



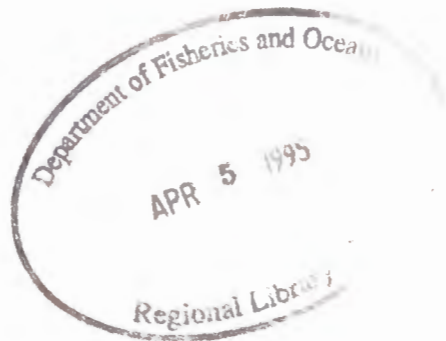
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## Production and growth efficiency of two burrowing invertebrates, Hexagenia limbata and Diporeia hoyi, in Batchawana Bay, Lake Superior

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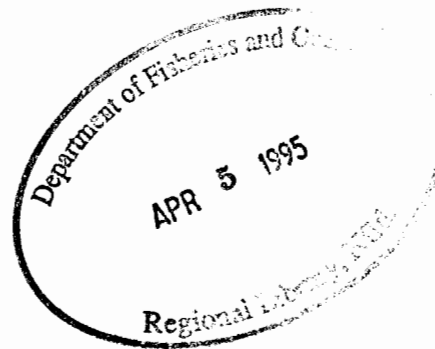
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PRODUCTION AND GROWTH EFFICIENCY OF TWO BURROWING INVERTEBRATES,  
HEXAGENIA LIMBATA AND DIPOREIA HOYI, IN BATCHAWANA BAY,  
LAKE SUPERIOR

by

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## ABSTRACT

Dermott, R. 1995. Production and growth efficiency of two burrowing invertebrates, Hexagenia limbata and Diporeia hoyi, in Batchawana Bay, Lake Superior. Can. Tech. Rep. Fish. Aquat. Sci. 2034: 28p.

Production (0.29 to 0.25 g m<sup>-2</sup> yr<sup>-1</sup>) and turnover ratios (P/B = 2.2 and 2.6) by the two dominant benthic invertebrates in oligotrophic Batchawana Bay, eastern Lake Superior were similar in spite of the difference in temperature at the two depth zones inhabited. Both burrowers are in the same trophic guild, with the populations being limited by the low algal production in the bay. Growth and growth efficiency (G.E.) of the mayfly Hexagenia were highly dependent on temperature, with growth occurring only when water temperature was above 10 to 13°C. As a result of seasonal growth, the average G.E. of the yearling Hexagenia at a depth of 7 m was 18%. Assimilation efficiency of this year-class of Hexagenia nymphs was highest in midsummer, ranging between 28 to 44% during this species' growing season. Temperature in the profundal zone (30 m) and hence, growth by one year old Diporeia, was more constant over the year, with G.E. of the amphipod averaging 34%.

## RÉSUMÉ

Dermott, R. 1995. Production and growth efficiency of two burrowing invertebrates, Hexagenia limbata and Diporeia hoyi, in Batchawana Bay, Lake Superior. Can. Tech. Rep. Fish. Aquat. Sci. 2034: 28p.

On a constaté que les deux invertébrés benthiques dominants de la baie Batchawana (oligotrophe) de l'est du lac Supérieur, ont une productivité (de 0,29 à 0,25 g m<sup>-2</sup> an<sup>-1</sup>) et un taux de renouvellement (P/B = 2,2 et 2,6) comparables, malgré la différence de température observée entre les deux zones de profondeur où ils vivent. Ces deux organismes fouisseurs font partie de la même guildes trophique, leurs populations étant limitées par la faible productivité des algues dans la baie. Par ailleurs, la croissance et le rendement de croissance de l'éphémère Hexagenia dépendent fortement de la température, la croissance ne s'observant que lorsque la température dépasse 10 à 13°C. En raison de la croissance saisonnière, le rendement de croissance moyen des Hexagenia de l'année à 7 m de profondeur a atteint 18%. Le taux d'assimilation chez les nymphes d'Hexagenia de cette classe d'âge était maximal au milieu de l'été, sa valeur allant de 28 à 44% durant la saison de croissance de l'espèce. La température dans la zone profonde (30 m) et, dès lors, la croissance des Diporeia d'un an, ont été plus constantes au cours de l'année, le rendement de croissance de l'amphipode se situant en moyenne à 34%.

## INTRODUCTION

Benthic invertebrates play an important role in processing deposited organic matter and recycling it back into the water column. Three of the largest benthic invertebrates; Amphipods, Chironomus, and Hexagenia nymphs, which are selectively consumed by fish, are important in the energetic flow through the lakes where they are common. The burrowing mayflies, Hexagenia spp., where common, are important prey for fish in large rivers and shallow lakes (Clady and Hutchinson 1976). In previous years, Hexagenia were prominent in shallow regions of the Great Lakes, such as Green Bay (Howmiller and Beeton 1971), Saginaw Bay (Schneider et al. 1969), and western Lake Erie (Carr and Hiltunen 1965; Manny 1991). Hexagenia nymphs are still important components of the benthic fauna in the St. Marys River, connecting Lake Superior to Lake Huron (Schloesser and Hiltunen 1984); Lake St. Clair; and have recently reappeared in the Detroit River (Thornley 1985).

In the deeper portions of the Great Lakes and many large lakes on the Canadian Shield, the benthic fauna is dominated by the burrowing amphipod, Diporeia hoyi, formerly in the genus Pontoporeia. Below the thermocline, Diporeia can represent up to 80% of the benthic biomass present and have populations in excess of 10 000 m<sup>-2</sup> (Cook and Johnson 1974). Like Hexagenia, Diporeia forms a major portion of the diet of fish in northern lakes (Larkin 1948). In the Great Lakes basin, both Hexagenia and Diporeia normally have a generation time of two years, resulting in two cohorts coexisting at any one time. In the upper Great Lakes, the emergence of the Hexagenia limbata occurs by the first week of July. The newly hatched young of Diporeia are released by the gravid females in late March. Both species burrow into soft sediments, consuming settled algae, fine particles, and associated bacteria (Ankar 1977). However, the two species rarely compete, as their niches are separated by temperature preferences. During summer, Diporeia is restricted to the area below the thermocline where Hexagenia is rarely collected. Adult Diporeia have an upper temperature tolerance of 14°C (Dadswell 1974), while Hexagenia requires temperatures above 13°C to complete its life cycle (Fremling 1970).

The benthic biomass of an aquatic system is dependent on the amount of settling phytoplankton, imported material, and benthic algae (Strayer and Likens 1986). Individual growth rate and assimilation efficiency are dependent on the amount and nature of the food source, while growth rate, generation time, and assimilation rate are temperature dependent. Total production by two species within the same functional guild and living in the same habitat is limited by the food supply available. However, the efficiency at which energy is used by each species is dependent on the physiology and temperature requirements of each.

The present study compared the production and turnover ratio of Hexagenia limbata and Diporeia hoyi inhabiting different depth zones of the relatively shallow Batchawana Bay in eastern Lake Superior. In the bay, these two silt-inhabiting species account for over 40% of the benthic biomass. Because of the importance of both species in the diets of fish, a bioenergetic model for Hexagenia and Diporeia would be useful in trophic transfer studies for estimating potential fish production. The growth efficiencies (G.E.) of the yearling cohorts of the two species were compared from September 1977 until October 1978. Additional data on Hexagenia and Diporeia allowed the calculation of seasonal ingestion and assimilation efficiency for the yearling cohorts.

## METHODS

### DESCRIPTION OF STUDY AREA

Batchawana Bay, located 40 km north of Sault Ste. Marie, is surrounded by forested hills of Precambrian granitic rocks. The bay has limited human influence, consisting primarily of scattered cottages along the east shoreline. No settlements occur on the banks of the rivers entering the bay. The maximum depth in the bay to the east of Batchawana Island is 46 m. An enclosed basin having a depth of 30 m is situated to the north-east of the island. Much of the bay is less than 6 m deep, with extensive sand shoals separating the bay from Lake Superior (Fig. 1). As a result, warm surface water as high as 22°C (J.R.M. Kelso, unpublished) accumulates in the bay during the summer. Algal biomass peaks during late August (Fig. 2). The maximum recorded algal biomass at the surface was 595 mg m<sup>3</sup> (R.J. Love, unpublished) classifying the bay as oligotrophic according to Vollenweider (1968). The potential photic depth in the bay is below 20 m, while oxygen levels at 20 m depth remained above 9 mg L<sup>-1</sup>. The benthic fauna in the bay was composed of three community assemblages dependent primarily on depth (Dermott 1984). These communities were: a profundal community below 20 m dominated by Diporeia hoyi; a community at intermediate depth (5 to 20 m) on fine sediments dominated by Hexagenia limbata; and that inhabiting the sandy sediments at depths less than 5 m dominated by the molluscs Elimia livescens and Sphaerium spp. The inshore fauna of the bay is more typical of that which was historically present in the now eutrophic, shallow embayments of the lower Great Lakes, than the fauna inhabiting the nearshore of Lake Superior.

### METHODOLOGY

Sampling was conducted in the enclosed north-eastern section of the bay (Fig. 1) at three sites for each species. The sampling depths represented two of the three communities in the bay. Each site was homogeneous in depth and substrate (silt) over a large area. At periodic



intervals from September 1977 until November 1978, five replicate Ponar samples ( $0.05 \text{ m}^2$ ) were taken from both the profundal sites (28 to 30 m) and intermediate depth sites (average depth 7 m). The sediments were washed through a sieve of 0.18 mm mesh and the retained organisms were preserved in 10% formalin. The organisms were identified, enumerated, and their lengths measured. Two of the sampling sites supported the second largest densities of the two study species at 27 sites examined in the bay (Dermott 1984). Bulk collections were made at these two sites in order to get sufficient animals for size-frequency analysis, length-weight regressions, and use in laboratory experiments. The length-weight regressions for the two dominant species were calculated from the lengths and dry weights of unpreserved animals.

Growth rates of three size-classes of Hexagenia limbata (< 8 mm, 8 to 15 mm, and > 15 mm) and that of three sizes of Diporeia hoyi (< 3 mm, 3 to 5 mm, and > 5 mm) were calculated based on the average lengths present on each sample date. For the respective species, these size-classes represent animals of less than one year old, the yearling, and mature-size cohorts. Production was calculated for the interval between October 15, 1977 and October 25, 1978. Continuous exponential production (Gillespie and Benke 1979) was calculated as the sum of the production of each of the three size-classes using growth (G), mortality (M), and change in average biomass ( $\Delta B$ ) as:

$$P = G / (G - M) \cdot \Delta B$$

The growth rates of yearling (initial length 11 mm) Hexagenia nymphs collected during late September were measured biweekly from October 1978 until January 1979 in the laboratory at 5, 10, 15, and 20°C. Individual nymphs were placed into silt-filled chambers (9 cm diameter) covered with 1 mm mesh and submerged in aquaria. Dried maple leaves (Acer saccharinum) ground into particles < 100  $\mu\text{m}$  were fed to the nymphs at a rate of 9.1 mg per week to supplement the algae and bacteria in the native silt from Batchawana Bay. This addition of organic matter per unit area would represent about  $200 \text{ mg m}^{-2} \text{ day}^{-1}$ , a level similar to the algal biomass in the bay during early summer (Fig. 2). Ingestion rates of the Hexagenia population in Batchawana Bay were calculated following the method of Dermott (1981), using the average monthly water temperature.

$$\text{Volume ingested } (\mu\text{L nymph}^{-1} \text{ d}^{-1}) = 2.3 e^{(0.178 \text{ Temp} + 2.331 \text{ Ln length (mm)} - 5.720)} \quad r^2 = 0.78$$

where Ln is the natural log. The volume ingested was converted to dry weight using the average density ( $0.355 \text{ mg } \mu\text{L}^{-1}$ ) of the silty sand sediment at the Hexagenia collection sites. The organic content of this sediment was 4.09%.

Particle size and algal composition of the gut contents were examined in both Hexagenia and Diporeia. The alimentary tract of the thorax was dissected out and the contents were mixed with a measured volume of water and examined at 200 x under a microscope using a Levy-Hausser counting chamber. The volume of all particles greater than 2  $\mu\text{m}$  were measured using an ocular micrometer.

Live mayflies were collected during May, July, and October 1978 to calculate the feeding rate and organic content of their fecal pellets. To estimate assimilation efficiency, the organic content of the foreguts and hindguts were determined by weight loss on ignition at 500°C. Assimilation efficiency was calculated following the method of Conover (1966). Ingestion rates of yearling Diporeia (3 mm to 6 mm length) were calculated using the regression

$$\text{Ingestion mg animal}^{-1} \text{ d}^{-1} = 0.024 e^{(0.106 \text{ Temp} + 2.8308 \text{ Ln (length mm)} - 2.9866)} \quad r^2 = 0.66$$

from the ingestion of animals in Lake Ontario (Dermott and Corning 1988). The sediments at the study sites for Diporeia in Batchawana Bay had an organic content of 5.3%.

Respiration (R) by the Diporeia population was calculated using the regression of Johnson and Brinkhurst (1971):

$$R (\mu\text{g O}_2 \text{ mg}^{-1} \text{ d}^{-1}) = e^{(1.4782 + 0.1376 \text{ Temp} - 0.3433 \text{ Ln AFDW mg})}$$

The ash-free dry weight (AFDW) of Diporeia was calculated as 0.789 of the dry weight for young (< 4 mm) and 0.810 of the dry weight for juvenile (> 4 mm length) amphipods.

The respiration by Hexagenia was calculated using a multiple regression derived from data of Eriksen (1963a), Walker and Burbank (1971), and Zimmerman et al. (1975):

$$R (\text{mg O}_2 \text{ mg}^{-1} \text{ d}^{-1}) = e^{(-4.4453 + 0.1340 \text{ Temp} - 0.4705 \text{ Ln dry weight mg})} \quad r^2 = 0.86$$

A model of the assimilation (A) by the yearling cohort (hatched in 1977) of both species was calculated as the sum of growth (G) and calculated respiration (R) over the 1978 growing season. Growth was calculated from the change in mean individual weight between successive dates. Respiration was calculated using mean individual weight and water temperature on each sample date, as well as the average weight and temperature calculated between successive dates. The interval respiration is the sum of the three regression results, each multiplied by one-third of the sample interval (days). The young-of-the-year cohort (YOY) of Hexagenia are not sampled until August of each year, while the adult-size cohort in both species either die or emerge by early summer. Therefore, seasonal trends in growth efficiency (G.E. = G/A) were calculated only for the yearling-size class. Growth was converted to calories using conversions

of 4.870 and 6.114 cal mg<sup>-1</sup> for Hexagenia and Diporeia respectively (Cummins and Wuycheck 1971; Johnson and Brinkhurst 1971). Respiration was converted to calories using a coefficient of 3.38 cal mg<sup>-1</sup> O<sub>2</sub> (Teal 1957). The organic matter in the sediments was converted to calories (3.15 cal mg<sup>-1</sup> organic matter) based on a regression between the sediment organic content and calorie content from the data on sediments from oligotrophic lakes in Cummins and Wuycheck (1971), Johnson and Brinkhurst (1971), and Zimmerman et al. (1975). The assimilation efficiency (A.E.) of the Hexagenia nymphs was calculated as:

$$\frac{\text{assimilation}}{\text{ingestion}} \times 100 \%$$

## RESULTS

### HEXAGENIA

The length-frequency distributions of both species indicated a two year life cycle in Batchawana Bay, with two overlapping generations present (Figs. 3 and 4). Hexagenia emergence was synchronized during the first week of July, with emerging nymphs all being longer than 18 mm, averaging 23.4 mm (14.8 mg dry weight). After an incubation period of about 20 days (Friesen et al. 1979) the YOY nymphs appeared in the samples by August at a length of 2.0 mm (0.02 mg). The YOY nymphs attained a maximum length of 14 mm the following August.

The length-weight regressions for Hexagenia limbata from Batchawana Bay were:

nymphs < 11 mm

$$\text{dry weight (mg)} = e^{(3.1488 \times \text{Ln length (mm)} - 6.8908)} \quad r^2 = 0.87$$

nymphs > 12 mm

$$\text{dry weight (mg)} = e^{(2.8682 \times \text{Ln length (mm)} - 6.2964)} \quad r^2 = 0.94$$

all nymphs

$$\text{live wet weight (mg)} = e^{(2.8430 \times \text{Ln length (mm)} - 4.1134)} \quad r^2 = 0.96$$

The population of Hexagenia limbata at the study sites in north-east Batchawana Bay (Fig. 5) averaged 112 ± 29 m<sup>-2</sup>. Total annual production between October 19, 1977 and October 24, 1978 amounted to 0.297 ± 0.148 g m<sup>-2</sup> over a period of 3427 degree days, at a mean temperature of 9.2°C. Average standing stock during the same period was 0.133 ± 0.045 g m<sup>-2</sup> (dry), resulting in an annual production/biomass (P/B) ratio of 2.2 yr<sup>-1</sup>. Production by the 1978 YOY cohort from July until October 24 (85 days) was 2.5 ± 1.5 mg m<sup>-2</sup>, with a seasonal P/B ratio of 0.8. Production by the yearling cohort (1977 year-class) amounted to 0.198 ± 0.090 g m<sup>-2</sup> yr<sup>-1</sup>.

The yearling Hexagenia (11 mm initial length and 2.1 mg initial dry weight) maintained in the laboratory showed rapid initial growth at 15 and 20°C (Fig. 6). Growth was minimal at 10°C, while zero or negative growth occurred at 5°C. Initial growth as wet weight over a 70 day period averaged 0.56 mg d<sup>-1</sup>, 0.30, and 0.03 mg d<sup>-1</sup> at 20, 15, and 10°C. The dry weight equivalents of the growth rate were: 0.067 mg d<sup>-1</sup>, 0.036 and 0.004 mg d<sup>-1</sup> at 20, 15, and 10°C, respectively. The initial growth rate of the nymphs in the laboratory at 15 and 20°C was close to that in Batchawana Bay at comparable temperatures. When regressed against the seasonal temperatures in the bay, these growth rates verified that two summers are required for the nymphs to reach reproductive size. The laboratory growth rates slowed dramatically after the nymphs reached 16 mm (42 mg wet or 5.2 mg dry). After a period of 120 days, few of the nymphs attained a length of 19 mm (8.8 mg), while none matured to develop the darkened wing pads of the final instars. The weights of the nymphs after 120 days in the laboratory were lower (57%) than that for nymphs of equal size collected in Batchawana Bay, suggesting inferior conditions in the laboratory.

Calculated growth efficiencies for the Hexagenia yearling cohort (Table 1) averaged 17.7%, ranging from 2.5 to 41% during 1978, with the lowest efficiencies occurring when water temperature was below 10°C. Growth and G.E. were greatest for the larger immature nymphs (> 13 mm) during August, while that of the YOY nymphs was slightly less during the same period. G.E. remained high during midsummer and early fall, decreasing rapidly as the temperature dropped below 13°C. Although the mean length of the yearling nymphs increased between October and May, growth was marginal over the winter period. There was no statistically significant increase ( $p < 0.01$ ) in the mean size of the nymphs between October and the following June.

Analysis of the surface sediments from 7 m in Batchawana Bay indicated that during midsummer, large populations of benthic diatoms were present, averaging  $2.4\% \pm 0.6\%$  of the surface sediment volume. Common diatom genera on the sediments above the thermocline were Navicula, Cocconeis, and Achnantes. Gut analysis of the Hexagenia nymphs indicated that algae and algal remains represented only 4% of the gut volume, with Navicula (0.7%), Stephanodiscus (0.3%), Cymbella (0.2%), and Cocconeis (0.1%) dominating. Bacteria and clay-size particles (mean size 0.002 mm diameter) formed  $63\% \pm 3.4\%$  of the foregut volume compared with  $34\% \pm 6.7\%$  in the sediments. Sand and silt (diameter > 0.004 mm) together accounted for  $33\% \pm 1.6\%$  of the Hexagenia gut volume, compared with  $63\% \pm 3.5\%$  in the sediments at the collection sites in Batchawana Bay.

During the growing season, Hexagenia ingestion ranged from 1.855  $\mu\text{L}$  sand nymph<sup>-1</sup> d<sup>-1</sup> for 6.71 mm nymphs at 6°C in May, to 110.921  $\mu\text{L}$  nymph<sup>-1</sup> d<sup>-1</sup> by 16.8 mm nymphs at 16.9°C on September 8. The ingestion rate of the Hexagenia population at 7 m depth in Batchawana Bay rose rapidly during May, after water temperatures exceeded 10°C. The decrease in total

ingestion during early July (Fig. 7) was due to the emergence of the large two year old nymphs. The later increase in total ingestion during late July occurred during the maximum bottom temperatures of the season (19°C). Total respiration by the Hexagenia population displayed a similar drop in early July (Fig. 7), followed by peak respiration at the end of the month due to the same factors that controlled total ingestion by the population. Over the study period, total respiration by the Hexagenia population amounted to 2.95 g O<sub>2</sub> m<sup>-2</sup> yr<sup>-1</sup> (9.97 kcal m<sup>-2</sup> yr<sup>-1</sup>), while the estimated amount of organic matter ingested was 10.56 g m<sup>-2</sup> yr<sup>-1</sup> (33.26 kcal m<sup>-2</sup> yr<sup>-1</sup>).

The organic content of the foreguts of the Hexagenia was as high as 65%. However, the organic content of fecal pellets produced by live mayflies feeding on organically enriched silt and ashed diatomous earth averaged 33.8% and 11.2% respectively. The organic content of this silt and diatomous earth prior to ingestion averaged only 28.6 and 1.4%, respectively. This indicates that organic matter, such as the durable peritrophic membrane on the outside of the fecal pellets, is added to the material as it passes through the mayflies' guts. The calculated assimilation efficiencies based on the ash ratio method were: on May 19,  $x_7 = 41.7\% \pm 11.5\%$ ; in July at 20°C,  $x_7 = 39.5 \pm 7.6\%$ ; and during October 1978,  $x_6 = 32.0\% \pm 2.3\%$ .

The assimilation efficiency of yearling Hexagenia (Table 1) remained between 28 and 44% during the summer growing period, with very high values calculated for the winter period. These values are based on the organic content of the sediment (4.09%) and not the organic content of the material that is selectively ingested by the nymphs. The calculated A.E. by Hexagenia during the winter months may be elevated because respiration at temperatures below 5°C may be much lower than that calculated. Although ingestion rates were not directly measured at low temperatures, Hexagenia collected from Batchawana Bay during the winter had a gut-filling-time of less than 24 h at 4°C. This was similar to that calculated at 4°C using the ingestion regression. The estimated annual A.E. for the Hexagenia population in the study area of Batchawana Bay was 34.2%. Over the same period (371 days), the population's annual G.E., calculated as total production divided by assimilation per m<sup>2</sup>, was only 12.4%.

## DIPOREIA

In Batchawana Bay, Diporeia hoyi reproduce during late winter with the young being released from the brood pouches during April. The YOY grew from 1.7 mm (0.02 mg dry weight) after release, to 3 mm by the end of October, reaching 4 mm (0.2 mg) the following May. Reproduction was restricted to amphipods in excess of 6 mm (0.37 mg) during the end of their second winter. The maximum length attained by Diporeia in Batchawana Bay was 8.1 mm (0.96 mg).

The length-weight regression for Diporeia hoyi in Batchawana Bay was:

$$\text{dry weight (mg)} = e^{(3.1516 \times \text{Ln length (mm)} - 6.3189)} \quad r^2 = 0.98$$

The abundance of Diporeia at 30 m in north-east Batchawana Bay is displayed in Fig. 8 where the population averaged  $548 \pm 222 \text{ m}^{-2}$  ( $\pm 2$  SE). Total annual production (from October 15, 1977 to October 25, 1978) amounted to  $0.253 \pm 0.120 \text{ g m}^{-2}$  over a period of 2097 degree days (mean annual temperature of  $5.6^\circ\text{C}$ ). As the standing stock biomass (B) averaged  $0.097 \text{ g m}^{-2}$ , the estimated annual P/B ratio was  $2.6 \text{ yr}^{-1}$ . Production by the YOY during 1978 over a period of 162 days (May to October) was  $11.3 \pm 2.5 \text{ mg m}^{-2}$ , with a seasonal P/B ratio of 2.8 for that cohort. The annual production by the yearling cohort amounted to  $0.149 \pm 0.06 \text{ g m}^{-2} \text{ yr}^{-1}$ .

The growth efficiency of yearling Diporeia (Table 2) averaged 34.2%. The G.E. reached its highest level in the YOY during their first summer of growth. G.E. was greater in the spring or late fall over a narrow range of water temperature ( $5$  to  $10^\circ\text{C}$ ), but it was reduced during midsummer. The total respiration by the Diporeia population over the study period amounted to  $1.25 \text{ g O}_2 \text{ m}^{-2} \text{ yr}^{-1}$ . As a result, the estimated G.E. of the Diporeia population between October 1977 and October 25, 1978 was 26.7%.

The gut contents of Diporeia from Batchawana Bay were composed mainly of dark amorphous material (98%) with an average particle size of less than  $0.002 \text{ mm}$ . Algae and algal remains accounted for less than 2% of the gut material and were composed mostly of diatoms. The organic content of the silt at the collection sites was 5.3%.

Diporeia ingestion ranged from  $0.075 \text{ mg silt animal}^{-1} \text{ d}^{-1}$  by  $4.06 \text{ mm}$  amphipods at  $1.5^\circ\text{C}$  in February, to  $0.484 \text{ mg animal}^{-1} \text{ d}^{-1}$  by  $5.88 \text{ mm}$  amphipods at  $9.2^\circ\text{C}$  on October 25. The estimated assimilation efficiencies of Diporeia feeding on silt, having an organic content of 5.3%, ranged between 49.7% and 65.7% during 1978. The very high A.E. of 92.6% calculated for  $3.1 \text{ mm}$  amphipods during September 15, 1977 is probably an error in the regression for small amphipods. Ignoring this initial high value, the average A.E. for the yearling Diporeia in Batchawana Bay was calculated as 55.7% (Table 3). The only measured organic content of the foreguts of the amphipods examined for gut contents was 12.9%. Using 12.9% as the organic content of the sediment particles selectively ingested by the amphipods, the average A.E. over the study period would be reduced to 36%.

## DISCUSSION

### PRODUCTION

Annual production by Hexagenia limbata in Batchawana Bay ( $0.29 \text{ g m}^{-2} \text{ yr}^{-1}$ ) was much less than that by the same species in most other lakes in North America (Table 4). However, the species had similar P/B turnover ratios (2.1 to 2.7) in areas where the generation time was also two years. The increased biomass in a shallow boreal lake at a similar latitude as Batchawana Bay (Riklik and Momot 1982) reflected the greater inputs of allochthonous material as compared to the oligotrophic status of Batchawana Bay, Lake Superior. The size of the populations are dependent on the food resources of their habitat, but the life cycle and annual P/B ratios which were similar to that in this study are dependent on mean temperature.

A reduction in the generation time of H. limbata to one year is common in more southern latitudes, as a result of increased temperature. Under conditions of unlimited food, Hexagenia spp. can grow to maximum length within 80 days at  $27^{\circ}\text{C}$  (Fremling 1967). Conversely, eggs maintained below  $8^{\circ}\text{C}$  cease their development and they require 127 days to hatch at  $12^{\circ}\text{C}$  (Friesen et al. 1979). As Riklik and Momot (1982) pointed out, latitude and the resulting heat inputs to a body of water greatly influence growth rates and generation time resulting in higher P/B ratios in populations at lower latitudes. With increasing latitude, Hexagenia is limited to suitable habitats where the temperature remains above  $8\text{-}10^{\circ}\text{C}$  long enough to allow the species to complete its life cycle, which can be four years in lakes near the species' northern limits (Gilbertson et al. 1991).

The shortening of the life cycle to one year also occurs with Diporeia hoyi or its Palaearctic analog, Monoporeia affinis, as a result of higher mean annual temperature in shallow habitats (depth  $< 15 \text{ m}$ ) within the lakes of eastern North America (Winnell and White 1984; Siegfried 1985) or in the shallow lakes of north Europe (Kuz'menko 1969; Johnson 1987). Production can be as high as  $14.8 \text{ g m}^{-2} \text{ yr}^{-1}$  (Siegfried 1985) for populations with a one-year life cycle under warmer temperatures. Annual production by Diporeia in Batchawana Bay was low compared to other study areas with a two-year life cycle (Table 5), again reflecting the oligotrophic status of the bay.

The magnitude of the abundance and hence the production of Diporeia is dependent on the available food supply. Annual production and standing biomass of D. hoyi at a depth of 28 m in eastern Lake Ontario,  $5 \text{ g m}^{-2}$  (Johnson and Brinkhurst 1971), was greater than 30 times that at a similar depth in Batchawana Bay, although the P/B ratio was only slightly less. Phytoplankton biomass in Lake Ontario averaged  $2700 \text{ mg m}^{-3}$  (Vollenweider et al. 1974) compared with an average phytoplankton biomass in Batchawana Bay of  $248 \text{ mg m}^{-3}$ . As a result, Lake Ontario is capable of supporting a much larger benthic population than is

Batchawana Bay. Johnson (1988) showed a similar increase in the biomass of D. hoyi with increases in the levels of algal production in the Bay of Quinte as compared to the more oligotrophic South Bay, Lake Huron. The turnover rate (P/B) is dependent on mean temperature and hence, generation time. In Batchawana Bay, the P/B of Diporeia was  $2.6 \text{ yr}^{-1}$  at a mean temperature of  $5.6^{\circ}\text{C}$ . This was higher than that predicted in the regression analysis, between turnover ratio and mean annual temperature of Johnson (1988).

## GROWTH EFFICIENCY

The growth efficiency (32%) of the detritivore Hexagenia over the summer months was much lower than that found by Zimmerman et al. (1975) in a small Ohio pond (88%) where summer temperature averaged  $23^{\circ}\text{C}$ . The periods of high G.E. in the bay during August and September coincided with both favourable water temperatures and high algal production. Food quality in Batchawana Bay is high, with diatoms as the main source of organic matter in the bay. The physiology of most Hexagenia species restricts growth to temperatures above  $10^{\circ}\text{C}$  (Hunt 1953) with the laboratory growth rates verifying the cessation of growth below this thermal limit. In Batchawana Bay, growth of Hexagenia slowed considerably during October, as temperature dropped. Similarly, Riklik and Momot (1982) found the instantaneous growth rate of Hexagenia to be negative in late fall, implying that growth ceased between September and June in the small boreal lake they studied.

Unlike Hexagenia, the physiology of Diporeia is adapted to the narrow temperature range ( $1\text{-}12^{\circ}\text{C}$ ) in the profundal zone. Thus, there was a limited effect of temperature on the G.E. of this species which changed little throughout the year. Johnson and Brinkhurst (1971) found that at a depth of 28 m in Lake Ontario, the annual G.E. of the Diporeia population averaged 0.38, compared with  $0.34 \pm 0.06$  for the yearling Diporeia in the more oligotrophic Batchawana Bay, Lake Superior. The instantaneous growth rate of D. hoyi in the Great Lakes (Johnson and Brinkhurst 1971; Johnson 1988) is highest during the spring of their first year, thereafter declining with age, with a minor increase in growth rate occurring during their second spring. Growth of Diporeia in Batchawana Bay was similar, with the highest G.E. of yearling Diporeia occurring during May and June.

There was little agreement between the period of maximum phytoplankton biomass and the G.E. of Diporeia in Batchawana Bay, with the G.E. being lower (21.7%) during the period of peak phytoplankton biomass than during the spring or fall. In addition, the sedimentation of the midsummer algal bloom to the profundal sediments would also be delayed until the erosion of the thermocline during early September. As a result, the seston reaching the bottom in midsummer would have a lower quality than that settling during isothermal conditions in the spring or fall. Gut analysis of Diporeia in Batchawana Bay, as well as in previous studies (Ankar 1977; Moore 1977) indicated that identifiable algae may represent less than 1% of the



gut contents, with silt and clay-size particles ( $< 10 \mu\text{m}$ ) predominating. However, studies of this genera's gut contents seriously underestimate the importance of diatoms in the amphipods' diet (Quigley and Vanderploeg 1991). The large cusps on the elephant-like molars at the base of the mandibular tusks of Hexagenia nymphs indicate that they can effectively grind up algal and plant material. As a result, like Diporeia, studies on the gut contents of Hexagenia may underestimate the importance of diatoms in the species' diet.

## ASSIMILATION EFFICIENCY

The apparently very high A.E. of the Hexagenia nymphs over winter occurs during a period of limited growth. Although ingestion, growth, and respiration rates of the nymphs are all dependent on temperature, growth ceases at low temperature. Many aquatic poikiotherms overwinter either in quiescence or actual diapause, with their maintenance energy derived from previously stored energy reserves. The use of length-weight regressions is not suitable to estimate the weight of the nymphs over the winter, as their actual weight or energy reserves may be dropping. With the methods used, any use of energy reserves during periods of low growth would result in an error in the calculated A.E. At higher temperature, growth only occurs when the energy assimilated exceeds that required for maintenance. Calculations of the ingestion rate (Dermott 1981) indicated that 16 mm H. limbata nymphs consume about 0.7 mg organic matter  $\text{d}^{-1}$  at  $16^{\circ}\text{C}$ . In the laboratory growth experiments, this amount of organic matter was just matched in the form of added leaves ( $0.67 \text{ mg organic } \text{d}^{-1}$ ). After the nymphs reached this critical length, their growth slowed. The energy requirements of nymphs greater than 17 mm length exceeded that available, resulting in a cessation of their growth at both  $15^{\circ}\text{C}$  and  $20^{\circ}\text{C}$ .

During summer, both the G.E. and A.E. of Hexagenia peaked between July and early September, coinciding with the maximum water temperatures and algal biomass in the bay. Temperature was the most important factor controlling the amount of material ingested (Zimmerman and Wissing 1978); hence, assimilation by Hexagenia occurred. This high A.E. results in a maximum amount of energy being converted into growth during summer. However, during midsummer the A.E. by H. limbata in Batchawana Bay never reached the high values (68%) found by Zimmerman et al. (1975). This was probably due to the much lower organic and calorific content of the sediments in Batchawana Bay compared with the small pond studied by Zimmerman et al. During the spring, the G.E. was much lower than in the fall at similar temperatures, while the A.E. was greater in the spring. The family Ephemeridae demonstrate a rapid rise in metabolic activity during spring (Morgan and Wilder 1936; Eriksen 1963b). This surge in metabolism is suggested as being responsible for rapid growth and gonad development that occurs in mature nymphs during May despite the low temperature.

The A.E. values calculated for the amphipods feeding on silt with an organic content of 5.3% are probably too high, given the feeding selectivity demonstrated (Quigley and Vanderploeg 1991) and the periods of intermittent feeding by the Diporeia (Evans et al. 1990). The organic content of the foreguts of amphipods from Lake Ontario feeding in sediments having an organic content of 9.7% was above 22% (Dermott and Corning 1988) indicating selective ingestion of organic rich particles. However, unpublished work on the feeding of Lake Ontario amphipods using dual labelled food, following the methods of Cammen (1977) indicate the A.E. of algae mixed with silt can be as high as  $x_g = 65.7\%$  (SE 10.5%) at 10°C. Lopez and Elmgren (1989) found Monoporeia affinis to have an assimilation efficiency of 40% when feeding on freshly deposited phytoplankton in sediments of the Baltic Sea. Therefore, the high A.E. calculated in Batchawana Bay during the summer months could be truly representative of the assimilation efficiencies of Diporeia.

The biomass of the two detritivores (0.10 and 0.13 g m<sup>-2</sup>) and their production (0.25 and 0.29 g m<sup>-2</sup> yr<sup>-1</sup>) were similar at the two study depths in Batchawana Bay. This was expected as the populations and production of both species is food-limited in Batchawana Bay, with the quantity and nutritional quality of the sparse phytoplankton in the bay determining how much energy is available for respiration and growth. Both species, one a cold water organism and the other associated with warm shallow water, had a similar life span; hence, turnover ratios in Batchawana Bay. In spite of the warmer temperatures experienced by the Hexagenia nymphs, their production was not greater than Diporeia due to the much larger body size required for reproduction and the fact that their physiology causes their growth to cease for six months each winter.

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Table 1. Growth, Respiration ( $\text{mg O}_2 \cdot \text{nymph}^{-1} \cdot \text{interval}^{-1}$ ), Assimilation ( $\text{cal. nymph}^{-1} \cdot \text{interval}^{-1}$ ) and Ingestion ( $\text{mg organics} \cdot \text{nymph}^{-1} \cdot \text{interval}^{-1}$ ), for a series of time intervals, and corresponding Growth Efficiencies (G.E.), and Assimilation Efficiencies (A.E.) of yearling Hexagenia limbata in Batchawana Bay. Caloric equivalents are in parenthesis (weight as  $4.87 \text{ cal} \cdot \text{mg}^{-1}$  dry) and sediments are calculated as  $3.15 \text{ cal mg}^{-1}$  ash free.

Date	Num. $\text{m}^{-2}$	Temp. $^{\circ}\text{C}$	Dry wt. $\text{mg} \cdot \text{n}^{-1}$	Growth mg	Resp. $\text{mg O}_2 \cdot \text{n}^{-1}$	Assim. (G+R)	G.E.% (G/A)	Ingestion $\text{mg} \cdot \text{n}^{-1}$	A.E.% (A/I)
Sept 16	44.1	16.0	0.22	.13 ( 0.64)	1.20 ( 4.05)	4.69	13.6	2.19 ( 6.90)	67.9
Oct. 19	56.0	10.2	0.35	.04 ( 0.21)	1.36 ( 4.61)	4.83	4.4	1.71 ( 5.38)	89.5
Feb. 8	37.0	0.6	0.39	.02 ( 0.07)	0.85 ( 2.87)	2.94	2.5	1.21 ( 3.83)	76.8
May 1	48.2	6.0	0.41	.02 ( 0.08)	0.33 ( 1.13)	1.21	6.8	0.60 ( 1.92)	63.9
May 16	-	9.3	0.43	.26 ( 1.26)	2.30 ( 7.79)	9.05	13.9	6.51 ( 20.52)	44.1
June 20	17.8	18.6	0.68	.26 ( 1.25)	2.70 ( 9.13)	10.38	12.1	9.17 ( 28.89)	35.9
July 10	11.5	19.4	0.94	.80 ( 3.90)	2.62 ( 8.84)	12.75	30.6	9.87 ( 31.10)	41.0
July 24	20.4	19.5	1.74	.47 ( 2.30)	1.57 ( 5.31)	7.60	30.1	6.70 ( 21.09)	36.0
Aug. 1	16.8	19.1	2.21	1.76 ( 8.55)	3.70 (12.49)	21.04	40.6	18.04 ( 56.82)	37.0
Aug. 16	13.9	18.6	3.97	2.14 (10.39)	6.58 (22.25)	32.64	31.8	36.26 (114.21)	28.6
Sept 8	10.4	16.9	6.11	1.94 ( 9.45)	6.92 (23.39)	32.84	28.8	36.70 (115.60)	28.4
Oct. 4	10.0	13.6	8.05	.35 (1.68)	4.56 (15.41)	17.09	9.8	21.63 ( 68.14)	25.1
Oct. 24	7.3	9.8	8.40	0.05 (0.22)	1.17 (3.97)	4.19	5.3	5.14 ( 16.21)	28.9
Nov 5	-	6.0	8.45						

Table 2. Growth, respiration ( $\mu\text{g O}_2 \text{ animal}^{-1}$ ), assimilation ( $\text{cal. animal}^{-1} \text{ interval}^{-1}$ ) for a series of time intervals and corresponding growth efficiencies (G.E.) of yearling (3-6 mm) Diporeia hoyi in Batchawana Bay, Lake Superior, Sept. 1978 to Oct. 1978. Caloric equivalents are in parenthesis, weight as  $6.114 \text{ cal}\cdot\text{mg}^{-1}$  dry, respiration as  $3.38 \text{ cal}\cdot\text{mg}^{-1} \text{ O}_2$ .

Date	Num. m <sup>2</sup>	Temp. °C	Dry wt. mg	Growth mg	Resp. $\mu\text{g O}_2 \text{ ind}^{-1}$	Assim. (G+R)	G.E. % (G/A)
Sept 15	192.0	9.0	0.063				
Oct. 15	480.1	9.5	0.098	.035 (0.214)	70.43 (0.238)	(0.452)	47.3
Feb 8	283.5	1.5	0.149	.053 (0.324)	389.04 (1.315)	(1.639)	19.8
May 16	288.8	4.5	0.205	.056 (0.342)	182.79 (0.618)	(0.960)	35.6
June 20	276.9	5.5	0.252	.047 (0.287)	102.67 (0.347)	(0.634)	45.3
July 10	207.9	7.1	0.287	.035 (0.214)	77.34 (0.261)	(0.475)	45.0
July 24	207.0	7.5	0.297	.010 (0.061)	65.07 (0.220)	(0.281)	21.7
Aug 22	264.6	8.2	0.331	.034 (0.208)	152.33 (0.515)	(0.723)	28.7
Sept 8	172.6	9.4	0.364	.033 (0.202)	108.75 (0.367)	(0.569)	35.4
Oct. 4	166.3	10.2	0.399	.035 (0.220)	201.69 (0.682)	(0.902)	24.4
Oct. 25	179.5	9.2	0.461	.061 (0.373)	174.48 (0.589)	(0.963)	38.7



Table 3. Calculated ingestion ( $\text{mg sediment} \cdot \text{animal}^{-1} \cdot \text{interval}^{-1}$ ), Organic matter ingested, Assimilation as Growth + Respiration ( $\text{cal} \cdot \text{animal}^{-1} \cdot \text{interval}^{-1}$ ), and Assimilation efficiency (A.E) of yearling (3-6 mm) Diporeia hoyi in Batchawana Bay, Lake Superior over a series of time intervals from Sept. 1977 to Oct. 1978. Caloric equivalents are in parenthesis. Sediments had an organic content of 5.3 % dry weight and  $3.15 \text{ cal} \cdot \text{mg}^{-1}$  organics.

Date	Temp. °C	Length mm	Interval days	$\Sigma$ Ingestion $\text{mg} \cdot \text{anim} \cdot \text{int.}$	Organics Ingested $\text{mg} \cdot \text{anim} \cdot \text{interval}$	Assim. G+R	A. E. % A/I
Sept 15	9.0	3.11	29	2.9282	0.1552 (0.4889)	(0.4521)	92.4
Oct. 15	9.5	3.28	176	17.4328	0.9239 (2.9104)	(1.6389)	56.3
Feb. 8	1.5	4.06	97	9.4579	0.5013 (1.5789)	(0.9598)	60.8
May 16	4.5	4.53	35	6.7321	0.3568 (1.1239)	(0.6340)	56.4
June 20	5.5	4.84	20	4.3297	0.2295 (0.7228)	(0.4754)	65.7
July 10	7.1	5.04	14	3.6056	0.1911 (0.6019)	(0.2809)	46.7
July 24	7.5	5.10	29	8.3970	0.4450 (1.4018)	(0.7229)	51.6
Aug. 22	8.2	5.28	17	5.9017	0.3128 (0.9853)	(0.5696)	57.8
Sept 8	9.4	5.45	26	10.8919	0.5773 (1.8184)	(0.9017)	49.6
Oct. 4	10.2	5.57	21	10.1907	0.5401 (1.7013)	(0.9627)	56.6
Oct. 25	9.2	5.88					

Table 4. Summary of several studies on the production of the mayfly Hexagenia limbata.

Density no.m <sup>-2</sup>	Biomass dry g m <sup>-2</sup>	Production dry g m <sup>-2</sup>	P/B	Depth m	Life span yr	Location	Reference
47	0.08	0.45	5.4	8	1	Kansas Reservoir	Horst and Marzolf 1975
189	0.58	1.40	2.7	5	1 & 2	South Dakota	Hudson and Swanson 1972
473	2.15	-	-	2	1 & 2	Ohio pond	Rutter and Wissing 1975
107	0.29	0.68	2.1	3	2	NW Ontario	Riklik and Momot 1982
112	0.13	0.29	2.2	7	2	Batchawana Bay	this study

Table 5. Summary of some studies on the production of the amphipod Diporeia (formerly Pontoporeia affinis).

Density no.m <sup>-2</sup>	Biomass dry g m <sup>-2</sup>	Production dry g m <sup>-2</sup>	P/B	Life span yr	Depth m	Location	Reference
232	0.13	0.34	2.6	1	6	NW Russia	Kuz'menko 1969
-	4.87	9.20	2.0	2	30	NE Lake Ontario	Johnson & Brinkhurst 1971
3602	1.66	3.17	1.9	2	45	N Baltic proper	Cederwall 1976
3234	0.90	2.82	3.1	1	15	SE Lake Michigan	Winnell and White 1984
8292	5.58	7.07	1.3	2	42	"	"
662	0.12	0.40	3.4	1	12	Stockholm Sweden	R.K. Johnson 1987
54	0.01	0.03	3.1	1	14	South Bay L.Huron	M.G. Johnson 1988
2173	0.82	1.15	1.4	2	42	"	"
548	0.10	0.25	2.6	2	30	Batchawana Bay	this study

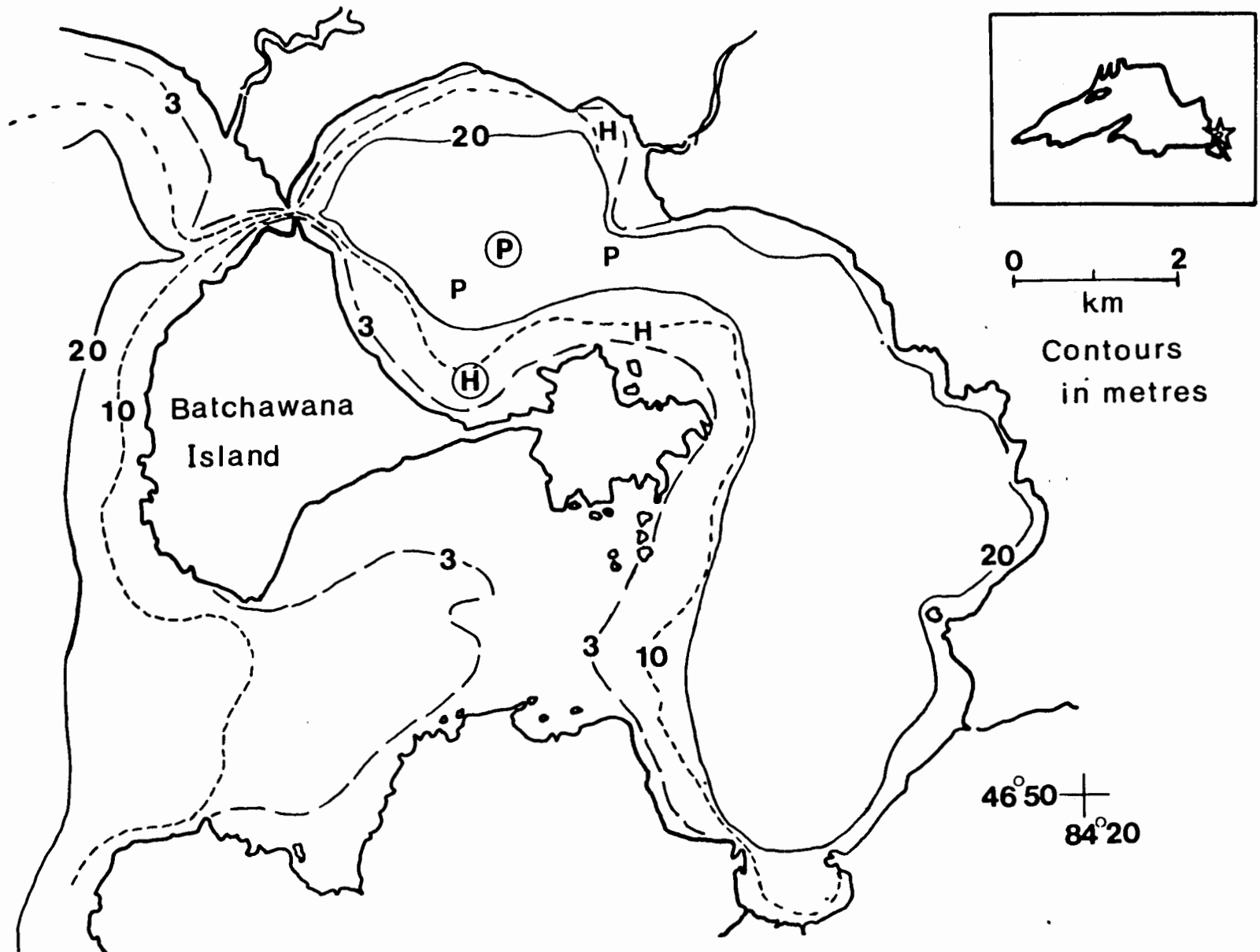
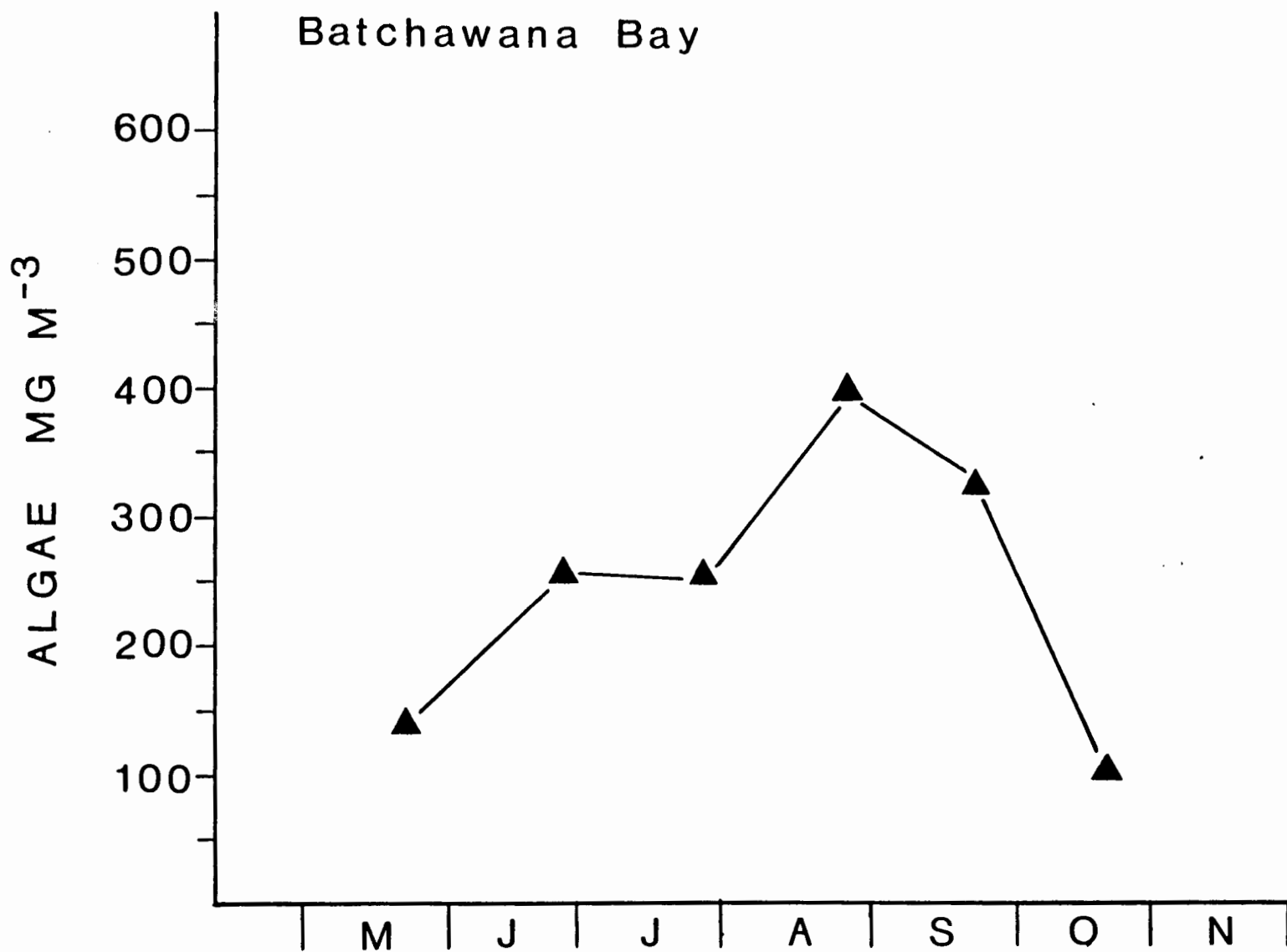


Figure 1. Sampling sites for production estimates of the *Diporeia* (P) and *Hexagenia* (H) populations. Bulk collections were made at the circled sites for animals used in laboratory experiments, size-frequency analysis and length-weight relationships.

Figure 2. Depth integrated algal biomass in north-east Batchawana Bay, 1978.



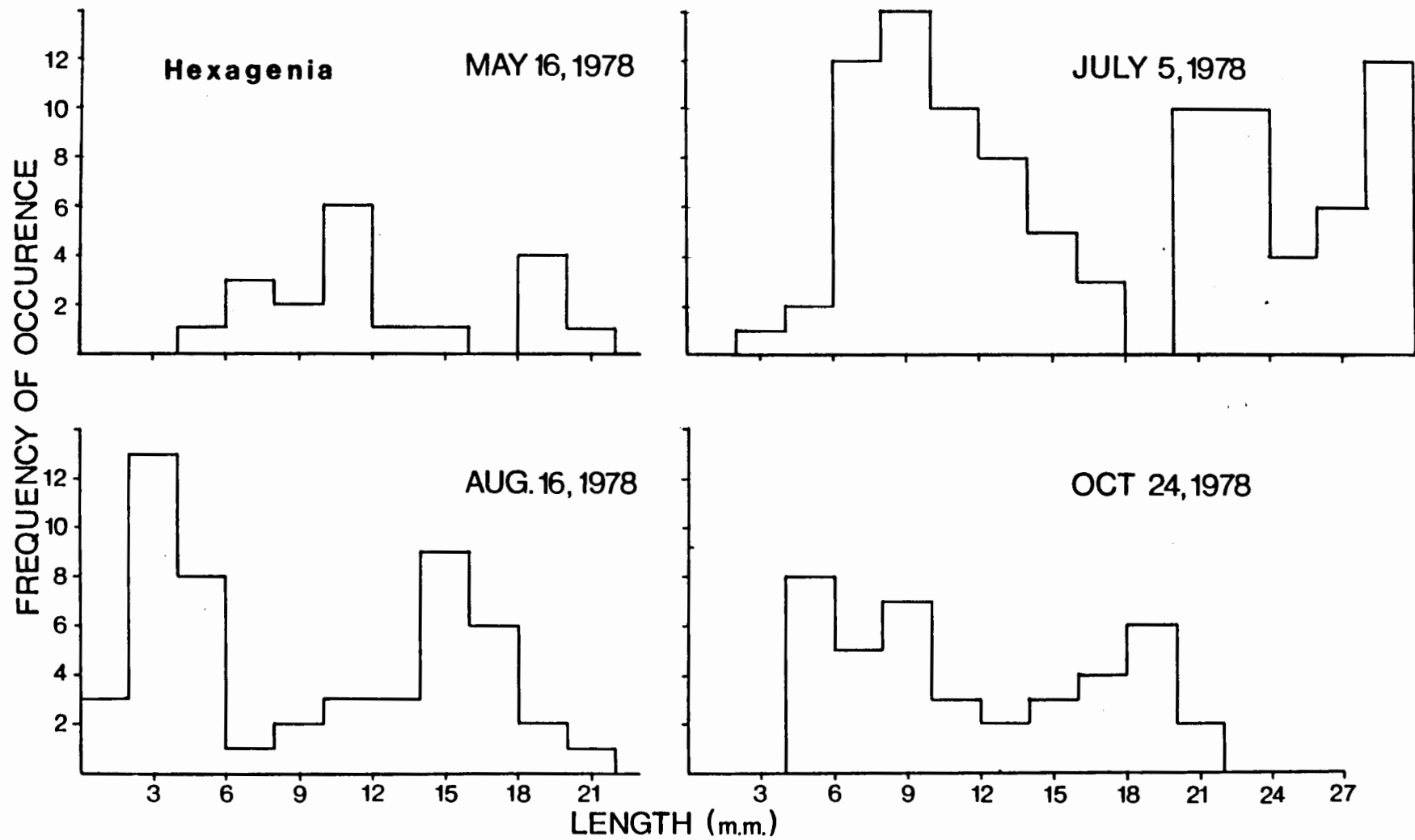
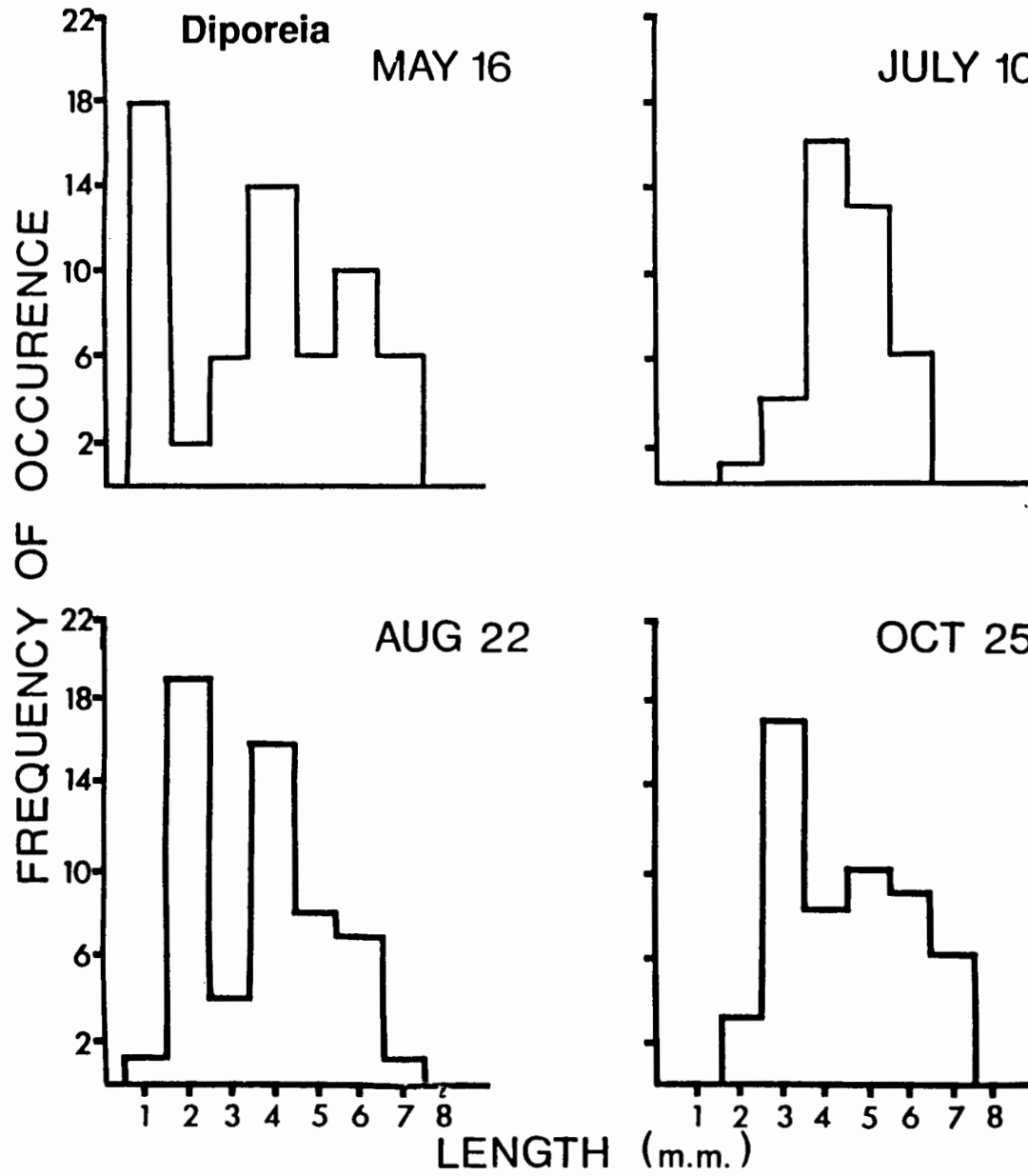


Figure 3. Length-frequency distribution of Hexagenia limbata in north-east Batchawana Bay.

Figure 4. Length-frequency distribution of *Diporeia* in north-east Batchawana Bay.



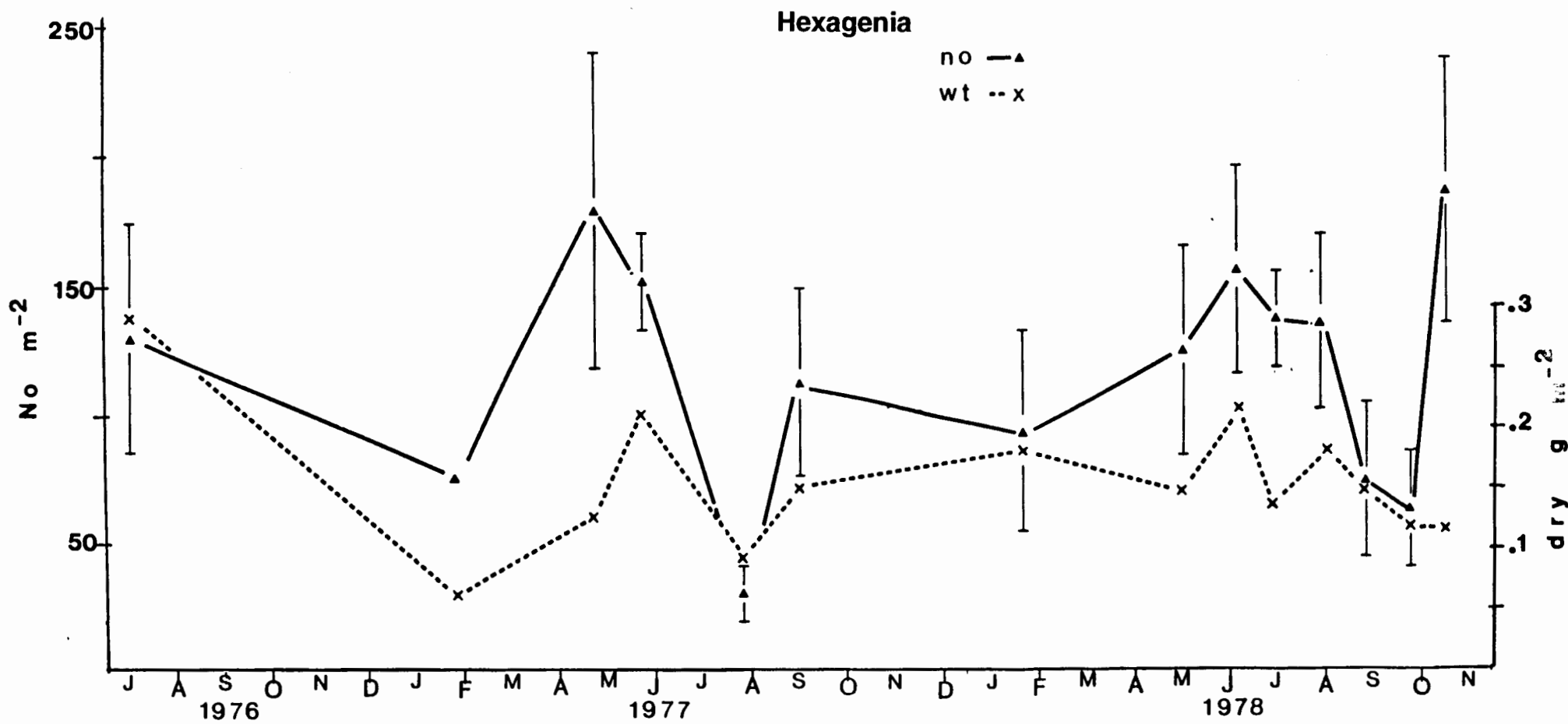


Figure 5. Abundance of Hexagenia and biomass (dashed line) in north-east Batchawana Bay at 7 m depth.

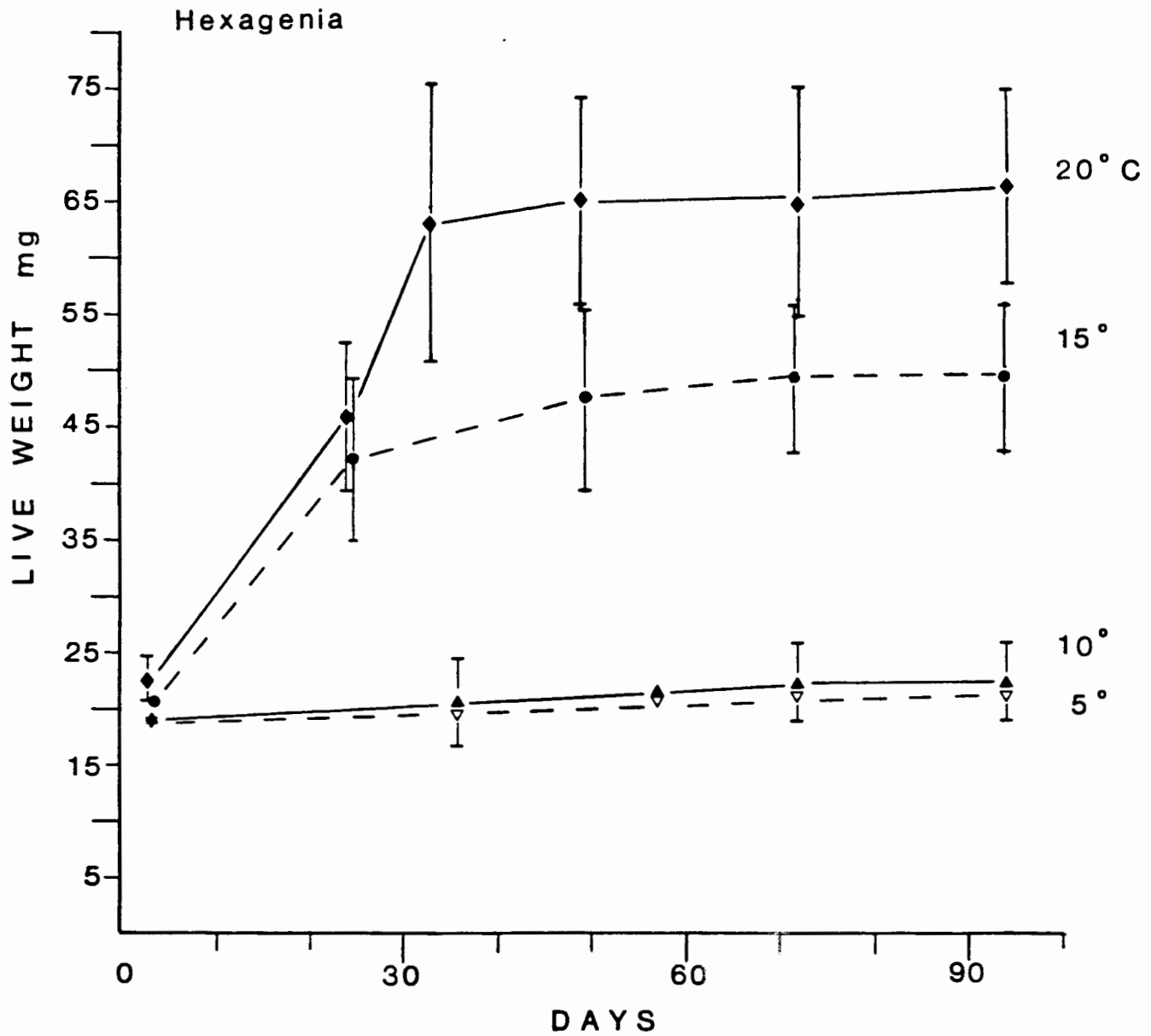


Figure 6. Laboratory growth rates of yearling *Hexagenia* nymphs at four temperatures.



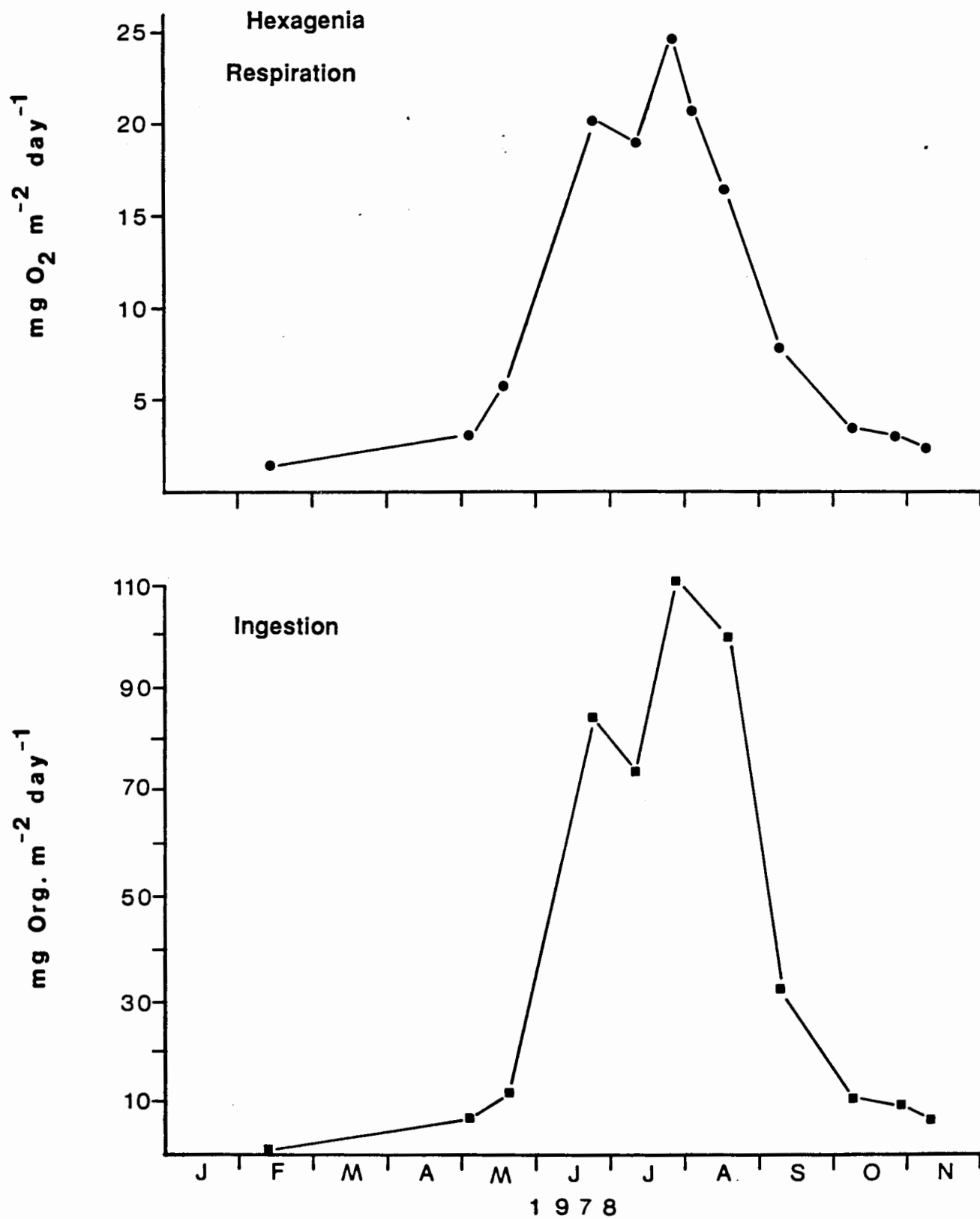


Figure 7. Calculated respiration (mg O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and ingestion rate (mg dry organic matter m<sup>-2</sup> d<sup>-1</sup>) by the *Hexagenia* population at 7 m depth in Batchawana Bay, 1978.

Figure 8. Abundance of *Diporeia* and biomass (dashed line) at 30 m depth in north-east Batchawana Bay.

