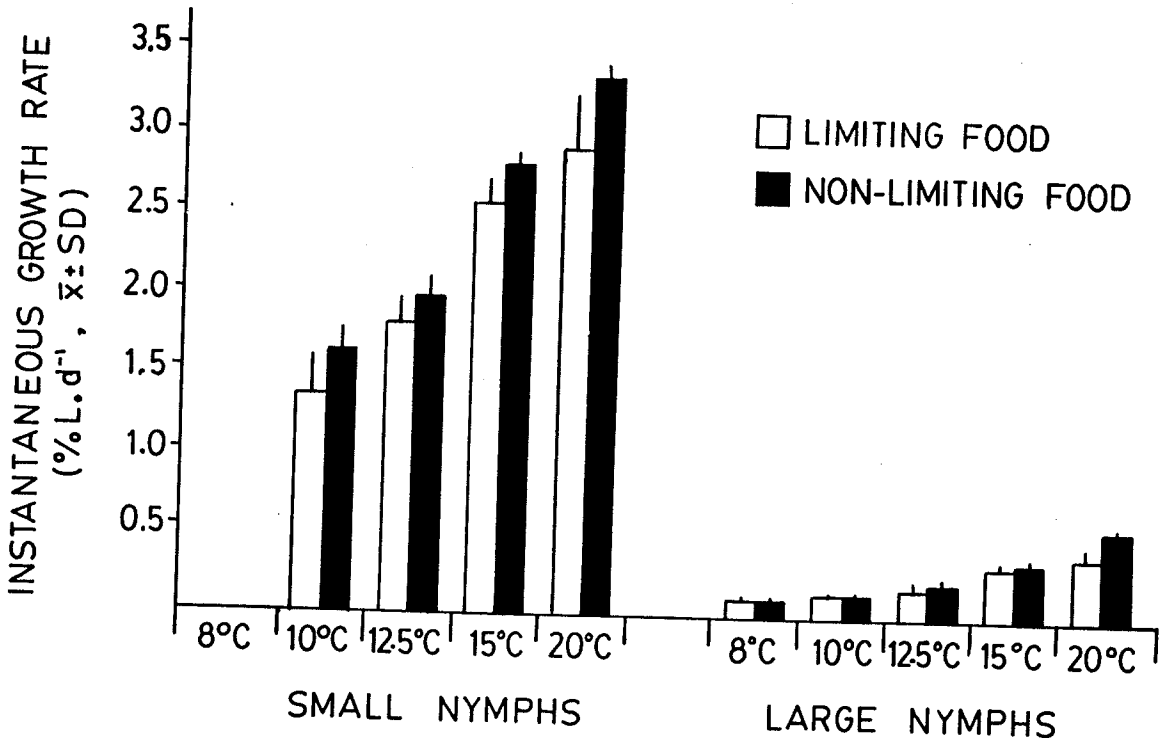

Fig. V-2. Instantaneous growth rates (%length/d) of two size-classes of *Hexagenia limbata* nymphs reared in the laboratory at two food levels over a range of temperatures (Experiment 3).

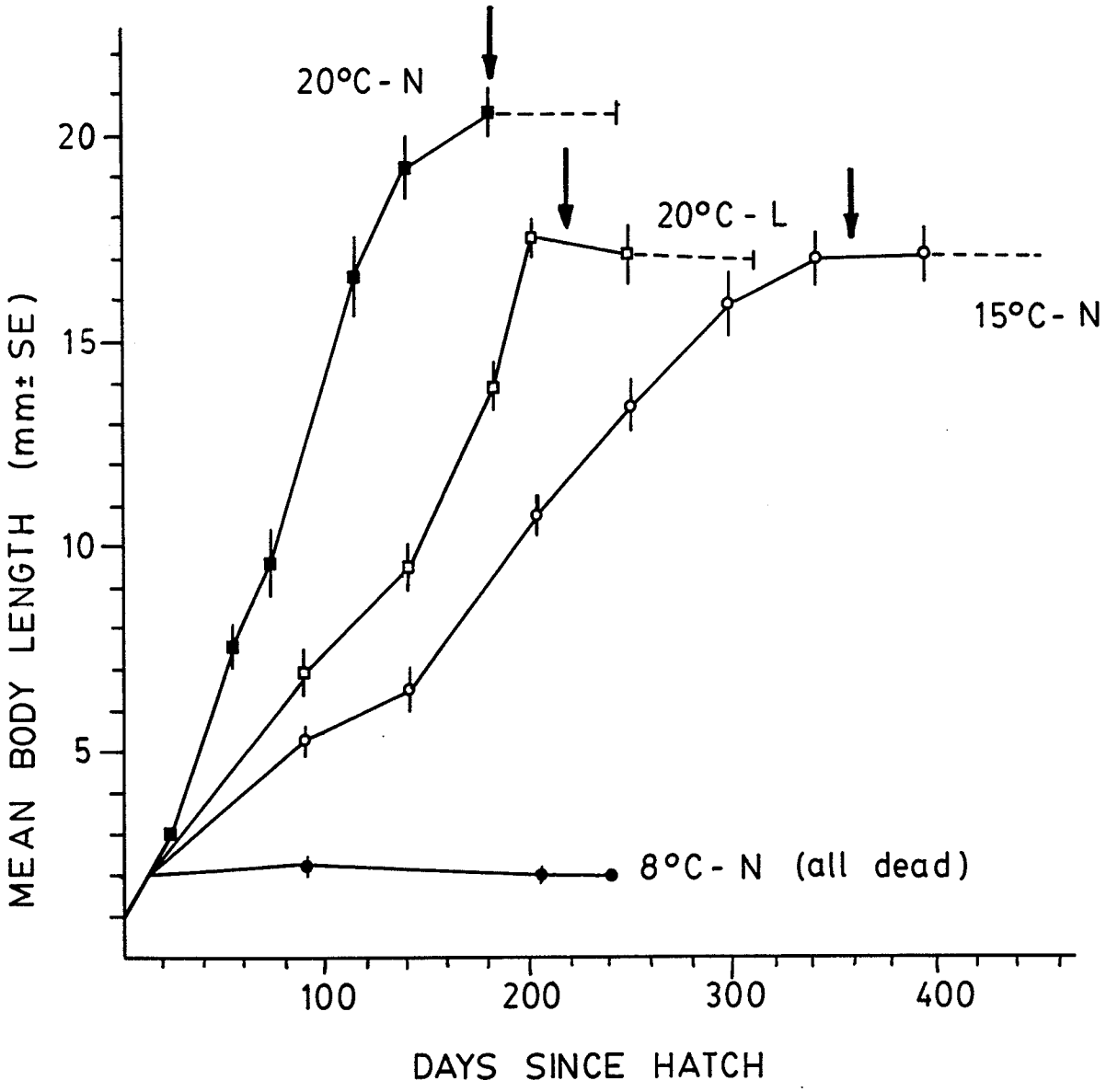

Fig. V-3. Growth of *Hexagenia limbata* at three constant temperatures (8°, 15°, and 20°C), and two food levels (L=limiting, N=nonlimiting; see text for explanation). Arrows point to time of first emergence; dashed lines represent continuation of emergence period following last sampling date (only 60% of emergence was complete in the 15°C trial at the time experiments were terminated (450 d), but the entire emergence period is shown for the 20°C trials.

very slow at 8°C. Small *H. limbata* did not grow at 8°C (Fig. V-2).

For mid-sized *Hexagenia* in Experiment 1, sex had a significant effect on growth in both species (Table V-4, Fig. V-1), so care was taken in later trials to include equal proportions of males and females. *Hexagenia limbata* consistently grew faster than *H.rigida*, though this trend was not quite statistically significant at $p < 0.05$ ($p = .055$; Table V-1).

In Experiment 3, no significant density effect was observed on growth for either size class of *H. limbata* (Table V-4), so the density treatments were combined to analyse the relative effects of temperature and food (Fig. V-2). Nymphs given more food grew faster, and for large nymphs, the response to food was stronger at higher temperatures (Table V-4, Fig. V-2). No other significant interactions were noted.

Mortality

Nymphal mortality in the rearing trials was related to rearing temperature and size class, but not to density, food level, species, or sex (Tables V-1, V-2, and V-3). Mortality was generally higher for small nymphs than for large ones (Tables V-2, V-3). Within size classes, mortality of large nymphs was highest at 20°C (Tables V-1, V-3), and mortality of small nymphs was highest at 8° and 10°C (Table V-2).

Development

Development of *H.limbata* was related to both food and rearing temperature. In Experiment 2, nymphs grown at non-limiting food levels at 20°C began emerging in less than half the time (183 d) of those reared at 15°C (380 d; Fig.V-3, Table V-5). Temperature thresholds for developing nymphs varied with nymphal size; the large nymphs in Experiment 3 achieved measurable

Table V-5. Size, fecundity, and time from egg hatch to first emergence of *Hexagenia limbata* adults reared in the laboratory at 15° and 20°C ($\bar{x}$±SD); N=Non-limiting food level, L=Limiting food level; see text for explanation (Experiment 2).

	Temp	Body Length (mm)				Fecundity	Development time		Mortality
Food	(°C)	females	n	males	n	(# eggs/♀)	(days)	(dd>10.4°C)	(%/d)
N	15	23.71±1.8	14	18.20±1.3	12	2873±633	380-?	1750-?	0.27
N	20	25.34±2.1	15	20.24±1.7	11	3433±520	183-243	1745-2333	0.07
L	20	22.64±2.2	16	17.76±1.1	14	2506±515	220-310	2111-2976	0.18

growth and development at 8°C (Fig. V-2), but no growth or development was noted at 8° in the small nymphs in either Experiment 2 (Fig. V-3) or Experiment 3 (Fig. V-2). Actual developmental thresholds for SIL *H. limbata*, therefore, are probably about 9°C for small nymphs and just below 8°C for large nymphs. The developmental threshold for *H. rigida* nymphs was not determined, but the pattern of growth for mid-sized nymphs in Experiment 1 was similar to that of *H. limbata*, with measurable growth at 10°C. Thus, the threshold for *H. rigida* development must also lie below 10°C.

The derived threshold for total development for *H.limbata* nymphs in this study (by extrapolation from the dd model) was 10.4°C. Development (from egg hatch to start of emergence period) required ≈1750 dd >10.4C under non-limiting food conditions (Table V-5). Virtually all emergence was complete within 60 d at 20°C (non-limiting food) resulting in a total dd range of 1745-2333 (>10.4°C) for all individuals at that temperature (Table V-5). Only ≈60% of nymphs had emerged by 60 d after the start of emergence at 15°C. Experiments were terminated at this time, so the full dd range for emergence at 15°C is not known, but ranged from 1750->2100 dd>10.4°C.

Development rates of *H. limbata* were slowed by limiting the availability of food. The emergence period started later and extended for a longer period under limiting food levels at 20°C than under non-limiting levels (Fig. V-3). However, there was a high degree of overlap between emergence periods for the two food treatments (non-limiting food: 183-243 d or 1745-2333 dd; limiting food: 220-310 d or 2112-2976 dd, Table V-5).

Adult size and fecundity

Temperature and food quantity affected adult size and fecundity of *H. limbata*. Nymphs reared at a non-limiting food level but at 15°C grew into

significantly smaller and less fecund adults (Students t, $P < .01$) than those reared at non-limiting levels and 20°C (Table V-5). Similarly, those reared at 20 °C but under limiting food conditions were smaller and less fecund as adults (Student's t, $P < .01$) than those at 20°C at non-limiting food conditions (Table V-5). No significant differences were seen in adult size or fecundity between those reared at 15°C at non-limiting food levels and at 20°C at limiting food levels.

DISCUSSION

Temperature and food are known to affect aquatic insect life histories through their effects on growth and development (Sweeney 1984). In this study, growth rates increased with increasing temperature for both *H.limbata* and *H.rigida*. Food availability also influenced growth rates of *H. limbata*, and increased growth rates resulted in shorter developmental periods, larger size at maturity, and higher adult fecundity. Although these traits were not investigated for *H. rigida*, the two species have virtually identical life cycles in Lake Winnipeg (Neave 1932) and SIL (Chapter III), and similar growth/temperature responses between 10° and 20°C. Therefore temperature and food probably have a similar influence on life history traits of *H. rigida*. The effect of food quantity on growth of *H. limbata* was more pronounced at higher temperatures, particularly for the larger nymphs. Temperature may have affected the quality of the available food, perhaps by stimulating microbial growth. Rosillon (1988) also noted an interaction between food and temperature for *Ephemerella ignita* and suggested that the rate of acceleration of growth with temperature may depend on diet.

Growth of *H. limbata* was not affected by nymphal rearing density, at

least at the densities evaluated. In natural *Hexagenia* populations, densities may range from <5/m² to >2000/m², with averages generally from 60-300/m², depending upon location and time of year (Carlander *et al.* 1967, Craven and Brown 1969, Heise *et al.* 1988, Horst and Marzolf 1975, Hudson and Swanson 1972, Hunt 1953, Neave 1932). Aquarium densities of 430-1290/m² (small nymphs) and 215-430/m² (large nymphs), therefore, were within the natural range. If density had an effect on growth, for example through competitive interactions, decreased growth rates or increased variability in the rates should have been noted with increasing density, particularly at the limiting food level. However, there was no consistent growth pattern with density at any of the temperatures or food levels evaluated. Rosillon (1988) noted differences in growth rates and other life history parameters in *Ephemerella ignita* nymphs that were reared individually and in groups, so it is likely that interactions may play a role in some cases. However, for *H. limbata*, competitive interactions may be unimportant or only become important at extremely high densities or low food levels.

When insect development is strictly temperature dependent, development can be predicted using a dd model. The relationship between temperature and the time required for insects to complete development usually follows a sigmoidal, or logistic pattern, although it can be described by a linear equation over temperatures in the middle part of the range (Davidson 1944, Pruess 1983, Rosillon 1988). Total development (egg to adult) was followed for *H. limbata* at 15° and 20°C, and the linear equation describing development between those temperatures was used to derive the lower developmental threshold temperature (by extrapolating the line to the point where the development rate approached 0). Even though ony two study temperatures were evaluated, the derived threshold of 10.4°C for the SIL population was very

near the published value of 10.0°C for *H. limbata*. However, it is difficult to make comparisons with southern populations since the literature value is based on field data (Hunt 1953) and has not previously been experimentally determined.

The derived threshold temperature is usually higher than the actual threshold. Because of the sigmoidal relationship of development rate and temperature, development will be faster at temperatures at the low end of the temperature range than predicted from the linear model, and some development will occur at temperatures below the predicted developmental zero (Davidson 1944, Higley *et al.* 1986, Pruess 1983). Both *Hexagenia* species showed measurable growth at 10°C, and for large *H. limbata*, growth was also observed at 8°C. Therefore, the true developmental threshold for both species must lie below 10.°C, and perhaps approaches 8°. In populations where temperatures in spring and fall change rapidly, and little time is spent at temperatures near the true threshold, the linear model provides a good predictor of insect development (e.g. Higley *et al.* 1986, Pruess 1983). However, in situations where populations spend more time at or near the developmental threshold, the ≈2°C difference between the true and derived developmental threshold temperatures means that development will proceed more rapidly than predicted from a linear degree day model (Chapter III).

Life-cycle duration varies in *H. limbata* depending on environmental temperatures, although temperature may not be the only factor controlling the length of the life cycle. Over most of its geographic range, ≈1900-2600 dd>10°C are required to complete development from egg through to adult (Heise *et al.* 1987, McCafferty and Pereira 1984, and calculated from data in Hunt 1953, Hudson and Swanson 1972, Welch and Vodopich 1989). The reported 10°C threshold has become accepted because of generally good agreement between dd

accumulations for widely separated populations. Latitudinal differences in the thermal regime then result in variations in life cycle length with latitude; these range from <1 yr in the southern part of the range (Hunt 1953, Craven and Brown 1969, Horst and Marzolf 1975) to 2 yr in mid-latitude locations (Flannagan 1979, Heise *et al.* 1987, Riklik and Momot 1982), and at least 3 yr in the far northern part of the range (Chapter III).

Laboratory dd accumulations for SIL *H. limbata* at non-limiting food levels were only ≈1750 dd above the derived threshold (10.4°C), compared to the 1900-2600 indicated above. Most researchers have assumed a 10°C threshold for calculations of *H. limbata* dd requirements, rather than derive the threshold experimentally (e.g. Heise *et al.* 1987). Assuming a 10°C threshold temperature for the SIL lab population, a minimum of ≈1830-1900 dd>10°C was required to complete development at 15° and 20°C. These values are similar to those reported by Heise *et al.* (1987) for *H. limbata* in Dauphin Lake, Manitoba, but generally lower than those reported for other southern populations.

Degree day accumulations for field populations, however, vary from site to site and from year to year. Heise *et al.* (1987) noted a trend for declining dd requirements with increasing latitude over the geographic range of *H. limbata*. Within a site, Heise *et al.* (1987) reported mean dd accumulations >10°C of 1728, 1806, 1848, and 2030 for different cohorts in Dauphin Lake, Manitoba, and 2370 and 2604 dd>10°C were needed for successive cohorts in South Dakota/Nebraska (calculated from Hudson and Swanson 1972). The trend for lower apparent dd requirements at higher latitudes is probably related to increased time spent near the lower developmental threshold by northern populations (Chapter III). Within site differences, however, may be related to food availability. In this study, nymphs reared at limiting food

levels required 20-30% more dd to complete development than those grown at non-limiting food levels. Furthermore, although density had no effect on growth in this study, it is possible that, at higher densities and lower food levels, competition for food may limit growth and result in greater dd differences. Hunt (1953) hypothesized that slower growth of a lab population of *H. limbata* compared to a field population under similar temperatures may have been due to overcrowding and food limitation.

Fecundity and adult size are also important life-history parameters that affect overall success of field populations. Fecundity is directly related to female body size in *Hexagenia* (Clifford and Boerger 1974, Chapter III), so differences in fecundity with temperature should correlate with differences in adult size. For hemimetabolous aquatic insects, the temperature regime for nymphs that produces the largest and most fecund adults has been viewed as optimal (Sweeney and Vannote 1978). The optimum temperature for growth of *H. limbata* is probably between 20° and 25°C (McCafferty and Pereira 1984, Zimmerman and Wissing 1978), and both size and fecundity of adults reared from SIL eggs were significantly greater at 20°C than at 15°C. Limiting food quantity had the same effect as rearing at lower temperatures: at 15°C, under non-limiting food conditions, emerging adults were similar in size and fecundity to those grown at 20°C under limiting food conditions. Therefore, food quantity must also be considered when comparing growth/temperature responses in different populations.

Mortality of laboratory-reared *Hexagenia* nymphs was unrelated to density or food level, but was related to temperature and body size. Mortality (%/d) was highest at 20°C for the large nymphs, and was highest at 8° and 10°C for the small nymphs. High mortality of large nymphs at 20°C may have been related to accumulations of metabolic wastes in aquarium water at that

temperature, since growth rates were highest at 20°C and the water in each aquarium was only renewed monthly. It is not clear why survival of small nymphs should have been lower at low temperatures, but it is possible that newly hatched nymphs need to accumulate food reserves in order to survive a long period of dormancy or low-temperature quiescence.

In summary, temperature and food availability during nymphal development had an important effect on life-history traits such as growth and development rates and adult size and fecundity of *Hexagenia*. Higher growth and development rates at higher temperatures resulted in larger and more fecund adults. Insufficient food supply generally modified the temperature response by reducing growth rates, and ultimately adult size and fecundity, by approximately the same magnitude as lowering temperatures by ≈5°C. Fecundity, and its effect on reproductive effort, is an important factor when considering the success of natural populations, so food and temperature effects on this parameter may have important implications for field populations. Development rates were also slowed by limiting food quantity, but this effect was not as pronounced as the effect on growth. However, differences in food availability may account for some of the reported variability in dd accumulations for *Hexagenia* development. Rearing density, at least within the range of 430–1290 nymphs/m² (small nymphs) and 215–430 nymphs/m² (large nymphs) had no effect on growth or development. The experimental threshold temperature for *H. limbata* was <8°C for nymphs that were approximately half grown, and ≈9°C for newly hatched nymphs, compared to the derived threshold of 10.4°C from the linear dd model, and the published threshold of 10°C. However, due to a lack of information on food levels and experimentally determined threshold temperatures in other studies, it cannot be stated whether growth patterns in the SIL population do or do not differ from southern populations.

CHAPTER VI

LONG-TERM ABUNDANCE PATTERNS OF *HEXAGENIA* IN SOUTHERN INDIAN LAKE: THE EFFECTS OF WEATHER AND HYDROELECTRIC DEVELOPMENT

ABSTRACT

Hexagenia abundance in Southern Indian Lake (SIL) between 1972 and 1987 was strongly correlated to air temperature. Air temperature itself was not the controlling variable for *Hexagenia* abundance, but acted through its relationship with the variables that actually controlled abundance. Summer air temperatures correlated with weather during the emergence period, which subsequently affected emergence and mating success. Air temperatures were also related to water temperatures in the lake, since the lake did not stratify thermally, and water temperature affected life cycle length and accumulated nymphal mortality, timing of emergence, and egg hatching success. Water temperatures were also affected by the impoundment of SIL and Churchill River diversion. In some areas temperature accumulations were reduced, while in others, incipient stratification or high temperatures coupled with increased oxygen demand from flooded organic material probably affected oxygen concentrations. Populations in regions 0, 1, 2, 6W, and probably 5 were primarily related to weather (expressed as air temperature accumulation), whereas those in regions 3, 4, 6E, and possibly 7, were affected by the impoundment or diversion. However, standing stocks in the latter regions traditionally made up only a small portion of the lake-wide standing stocks, so the impact of the hydroelectric development was masked by the much larger weather-related response.

INTRODUCTION

From studies on the life history and population dynamics of *Hexagenia limbata* and *H. rigida* in Southern Indian Lake (Chapters III, IV, and V), it is known that effects of weather on life history features ultimately affect population abundance. These effects include: 1) the influence of water temperature on life-cycle length and accumulated mortality, adult body size and fecundity, and egg-hatching success, 2) effects of air temperature on length of subimaginal life and moulting success, and 3) effects of wind on emergence-related mortality. One method of determining the relative importance of weather to the SIL population is to compare the long-term SIL weather patterns with long-term *Hexagenia* abundance in the lake. Benthic macroinvertebrates were surveyed approximately every second year in SIL from 1972 to 1987 (Giberson *et al.* 1991, Hamilton 1974, Wiens and Rosenberg 1984). In addition, a number of physical parameters, including water temperature and turbidity, were monitored during the same period, both at the time of the benthic surveys and in conjunction with other studies (e.g. Hecky 1984, McCullough 1981, S.J. Guildford, Freshwater Institute, personal communication). Because the lake does not stratify, there was a direct relationship between water temperature and air temperature during the ice-free season (Hecky 1984). Therefore, where gaps in the water temperature record occurred, temperatures could be estimated from air temperatures. An Environment Canada Weather Station was in place on SIL from 1978 to 1989, collecting data on air temperatures, precipitation, and wind speeds and directions, and longer-term weather data are available from the towns of Lynn Lake (130 km west) and Thompson (130 km southeast). Consequently, it is possible to look for possible correlations between weather variables and the abundance of *Hexagenia* over the period of record.

In addition to weather effects, water temperature was influenced by impoundment of SIL and the diversion of the Churchill River into the Nelson catchment (Hecky 1984). Impoundment affected water temperatures throughout the lake by increasing the water volume to be heated, and by increasing light reflectance because of higher turbidity caused by eroding shorelines. However, impoundment effects on temperature were not as pronounced as those due to diversion. The diversion resulted in the redirection of most of the flow of the Churchill River southward, which delayed ice break-up in spring in the large northern basins (Regions 3 and 4 and the northern portion of Region 2; Fig VI-1), and resulted in cooler overall water temperatures (Hecky 1984). In contrast, Churchill River water moving out of Region 2 is cooler than the pre-diversion condition in Region 6W, so diversion has caused a cooling in this southern region as well (Hecky 1984). Therefore, in addition to the potential for large population fluctuations of SIL *Hexagenia* in response to weather factors, temperature-related effects from the hydroelectric development must also be considered. The objective of this chapter is to quantify weather effects on SIL populations of *Hexagenia*, and to distinguish these from effects caused by the hydroelectric development.

MATERIALS AND METHODS

Hexagenia were sampled in 1972 (before impoundment and diversion), 1977 (after impoundment), 1979 (after diversion, and every two years thereafter until 1987. Samples were collected during mid-July with a 15 X 15 cm modified Ekman grab, along with physical data (temperature, turbidity, particle size distribution), at 58 stations throughout the lake (Fig. VI-1; Giberson *et al.* 1991, Wiens and Rosenberg 1984). For comparison with earlier chapters,

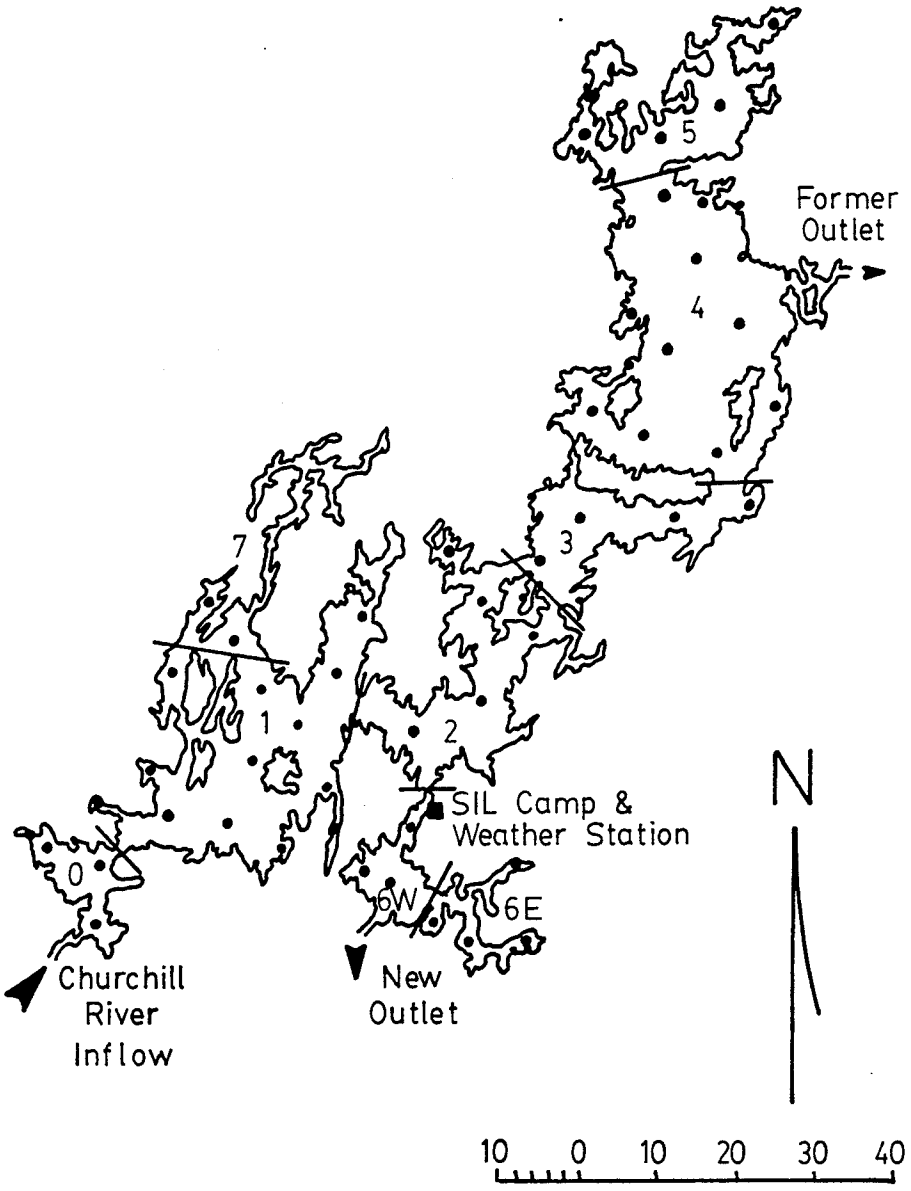

Fig. VI-1. Southern Indian Lake, with regions (numbers), whole-lake survey sampling stations (dots), and location of SIL camp and weather station. Arrows refer to major inflow and outlets.

region 0 in this section corresponds to Opachuana, Wupaw Bay is a small bay of the main flow of the Churchill River in region 1, region 6E is South Bay East, and region 6W is South Bay West.

Air temperature was chosen as the primary weather variable in correlation analyses with *Hexagenia* abundance both because of its effect on life history and because of the complete record of air temperatures that existed for the area. Although water temperature affected many aspects of the life history of *Hexagenia*, water temperature data were not continuous through the period of record because of changes in the focus of studies at SIL. Water temperatures for each region were estimated from relationships between air and regional water temperatures from the periods for which records existed (A.P. Wiens, Freshwater Institute, personal communication). However, rather than use derived relationships for correlation analyses, it was simpler and more direct to use air temperatures, especially because air temperature also influenced *Hexagenia* abundance (Chapter III).

Calculation of atmospheric degree days

Summer daily temperatures for each year subsequent to 1978 were taken directly from the Environment Canada weather summaries for SIL. Prior to 1978, temperatures were estimated from the mean of Lynn Lake and Thompson data (McCullough 1981). Because *Hexagenia* is affected not only by the temperature during the growing season, but also by the length of the growing season, daily temperatures were summed over the length of the ice-free season to give the air degree days (dd) >0°C. Air dd >0°C are roughly equivalent to the mean summer temperature multiplied by the number of ice-free days, and give a relative measure of the amount of heat available each year for growth.

Air dd >0°C were used for the whole open-water season, rather than just

the period when water temperatures were above the developmental threshold temperature (≈8°C; Chapters IV & V), because any air temperatures above freezing in the spring influence the rate of warming after ice-out. Similarly, in fall, rates of cooling may have an effect on life history features such as egg hatch, and adults may still be emerging despite the cool temperatures (Chapter III).

The ice-free periods for 1972-1979 are given in McCullough (1981), and were calculated according to the formula in McCullough (1981) for 1980-1987. Date of average break-up for the lake is considered to be the intersection of the forty day running mean temperature with 5°C, and freeze-up corresponds to the intersection in the fall with 0°C; these dates corresponded well to observed dates of break-up and freeze-up (McCullough 1981).

Correlations between air temperature and Hexagenia abundance - whole lake

There was high year-to-year variability in air temperature patterns (air dd>0°C) during the period 1972-1987 (Fig. VI-2). *Hexagenia* abundance appeared to track the temperature data, although with a time lag of two to three years. Consequently, a series of "lagged" regressions were performed to determine the relationship that explained (statistically) the most variation in *Hexagenia* abundance.

Two series of regressions were performed. The first consisted of regressing *Hexagenia* abundance against single-year temperature accumulations (May-Nov) for the year prior to the sampling date, 2 yr prior to the sampling date, and 3 yr prior to the sampling date. The second series was based upon the fact that temperature has an important influence on *Hexagenia* abundance over the entire life cycle. In this series, *Hexagenia* abundance was regressed against accumulated temperature (ice-free season) for the one-year period from

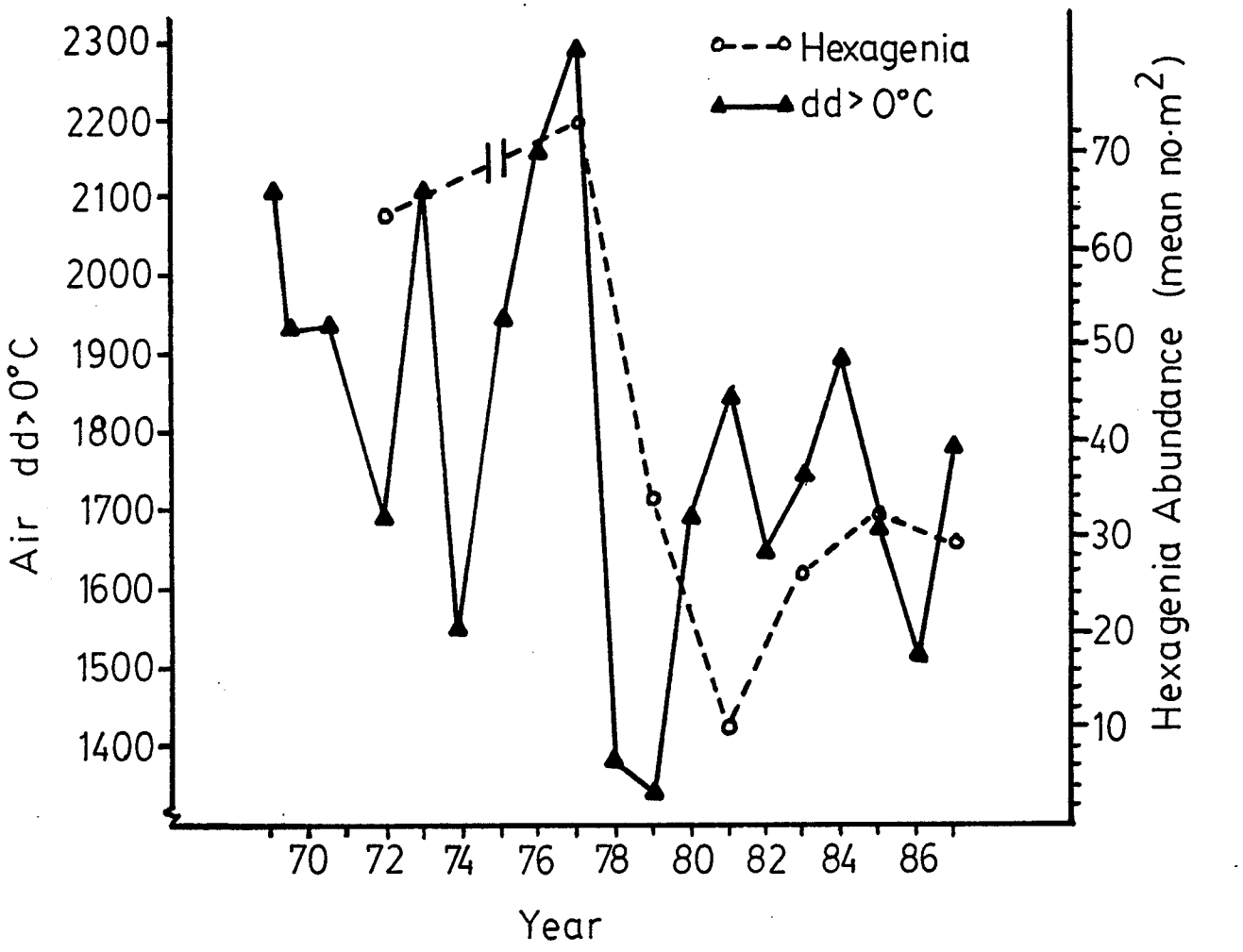

Fig. VI-2. Annual air temperature accumulations >0°C (1969-1987), and whole-lake *Hexagenia* abundance (no.m^{-2}, 1972-1987) for Southern Indian Lake.

July-July prior to the sampling date, and against the mean annual accumulated temperatures for 2 yr and 3 yr prior to sampling.

The strongest correlation was observed between *Hexagenia* abundance and the 3-yr accumulated air temperature. Therefore, that correlation was used to predict *Hexagenia* abundance relative to weather, and predicted abundances were plotted along with the observed values and compared visually. The 3-yr mean temperature correlation was also used in subsequent regional analyses.

Correlations between abundance and 3-yr mean temperature - regions

Hexagenia mean abundance was calculated annually for each lake region and regressed against the 3 yr mean accumulated temperature. Regions in which abundance was not significantly correlated to the air-temperature model were assumed to be affected by factors other than weather.

RESULTS

Mean summer temperatures for the SIL region varied from 10.8 to 13.8°C, and the length of the ice-free season ranged from 120-190 d between 1972 and 1987 (Table VI-1). Air dd>0°C ranged from 1344-2125 in that period ($\bar{x}$ = 1777) with high year-to-year variability (Fig. VI-2, Table VI-1). *Hexagenia* abundance was high in 1972 and 1977, following periods of generally above average temperature accumulations, but dropped dramatically following two consecutive extremely cold years in 1978 and 1979 (Fig. VI-2). Temperature accumulations since 1980 have hovered near the 19-yr mean, and standing stocks of *Hexagenia* appear to be gradually recovering.

There were significant correlations ($P<.05$) between whole-lake *Hexagenia* abundance and air temperatures only for multiple year accumulations of 2 or 3

Table VI-1. Average dates of break-up and freeze-up, length of ice-free season, and mean summer temperatures (°C) for Southern Indian Lake, 1972-1987.

Year	Break-up Date	Freeze-up Date	Ice-free Days	Mean Summer Temp.
1972	25 May	20 October	148	11.4
1973	28 May	5 November	161	13.2
1974	7 June	20 October	135	11.4
1975	29 May	3 November	158	12.2
1976	26 May	3 November	161	13.5
1977	12 May	18 November	190	12.3
1978	31 May	13 October	135	10.8
1979	10 June	7 October	120	11.2
1980	10 May	9 October	151	11.3
1981	2 June	20 October	140	13.3
1982	1 June	19 October	141	11.7
1983	19 June	24 October	127	13.8
1984	5 June	22 October	139	13.7
1985	24 May	14 October	143	11.8
1986	31 May	10 October	133	11.4
1987	5 June	3 November	137	13.1

yr (Table VI-2). The strongest correlation was obtained from the regression of abundance on the average accumulated temperature for the 3 yr prior to each sampling date (Table VI-2, Fig. VI-3). That relationship explained, in a statistical sense, nearly 95% of the variation in abundance between 1972 and 1987. The resulting regression equation:

$$Y = 0.152\ (X) - 235 \qquad \text{where } Y = \text{abundance and } X = dd{>}0°C,$$

was used to predict abundance values for that period, based solely on the temperature relationship (Fig. VI-4). Close agreement can be seen between the plots for predicted *vs* observed abundance, with the possible exception of early in the study period, when there was a long (5 yr) gap in the sampling record.

Hexagenia abundance was also related to air temperature in many of the regions in the lake (Fig. VI-5). Correlations were significant ($P<.05$) in all regions except for 3 and 4, although correlations were relatively weak in regions 5 and 7. Note, however, that in region 6E, a relatively strong correlation ($r^2=.64$, $P=.03$; Fig. VI-5) resulted from two clusters of points rather than a smooth linear distribution. When relationships obtained from Fig. VI-5 were used to predict regional abundances on the basis of air temperature (Fig. VI-6), the patterns became clearer. Regions 0, 1, 2, and 6W agreed closely with the temperature model. Regions 5 and 7 had generally higher than predicted mean *Hexagenia* abundance for the first half of the study period, and then lower than predicted for the second half. Region 6E had higher standing stocks than predicted early in the study period, and standing stocks declined earlier than predicted, although they did not reach the very low levels expected from the temperature model. Subsequently, abundance in this zone did not recover to the level predicted by the model. The patterns in regions 3 & 4 were similar to region 6E.

Table VI-2. Results of correlation analyses between whole lake *Hexagenia* abundance and air temperatures in Southern Indian Lake, 1972-1987. See text for explanation.

	Atmospheric dd>0°C for open water season					
	Single year accumulations			Multi-year means		
	yr-1	yr-2	yr-3	1-yr	2-yr	3-yr
r^2	0.49	0.22	0.06	0.34	0.75	0.95
P	0.08	0.29	0.61	0.17	0.01	<0.001

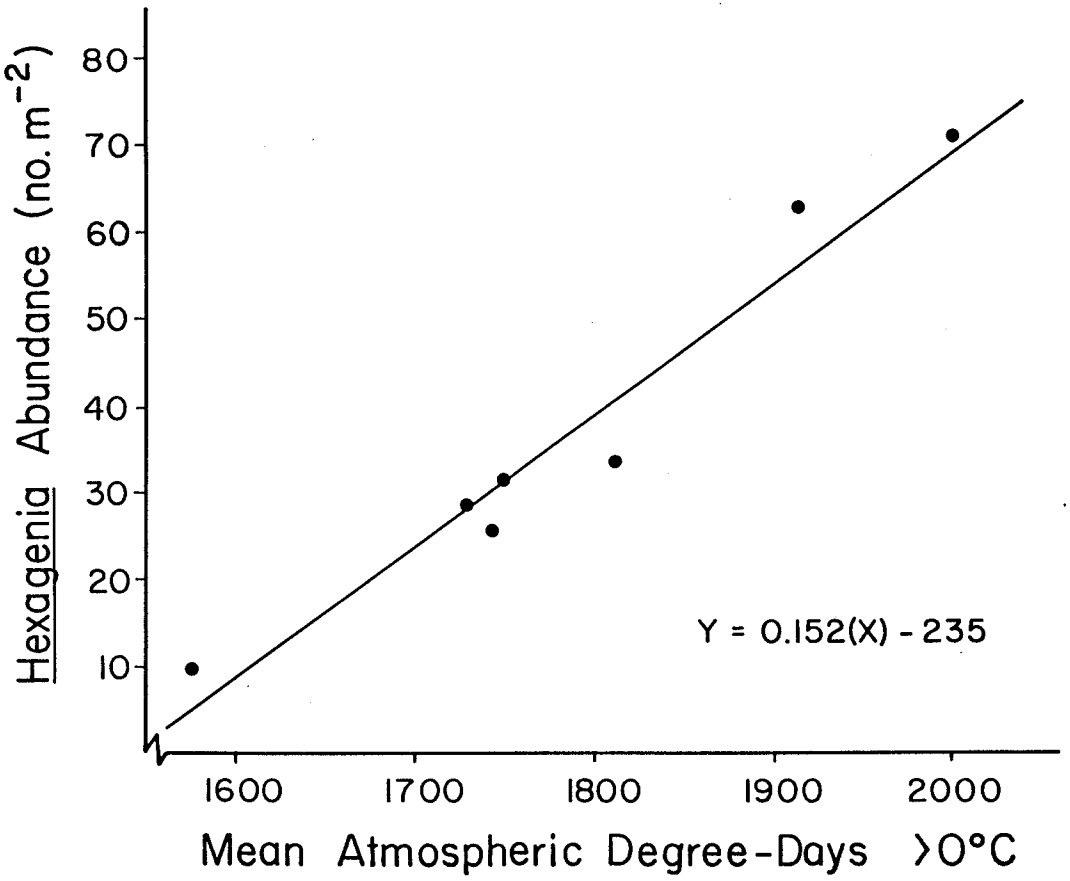

Fig. VI-3. Relationship between *Hexagenia* whole-lake abundance (mean no.m^{-2}) and mean 3-yr accumulated air temperatures (>0°C) in Southern Indian Lake, 1972-1987.

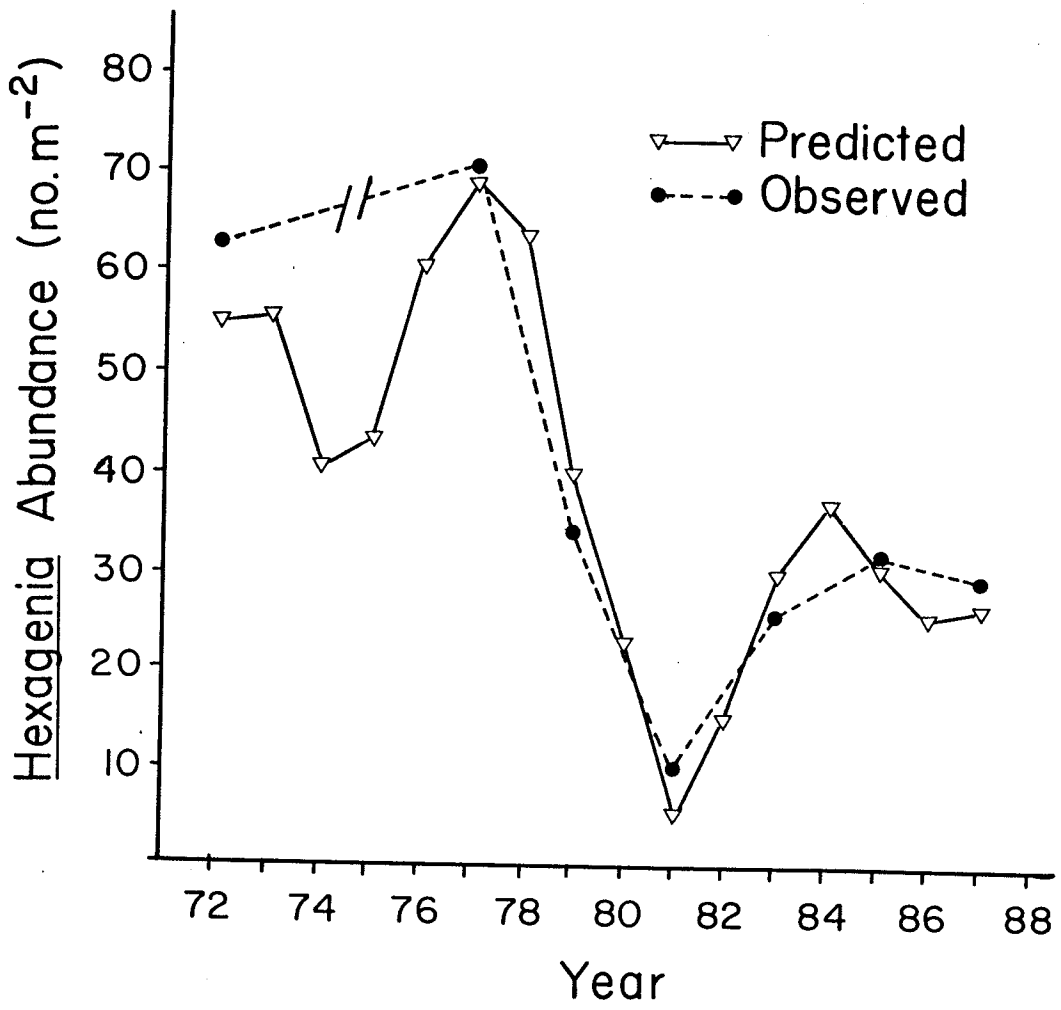

Fig. VI-4. Comparison between observed *Hexagenia* densities and those predicted from the relationship in Fig. VI-3.

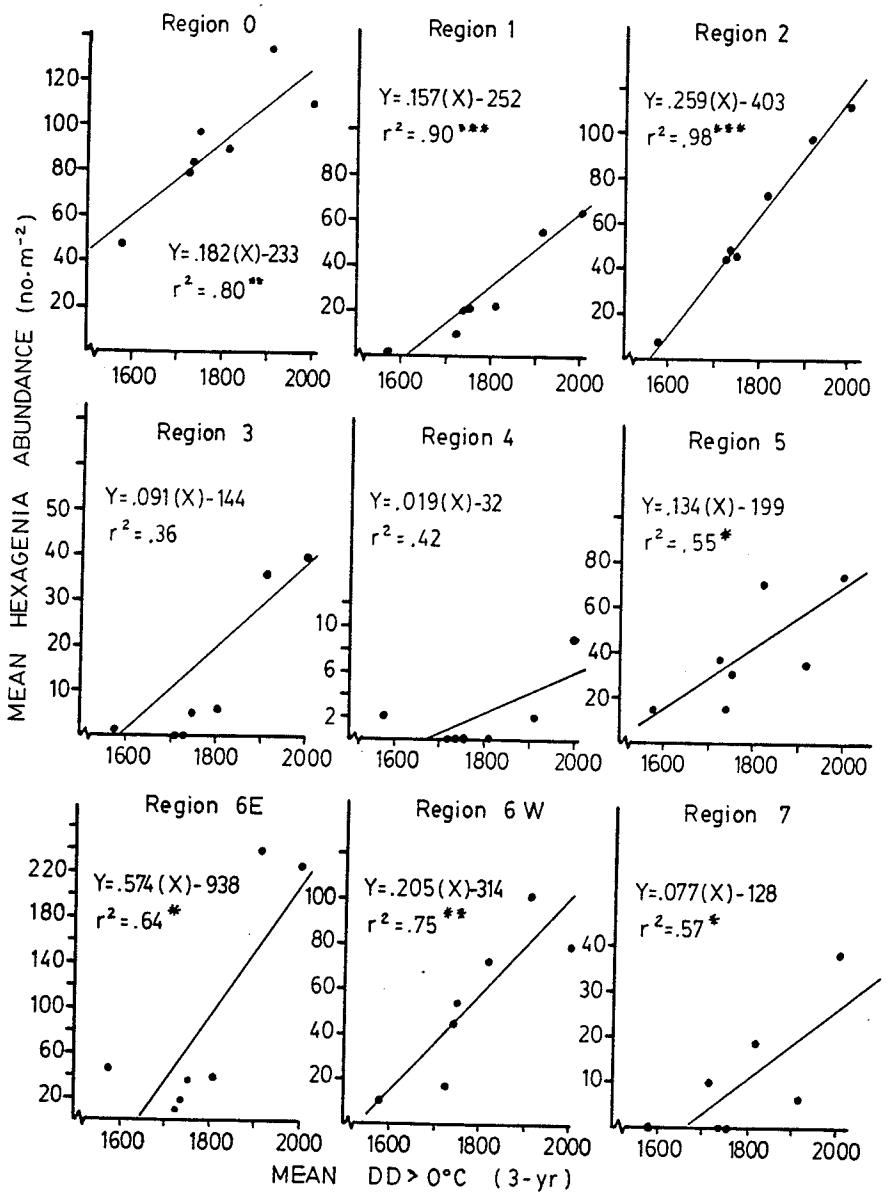

Fig. VI-5. Relationships between *Hexagenia* abundance and 3-yr accumulated air temperatures for the 9 Regions in Southern Indian Lake, 1972-1987. Asterisks refer to level of statistical significance: *$p<.05$; **$p<.01$; ***$p<.001$.

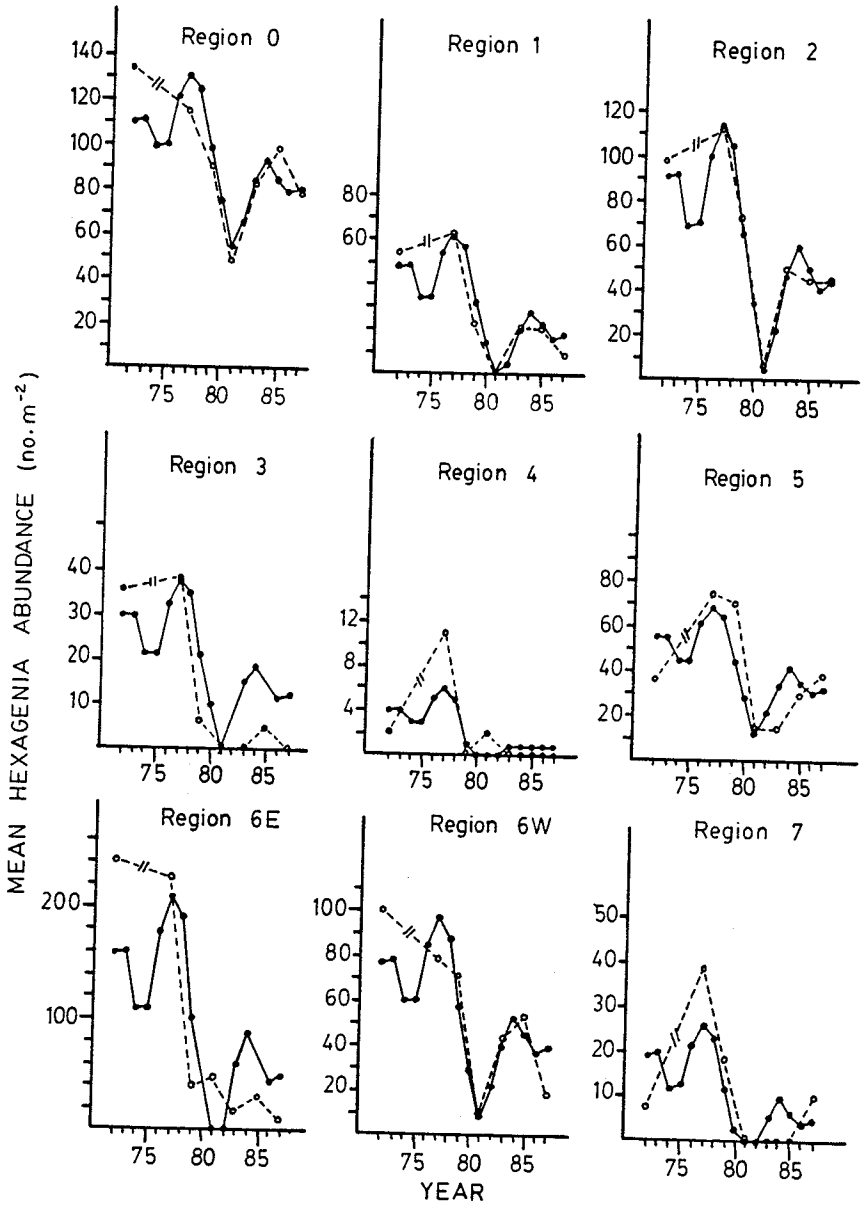

Fig. VI-6. Comparison between observed *Hexagenia* densities and those predicted from the relationships in Fig. VI-5. Solid lines = predicted; dashed lines = observed.

DISCUSSION

The correlations between accumulated air temperatures and *Hexagenia* abundance in SIL stem from weather effects on the life history (Chapter III). Air temperature during the ice-free season is directly related to water temperature because the lake does not stratify, and water temperature influences life-cycle length (Chapter III), egg-hatching success (Chapter IV), emergence timing (Chapter III), and body size and fecundity (Chapters III, V). Air temperature also affects the length of the subimaginal stage, and consequently the length of time that *Hexagenia* was susceptible to predation in the winged stages (Chapter III). Finally, cool summers tend to be relatively windy compared to warm summers, so air temperature was also related indirectly to emergence success (Chapter III). These temperature effects occur throughout the life cycle, so it is not surprising that the multiple-year temperature correlations produced statistically significant ($P<.05$) results. Moreover, the majority of the burrowing mayflies in SIL have a 3 yr life cycle, rather than 4-yr, which explains the good fit between abundance and 3-yr temperature accumulations.

The temperature model was less useful when mean abundances were considered regionally, rather than for the whole lake, despite significant ($p<.05$) correlations between temperature and abundance in all regions except 3 and 4. Region 6E had a significant correlation only because the data points fell into two clumps at either end of the regression line. Good correlations were expected in regions essentially unaffected by diversion (0,1, and most of 2). However, the strong correlation between air temperatures and *Hexagenia* standing stocks in Region 6W was unexpected, because inputs of cool Churchill River water resulted in cooler summer temperatures there than before diversion. It is possible that Churchill River inputs opened up the area

sooner in spring than in the pre-diversion condition, resulting in a longer growing season and similar total temperature accumulations to the period before the diversion became operational. In addition, river flow may have increased organic inputs to the region. Food supply affects growth and development, although to a lesser degree than temperature (Chapter V), and an abundance of food may compensate for lower temperatures.

Alternatively, temperature declines due to the diversion may have changed the life cycle pattern in Region 6W. Information on pre-diversion life cycle patterns and temperature accumulations in 6W is not available, but if pre-diversion temperatures in 6W were similar to those in 6E, a 3-yr life cycle would have been expected. Nymphs in Region 6W now require 4 yr to complete development, so diversion may have also resulted in a lengthening of the life cycle. If the life cycle did change as a result of diversion effects on temperature, expected declines in abundance from a lowered temperature regime may have been offset by higher fecundity. Overall body sizes (particularly for *H. limbata*) associated with the longer life cycle are larger, resulting in higher fecundity as well.

The pattern in Region 6E was also unexpected, but for the opposite reason. That region was unaffected by diversion, so *Hexagenia* abundance was expected to correlate well with weather patterns. However, numbers fell earlier than predicted from the weather model, and did not rebound to the same extent as other unaffected regions after the cold years of 1978 and 1979. This pattern may be due to effects of hydroelectric development in 6E. Grab samples in parts of Region 6E were highly organic, and had a strong hydrogen sulfide smell, particularly in mid-summer. The addition of organic matter from shoreline erosion to these shallow, sheltered bays may have produced a high oxygen demand, resulting in anoxic conditions that directly affected

Hexagenia. *Hexagenia* cannot survive oxygen concentrations less than ≈1.2 ppm (Eriksen 1968, Hunt 1953), so their low densities in this area could be related to low oxygen.

Standing stocks in Regions 5 and 7 were only weakly correlated to air temperature compared to regions directly in the flow of the Churchill River. Neither region should have been affected by the diversion, and so both were expected to conform well to the weather model. In Region 5, the weaker correlation could stem from the fact that it is located nearly 100 km north of the weather station, and weather patterns may have been different for this portion of the lake. Region 7 was not sampled regularly, so little is known about physical conditions there and it is difficult to speculate on the reasons for the poor correlation. However, Region 7 is deep and many parts are relatively sheltered, so impoundment may have resulted in occasional stratification and oxygen deficits.

Regions 3 and 4 were directly affected by the diversion of the Churchill River southward, so the decline in standing stocks in these areas was probably related to a combination of weather and diversion effects. The decline was first noted in 1979, earlier than for areas primarily affected by weather. Diversion may have had an immediate effect. The combination of two consecutive cold years and lowered temperatures because of diversion essentially eliminated *Hexagenia* from these regions. Standing stocks in these regions originally were lower than in most parts of the lake, so the patterns identified in Regions 3 and 4 would have had little noticeable effect on the whole-lake response.

To summarize, the dramatic decline in *Hexagenia* standing stocks in SIL following lake manipulation for hydroelectric development appears to be largely a weather-related anomaly and not one caused by the development. 95% of the variation in lake-wide standing stocks could be attributed to weather. Some of the mechanisms for population control by weather were revealed by intensive study on *Hexagenia*, with water temperature an important controlling variable. Since the development also influenced water temperatures in SIL, particularly in certain regions, a regional analysis identified localized development effects within specific regions. *Hexagenia* abundance in regions 0, 1, 2, 5, 6E, 6W, and 7 was significantly correlated to weather, whereas abundance patterns in regions 3 and 4 were apparently related to a combination of weather and diversion effects. Despite the apparent correlation between abundance and weather in region 6E, however, the pattern there was also most likely related to the hydroelectric development. *Hexagenia* abundance declined sharply after lake manipulation and did not subsequently recover, possibly because of development of anoxia caused by decomposition of organic matter. Weaker correlations in regions 5 and 7 may have resulted from distance from the weather station to region 5 and a possible hypolimnetic oxygen deficit in region 7 if stratification occurred due to impoundment.

Large fluctuations in standing stocks of natural populations occur commonly in response to a variety of natural phenomena, many of which cannot be predicted (Bakun 1986, Iker 1983, see Buchanan *et al.* 1978, Macan 1977, Oliver 1960, Schneider 1965, Stahl 1986, Wright 1978 for examples). Many environmental monitoring studies operate on relatively short time frames and simply set out to record change, without giving much thought to the actual causes of those changes (Green 1984). This research has demonstrated how easy it is to confuse responses to natural variability with responses to

anthropogenic perturbations, particularly when a large weather response overshadows one relating to development. A combination of long-term basic monitoring, intensive surveys, and experimental studies allowed the error in interpretation of the monitoring data to be identified, and the mechanisms responsible for fluctuations in standing stocks of *Hexagenia* to be elucidated.

CHAPTER VII

OVERALL SUMMARY

SUMMARY

1. The life cycles of *Hexagenia limbata* (Serville) and *H. rigida* McDunnough were virtually identical in the study regions investigated in SIL. Life cycles took 3 yr to complete in the warmer areas of the lake, and ≥4 yr in cooler regions. Three year life cycles have been alluded to in the literature for *H. limbata* (McCafferty 1975, Mozely and Ladronka 1988), but I am not aware of any other verified examples of a ≥3-yr life cycle for either species.

2. Life cycle length was related to water temperature during development. Development took longer at lower temperatures, resulting in higher potential accumulated mortality due to longer times spent exposed to mortality factors.

3. Degree day requirements (>10°C) over the life cycle of *H. limbata* were lower for SIL field populations than reported for populations further south, confirming a pattern noted by Heise *et al.* (1987) of declining dd requirements with increasing latitude. This pattern is probably not related to physiological differences between populations, since the development/temperature response for laboratory reared SIL *H. limbata* was similar to that reported in southern populations (for temperatures in the middle of the temperature range). Instead, it is likely due to differences in thermal regime in northern habitats when compared to southern ones. The dd model is only valid for temperatures within the middle portion of the temperature ranges, and growth is faster than predicted when temperatures are near the lower threshold for

development. In northern habitats, temperature changes in spring and fall are gradual, so more time may be spent at temperatures near the lower threshold than in habitats located further south. Therefore field dd comparisons between northern and southern populations with the linear model may not be valid.

4. Emergence timing was related to dd accumulation over the whole life cycle, but it was more closely related to dd accumulation in the final weeks before emergence. Although development is largely temperature controlled, the population may be synchronized by an environmental cue in the last year. Nymphs of a certain size may respond to this cue, perhaps an abrupt change in temperature, to begin adult tissue maturation necessary for emergence.

5. Emergence of subimagos from the lake and subsequent mating success were influenced by the weather during and prior to emergence. Subimagos were observed emerging throughout the day, but the majority emerged during mid-morning. If conditions were windy enough at that time to produce waves of >1m in height, most of the newly emerged subimagos drowned. For those that successfully emerged, the duration of the winged stages was dependent on air temperature. The moult from subimago to imago took longer at lower temperatures, resulting in longer potential exposure to predation. Moreover, the final moult was unsuccessful when air temperatures were near freezing. Cool summers at SIL were generally windier than warm summers, leading to a higher probability of emergence-related mortality in cool summers. High winds also hindered mating success if windy conditions persisted into evenings when swarming

occurred. In addition, weather in the fall tended to be more severe than in mid-summer, so in the years in which low temperatures delayed emergence until fall, both emergence mortality and moulting mortality (from subimago to imago) would probably increase.

6. As suggested from the field data, There was a strong relationship between temperature and growth and development in the laboratory. Higher temperatures resulted in higher growth rates and faster development, and also in larger size at maturity. Food availability modified the temperature response; rearing nymphs under limiting food conditions had about the same effect as lowering the thermal regime by ≈5°C.

7. Mature body size was also related to thermal regime in the field. Nymphs were generally largest in Opachuana, the warmest area investigated, and declined in size with decreasing annual thermal accumulations for Wupaw Bay and South Bay East, locations where the life cycle was 3 yr in length. Body size increased again in South Bay West, despite the cooler temperatures, where the life cycle switched to 4 yr. This pattern was most pronounced for *H. limbata* where body size in South Bay West was very similar to that for Opachuana. Nymphs of *H. rigida* from South Bay West, on the other hand, were smaller than those from Opachuana, perhaps responding more strongly to the lower temperatures than *H. limbata*.

8. Mature nymphal body size in both species was strongly related to adult body length, which in turn, was related to fecundity. Therefore, the same relationship to thermal regime existed for fecundity as body size. Fecundity was highest in Opachuana and South Bay West for *H. limbata*, and in Opachuana for *H. rigida*, and generally declined with declining temperature for Wupaw Bay and South Bay East. The higher fecundity in South Bay West for both species may have at least partially offset the higher potential accumulated mortality due to the longer life cycle.

9. Egg hatching success and time required for hatching were both related to water temperature for *H. limbata*. Fewer eggs hatched at lower temperatures, over a longer period of time, but hatching success at 8°C (believed to be near the lower threshold for hatching), was improved following exposure to winter temperatures. Hatching success at all temperatures investigated >8°C was improved after exposure to a cold period. Only about half of the eggs hatched immediately at 20°C, and the remainder apparently entered diapause and hatched after exposure to cold. This type of bimodal hatching response is thought to be an adaptation to extreme environments. In SIL, in warm years or warm locations, some eggs hatch within 3-6 wk after oviposition and are likely able to achieve sufficient growth to successfully overwinter. The remaining eggs overwinter and hatch the next spring. In cold years or locations, eggs may still hatch in the season of oviposition, but very young nymphs experience high overwintering mortality. The presence of overwintering eggs in this instance ensures that at least some members of the new cohort will survive the first winter.

10. Weather effects on the abundance of *Hexagenia* in SIL may be summarized as follows: Air temperature affects water temperature, which influences life cycle duration and potential accumulated mortality, egg hatching success and timing, body size and fecundity, and timing and subsequent success of emergence. Air temperature is indirectly related to emergence and mating success because warm summers are generally less windy than cool ones. Air temperature also affects the length of the subimaginal stage and consequently the amount of time the winged stages are exposed to predation pressure.

11. A combination of long-term basic monitoring and intensive study on *Hexagenia* was required to separate the effects of weather and hydroelectric development. Lake-wide abundance was strongly correlated with accumulated air temperature for the 3 yr prior to each sampling date (r^2=0.95). The strong relationship stemmed from the fact that air temperature was correlated with both water temperature and weather during emergence, and temperature effects were felt throughout the 3-yr life cycle. The correlation between air temperature and *Hexagenia* abundance, supported by intensive study on the mechanisms for weather control of the population, indicated that weather rather than hydroelectric development was primarily responsible for the long-term abundance pattern in the lake. However, the development did have an effect in some areas, although that response was masked by the larger natural variability response for the whole lake. Diversion caused a cooling in regions 3 and 4 that, when combined with the weather response, has apparently eliminated *Hexagenia* from those areas. Diversion in region 6W may also have resulted in cooling, with a

subsequent lengthening of the life cycle there from 3 yr to 4 yr. No apparent diversion-related decline in standing stocks was noted, however, possibly due to higher fecundity offsetting higher accumulated mortality associated with the longer life cycle. In region 6E organic matter decomposition likely resulted in oxygen deficits that led to a decline in the *Hexagenia* population. Oxygen deficits may also have occurred in region 7, if occasional thermal stratification resulted from impoundment.

LITERATURE CITED

Anderson, N.H. and A.S. Cargill. 1987. Nutritional ecology of aquatic detritivorous insects. Chapter 30, *in* F. Slansky and J.G. Rodriguez (editors). Nutritional Ecology of Insects, Mites and Spiders. John Wiley and Sons, Inc.

Anderson, N.H. and K.W. Cummins. 1979. Influences of diet on the life histories of aquatic insects. Journal of the Fisheries Research Board of Canada 36:335-342.

Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by macro-invertebrtates in stream ecosystems. Annual Review of Entomology 24:351-377.

Baker, R.L. and B.W. Feltmate. 1987. Development of *Ischnura verticalis* (Coenagrionidae: Odonata): effects of temperature and prey abundance. Canadian Journal of Fisheries and Aquatic Sciences 44:1658-1661.

Bakun, A. 1986. Definitions of environmental variability affecting biological processes in large marine ecosystems. Chapter 6 *in* K. Sherman and L.M. Alexander (editors), Variability and Management of Large Marine Ecosystems. AAAS Selected Symposium, Westview Press Inc. Colorado

Berner, L. and M.L. Pescador. 1988. The Mayflies of Florida (Revised Edition) University Presses of Florida, Tallahassee and Gainsville. 415 pages.

Bird, G.A. and N.K. Kaushik. 1984. Survival and growth of early instar nymphs of *Ephemerella subvaria* fed various diets. Hydrobiologia 119:227-233.

Bodaly, R.A., T.W.D. Johnson, R.J.P. Fudge, and J.W. Clayton. 1984. Collapse of the lake whitefish (*Coregonus clupeaformis*) fishery in Southern Indian Lake, Manitoba, following lake impoundment and river diversion. Canadian Journal of Fisheries and Aquatic Sciences 41:692-700.

Bowman, R.S. 1978. Dounreay oil spill: Major implications of a minor incident. Marine Pollution Bulletin 9:269-273.

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, Volume 1 (New Series), #5, 70 pp.

Brittain, J.E. 1976. Experimental studies on nymphal growth in *Leptophlebia vespertina* (L.) (Ephemeroptera). Freshwater Biology 6:445-449.

Brittain, J.E. 1990. Life history strategies in Ephemeroptera and Plecoptera. Pages 1-12, *in* I.C. Campbell (editor), Mayflies and Stoneflies: Life History and Biology. Proceedings of the 5th International Conference on Ephemeroptera and 9th International Conference on Plecoptera, Marysville, Australia, February 1987; Series Entomologica, Volume 44, Kluwer Academic Publishing, Norwell, MA.

Buchanan, J.B., M. Sheader, and P.F. Kingston. 1978. Sources of variability in the benthic macrofauna off the south Northumberland coast, 1971-1976. Journal of the Marine Biological Association of the U.K. 58:191-209.

Burton, W. and J.F. Flannagan. 1973. An improved Ekman-type grab. Journal of the Fisheries Research Board of Canada 30:287-290.

Butler, M.G. 1984. Life histories of aquatic insects. pages 24-55 *in* V.H. Resh and D.M. Rosenberg (editors) The Ecology of Aquatic Insects. Praeger, New York.

Cairns, J., Jr. 1984. Are single species toxicity tests alone adequate for estimating environmental hazard? Environmental Monitoring and Assessment 4:259-273.

Callahan, J.T. 1984. Long-term ecological research. BioScience 34:363-367.

Carlander, K.D., C.A. Carlson, V. Gooch, and T.L. Wenke. 1967. Populations of *Hexagenia* naiads in pool 19, Mississippi River, 1959-1963. Ecology 48:873-878.

Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35:634-639.

Clifford, H.F. and H. Boerger. 1974. Fecundity of mayflies, with special reference to mayflies of a brown-water stream on Alberta, Canada. Canadian Entomologist 106:1111-1119.

Coull, B.C. 1985. The use of long-term biological data to generate testable hypotheses. Estuaries 8:84-92.

Coull, B.C. 1986. Long-term variability of meiobenthos: value, synopsis, hypothesis generation and predictive modelling. Hydrobiology 142:271-279.

Craven, R.E. and B.E. Brown. 1969. Ecology of *Hexagenia* naiads (Insecta: Ephemeridae) in an Oklahoma reservoir. American Midland Naturalist 82:346-358.

Crawford, P.J. and D.M. Rosenberg. 1984. Breakdown of conifer needle debris in a new northern reservoir, Southern Indian Lake, Manitoba. Canadian Journal of Fisheries and Aquatic Sciences 41:649-658.

Cullinane, J.P. and P.M. Whelan. 1983. An example of drastic natural changes in the intertidal biota and the implications for monitoring programs. Estuarine, Coastal and Shelf Science 17:479-481.

Danks, H.V. 1987. Insect Dormancy: An Ecological Perspective. Biological Survey of Canada Monograph Series #1, 439 pages.

Davidson, J. 1944. On the relationship between temperature and rate of development of insects at constant temperatures. Journal of Animal Ecology 13:26-38.

Edmunds, G.F., S.L. Jensen, and L. Berner. 1976. The Mayflies of North and Central America. University of Minnesota Press, Minneapolis. 330 pages.

Elliott, J.M. 1984. Hatching time and growth of *Nemurella pictetii* (Plecoptera: Nemouridae) in a Lake District stream. Freshwater Biology 14:491-499.

Elliott, J.M. 1987. Temperature induced changes in the life cycle of *Leuctra nigra* (Plecoptera: Leuctridae) from a Lake District stream. Freshwater Biology 18:177-184.

Elliott, J.M. and U.H. Humpesch. 1980. Eggs of Ephemeroptera. Report of the Freshwater Biological Association 48:41-52.

Eriksen, C.H. 1963. Respiratory regulation in *Ephemera simulans* Walker and *Hexagenia limbata* (Serville) (Ephemeroptera). Journal of Experimental Biology 40:455-467.

Eriksen, C.H. 1968. Ecological significance of respiration and substrate for burrowing Ephemeroptera. Canadian Journal of Zoology 46:93-103.

Flannagan, J.F. 1979. The burrowing mayflies of Lake Winnipeg, Manitoba, Canada. Pages 103-114 *in* K. Pasternak and R. Sowa (editors). Proceedings of the 2nd International Conference on Ephemeroptera, Pol. Akad. Navk, Krakow.

Flattum, R.F. 1963. Apparent effects of refrigeration on the rate of embryonic development of mayfly (*Hexagenia limbata*) eggs. Proceedings of the Minnesota Academy of Sciences 31:81-83.

Fremling, C.R. 1973. Factors influencing the distribution of burrowing mayflies along the Mississippi River. pages 12-25 *in* W.L. Peters and J.G. Peters (editors). Proceedings of the 1st International Conference on Ephemeroptera. E.J. Brill, Leiden.

Fremling, C.R. and D.K. Johnson. 1990. Recurrence of *Hexagenia* mayflies demonstrates improved water quality in pool 2 and Lake Pepin, upper Mississippi River. pages 243-248 *in* I.C. Campbell (editor) Mayflies and Stoneflies: Life History and Biology. Proceedings of the 5th International Conference on Ephemeroptera and the 9th International Conference on Plecoptera, Marysville, Australia, February 1987. Series Entomologica, Volume 44, Kluwer Academic Publishing, Norwell, MA.

Friesen, M.K. 1981. *Hexagenia rigida* (McDunnough). Pages 127-142 *in* S.G. Lawrence (editor). Manual for the culture of selected freshwater invertebrates. Canadian Special Publication of Fisheries and Aquatic Sciences 54, 169pp.

Friesen, M.K., J.F. Flannagan, and T.D. Galloway. 1979. Effects of temperature and cold storage on developmental time and viability of eggs of the burrowing mayfly *Hexagenia rigida* (Ephemeroptera: Ephemeridae). Canadian Entomologist 111:665-673.

Fuller, R.L. and R.J. Mackay. 1981. Effects of food quality on the growth of three *Hydropsyche* species (Trichoptera: Hydropsychidae). Canadian Journal of Zoology 59:1133-1140.

Giberson, D.J., D.M. Rosenberg, and A.P. Wiens. 1991. Changes in abundance of burrowing mayflies in Southern Indian Lake: Lessons for environmental monitoring. Ambio, in press.

Golladay, S.W., J.R. Webster, and E.F. Benfield. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. Holarctic Ecology 6:157-162.

Green, R.H. 1984. Statistical and non-statistical considerations for environmental monitoring studies. Environmental Management and Assessment 4:293-301.

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 16, 32 pages.

Hecky, R.E. 1984. Thermal and optical charactristics 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. and S.J. Guildford. 1984. Primary productivity of Southern Indian Lake before, during and after impoundment and Churchill River diversion. Canadian Journal of Fisheries and Aquatic Sciences 41:591-604.

Hecky, R.E. and G.K. McCullough. 1984. Effect of impoundment and diversion on the sediment budget and nearshore sedimentation of Southern Indian Lake. Canadian Journal of Fisheries and Aquatic Sciences 41:567-578.

Hecky, R.E., R.W. Newbury, R.A. Bodaly, K. Patalas, and D.M. Rosenberg. 1984. Environmental impact prediction and assessment: the Southern Indian Lake experience. Canadian Journal of Fisheries and Aquatic Sciences 41:720-732.

Heise, B.A., J.F. Flannagan, and T.D. Galloway. 1987. Life histories of *Hexagenia limbata* and *Ephemera simulans* (Ephemeroptera) in Dauphin Lake, Manitoba. Journal of the North American Benthological Society 6:230-240.

Heise, B.A., J.F. Flannagan, and T.D. Galloway. 1988. Production of *Hexagenia limbata* (Serville) and *Ephemera simulans* Walker (Ephemeroptera) in Dauphin Lake, Manitoba, with a note on weight loss due to preservatives. Canadian Journal of Fisheries and Aquatic Sciences 45:774-781.

Hengevold, R. 1987. Scales of variation: their distinction and ecological importance. Annales Zoologci Fennici 24:195-202.

Herman, P.M.J. and C. Heip. 1986. The predictability of biological populations and communities: an example from the meiobenthos. Hydrobiologia 142:281-290.

Higley, L.G., L.F. Pedigo, and K.R. Ostlie. 1986. DEGDAY: a program for calculating degree days, and assumptions behind the degree day approach. Environmental Entomology 15:999-1016.

Horst, T.J. and G.R. Marzolf. 1975. Production ecology of burrowing mayflies in a Kansas reservoir. Verhandlungen der Internationalen Vereinigung fur Theoretische und Angewandte Limnologie 19:3029-3038.

Hudson, P.L. and G.A. Swanson. 1972. Production and standing crop of *Hexagenia* (Ephemeroptera) in a large reservoir. Studies in Natural Sciences, Eastern New Mexico University, Portales 1:1-36.

Humpesch, U.H. 1979. Life cycles and growth rates of *Baetis* spp. (Ephemeroptera: Baetidae) in the laboratory and in two stony streams in Austria. Freshwater Biology 9:467-479.

Humpesch, U.H. 1981. Effect of temperature on larval growth of *Ecdyonurus dispar* (Ephemeroptera: Heptageniidae) from two English lakes. Freshwater Biology 11:441-457.

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 pages.

Iker, S. 1983. A lifetime of listening. Mosaic 14(4):8-13, reprinted in the Bulletin of the Ecological Society of America 65(1):7-12 (1984).

Keegan, B. 1986. The COST 647 Project on coastal benthic ecology - a perspective. Hydrobiologia 142:ix-xii.

Leggott, M. and G. Pritchard. 1985. The effect of temperature on the rate of egg and larval development in populations of *Argia vivida* Hagen (Odonata: Coenagrionidae) from habitats with different thermal regimes. Canadian Journal of Zoology 63:2578-2582.

Likens, G. 1983. A priority for ecological research. Bulletin of the Ecological Society of America. 64:234-243.

Lincoln, R.J., G.A. Boxshall, and P.F. Clark. 1982. A dictionary of ecology, evolution and systematics. Cambridge Univ. Press, Cambridge. 298 pages.

LWCNR 1975. Lake Winnipeg, Churchill and Nelson Rivers Study Board. Technical Report. Queen's Printer, Winnipeg, Manitoba. 398 pages and 8 appendices.

Lyman, F.E. 1944. Notes on emergence, swarming and mating of *Hexagenia* (Ephemeroptera). Entomological News 55:207-210.

Macan, T.T. 1977. A twenty year study of the fauna in the vegetation of a moorland fishpond. Archives für Hydrobiologie 81:1-24.

McCafferty, W.P. 1975. The burrowing mayflies of the United States (Ephemeroptera: Ephemeroidea). Transactions of the American Entomological Society 101:447-504.

McCafferty, W.P. 1984. A new synonym in *Hexagenia* (Ephemeroptera: Ephemeridae). Proceedings of the Entomological Society of Washington 86:789.

McCafferty, W.P. and C. Pereira. 1984. Effects of developmental thermal regimes on two mayfly species and their taxonomic interpretation. Annals of the Entomological Society of America 77:69-87

McCullough, G.K. 1981. Water budgets for Southern Indian Lake, Manitoba, before and after impoundment and Churchill River diversion 1972-1979. Canadian Manuscript Report of Fisheries and Aquatic Sciences #1620, 22 pages.

Mozley, S.C. and R.M. Ladronka. 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. and G.K. McCullough. 1984. Shoreline erosion and restabilization in the Southern Indian Lake reservoir. Canadian Journal of Fisheries and Aquatic Sciences 41:558-565.

Newbury, R.W., G.K. McCullough, and R.E. Hecky. 1984. The Southern Indian Lake Impoundment and Churchill River Diversion. Canadian Journal of Fisheries and Aquatic Sciences 41:548-557.

Nichols, F.H. 1985. Abundance fluctuations among benthic invertebrates in two pacific estuaries. Estuaries 8(2A): 136-144.

Northcote, T.G. 1952. An analysis of variation in quantitative sampling of bottom fauna in lakes. MA thesis, University of British Columbia, Vancouver, B.C.

Oliver, D.R. 1960. The macroscopic bottom fauna of Lac La Ronge, Saskatchewan. Journal of the Fisheries Research Board of Canada 17:607-624.

Park, S.O. 1988. Effects of temperature on the development of the water strider *Gerris paludum insularis* (Hemiptera: Gerridae). Environmental Entomology 17:150-153.

Pritchard, G. 1978. Study of dynamics of populations of aquatic insects: the problem of variability in life history exemplified by *Tipula sacra* Alexander (Diptera: Tipulidae). Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 20:2634-2640.

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 10:486-520.

Rempel, R.C. and J.C.H. Carter. 1986. An experimental study on the effect of elevated temperature on the heterotrophic and autotrophic food resources of aquatic insects in a forested stream. Canadian Journal of Zoology 64:2457-2466.

Rempel, R.C. and J.C.H. Carter. 1987. Modelling the effects of accelerated development and reduced fecundity on the population dynamics of aquatic Diptera. Canadian Journal of Fisheries and Aquatic Sciences 44:1737-1742.

Resh, V.H. and D.M. Rosenberg. 1989. Spatial-temporal variability and the study of aquatic insects. Canadian Entomologist. 121:941-963.

Riklik L. and W.T. Momot. 1982. Production ecology of *Hexagenia limbata* in Savanne Lake, Ontario. Canadian Journal of Zoology 60:2317-2323.

Robinson, W.R., R.H. Peters, and J. Zimmerman. 1983. The effect of body size and temperature on metabolic rate of organisms. Canadian Journal of Zoology 61:281-288.

Rosenberg D.M. and A.P. Wiens. 1985. Changes in populations of *Hexagenia limbata* and *Hexagenia rigida* (Ephemeroptera: Ephemeridae) in Southern Indian Lake, Manitoba. Paper presented to 33rd annual meeting of the North American Benthological Society, Corvallis, Oregon, June 1985.

Rosillon, D. 1988. Food preference and relative influence of temperature and food quality on life history characteristics of a grazing mayfly *Ephemerella ignita* (Poda). Canadian Journal of Zoology 66:1474-1481.

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, Ohio.

Scavia, D., G.L. Fahenstiel, M.S. Evans, D.J. Jude, and J.T. Lehman. 1986. Influence of salmonine predation and weather on long-term water quality trends in lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 43:435-443.

Schindler, D.W. 1987. Detecting ecosystem responses to anthropogenic stress. Canadian Journal of Fisheries and Aquatic Sciences 44, (Supplement 1):6-25.

Schloesser, D.W. and J.K. Hiltunen. 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.

Schneider, J.C. 1965. Further studies on the benthic ecology of Sugarloaf Lake, Washtenaw County, Michigan. Papers of the Michigan Academy of Sciences, Arts, and Letters 6:11-29.

Söderström, O. 1988. Effects of temperature and food quality on life history parameters in *Parameletus chelifer* and *P. minor* (Ephemeroptera): a laboratory study. Freshwater Biology 20:295-304.

Southwood, T.R.E. 1978. Ecological Methods, with Particular Reference to the Study of Insect Populations. 2nd Edition. Chapman and Hall, London. 524 pages.

Stahl, J.B. 1986. A six-year study of abundance and voltinism of Chironomidae (Diptera) in an Illinois cooling reservoir. Hydrobiology 134:67-79.

Stanley, E.H. and R.A. Short. 1988. Temperature effects on warmwater stream insects - a test of the thermal equilibrium hypothesis. Oikos 51:313-320.

Strayer, D., J.S. Glitzenstein, C.G. Jones, J. Kolassa, G.E. Likens, M.J. McDonnell, G.G. Parker, and S.T.A. Pickett. 1986. Long-term ecological studies: an illustrated account of their design, operation, and importance to ecology. Occasional Publications of the Institute of Ecosystem Studies, #2, August 1986, 38 pages.

Suter, P.J. and J.E. Bishop. 1990. Post-oviposition development of eggs of south Australian mayflies. Pages 85-84 *in* I.C. Campbell (editor), Mayflies and Stoneflies: Life Histories and Biology. Proceedings of the 5th International Conference on Ephemeroptera and the 9th International Conference on Plecoptera, Marysville, Australia, February 1987. Series Entomologica, Volume 44, Kluwer Academic Publishers, Norwell, MA.

Svensson, B. 1977. Life cycle, energy fluctuations and sexual differentiation in *Ephemera danica* (Ephemeroptera), a stream-living mayfly. Oikos 29:78-86.

Sweeney, B.W. 1984. Factors influencing life history patterns of aquatic insects. Pages 56-100 *in* V.H. Resh and D.M. Rosenberg (editors). The Ecology of Aquatic Insects. Praeger Publishers, New York. 625 pages.

Sweeney, B.W. and R.L. Vannote. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. Science 200:444-446.

Sweeney, B.W. and R.L. Vannote. 1984. Influence of food quality and temperature on life history characteristics of the parthenogenic mayfly *Cloeon triangulifer*. Freshwater Biology 14:621-630.

Sweeney, B.W., R.L. Vannote, and P.J. Dodds. 1986a. The relative importance of temperature and diet to larval development and adult size in the winter stonefly, *Soyedina carolinensis* (Plecoptera: Nemouridae). Freshwater Biology 16:39-48.

Sweeney, B.W., R.L. Vannote, and P.J. Dodds. 1986b. Effects of temperature and food quality on growth and development of a mayfly, *Leptophlebia intermedia*. Canadian Journal of Fisheries and Aquatic Sciences 43:12-18.

Tauber, M.J., C.A. Tauber, and S. Masaki. 1986. Seasonal Adaptations of Insects. Oxford University Press, New York. 411 pages.

Vannote, R.L., and B.W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. American Naturalist 115:667-695.

Wallace, J.B. and R.W. Merritt. 1980. Filter feeding ecology of aquatic insects. Annual Review of Entomology 25:103-132.

Walker, T.J. 1980. Mixed oviposition in individual females of *Gryllus firmus*: graded proportions of fast developing and diapause eggs. Oecologia 47:291-298.

Ward, J.V. and J.A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. Annual Review of Entomology 27:97-112.

Webb, K.M. and R.W. Merritt. 1987. The influence of diet on the growth of *Stenonema vicarium* (Walker) (Ephemeroptera: Heptageniidae). Hydrobiologia 153:253-260.

Welch C.L. and D.S. Vodopich. 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 (Ephemeridae, Ephemeroptera) in Irish waters. pages 187-199 *in* J.F. Flannagan and E. Marshall (editors). Advances in Ephemeroptera Biology. Proceedings of the 3rd International Conference on Ephemeroptera, Winnipeg, 1979. Plenum Press, New York.

Wiens, A.P. and D.M. Rosenberg. 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.

Wright J.F. 1978. Seasonal and between year variation in the chironomid larvae of a chalk stream. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 20:2647-2651.

Wright, L.L., J.S. Mattice, and J.J. Beauchamp. 1982. Effect of temperature and sex on growth patterns in nymphs of the mayfly *Hexagenia bilineata* in the laboratory. Freshwater Biology 12:535-545.

Zimmerman, M.C. and T.E. Wissing. 1978. Effects of temperature on gut-loading and gut-clearing times of the burrowing mayfly *Hexagenia limbata*. Freshwater Biology 8:269-277.

Zimmerman, M.C. and T.E. Wissing. 1980. The nutritional dynamics of the burrowing mayfly *Hexagenia limbata*. Pages 231-257 *in* J.F. Flannagan and K.E. Marshall (editors). Advances in Ephemeroptera Biology. Proceedings of the 3rd International Conference on Ephemeroptera. Plenum Press, New York.

Zimmerman, M.C., T.E. Wissing, and R.P. Rutter. 1975. Bioenergetics of the burrowing mayfly *Hexagenia limbata* in a pond ecosystem. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 19:3039-3049.

APPENDIX A

SEPARATION OF COHORTS FOR *HEXAGENIA LIMBATA* AND *H. RIGIDA* FOR EACH OF THE STUDY REGIONS ON EACH SAMPLING DAY

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COHORT SEPARATION

Cohorts were separated subjectively by visually comparing the frequency distributions through time for nymphal body length, head width, and mesothoracic wing-pad length. Body length was measured from the tip of the frontal process to the end of the abdomen, head width was measured immediately anterior of the eyes, and wingpad length was measured from the outside angle of the pad to the tip (Fig. A-1). Cohorts were assumed to correspond to peaks in the frequency distribution that were consistent through time. If overlap in frequency distributions occurred in one measure, but were clearly separated with another, the distribution with the strongest separation (if consistent with patterns for the month before and after) was assumed to be the cohort. This separation was then superimposed upon the frequency distributions for the other measures to check consistency. In the few cases where clear separation did not occur with any measure, sex of nymphs was also considered, to factor in the effects of sexual dimorphism. Males were smaller than females, so if a group of males overlapped with a group of females, the males were assumed to belong to the larger cohort.

Frequency histograms for body length, head width, and wingpad length for each species and each location are shown in Figs A-2 to A-9; cohort oviposition and emergence times are given in Table A-1.

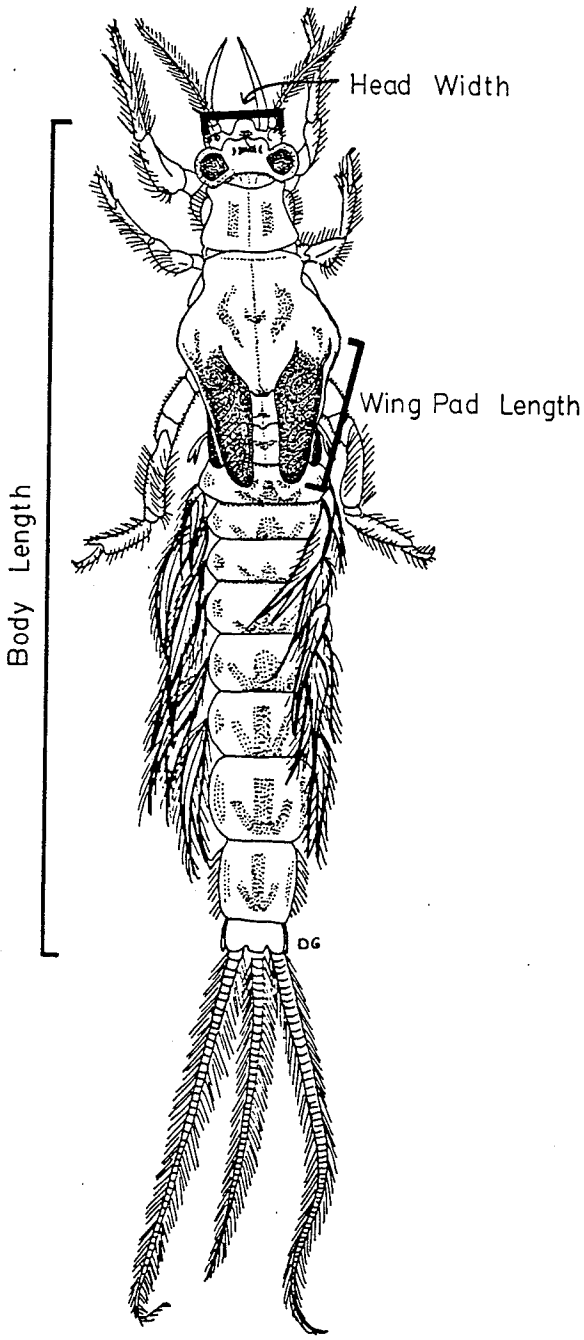

Fig. A-1. Hexagenia limabata nymph, showing measures used for cohort separation.

Table A-1. Summary of probable and observed oviposition and emergence years for each cohort, showing stipling patterns given in Figs. A-2 to A-9, and corresponding to cohort numbers in Table B-2 and Figs. B-1 to B-4.

a) Opachuana, Wupaw Bay and South Bay East

Cohort	Oviposited	Emerged	Stipling Pattern
1a	1983	1986	
2a	1984	1987	
3a	1985	1988	
1b	1986	1989	
2b	1987	1990	
3b	1988	1991	

b) South Bay West

Cohort	Oviposited	Emerged	Stipling Pattern
1a	1982	1986	
2a	1983	1987	
3a	1984	1988	
4a	1985	1989	
1b	1986	1990	
2b	1987	1991	
3b	1988	1992	

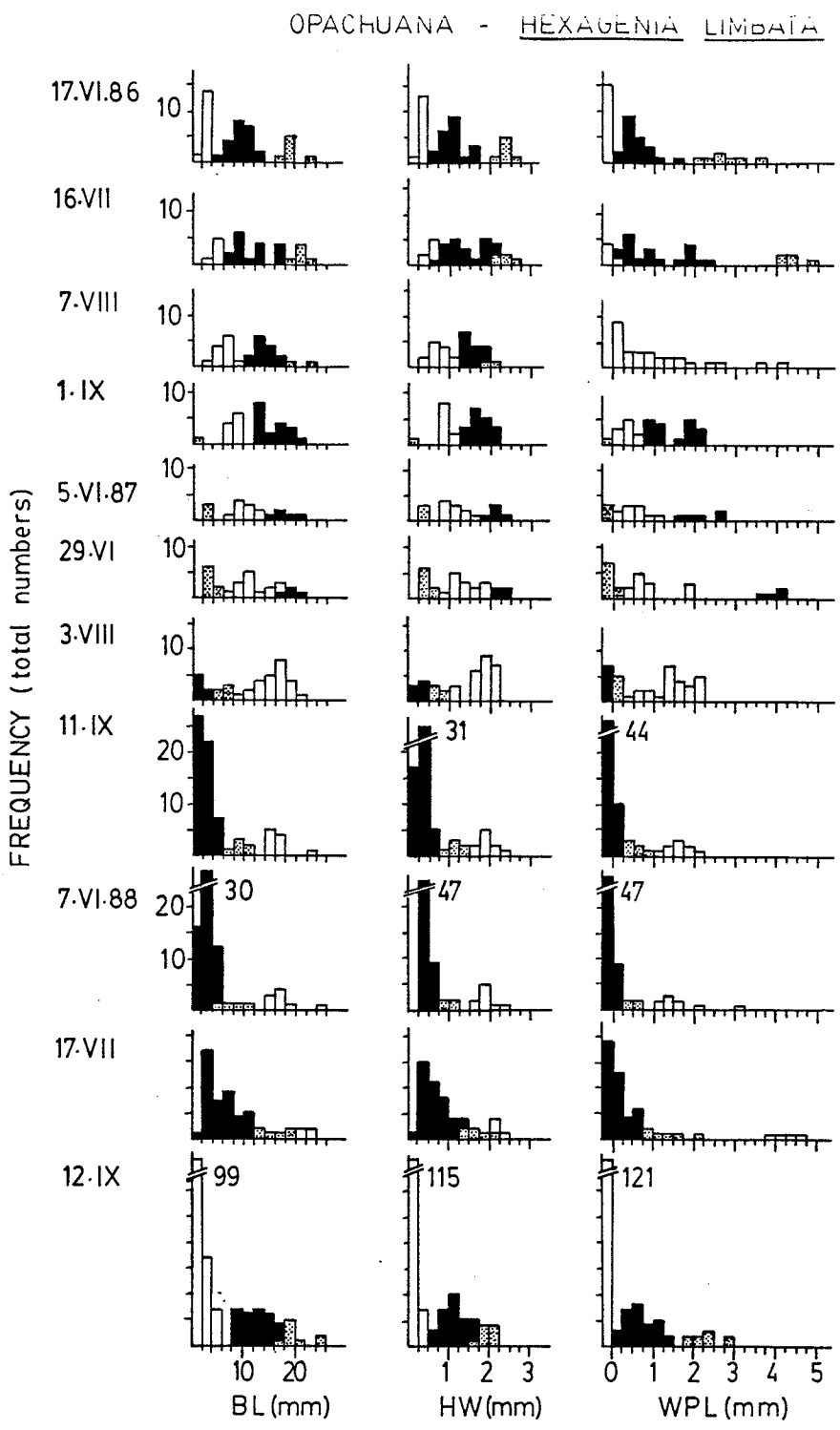

Fig. A-2. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for Hexagania limbata in Opachuana, 1986-1988. See Table A-1 for explanation of stipling pattern.

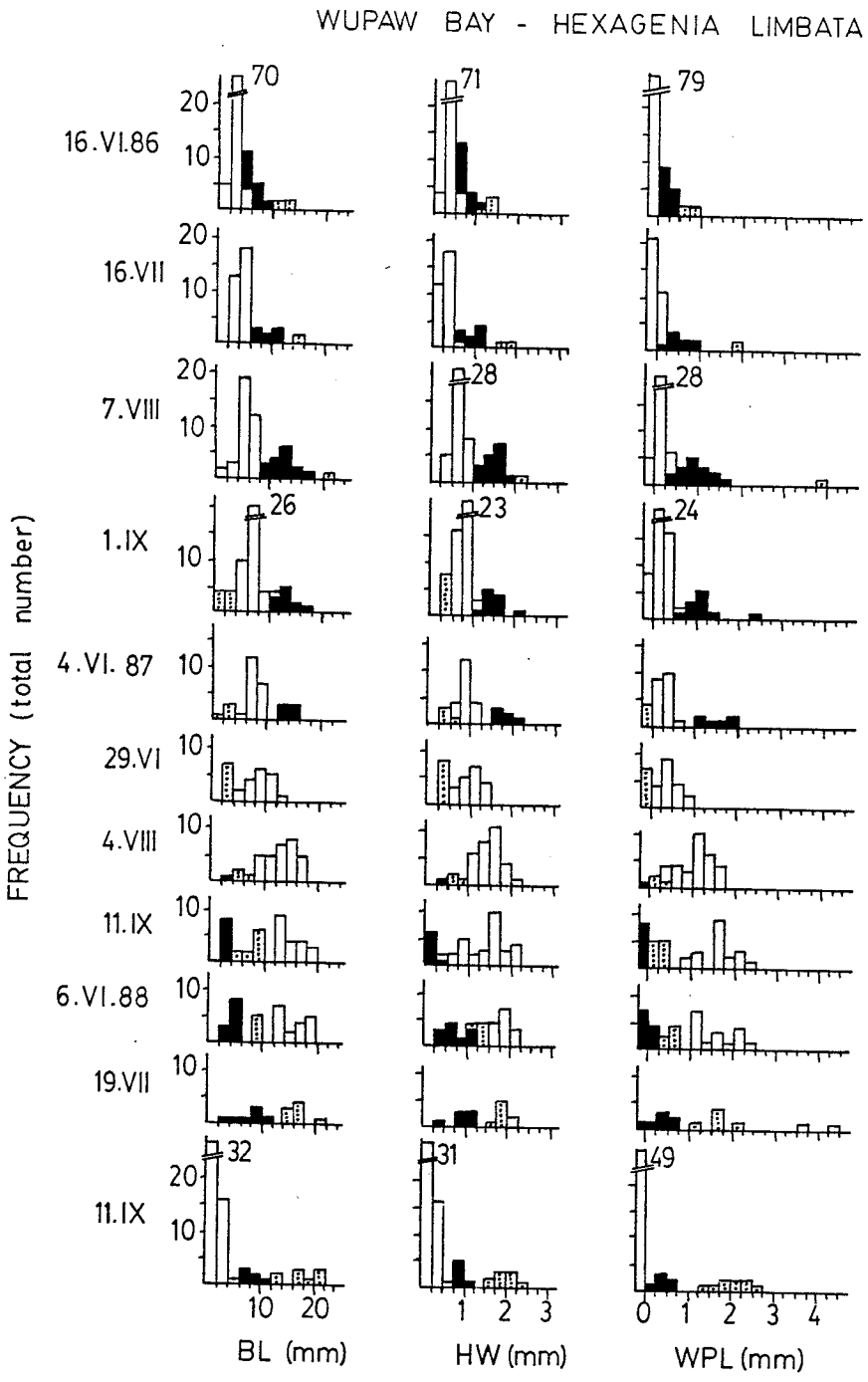

Fig. A-3. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for Hexagenia limbata in Wupaw Bay, 1986-1988. See Table A-1 for explanation of stipling pattern.

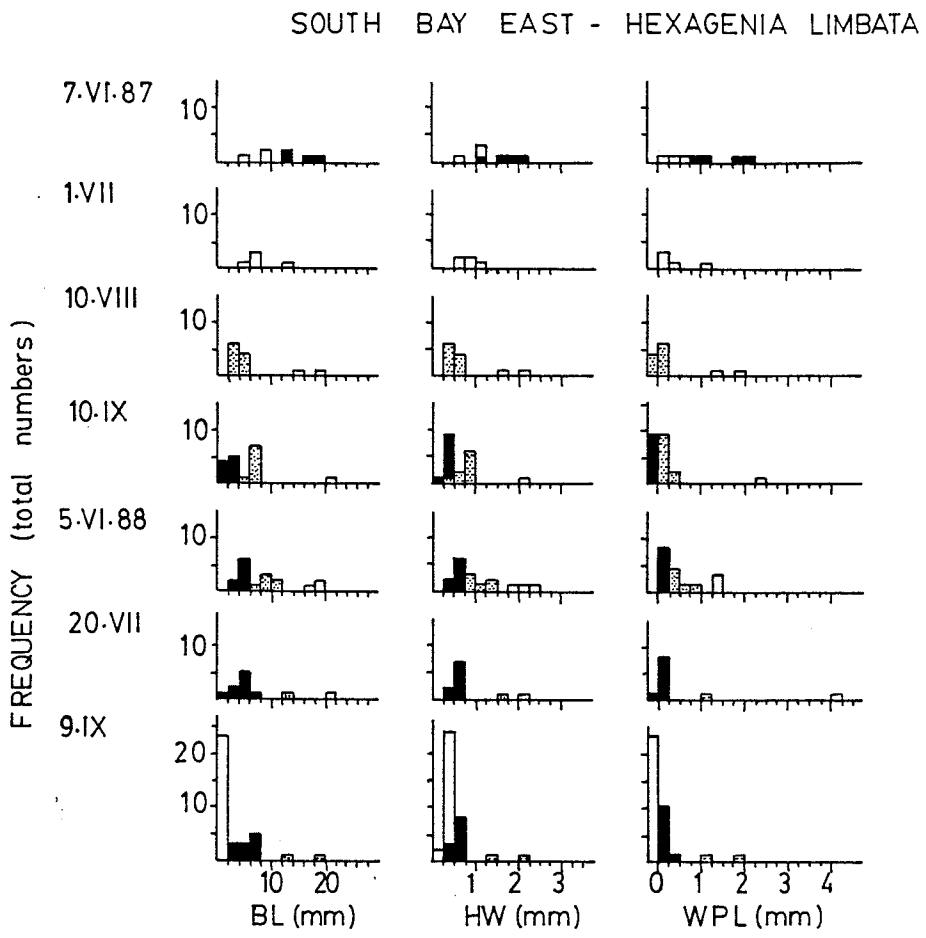

Fig. A-4. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for Hexagenia limbata in South Bay East, 1986-1988. See Table A-1 for explanation of stipling pattern.

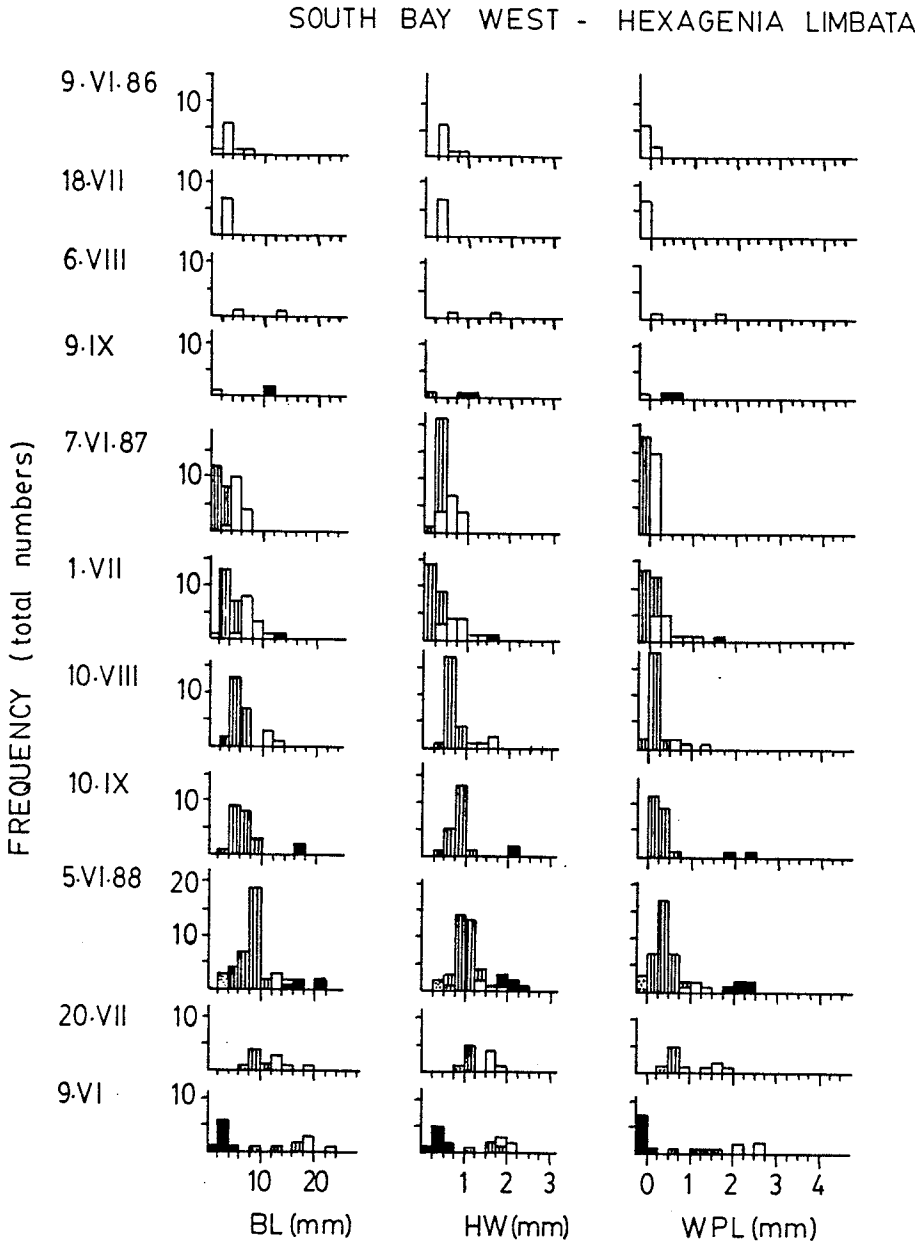

Fig. A-5. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for Hexagenia limbata in South Bay West, 1986-1988. See Table A-1 for explanation of stipling pattern.

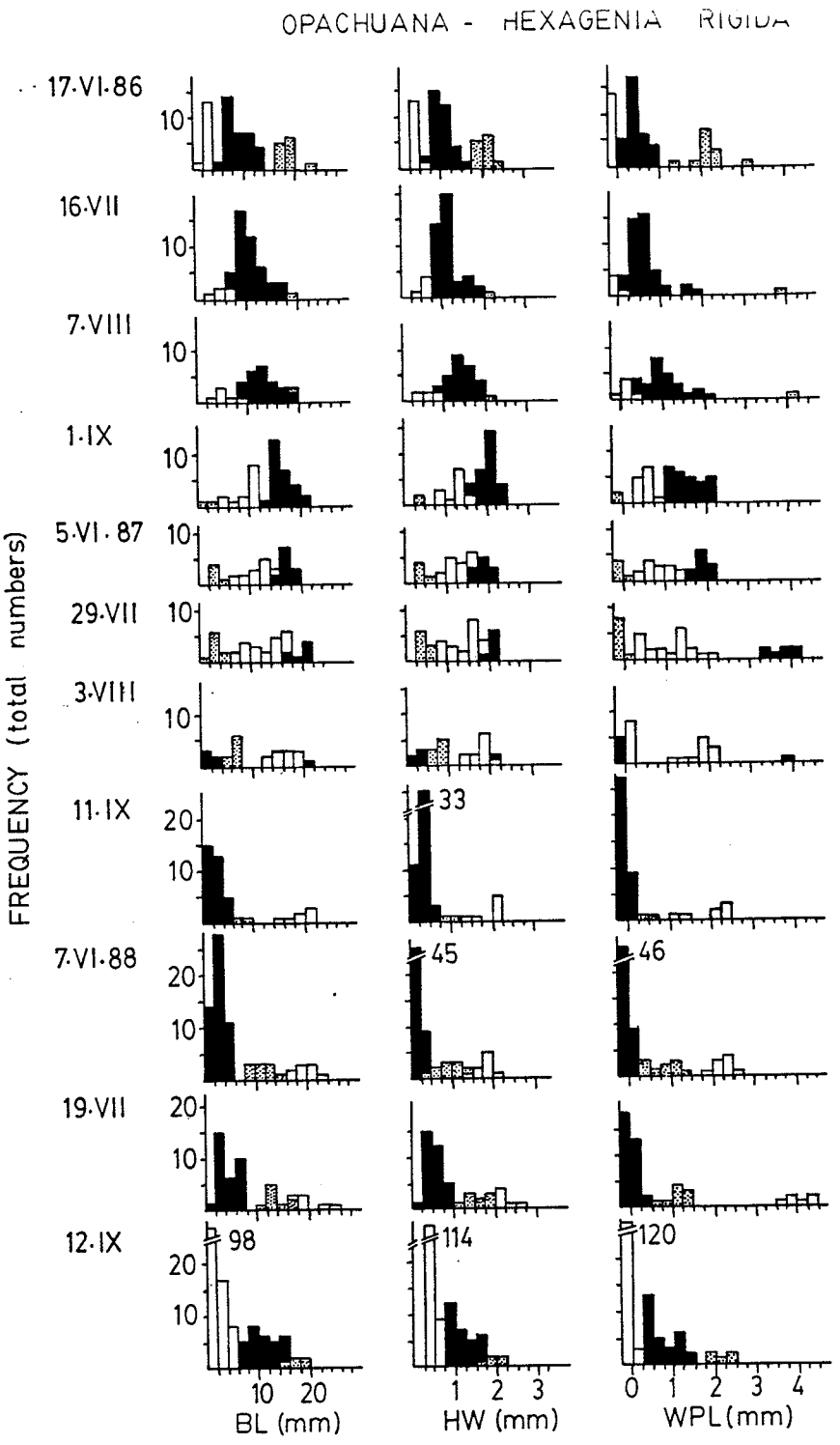

Fig. A-6. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for Hexagenia rigida in Opachuana, 1986-1988. See Table A-1 for explanation of stipling pattern.

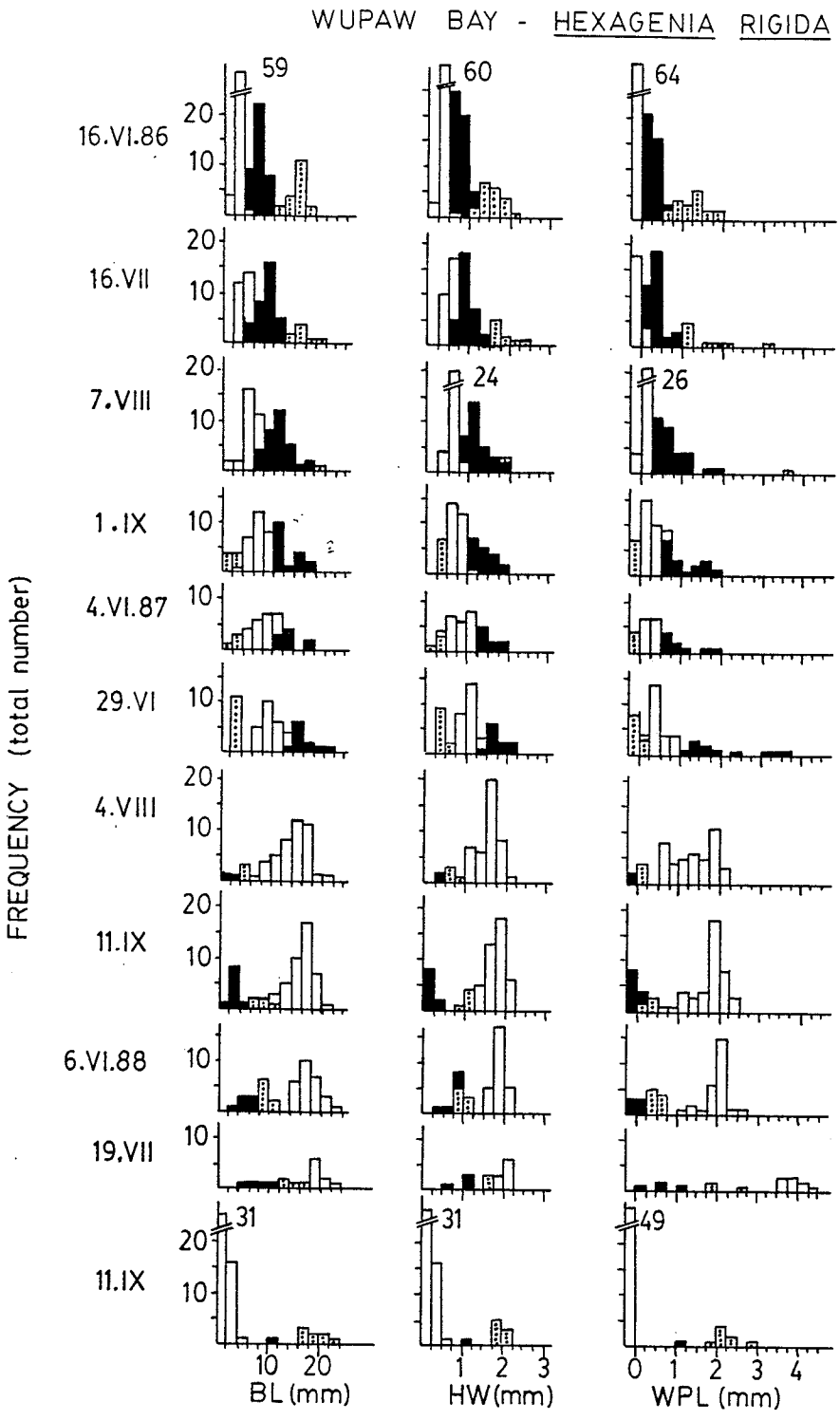

Fig. A-7. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for Hexagenia rigida in Wupaw Bay, 1986-1988. See Table A-1 for explanation of stipling pattern.

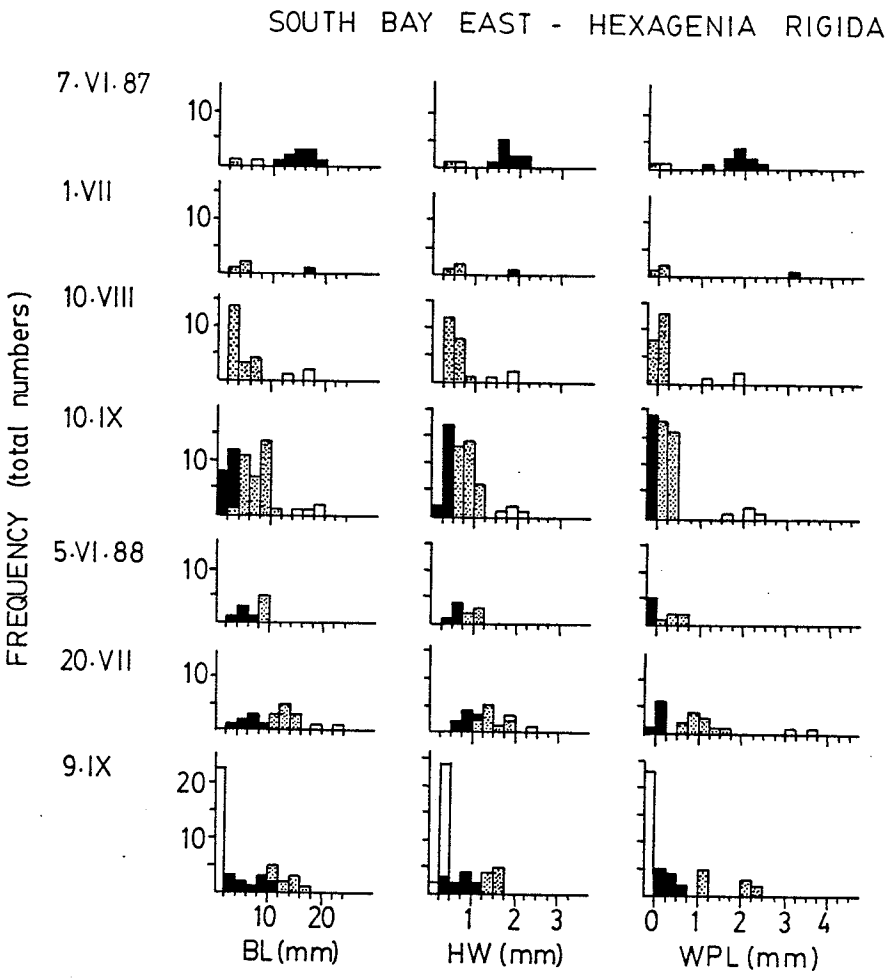

Fig. A-8. Frequency distribuions for body length (BL), head width (HW), and wingpad length (WPL) for Hexagenia rigida in South Bay East, 1986-1988. See Table A-1 for explanation of stipling pattern.

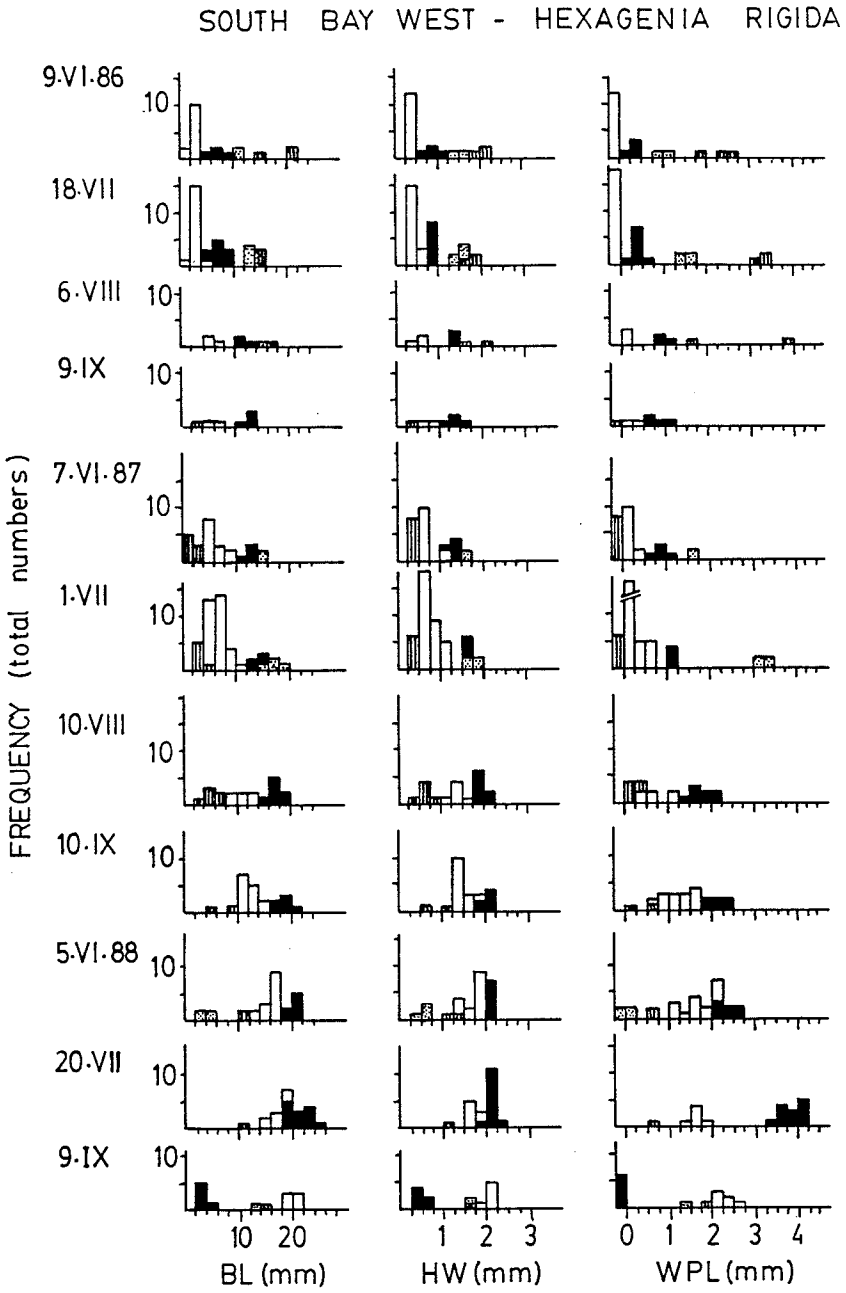

Fig. A-9. Frequency distributions for body length (BL), head width (HW), and wingpad length (WPL) for Hexagenia rigida in South Bay West, 1986-1988. See Table A-1 for explanation of stipling pattern.

APPENDIX B

MORTALITY CALCULATIONS AND SURVIVORSHIP CURVES

I. SURVIVORSHIP CURVES

Densities for each cohort for each species in each location were determined by counting the numbers in each assumed cohort (Appendix A), dividing by the numbers of samples collected at each site, and multiplying by 43 to obtain numbers/m^2 (the Ekman dredge sampled 1/43 m^2). Density (no/m^2) was then plotted against sample date for each study area (Figs. B-1 to B-4).

Overall *Hexagenia* abundance patterns (Table. B-1) indicated high variability, despite the collection of large numbers of samples (7-10 Ekman grabs in each of 4 sites in each location on each date). Once the nymphs were further divided into 3 or 4 separate cohorts, that variability increased; therefore, few statistically significant patterns could be seen. However, visual observation of the trends for each cohort indicated little change in abundance during the summer months, followed by sharp declines in abundance during the winter (Figs B-1 to B-4). Therefore, sample data were combined for the summer months to obtain a summer mean abundance for each cohort (Table B-2).

2. MORTALITY

Mortality was calculated between years by comparing summer mean abundance for each cohort from one year to the next. "1-yr old" nymphs came from eggs that were deposited the previous summer, whether or not the eggs overwintered; 2-yr old nymphs were those from eggs deposited 2 yr previously, etc. Mortality (%) was calculated as:

$$(N_{yr-1} - N_{yr} \;/\; N_{yr-1})\ 100$$ where N_{yr-1} = density in previous yr

N_{yr} = density in yr in question

Mortality was also estimated from one cohort to the next (3rd yr-1st yr and 4th yr-1st yr, Table B-3). The potential number of emerging adults was assumed to be equal to the density of nymphs (of the emerging cohort) just prior to emergence. Sex ratios were approximately 1:1 in all locations, so numbers of potential emerging females were estimated by dividing the total number by 2. Numbers of emerging females (no/m^2) were then multiplied by the mean number of eggs/female in each location (Chapter III) to estimate the fecundity (number of eggs that could be deposited /m^2) if all females emerged, mated, and deposited their eggs. Mortality was taken as the difference between this number and the number of newly hatched nymphs actually found in samples.

This mortality figure includes mortality from a number of sources that could not be determined independently. Emergence success could not be quantified because rough water conditions precluded the use of floating emergence traps and the mayflies apparently avoided submerged traps (A.P. Wiens, Freshwater Institute, personal communication). Predation during the winged stages was also observed, but not quantified, so it is not known how many adults survived to successfully mate and oviposit. Therefore a composite estimate including mortality from all these sources was calculated between the potential numbers of new recruits and the numbers actually observed.

Table B-1 . Mean *Hexagenia* abundance (no.m^{-2}, $\bar{x}$±S.E.) at each sampling site, on each sampling day, SIL, 1986-1988.

Location	Date	Mean Abundance (x ± S.E.) *Hexagenia limbata*	*Hexagenia rigida*
Opachuanau	17.VI.86	183 ± 59	127 ± 32
	6.VII.86	140 ± 25	108 ± 15
	7.VIII.86	129 ± 22	69 ± 7
	1.IX.86	133 ± 19	90 ± 16
	5.VI.87	39 ± 8	39 ± 9
	29.VI.87	37 ± 6	52 ± 11
	3.VIII.87	46 ± 11	32 ± 14
	11.IX.87	117 ± 40	75 ± 29
	7.VI.88	107 ± 25	111 ± 31
	17.VII.88	78 ± 11	72 ± 10
	12.IX.88	332 ± 144	340 ± 165
Wupaw Bay	16.VI.86	133 ± 21	173 ± 37
	16.VII.86	93 ± 20	135 ± 38
	7.VIII.86	114 ± 15	129 ± 39
	1.IX.86	129 ± 43	112 ± 40
	4.VI.87	65 ± 17	73 ± 41
	29.VI.87	47 ± 21	86 ± 45
	4.VIII.87	50 ± 4	71 ± 23
	11.IX.87	82 ± 13	123 ± 30
	6.VI.88	52 ± 17	65 ± 27
	19.VII.88	22 ± 6	24 ± 9
	11.IX.88	98 ± 19	89 ± 19
South Bay East	7.VI.87	14 ± 4	25 ± 6
	1.VII.87	7 ± 6	6 ± 3
	10.VIII.87	17 ± 8	34 ± 10
	10.IX.87	29 ± 9	91 ± 28
	5.VI.88	18 ± 3	11 ± 7
	20.VII.88	12 ± 5	22 ± 14
	9.IX.88	52 ± 21	62 ± 8
South Bay West	9.VI.86	18 ± 7	47 ± 12
	18.VII.86	15 ± 9	73 ± 13
	6.VIII.86	6 ± 2	23 ± 3
	9.IX.86	4 ± 2	15 ± 4
	7.VI.87	44 ± 38	35 ± 15
	1.VII.87	29 ± 16	39 ± 13
	10.VIII.87	23 ± 21	18 ± 1
	10.IX.87	25 ± 25	24 ± 5
	5.VI.88	38 ± 29	23 ± 6
	20.VII.88	10 ± 8	18 ± 4
	9.IX.88	9 ± 8	15 ± 10

Table B-2. Mean cohort summer densities (no.m², $\bar{x}$±S.E.). The first number in each cohort series is the density for the summer of 1986, followed by 1987, and 1988. b) second generation.

WUPAW BAY

	H. limbata			*H. rigida*		
Age	Cohort 1	Cohort 2	Cohort 3	Cohort 1	Cohort 2	Cohort 3
1 yr			86.4±10.0			65.9±9.5
2 yr		24.9±3.2	40.1±3.4		55.1±7.1	50.8±5.8
3 yr	4±1.1	4.8±4.1	15.3±12.0	16.9±6.0	16.1±4.4	27.4±14.1
b)1 yr	13.7±3.1	14.2±1.7		12.2±2.6	8.4±2.5	
2 yr	9.1±0.9			9.7±2.6		

OPACHUANA

1 yr			47.3±6.8			20.5±5.0
2 yr		74.7±7.5	21.9±2.7		69.4±9.2	18.7±5.1
3 yr	30.7±12.0	9.0±1.8	10.0±3.9	10.0±7.9	17.9±7.9	11.5±2.3
b)1 yr	8.9±1.3	75.2±7.3		9.7±1.9	62.3±6.8	
2 yr	10.9±4.8			10.8±2.6		

SOUTH BAY EAST

1 yr						
2 yr			4.5±1.3			3.2±1.4
3 yr		4.1±4.1	2.1±1.1		11.0±10	2.2
b)1 yr	13.5±8	12.1±1.7		22.6±12	14.4±5.6	
2 yr	3.5±1.6			10.5±2.7		

SOUTH BAY WEST

	Cohort 1	Cohort 2	Cohort 3	Cohort 4	Cohort 1	Cohort 2	Cohort 3	Cohort 4
1 yr				9.1±4.5				19.6±7.8
2 yr			0	9.5±4.6			11.7±3.3	16.2±4.5
3 yr		3.6±0.7	2.2±2.2	4.0±0.3		3.9±1.1	5.6±0.8	9.0±1.6
4 yr	0	0	1.4±1.4		5.2±1.1	2.1±1.1	4.9±2.5	
b)1 yr	20.4±2.4	1.5±0.5			5.8±1.7	5.0±0.4		
2 yr	11.7±7.9				1.6±0.4			

Table B-3. Year to year mortality (%) of *Hexagenia* nymphs from the four study regions in SIL for 1986-1988 calculated from Table B-2 (See text for explanation, note that this table also appears in Chapter III as Table III-3, and is repeated here for ease of comparison) NS=no sample; *densities too low to evaluate.

Species	Location	Year	1st-2nd year	2nd-3rd year	3rd-1st (4th) year	4th-1st year
H. limbata	Opachuana	86-87	53.7	87.9	99.9	
		87-88	*	54.3	99.5	
	Wupaw Bay	86-87	53.6	80.7	99.7	
		87-88	33.6	61.8	99.8	
	South Bay E.	86-87	NS	NS	NS	
		87-88	53.5	31.3	99.9	
	South Bay W.	86-87	*	57.9	99.8	*
		87-88	42.6	*	*	*
H. rigida	Opachuana	86-87	*	74.2	99.9	
		87-88	*	38.5	99.8	
	Wupaw Bay	86-87	22.9	70.8	99.8	
		87-88	20.5	46.1	99.9	
	South Bay E.	86-87	NS	NS	NS	
		87-88	53.5	31.3	99.9	
	South Bay W.	86-87	*	52.1	46.1	99.9
		87-88	72.4	44.0	12.5	99.8

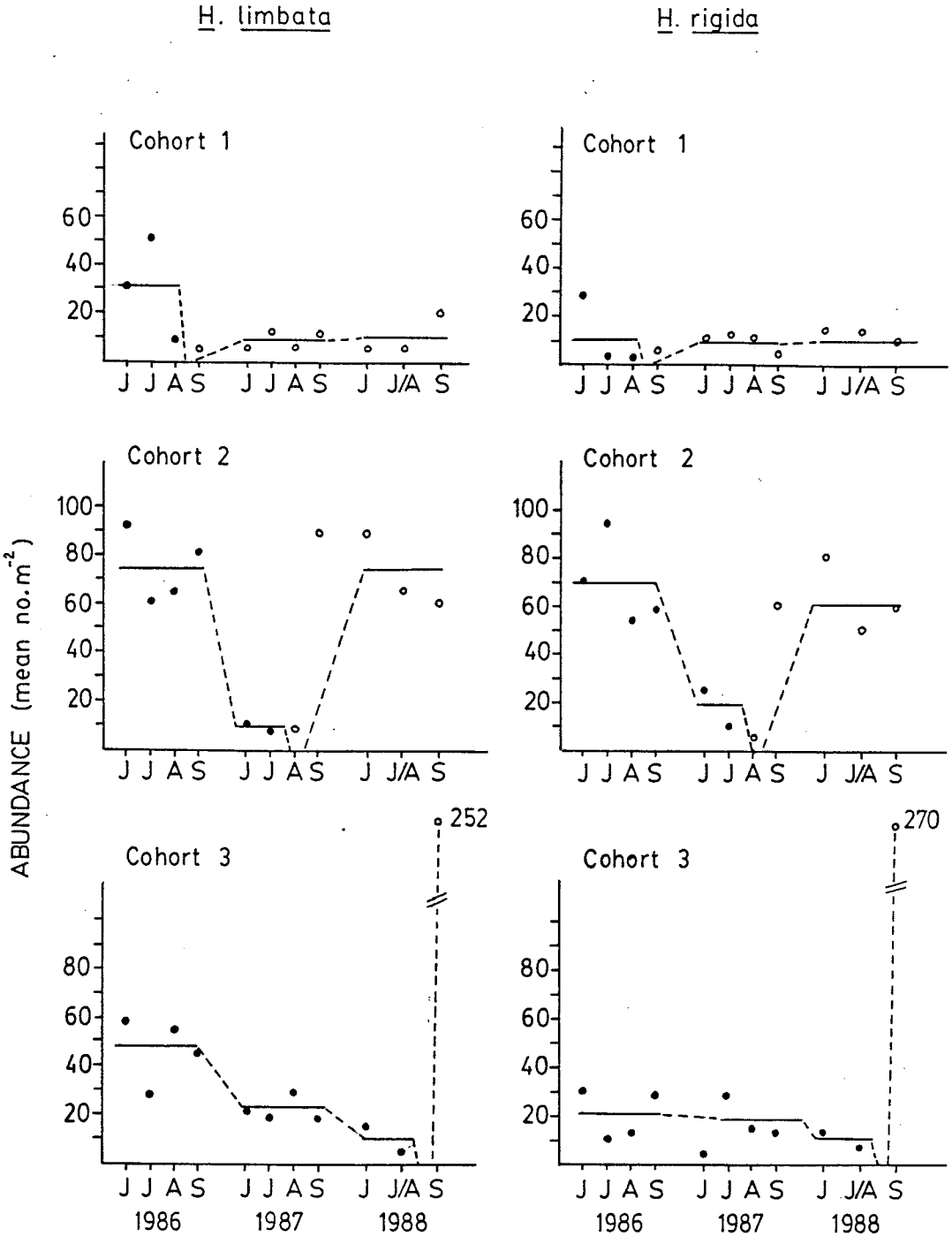

Fig. B-1. Densities and survivorship curves for Hexagenia from Opachuana, 1986-1988. Closed circles represent densities for the first generation (e.g. cohort 1a), and open circles are the second generation (e.g. cohort 1b). See Table A-1 for explanation of cohort numbers.

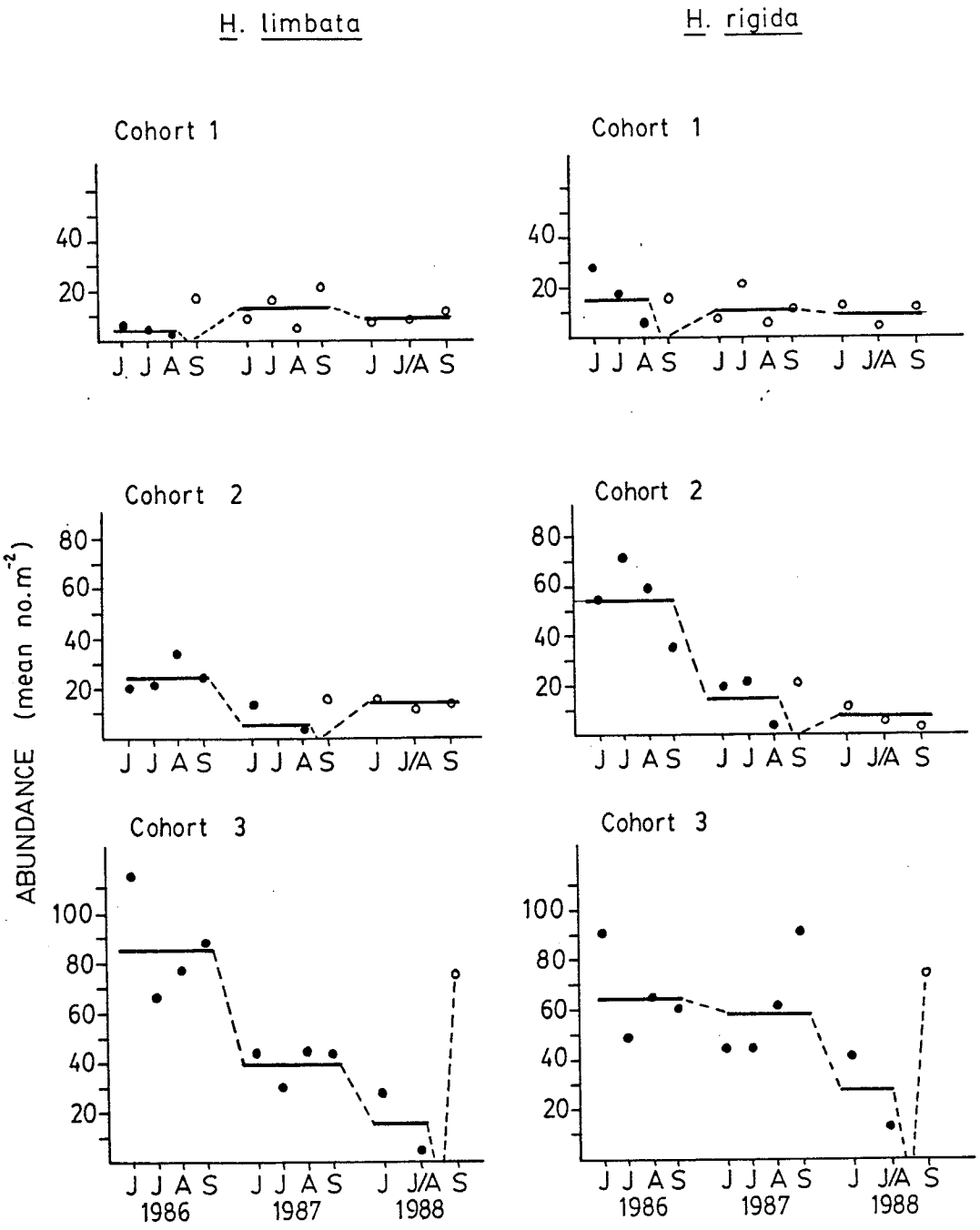

Fig. B-2. Densities and survivorship curves for Hexagenia from Wupaw Bay, 1986-1988. Closed circles represent densities from the first generation and open circles are the second generation. See Table A-1 for explanation of cohort numbers.

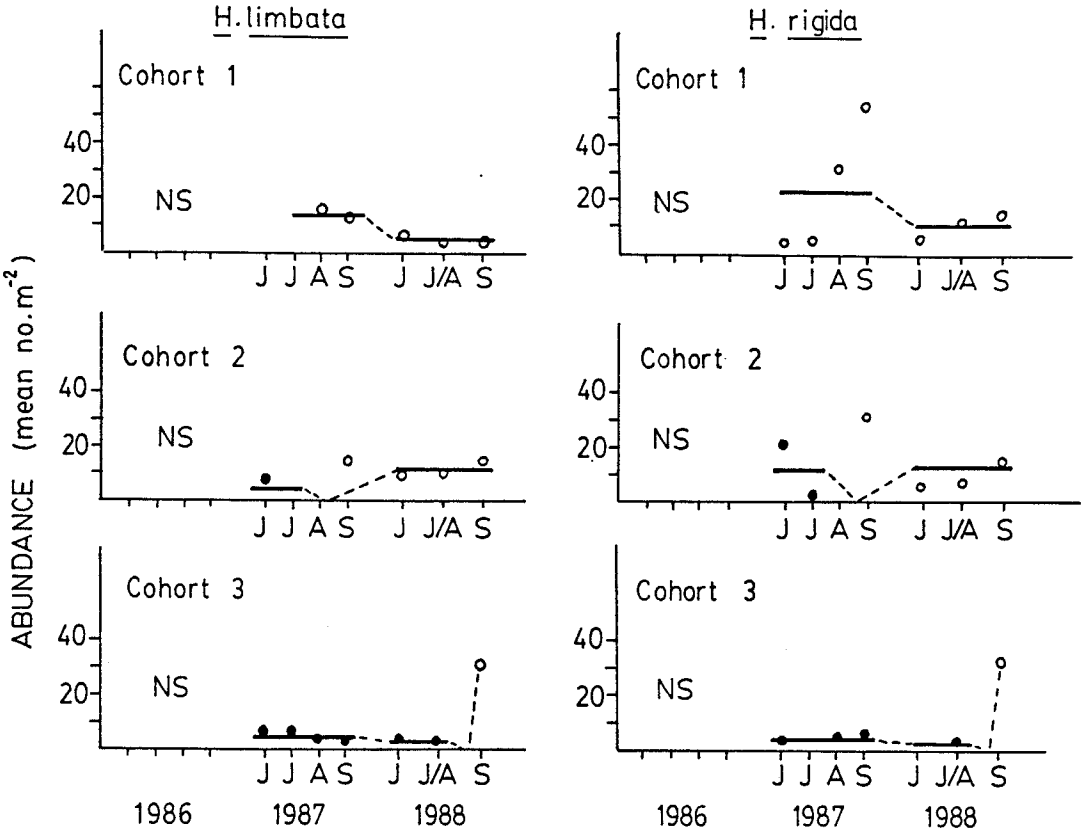

Fig. B-3. Densities and survivorship curves for Hexagenia from South Bay East, 1986-1988. Closed circles represent densities from the first generation and open circles are the second generation. See Table A-1 for explanation of cohort numbers. NS = no samples.

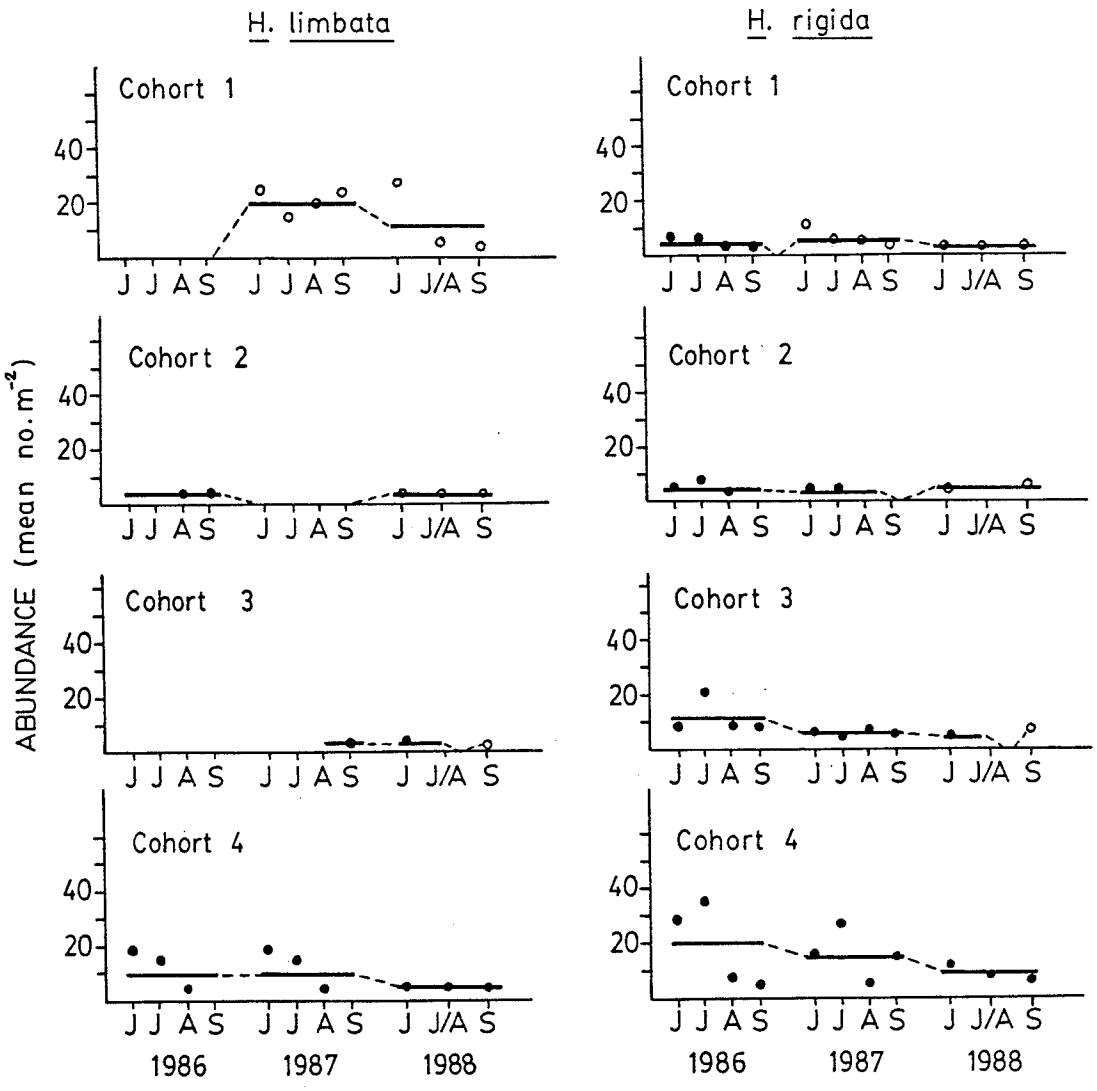

Fig. B-4. Densities and survivorship curves for Hexagenia from South Bay West, 1986-1988. Closed circles represent densities from the first generation and open circles are the second generation. See Table A-1 for explanation of cohort numbers.

APPENDIX C

RELATIONSHIP BETWEEN SUMMER TEMPERATURES AND WINDY WEATHER

ARE WARM SUMMERS ALSO CALM SUMMERS?

Researchers working at Southern Indian Lake suggested that warm summers around the lake tended to be relatively calm ones, and cool summers had a higher number of windy and stormy days. Both air temperature and wind speed affected emergence and mating success of *Hexagenia* in SIL, so it was important to determine the validity of this relationship in order to evaluate effects of long-term weather patterns.

The emergence periods in all locations and all study years occurred between July and September. Therefore, mean temperatures and numbers of windy days were calculated for that period for the years 1978-1987, which were the periods when data were directly available for the SIL site. Mean temperature was calculated from Environment Canada temperature summaries for SIL. Windy days were calculated from unpublished wind summaries (G. McCullough, Freshwater Institute, unpublished data). The day was considered to be "windy" if there were at least 2 consecutive hours with wind speeds exceeding 10 km/hr.

When mean summer temperature (July-September) was plotted against numbers of windy days for both July-August and July-September (Fig. C-1), a significant ($p<.05$) regression was noted. There was a trend for cool summers to have a higher number of windy days than warm ones.

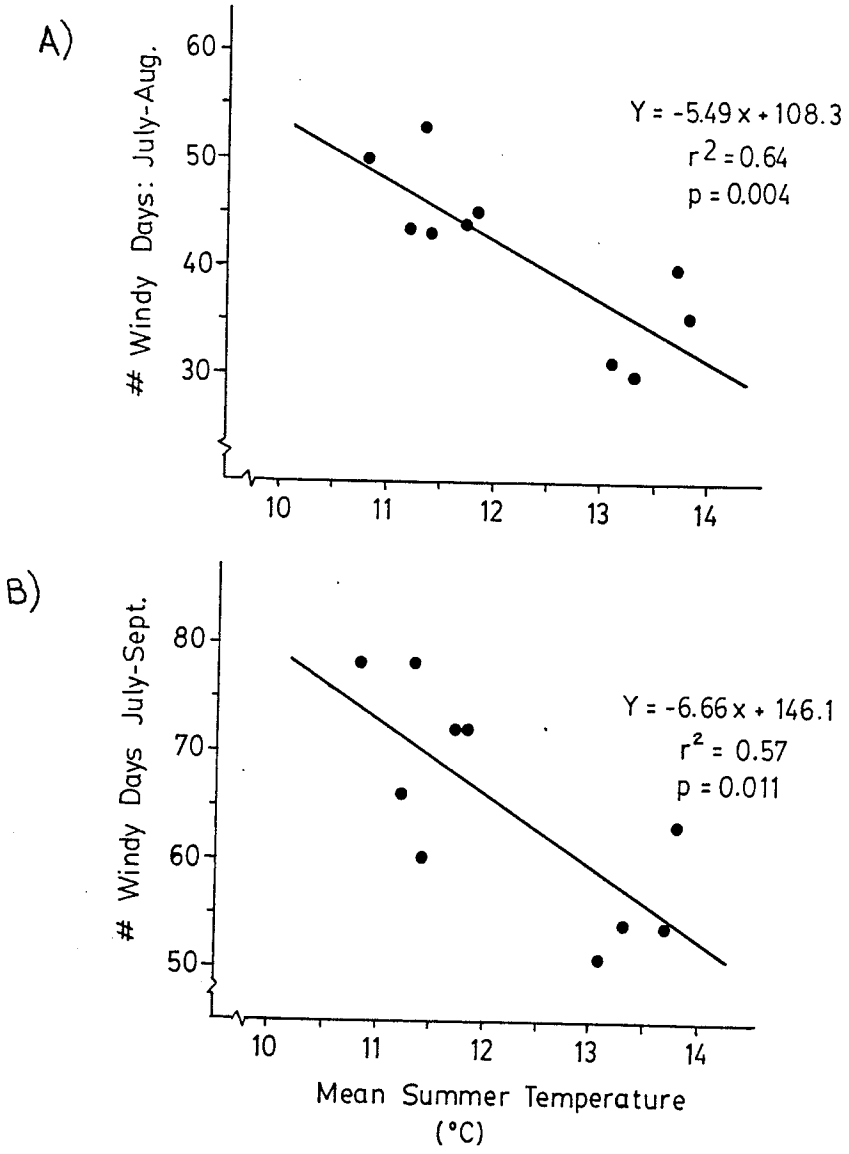

Fig. C-1. Relationships between number of windy days (days with wind speed 10 km/h for at least two consecutive hours) for July-August (A) and for July-September (B) with mean summer temperatures (July-September) for Southern Indian Lake weather station, 1978-1987.