Production ecology of the amphipod <u>Hyalella</u> <u>azteca</u> (Saussure)
in a Northern Ontario lake

by
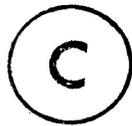
A thesis
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partial fulfillment of the requirements for the degree
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ABSTRACT

Annual production of the amphipod Hyalella azteca was estimated in the upper littoral zone of Dock Lake, Ontario, over a 2 year period (1980-1981). Population density (negligible below 1 meter) differed among the three habitats sampled. Cohort production by the size frequency method was 1.39 g/m^2 (dry weight), mean annual biomass was 0.36 g/m^2, and the P/$\bar{B}$ ratio was 3.9 for the 1980 year class. Six other methods for estimating production were applied to this cohort, providing comparable estimates ranging from 1.21 (instantaneous growth) to 1.65 (cohort G) g/m^2. Size frequency estimates of annual production for 1980 and 1981 were 1.24 and 1.40 g/m^2 respectively. The annual P/$\bar{B}$ ratios of 3.9 and 4.0 for these two years agree with the cohort value. A comparison of production estimates for Hyalella azteca in the literature shows a gradient of production correlating with habitat temperature regime.

This thesis is an original composition, based on research carried out by the author, and has not been previously submitted for credit toward any degree or diploma. Where the work of others has been included, it has been so acknowledged and appropriately cited.

August 16, 1982.

ACKNOWLEDGEMENTS

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INTRODUCTION

Production is "the means by which energy is made available for transmission from one trophic level to the next" (Waters, 1977). Studies of the production of detritivores thus form a link in the understanding of an energy pathway of major significance in aquatic ecosystem metabolism (Brinkhurst, 1974; Wetzel, 1975).

The common amphipod <u>Hyalella azteca</u> is a widely distributed freshwater detritivore. Often a major component of the benthos (see Anderson and Hooper, 1956), it is preyed upon by such fish as <u>Stizostedion vitreum</u>, <u>Perca flavescens</u>, <u>Oncorhynchus nerka</u>, and <u>Salmo gairdneri</u> (see Fedoruk, 1966; Cooper, 1965; Mathias, 1971), as well as invertebrate predators (Jackson, 1912).

Turnover, or P/$\bar{B}$ ratio values approximate 4 to 6 for most benthic invertebrates, and may thus be useful in estimating production (Waters, 1979). Calculation of the P/$\bar{B}$ ratio for <u>H. azteca</u> in different habitats and climates may help elucidate the interaction between environment and population dynamics; hence providing a way to develop predictive equations for estimating benthic production of lakes, as well as understanding the role of detritivores in aquatic ecosystems.

By comparing the production and turnover ratio of <u>H. azteca</u> in Northwestern Ontario with other available production estimates

(see Cooper, 1965; Mathias, 1971), the modifying effects of energy availability on life cycle and population dynamics of this important benthic species can be measured.

Life history of Hyalella azteca

H. azteca lives on or under the surface of detrital debris, and is particularly common among beds of emergent macrophytes. It feeds on dead and living plant material, especially filamentous algae, and epiphytic growth (Jackson, 1912; Embody, 1912; Cooper, 1965), although it will also consume fine detritus (Hargrave, 1970).

This amphipod is ubiquitously distributed in all North American permanent fresh water that reaches a monthly mean temperature of more than $10^{o}C$ (Bousfield, 1958). It has been reported from such northerly sites as Great Slave Lake (Moore, 1980), White Horse, Yukon, and lakes north of Rampart House, Alaska (Pearse, 1913). It is also common in Central and South America to Tierra del Fuego (Bulycheva, 1957).

H. azteca inhabits the littoral zone of lakes, but can be found to a depth of 10 meters (Bousfield, 1973). Cooper (1965) found it homogenously distributed above 1.75 m. in Sugarloaf Lake, Michigan. In Marion Lake, British Columbia, Mathias (1971) found it to be most numerous (up to $5000/m^2$) in very shallow water, but decreasing 10-fold from 0.5 m. to 3 m. Mean depth of Marion and

Sugarloaf Lakes are 2.4 m., and approximately 1.2 m.,
respectively.

The life cycle of this amphipod is univoltine. An
overwintering population begins to breed in early to late May,
or early June, depending on water temperature. The young grow
rapidly. Some broods may attain sexual maturity in their first
summer (Gaylor, 1922; Cooper, 1965; Biette, 1969), however, Mathias
(1971) found that in Marion Lake, which rarely goes above 20°C,
the amphipods did not mature until their second summer. Reproduction
is continuous during the summer for as long as temperature permits,
resulting in overlap of year classes and broods within a year class.

Sex recognition is primarily by touch (Holmes, 1903),
and amplexus precedes mating. The male carries the female until
she molts; immediately after which sperm is deposited in the
female's brood pouch, or marsupium. Eggs are subsequently passed
from the ovary to the marsupium, where they are fertilized (Jackson,
1912; Geisler, 1944). Clutch size varies from 4 to 40, being a
function of female body size (Mathias, 1971). Males can be dis-
tinguished from females by the enlarged second gnathopod, presence
of genital papillae ventrally on peraeon 7, and absence of coxal
oostegites (Bousfield, 1973). Breeding condition in females can
be estimated by the appearance of the oostegites, even when there
are no eggs in the marsupium. Non-breeding is indicated by poorly
developed oostegites which lack a fringe of long bristles (Geisler,
1944).

The eggs develop and hatch within the marsupium. The young remain within the pouch for one to three days, then work their way out (Geisler, 1944), or are released when the female molts (Gaylor, 1922). Cooper (1965) has shown that each juvenile instar has a characteristic mean number of antennal segments; however, adults are not as consistent. Instars 1 through 7 constitute the immature stages, instar 8 and above are considered adults. Instar 7 has nine or ten segments on the first antenna, with a maximum of twenty-two on the first and second antennae on one side of the head (Cooper, 1965; Geisler, 1944).

Temperature and photoperiod are critical factors regulating growth and reproduction. Cooper (1965) and Bovee (1950) demonstrated that the molt rate, incubation rate and age to maturity are a function of temperature; that growth is negligible at $10^{\circ}C$, and optimal ranges for growth and reproduction are 20 to $25^{\circ}C$.

Photoperiod determines reproductive state (active or resting), and temperature influences the rate of change from one state to the other. Breeding is initiated by a light regime of 12L-12D when temperature rises above $16^{\circ}C$ (breeding can be induced at $10^{\circ}C$ if this photoperiod is maintained for 10 weeks), similarly a return to this photoperiod from a longer day will halt breeding if the temperature drops (de March, 1977).

Size at maturity is dependent on the temperature experienced by the egg and embryo. Temperatures of 10 to $15^{\circ}C$ produce large adults with delayed reproductive development, 20 to $23^{\circ}C$ produces

small adults, and 18°C produces intermediate sized animals (de March, 1978).

Study area

Dock Lake (Figure 1) is one of four marl lakes situated 10.5 km. west of Lake Superior, within Thunder Bay, Ontario (lat. 48° 28', long. 89° 28'). It is 1.2 hectares in area, with a mean depth of 4.5 m. (Momot, 1973). Emergent macrophytes of the shoreline are dominated by <u>Carex aquatilis</u> and <u>Typha latifolia</u>. Submergent vegetation includes thick beds of <u>Potamogeton</u> spp. and <u>Chara</u> sp. Momot (1978) lists fish species, vegetation, and describes the limnology of this lake.

Beach temperatures during the ice-free seasons of 1980 and 1981 are shown in Figure 2. During the cool spring in 1981, the lake remained below the 20°C range until a much later date than in 1980.

The lake is stratified for most of the year. Conditions in the epilimnion vary with weather, but the hypolimnion is very stable. The thermocline is at 3 m., below which anoxia exists until turnover in the late fall. Winter conditions vary; in 1980 the lake was anoxic below 2 m., in 1981 it was oxic.

During the summer, conductivity readings in the epilimnion range from 280 to 310 micromhos. The hypolimnion exhibits a gradient of 300 micromhos at three meters, to 400 micromhos at the bottom. The water column as a whole drops briefly to 200 micromhos during turnover.

DOCK LAKE

N

Falls

1·5
3·0
4·5
6·5

A
B
C
D
E
F
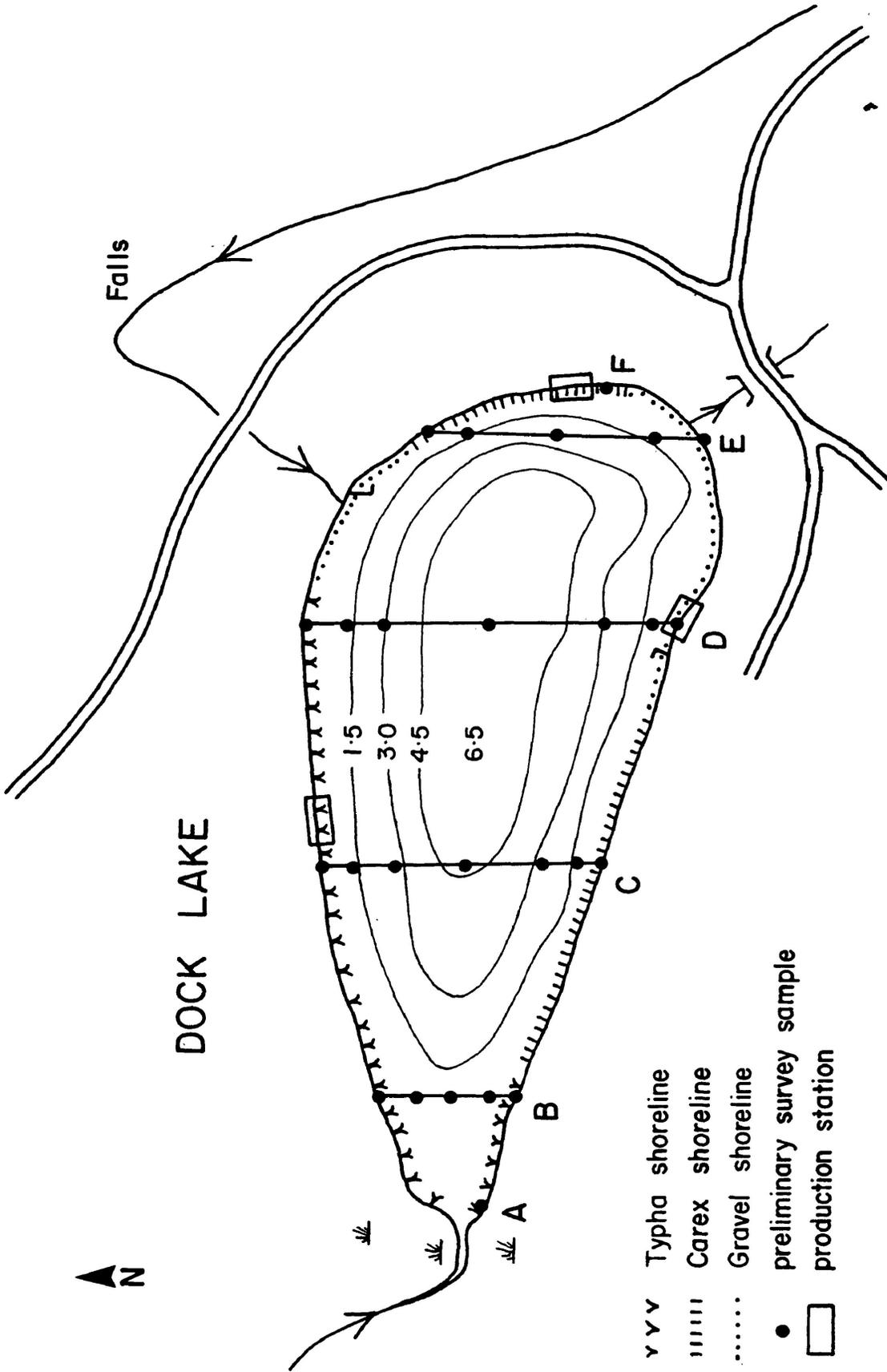
ʏ ʏ ʏ   Typha shoreline
ıııııı   Carex shoreline
· · · · ·   Gravel shoreline
●   preliminary survey sample
▯   production station

FIGURE 1: Depth contour map of Dock Lake, Ontario. Pro-

duction sampling stations consisted of three 5

meter lengths of shoreline (rectangles). Pre-

liminary survey transects ran north-south, with

two single-station transects at the east and west

ends of the lake. Depth distribution survey

transects (not shown) were taken perpendicular

to the shore at each production site.
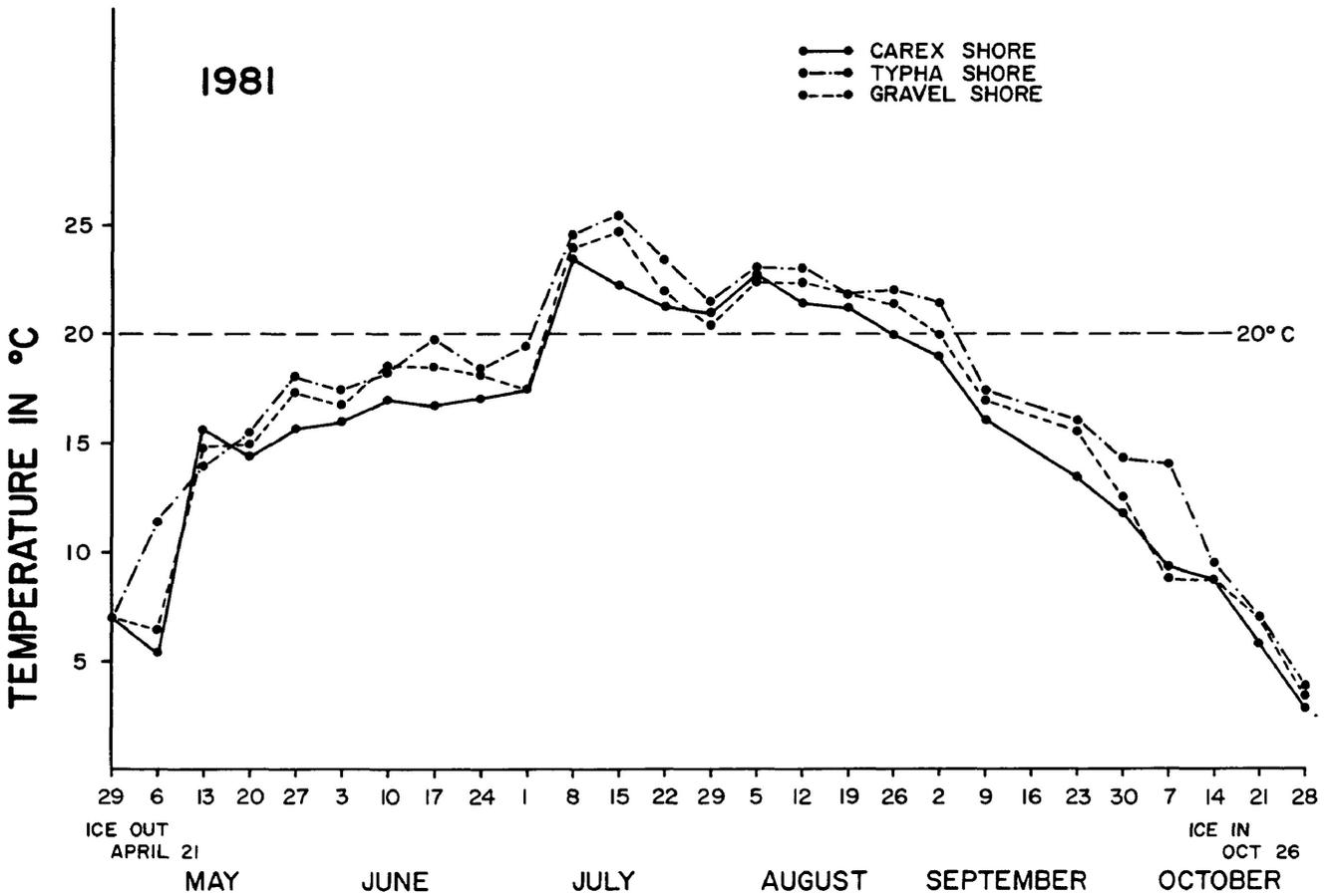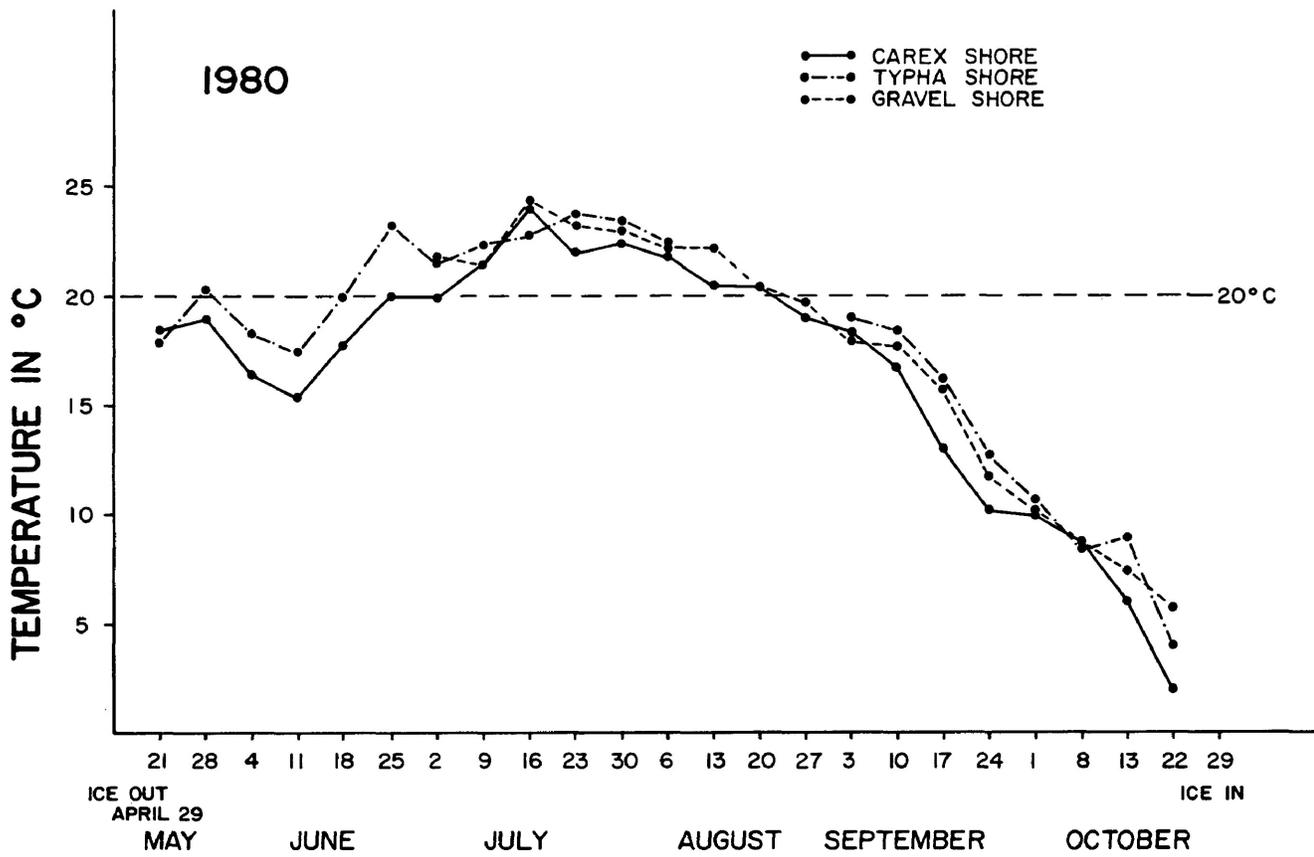
FIGURE 2:   Dock Lake shore temperatures for the ice-free

seasons of 1980 and 1981 on the three sample sites;

Carex, Typha and Gravel shores.

Secchi depth remains at 2 m. from breakup to mid-August, but ranges from 1.0 to 1.5 m. during fall.

Dock Lake exhibits a blend of marl, bog, and eutrophic characteristics. Wetzel (1975) describes the potential for rapid change in small marl lake ontogeny inherent in the development of littoral flora, especially Sphagnum. Approximately 50% of Dock Lake's shoreline is composed of floating vegetation mats containing this moss. The evidence suggests that Dock Lake is entering senescence, with the "pseudo-oligotrophy" (Momot, pers. comm.) imparted by marl chemistry giving way to eutrophic characteristics; eventually reaching a bog state.

MATERIALS AND METHODS

Limnology

Maximum/minimum thermometers were installed at three
stations, each representative of a shore type (see Figure 1).
The thermometers were read on a weekly schedule during the ice-
free seasons of 1980 and 1981. Mid-lake profiles of temperature,
oxygen and conductivity were taken using YSI Company meters, and
Secchi depth recorded, weekly, for the 1980 season.

Preliminary Survey

A survey was performed in early May, 1980, to establish
the distribution and density of H. azteca in Dock Lake. Transect
sampling was used to test for variability in depth distribution.
The survey consisted of four transects plus two single shore
stations (see Figure 1), for a total of 26 samples. Two replicates
were taken per station, as Cuff and Coleman (1979) found that survey
precision was increased by increasing the number of stations sampled
at the expense of the number of replicates per station.

Offshore stations were sampled with a small Ponar grab
(259 cm^2). Depths 0.5 m. or less were sampled using a cylindrical
box sampler (CBS) (Wilding, 1940; Hynes, 1970, p 238) of 919 cm^2
area. Samples were collected from the CBS using a fine mesh
(0.25 micrometer) hand net (Hynes, 1971, pp 69-70; Deacon, 1979).
To reduce variation in sampling effort a standardized method was
adopted; of heavy vegetation removal, counted sweeps with the net,

and a timed break between sets of sweeps. As H. azteca swims rapidly about when disturbed, this break proved a useful indicator of the preceding sweeps' effectiveness. Tests showed that the CBS was 90 to 100% effective in capturing amphipods on a gravel substrate; however, this value could be much lower in heavy vegetation.

Unpreserved field samples were transported to the laboratory in gallon jars, and washed in a #60 Tyler sieve (0.25 micrometer mesh), to remove silt. Cooper (1965) found this mesh size to retain the smallest size classes. Subsequently, measurements of head width of newly hatched individuals supported the use of the 0.25 micrometer mesh sieve (see Jonasson, 1955). Head width was greater than 0.25 micrometers for young within marsupiae, whereas free-swimming young are larger. The samples were stored in 10% formalin. Howmiller (1972), and Mills, Pitman and Munroe (1982) found that benthic organisms undergo the least weight loss in formalin.

Sugar flotation (Anderson, 1959) can be 90 to 99% effective in extraction of benthos from samples (Gerking, 1962; Cooper, 1965). In this study, the CBS samples contained large amounts of plant matter. As a result, the sugar flotation became a mere concentrating step, because the amphipods could not be skimmed from the surface of the sugar solution without also acquiring considerable plant material. This skimmed material was then hand-picked under a dissecting microscope to extract the amphipods.

Extracted amphipods were sorted into males, females and juveniles (instars 7 and younger), and counted. All samples in this study were treated similarly.

To check the preliminary survey, and test for seasonal habitat changes three additional depth distribution surveys were performed, in July, October and March. The former two consisted of one transect off each production station, with five stations per transect in July, and four in September. Due to adverse ice conditions, only three stations were sampled in March. In each survey, three replicates were taken at each station with the Ponar grab.

Taylor's Power Law was used to transform the density data (Elliot, 1977). The appropriate transformation is x^P, where x is the number of animals in the sample. Values of P obtained were 0.20 for the distributional data, and 0.25 for the production samples (see below). This agrees with the general transformation of $x^{0.25}$ calculated by Downing (1979). The distributional data were analyzed for trends in depth, transect, location and seasonality.

Length-Weight

Length-weight samples were collected in April, twice each in June and August, and in October, 1981, using a fine mesh D-net. Once extracted and sorted, the amphipods were stored in formalin except for a portion of the late June sample in which the animals were heat-killed, and processed immediately, to obtain fresh weight

measurements.

Head length was measured in profile as the arc between the tip of the rostrum and the dorsal margin of the head capsule, to the nearest hundredth of a millimeter using an ocular micrometer. Segment number counts for antenna 1, and first and second antennae were recorded. Total length measurements involved a mechanism similar to that described by Anderson and Hooper (1956). Slots of varying width were cut in a plexiglass plate, and sections of fine ruler (1 division = 0.42 mm.) were attached beside them. Each individual was inserted into the appropriate width slot, dorsal surface uppermost, and straightened by pressing gently on its back with fine forceps. Length was measured from the anterior of the rostrum to the tip of the telson.

Individuals were recorded as male, female, or juvenile. Eggs and/or young were removed from marsupiae by pressing them out through the interlocking hairs of the oostegites for counting.

Once measured, the animals were placed on weighing papers. Adults were treated individually and in groups of two to four animals of identical morphometrics and sex. Juveniles were similarly placed into groups of identical animals, in which the number of individuals per group was increased as size decreased; up to 100 or more for eggs and young from brood pouches. After drying for three days at $60^{\circ}C$, the amphipods were weighed on a five place Mettler electronic balance.

A total of 2861 individuals were measured for length-weight

analysis. With grouping, these animals gave 674 weight data.
Nine measurements of egg weight were obtained, involving 920 eggs.

The weight data were transformed, and analyzed for
differences between males and females, preserved and unpreserved
samples, and season. Linear regression was used to obtain a
length-weight equation.

Production

Restricted distributions and preferred habitats are
important factors to consider in designing sampling programs
appropriate to the life history of the organism under study
(Malley and Reynolds, 1979; Hall, Waters and Cook, 1980). Because
the largest number of $\underline{H}$. $\underline{azteca}$ occurred in less than 0.5 m. of
water, an extreme form of stratified random sampling, employing
the cylindrical box sampler, was used to obtain production
samples. Three strata of habitat-type were chosen (see Green, 1979;
Hall, Waters and Cook, 1980). The three main habitat types in
Dock Lake are beds of $\underline{Carex}$ $\underline{aquatilis}$, stands of $\underline{Typha}$ $\underline{latifolia}$,
and gravel beach containing sparse growths of $\underline{Equisetum}$ $\underline{sp}$. and
$\underline{Chara}$ $\underline{sp}$. Five meter sections of shoreline served as stations.
Samples were taken randomly within each station as in Green and
Hobson (1970); within the limitations of the sampler, and the
irregularities of the $\underline{Carex}$ and $\underline{Typha}$ vegetation mats.

Using the mean density of $\underline{H}$. $\underline{azteca}$ obtained from the
preliminary survey, and the area of the CBS (919 cm^2), the optimum

replicate number of three was obtained from Table 6 of Downing (1979). Therefore, three replicates were taken per station on each sampling date.

Waters (1969) recommends sampling schedules tailored to the growth type of the study organism. Cooper (1965) indicated that $\underline{H}$. $\underline{azteca}$ juveniles can molt every 5 days at 20°C, therefore the 1980 sampling schedule consisted of samples at five day intervals during the optimal season, and weekly to bi-weekly samples when water temperatures fell below this threshold. In 1981, a regular bi-weekly sampling schedule was adopted. Because the CBS did not function on ice-bound shores, samples could only be taken during the ice-free season.

Amphipod densities obtained in the production samples were tested for differences among stations on a sample by sample and total basis, and for trends in depth distribution within the range of the samples.

Once counted, the amphipods obtained from each replicate sample were stored in separate "adult" and "juvenile" vials. The three replicates of each sample were pooled, because size frequencies did not significantly differ among replicates. If the contents numbered more than approximately 100 individuals, adult and juvenile vials were subsampled using a plankton splitter, or a gridded petri dish and a table of random numbers. Cumulative subsampling revealed that a subsample of 75 to 100 animals accurately established the size frequencies of individuals within each vial.

Matching size classes to instars increases the accuracy of

production estimates which use the Hynes method (Hudson and Swanson, 1972; Resh, 1979). Therefore a graph of all measured animals of the 1980 data was examined for peaks indicative of mean instar sizes. Using mean instar antennal segment counts from Cooper (1965) as a criterion, the average head length and total length of instars 1 through 9 were calculated, compared to the graph peaks, and later checked against the length-weight data. From a total of 55,846 animals captured, 13,411 were measured for size frequency analysis.

After appropriate size classes were established, the measurement data were grouped into percentage frequencies for each size class. These were applied to the counts of juveniles and adults for each replicate, and to the sample means. Size frequency histograms of percentages and numbers for each sample were used in conjunction with lake temperature data (Figure 2), and the temperature dependent molt rates from Cooper (1965) to interpret life history.

Comparison of modal progressions of hatch peaks established that Cooper's molt data adequately fit the Dock Lake population. A modification of instar analysis (Cooper, 1965) was used to predict the expected location of hatch peaks in each sample, using mean temperatures over sample intervals and molt rates at those temperatures. The duration (in days) between samples was divided by the temperature-specific duration of instars (for juveniles) and incubation (an approximation of adult female molt rate, obtained from Cooper, 1965). The result is the potential number of instars (size classes)

the individuals of a hatch can grow through or into, during each sample interval. These calculations served to supplement the size frequency histograms, which were difficult to interpret. This information, together with temperature dependent size at maturity (de March, 1978) helped establish voltinism (see Table 3).

The numerical size frequency data, sampling schedule, and mean weight at mid length of each size class from the length-weight analysis were utilized in a computer program for estimation of production by the size frequency method (Krueger and Martin, 1980). Production for the 1980 and 1981 seasons, and for the 1980 year class (cohort) was estimated. A cohort is herein considered as "a group of individuals all hatched over the entire summer" (Hudson and Swanson, 1972). Separate production estimates for each of the three shores sampled were combined into a weighted mean, using the relative proportions of each habitat. Carex comprised 34%, Typha 42%, and Gravel 24% of the total shoreline perimeter.

The size frequency method (Hynes and Coleman, 1968; Hamilton, 1969), with the application of the cohort production interval voltinism correction (Benke, 1979), is comparable to other methods in accuracy. The size frequency method was chosen as the standard for this study.

For comparison, production was also estimated for the 1980 year class using the cohort G (Mathews, 1970), daily G (Hall, Waters and Cook, 1980; Waters, 1981), instantaneous growth (Ricker, 1946; Allen, 1949), Allen Curve (Allen, 1951), and removal summation

(Anderson and Hooper, 1956; Teal, 1957) methods, as outlined in Waters and Crawford (1973), and Wetzel and Likens (1979). Waters (1977) fully discusses the application of these methods. Year class production and biomass values were multiplied by 365/412 to obtain the annual values, because the 1980 year class was present in the samples for 412 days. Annual values are therefore 88.6% of year class values.

RESULTS

All statistical tests were performed at the 95% level
of significance.

Distribution

In Dock Lake, $\underline{H}$. $\underline{azteca}$ is restricted to shallow water,
with no individuals found below 1.5 meters (Figure 3).

No seasonal changes occur in depth distribution. The
Kruskal Wallis test and parametric analysis of variance showed
no significant difference in numbers of amphipods per m^2 (transformed
and untransformed data) at equal depths among transects, within
replicates, or among samples. Significant differences in numbers
of $\underline{H}$. $\underline{azteca}$ existed between depths in each sample. The 0 to
1 meter depth division significantly differed from all deeper
samples within each transect, and in the pooled data. A finer
depth scale was used for analysis of the May and July samples.
The 0 to 0.5 m range differed significantly from all deeper sets.

Separate production samples from each shore type were
analyzed for differences in depth distribution, and also as a
pooled set for each year. Depths of the production samples
ranged from 0.08 to 0.5 meters, as the CBS did not function in
less than 5 cm of water. The pooled sets for both years show a
similar trend, with few animals found in deeper samples, while
many occurred in the shallower samples; however the individual

DEPTH (METERS)

MEAN DENSITY (ANIMALS / m²)

FIGURE 3: Distribution of <u>Hyalella azteca</u> with depth in

Dock Lake; including all preliminary survey and

depth distribution samples (total number of

samples was 139). Zero values represent multiple

samples at all depths greater than 1 meter.

shores showed no significant difference among numbers of animals
at different depths. Using a 0.2 m increment scale of depth,
the following results were obtained for total numbers of animals,
and numbers of adults in each depth increment: parametric analysis
of variance showed no significant difference, the Kruskal Wallis
test gave significance, and three ranges tests (Duncan's Multiple
Range, Modified LSD, and Scheffe's tests) indicated that the Carex
shore differed from the Typha and Gravel shores.

Kruskal Wallis tests for differences among numbers of
animals on the three shores showed significance (pooled 1980 and
1981 data). Parametric ANOVA indicated significant differences
in total numbers of animals among the three shores for 1980 but
not 1981. Numbers of adults and juveniles in 1980, and adults
only in 1981 were significantly different among the three shores.
In all cases the ranges tests showed that the Carex samples were
different from those of Typha and Gravel (see Figure 5).

On a sample by sample basis, the 1980 samples showed
significant differences in numbers of H. azteca among the three shores
during the breeding season. In 1981, a majority of samples showed
no significant difference in total numbers of amphipods, or numbers
of adults or juveniles among the three shores.

Length-Weight

Statistical tests showed no significant difference
between the weights of males and females, nor between preserved
and unpreserved animals of the same size class. There were no
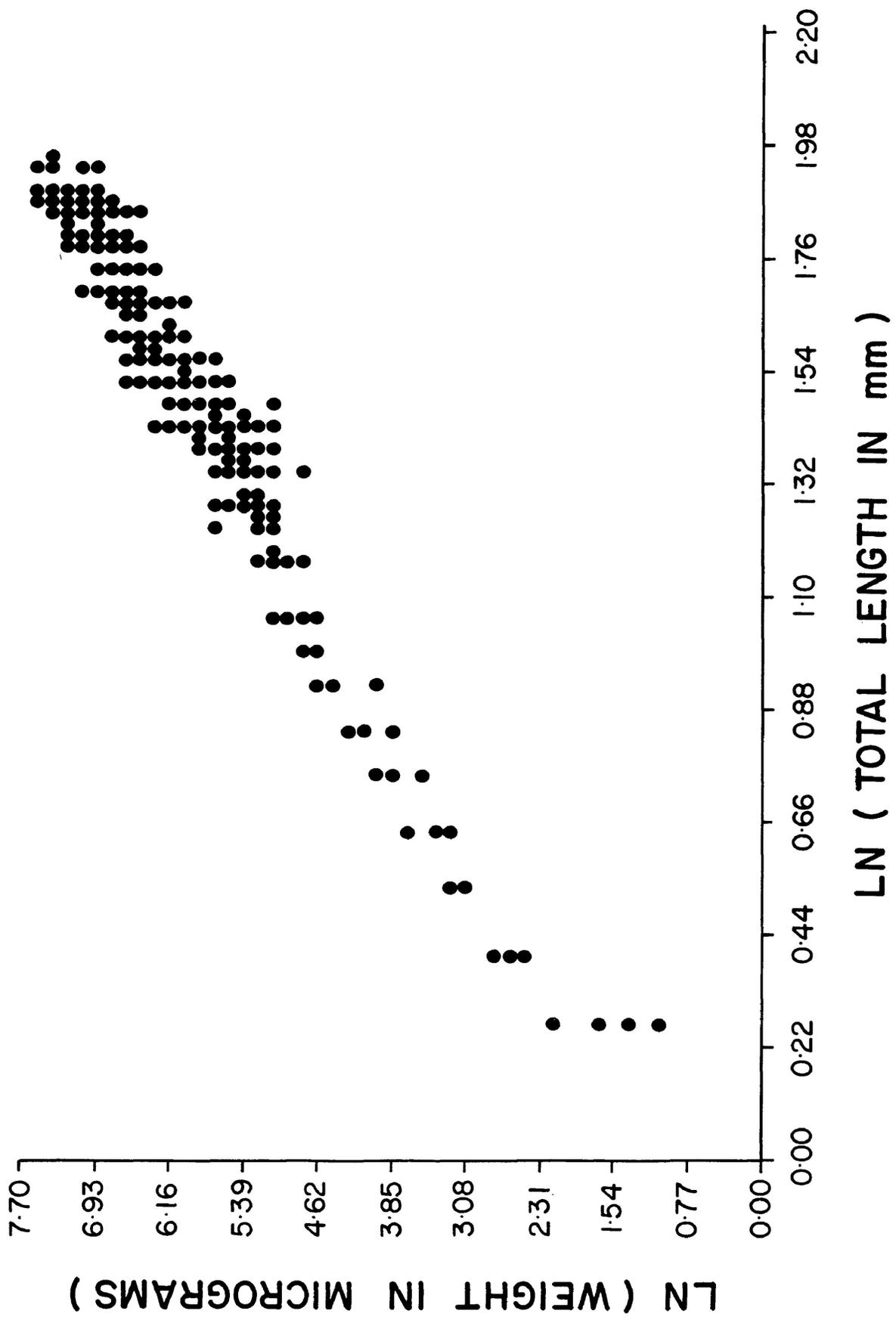
FIGURE 4: Relationship of the natural logarithms of weight

(micrograms) to total length (millimeters) for

Hyalella azteca in Dock Lake. (n = 588)

TABLE 1: Regression equations and correlation coefficients for selected morphometrics and length-weight of Hyalella azteca in Dock Lake, Ontario. The variables are as follows; W is dry weight in micrograms, TL is total length in mm, HL is head length in mm x 10^{-2}, A is antennal segment count (the ageing criterion).

REGRESSION

Number	Variables	Equation	CORRELATION COEFFICIENTS		
			Pearson	Kendal	Spearman
1	W,TL	ln W = 1.502 + 2.982 ln TL	0.98	0.87	0.97
2	W,HL	ln W = -10.367 + 4.000 ln HL	0.97	0.81	0.94
3	HL,TL	HL = 13.955 + 10.016 TL	0.97	0.88	0.97
4	A, HL	A = -25.569 + 12.379 ln HL	0.92	0.72	0.85
5	A,TL	A = 10.781 + 9.472 ln TL	0.93	0.72	0.85

seasonal weight differences within size classes, except for the April sample, in which the amphipods were significantly lighter than those of the same size classes from the June, August and October samples. On the assumption that these animals were lighter than the others due to depletion of body weight during winter, the April sample was omitted from the length-weight regression, leaving 588 weight data.

Figure 4 shows the relationship of weight in micrograms to total length in millimeters (see also Appendix A: 1 and A: 2). The regression equation is included in Table 1.

Total length and head length were judged effectively equivalent in accuracy (see Table 1), and total length chosen for subsequent analysis, as the more convenient measurement.

Mean egg weight was 5.4 ± 0.1 micrograms (920 eggs, 9 weight measurements).

Characteristics of the Population

Population Density

Figure 5 shows the density of <u>Hyalella</u> <u>azteca</u> on the three shores over the ice-free seasons of 1980 and 1981. On the <u>Carex</u> shore, peak population numbers occurred on August 6, 1980 (17,459 animals/m^2), and July 29, 1981 (10,579 animals/m^2).

Growth

Using the instar specific antennal segment counts from Cooper (1965) and Geisler (1944) to age specimens, average head
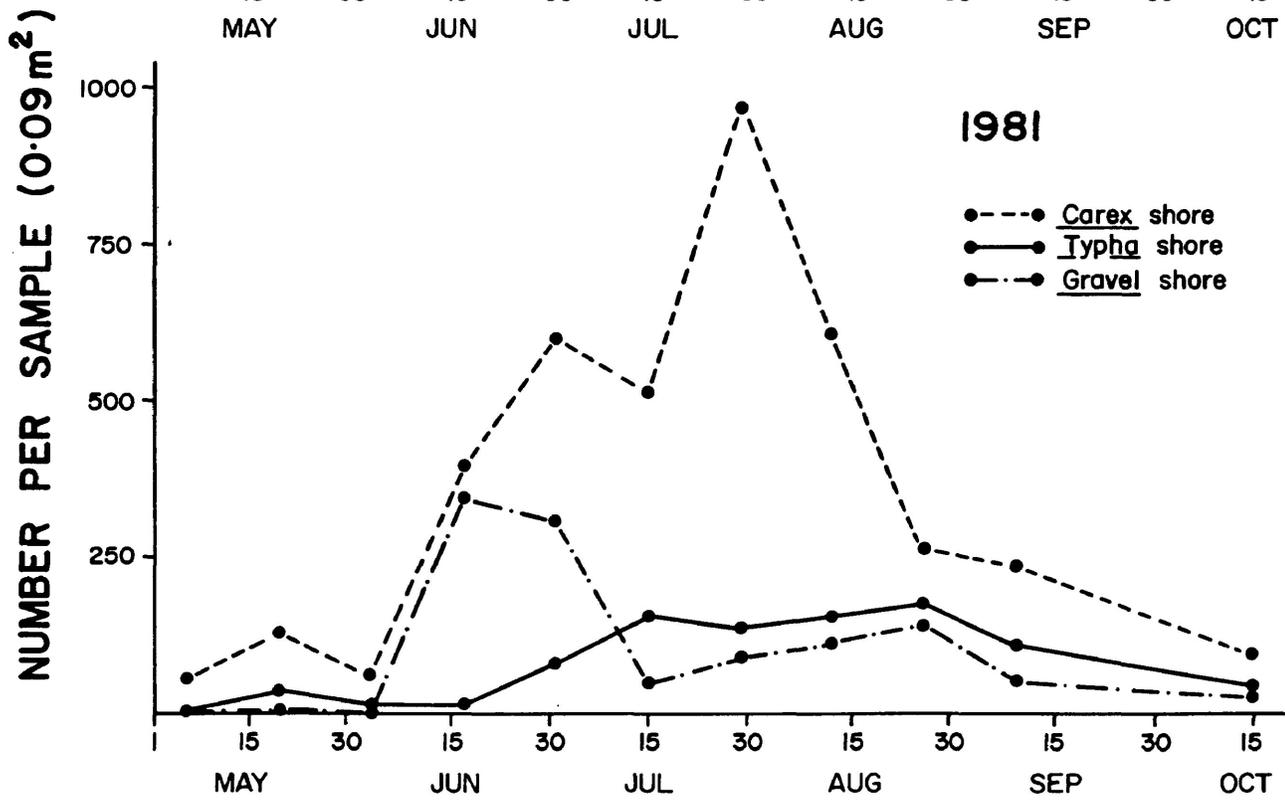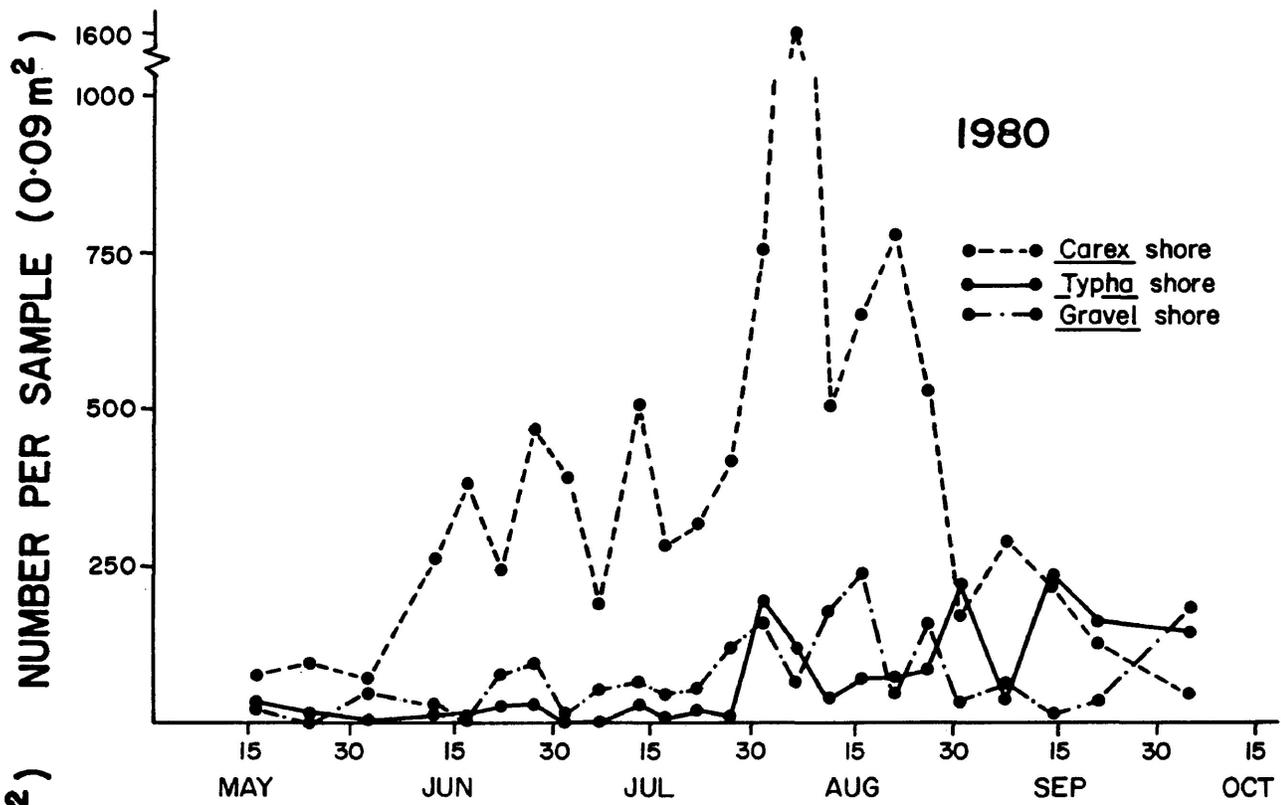
FIGURE 5:   Mean population densities of <u>Hyalella</u> <u>azteca</u>

in three habitat types of Dock Lake (<u>Carex</u> bed,

<u>Typha</u> stand and Gravel beach), for the ice-free

seasons of 1980 and 1981.

lengths and total lengths for instars 2 to 9 were calculated

from the 1980 production data and the length-weight data (Table

2). Up to instar 7, the head lengths agreed closely with Cooper's

data. Head length and total length plotted against antennal

segment count, as well as the length-weight data, display a great

deal of scatter in the adult sizes (see Appendix A: 1).

Growth is a function of temperature (Figure 6). Molt

rates (Cooper, 1965; Geisler, 1944) graphed against the weight

of each instar show that growth is much slower at $15^{\circ}C$ than at

$20^{\circ}C$.

All free-swimming young from the field, or observed in

the laboratory were instar 2 or older, and the majority of those

taken from brood pouches were instar 2 (13 antennal segments;

Cooper, 1965). No evidence of molting within the brood pouch

was found.

Table 2 was used to construct size classes for the size

frequency analysis. From instars 3 to 9, total lengths increase

in approximately 0.5 millimeter increments. The largest individuals

caught were 7.7 mm. Accordingly, thirteen size classes with mid-

lengths from 1.5 to 7.5 mm were constructed. Size classes 1 to 7

correspond to instars 3 to 9. Instars 2 and 3 (free-swimming sizes)

were combined into size class 1.

Age Composition

The size frequency histograms (Appendix B) show that three

TABLE 2: Mean head lengths and total lengths for instars 2 to 9 of Hyalella azteca in Dock Lake, 1980 and 1981. Antennal segment counts are used to age individuals (Cooper, 1965). n: number of animals of each instar used to calculate mean lengths; s: standard deviation.

Instar	Av. Antennal Segment No.	1980					1981				
		Head Length	s	Total Length	s	n	Head Length	s	Total Length	s	n
2	13	0.22	0.02	1.29	0.12	40	0.22	0.01	1.32	0.04	345
3	14	0.25	0.02	1.52	0.14	76	0.26	0.01	1.50	0.01	247
4	16	0.31	0.04	1.94	0.24	100	0.33	0.03	1.95	0.19	294
5	18	0.38	0.02	2.48	0.20	57	0.39	0.02	2.42	0.16	289
6	20	0.43	0.02	2.98	0.28	81	0.44	0.02	2.82	0.20	118
7	21.5	0.47	0.03	3.37	0.32	100	0.48	0.04	3.34	0.32	150
8	23.5	0.53	0.04	3.99	0.32	50	0.56	0.06	4.18	0.49	93
9	25.5	0.56	0.05	4.40	0.53	50	0.61	0.06	4.64	0.49	101
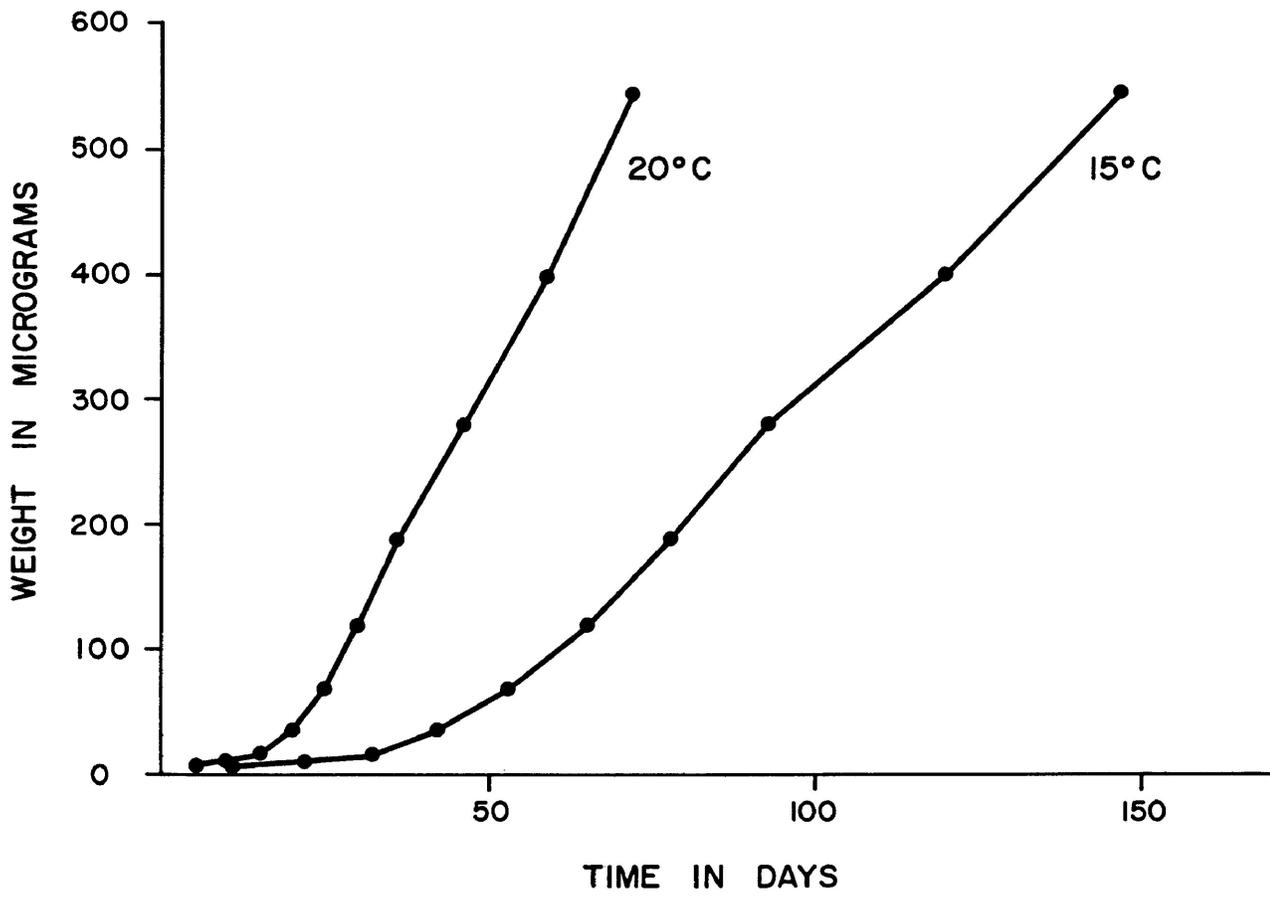
FIGURE 6:   Growth curve for <u>Hyalella</u> <u>azteca</u>, from instars

1 through 10. Molt rates for juveniles, and

incubation rates (corresponding to adult female

molt rates) are taken from Cooper (1965). Weight

is weight at average length for each instar, cal-

culated from the length-weight regression.

major hatch peaks occurred in both 1980 and 1981. Because May
1981 was colder, the first hatch occurred several days later
than in 1980. By the third hatch of either year, animals from
the first brood had grown into the adult size classes, and were
ovigerous. Comparison of the modal progression of hatches on the
histograms, instar analysis data (Cooper, 1965), and molt rate
calculations all confirm that the first hatch grows into and
merges with its parents, making the separation of year classes
difficult. Within a year class, each hatch eventually merges
indistinguishably into a "pool" of adults (see Appendix B).

In Table 3, the first hatch of 1981 can be followed
from its appearance until the last sample of the season. Molt rate
calculations are compared to the locations of the hatch peak in
each size frequency histogram (Appendix B). This first brood
of 1981 first appeared in sample 4, occupying the first three size
classes. Molt rate calculations and the histograms for the Typha
shore indicate that its remnants are still present in sample 10
(mid-October).

The first hatch of the 1980 year class occurred on
June 3-4, 1980. The last appearance of overwintered adults from
this cohort was on July 29, 1981; a total of 412 days. The
average life span of an individual is about 365 days, however
there is considerable individual variation.

Reproduction

Gravid females were captured in Dock Lake from May 23 to

TABLE 3: Growth of the first hatch, 1981 of Hyalella azteca in Dock Lake, Ontario, through successive size classes (1 to 13); using a modification of instar analysis (Cooper, 1965). Each sample interval is divided by the molt rate, or duration of instar, at mean interval temperature, to give the potential number of size classes any individual can grow into during the interval. The predicted location of the hatch peak is compared to its location in size frequency histograms. Duration of juvenile instars and incubation at given temperatures (^{o}C) are from Cooper (1965).

Sample	Date	sample interval (days)	mean temperature during sample interval	duration of juvenile instars at mean temperature	No. of juvenile molts during interval	duration of incubation at mean temp.	number of adult molts per interval	calculated size classes occupied by hatch	approximate size classes occupied by hatch (size frequency histograms)
4	Jun 17	14	17.1 a	6.8 b	2.1	19.5 b	0.7	1,2,3*	1,2,3
5	Jul 1	14	21.1	4.8	2.9	11.5	1.2	3,4,5	3,4,5
6	Jul 15	14	21.5	4.5	3.1	11.0	1.3	6,7,8	5,6,7,8
7	Jul 29	14	21.8	4.5	3.1	11.0	1.3	7,8,9	7,8,9
8	Aug 12	14	20.9	5.0	2.8	11.5	1.2	8,9,10	8,9,10
9	Aug 26	14	18.3	5.8	2.4	16.5	0.8	9,10,11	9,10,11
10	Sep 9	36	11.9	27.0	1.3	(28)	(1.3)	10,11,12	9,10
11	Oct 15							11,12,13	10,11,12,13

* Appearance of the first hatch, and the size classes occupied at that time, was obtained from size frequency histograms (1981 field samples)

a: data in ^{o}C

b: data in days

August 26 in 1980, and from May 20 to August 12 in 1981. First

age to maturity was 24 days in 1980, and 30 days in 1981. The

first hatch that matured, bred in their first summer in both years;

however, reproduction by the smaller adults of the second brood

ceased much earlier than among the larger ones (of the first hatch).

The third hatch failed to breed during its first summer.

Brood counts of gravid females correlated with animal size

(see Appendix A: 3). Mean brood size ranged from 5 to 36 eggs

for female total lengths of 3.8 and 7.0 mm. respectively. The

largest brood found in the subsampled animals was 42 eggs, in the

marsupium of a 6.7 mm. female. There was considerable variation

in brood size, particularly among the larger sized animals. Among

the three shores, brood counts for any given size class tended to

be highest on the Carex shore, slightly lower on the Gravel shore,

and lowest on the Typha shore; however, these trends were not

statistically significant.

Production

Waters (1977, 1979, 1981) indicates that use of the largest

size class of a benthic organism may lead to overestimates of

production, therefore the "times loss" factor in all size frequency

estimates was arbitrarily reduced (as suggested by Waters and

Crawford, 1973) from 13 to 12. The mean annual number of animals

in each size class (from the computer program output) was multiplied

by the mean weight of an individual of that size class, to compare

relative contributions to biomass. Size class 13 contributed less than size class 1, which supports the above decision. Similarly, instars 1 and 2 are not part of the free-swimming (and "catchable") population, therefore the first size class (mean length 1.5 mm) was used as the weight at hatching, since this is the length at which H. azteca leaves the marsupium.

Cohort G is calculated as the natural log of mean weight of the largest size divided by the mean weight at hatching. The mean weights of size classes 1 and 12 being 15 and 1487 micrograms, cohort G was therefore 4.596. This value was divided by the growing season (Waters, 1981); delimited by the length of time in which water temperatures are $10^{o}C$ or higher (150 days in 1980 plus 40 days to the disappearance of the cohort in 1981, for a cohort growth season of 190 days). The daily G was thus 0.024192.

Annual production was calculated for 1980 and 1981 using the size frequency and cohort G methods, for the three shores (Table 4, and Appendix C). To obtain a full year of samples as required by the size frequency method, the first sample of 1981 was used to represent the last sample of 1980. This gave a sampling year from ice-out 1980 to ice-out 1981. Since the fall 1980 and spring 1981 samples were almost identical, winter mortality was assumed to be minimal; and the fall 1981 sample was therefore used as an approximation of the April 1982 population, for the 1981 calculation. Production estimates for the littoral zone of Dock Lake were 1.24 and 1.40 g/m^2, for 1980 and 1981 respectively.

TABLE 4: Annual dry weight production (g/m²), by the size frequency and cohort G methods, biomass and P/B ratios; for 1980 and 1981 on three shores of Dock Lake. Annual means are calculated by weighting each shore value by the proportion of that shore type in the lake (Carex 34%, Typha 42%, Gravel 24%).

SHORE AND YEAR		BIOMASS (g/m²)	$P/\bar{B}$	METHODS	
				size frequency	cohort G
Carex	1980	0.452	4.096	1.851	2.077
Typha	1980	0.264	3.676	0.969	1.213
Gravel	1980	0.207	4.004	0.828	0.951
weighted mean	1980	0.314	3.933	1.235	1.478
Carex	1981	0.657	3.990	2.620	3.020
Typha	1981	0.230	3.892	0.894	1.057
Gravel	1981	0.123	4.425	0.543	0.565
weighted mean	1981	0.350	3.991	1.397	1.606

Cohort production was estimated for the 1980 year class using the size frequency (Table 5), daily G, cohort G, instantaneous growth, removal summation and Allen curve methods. These seven methods gave comparable estimates of annual production, ranging from 1.07 (instantaneous growth) to 1.46 (cohort G) g/m^2 (Table 6). Calculation of instantaneous growth, removal summation, Allen curve, and daily growth are given in Appendix D.

Annual $P/\bar{B}$ ratios on the three shores were: Carex 4.0, Typha 3.6, and Gravel 4.1 for the 1980 cohort. The weighted annual $P/\bar{B}$ ratio was 3.9. By the size frequency method, annual production of this year class was 1.23 g/m^2 (Table 6).

TABLE 5: Cohort size frequency production estimate calculations for _Hyalella azteca_ on three shores of Dock Lake, Ontario. The times loss factor has been reduced from 13 to 12 to avoid over-estimating the contribution by the rare 13th size class.

A: _Carex_ shore 1980 year class

SIZE CLASS	AV. NO. PER M²	NUMBER LOST	MEAN WEIGHT (G/INDIVIDUAL)	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION (G/M²/YEAR)
1	115.459	-23.959	0.000015	0.000023	-0.000549	
2	139.419	-60.674	0.000035	0.000049	-0.002982	
3	200.093	34.156	0.000069	0.000091	0.003095	
4	165.937	-82.376	0.000119	0.000150	-0.012321	
5	248.313	33.775	0.000188	0.000229	0.007749	
6	214.539	61.685	0.000280	0.000330	0.020358	
7	152.854	-6.602	0.000389	0.000460	-0.003040	
8	159.455	17.498	0.000545	0.000628	0.010992	
9	141.957	102.868	0.000724	0.000825	0.084817	
10	39.089	14.955	0.000939	0.001058	0.015822	
11	24.134	20.709	0.001192	0.001331	0.027572	
12	3.424	2.897	0.001487	0.001648	0.004775	
13	0.527	0.527	0.001827	0.001827	0.000964	
TOTAL					0.157251	
FINAL CALCULATIONS			12. ×	412./412. ×	0.157251	1.887

TABLE 5 (Continued)

B: _Typha_ shore 1980 year class

SIZE CLASS	AV. NO. PER M²	NUMBER LOST	MEAN WEIGHT (G/INDIVIDUAL)	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION (G/M²/YEAR)
1	5.797	-2.661	0.000015	0.000023	-0.000061	
2	8.458	-8.019	0.000035	0.000049	-0.000394	
3	16.478	-6.771	0.000069	0.000091	-0.000614	
4	23.249	-19.852	0.000119	0.000150	-0.000614	
4	23.249	-19.852	0.000119	0.000150	-0.002969	
5	43.101	-86.471	0.000188	0.000229	-0.019839	
6	129.572	3.164	0.000280	0.000330	0.001044	
7	126.409	0.396	0.000389	0.000460	0.000182	
8	126.013	-49.396	0.000545	0.000628	-0.031028	
9	175.408	137.558	0.000724	0.000825	0.113419	
10	37.850	33.596	0.000939	0.001058	0.035544	
11	4.254	3.985	0.001192	0.001331	0.005306	
12	0.269	0.269	0.001487	0.001648	0.000443	
13	0.000	0.000	0.001827	0.001827	0.000000	
TOTAL					0.101033	

FINAL CALCULATIONS   12.   ×   412./412.   ×   0.101033   =   1.212

TABLE 5 (Continued)

C: Gravel shore 1980 year class

SIZE CLASS	AV. NO PER M^2	NUMBER LOST	MEAN WEIGHT (G/INDIVIDUAL)	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION (G/M^2/YEAR)
1	23.437	-7.012	0.000015	0.000023	-0.000161	
2	30.449	-40.875	0.000035	0.000049	-0.002009	
3	71.324	-6.697	0.000069	0.000091	-0.000607	
4	78.022	12.230	0.000119	0.000150	0.001829	
5	65.792	-121.091	0.000188	0.000229	-0.027782	
6	186.884	23.023	0.000280	0.000330	0.007598	
7	163.861	50.573	0.000389	0.000460	0.023286	
8	113.287	85.381	0.000545	0.000628	0.053632	
9	27.907	20.665	0.000724	0.000825	0.017038	
10	7.242	-1.712	0.000939	0.001058	-0.001812	
11	8.954	8.140	0.001192	0.001331	0.010837	
12	0.815	0.693	0.001487	0.001648	0.001142	
13	0.122	0.122	0.001827	0.001827	0.000223	
TOTAL					0.083215	

FINAL CALCULATIONS   0.083215 = 12. x 412./412. x   0.999

TABLE 6: Biomass, and production (g/m^2) using 7 methods, for the 1980 year class of Hyalella azteca on three shores in Dock Lake, Ontario. Allen curves 1 and 2 are calculated from hand smoothed curves, and data connected by straight lines, respectively. Cohort G is 4.596 and daily G is 0.024192. Cohort values are calculated over a 412 day period (presence of the 1980 year class in the environment) and annual values are cohort figures x 365/412.

METHODS

	BIOMASS	size frequency	instantaneous growth	Cohort G	daily G	removal summation	Allen Curve 1	Allen Curve 2
COHORT								
Carex	0.468	1.887	2.533	2.153	2.979	2.557	2.579	2.171
Typha	0.335	1.212	0.744	1.541	0.931	0.745	0.862	0.746
Gravel	0.245	0.999	0.138	1.127	0.651	0.124	0.551	0.378
weighted mean	0.359	1.391	1.206	1.650	1.560	1.212	1.371	1.142
ANNUAL								
Carex	0.415	1.672	2.244	1.907	2.634	2.265	2.285	2.284
Typha	0.297	1.074	0.659	1.365	0.825	0.660	0.764	0.659
Gravel	0.217	0.885	0.122	0.998	0.577	0.110	0.488	0.296
weighted mean	0.318	1.231	1.069	1.462	1.382	1.074	1.215	1.124

DISCUSSION

Distribution

Hyalella azteca is rarely found below 2 to 3 meters (Hargrave, 1970). For example, higher densities of this amphipod occurred in the shallower areas of both West Blue Lake, Manitoba (Biette, 1969), and Marion Lake, British Columbia (Mathias, 1971). A similar distribution occurred in Dock Lake. Shallow water seems to be the preferred habitat for this amphipod.

Habitat preference and depth distribution relates to environmental heterogeneity. Macrophyte beds offer refugia from predation for both young and adult macrobenthos, as well as increased surface area for periphyton growth (Hall, Cooper and Werner, 1970). Among the three shore habitats of Dock Lake, the gravel substrate provided the least structural complexity, and the Carex beds the greatest, while Typha was intermediate. The substrate between stalks of Typha was a flocculent ooze quite different from the structured litter of the Carex beds. These habitats thus form a gradient of shelter and food.

In Dock Lake H. azteca does not occur below 1.5 meters (Figure 3). This corresponds to the depth limit of macrophytic growth. Below this depth, only soft lake sediments are found. Mathias (1971) states that H. azteca displays poor growth when

fed on such lake sediments, but does grow well on a diet of periphyton. Light attenuation causes epibenthic periphyton production to decrease with depth (Hargrave, 1970). Below 1.5 meters in Dock Lake, there is little periphyton (preferred food) or substrate (macrophytes) available; thus H. azteca is apparently limited to depths less than 1.5 meters by a combination of food and substrate.

Food may be the most important factor of habitat quality affecting distribution and population density of H. azteca in any given body of water. Differences in density with habitat type (see Figure 5) suggest that both type and quantity of vegetation (food) are important to the distribution and standing crop of H. azteca. Growth and production of Asellus racovitzae and Gammarus fasciatus in the lab were "profoundly affected" by the type of algae available as food (Swiss and Johnson, 1976). In Gammarus pulex, weight increase and molt rate at a given temperature also reflect the varying nutritional values of different diets (Willoughby and Sutcliffe, 1976). Hargrave (1970) found that in H. azteca, the ingestion rate and assimilation efficiency were lower on a diet of blue-green algae than on green algae and diatoms. The latter are a major component of the periphyton, which encrust the surface of macrophytes as well as other submerged substrates (Wetzel, 1975). Gerking (1962) has commented on the causal relationship of variability in abundance and distribution of macrophytes to the spatial distribution of benthos. Further studies involving

surveys of available food in different habitats, and analysis of the diet of H. azteca captured from these habitats, would test the hypothesis that food is the most important limiting factor.

Life Cycle

Growth

The mean instar sizes for H. azteca listed in Table 2 are based on an entire growing season, and can be considered "annual" means. The slight differences between the two years possibly represents bias introduced by using different numbers of animals from different seasons within each calculation. Although the weight of animals within a size class was the same from month to month, variations in length at a given age, caused by the temperature dependent growth (Figure 6), may have been present.

Antennal segment count could not be used to accurately age adult H. azteca, because head length and total length plotted against antennal segment count (Appendix A: 1) showed great scatter as antennal segment count increased. Wilder (1940) and Geisler (1944) also disclaim the effectiveness of antennal segment number as an ageing criterion. The standard deviation of head and total length for each instar also increased with age (Table 2). This increased variability with age could be a function of the inter-action between temperature control of growth (ie, molt) rates and of maximum size in older animals (see de March, 1978).

Juvenile instars were identified by antennal segment counts.

Very few young H. azteca taken from marsupiae corresponded to the

first instar (12 antennal segments) as reported by Cooper (1965).

The first visible segment of antenna 2, which is actually the

third segment (Bousfield, 1973, p. 20), is recessed in newly hatched

animals, and becomes more evident after several days. Wilder (1940)

lists instar 1 as having 13 antennal segments and total length of

1.3 mm, which agrees with Table 2. All other Dock Lake instars

match the Sugarloaf Lake data (Cooper, 1965). A carefully planned

rearing experiment would resolve the discrepancy in antennal segment

count.

Growth in H. azteca is approximately linear, for instars

1 through 10 (Figure 6). Higher water temperature results in a

steeper growth curve due to the increased rate of growth. Similar

temperature dependent growth (with no growth at 10°C) has been

demonstrated for crayfish by Pratten (1980). Growth rates, adult

body size and fecundity of some aquatic insects are also dependent

on temperature during development (Sweeney and Vannote, 1978).

In Dock Lake, the first brood of 1980 developed at 18 to

20°C, after which the temperature dropped to approximately 16°C

for a week (Figure 2). According to de March (1978), this temperature

regime should produce medium sized adults (5 to 6 mm.). The first

brood of 1981 developed at 15 to 18°C, which should give large

adults (5.5 to 7 mm.). In the size frequency histograms (Appendix

B), these growth patterns were evident as an accumulation of small

adults in 1980; and the presence of large adults in the last
sample of 1981, identified by molt rate calculations as belonging
to the first brood. Temperature control of adult length made it
impossible to separate the contribution from each brood to the
pool of adults, since all adults do not grow to the same maximum
size.

Temperature dependent growth rates may be modified by
population density. Wilder (1940) has shown that, given the same
temperature, lab populations of H. azteca tend to produce somewhat
smaller adults at high density than at low density. This could
explain the very large individuals that appeared on the Typha
and Gravel shores, but were not evident in Carex samples, in fall,
1981.

Voltinism

Cooper (1965) interpreted the Sugarloaf Lake population as
bivoltine, with separate summer and winter cohorts. The Marion
Lake (Mathias, 1971) and West Blue Lake (Biette, 1969) populations
were both univoltine. The Dock Lake population was interpreted
as univoltine, based on the size frequency histograms and molt
rate calculations. Temperature dependent mean size of adult instars
(de March, 1978) contributes to the difficulty of interpreting
these data. Waters (1981) also comments on the difficulty of
stating exact life cycle length in an amphipod with continuous
reproduction and high individual variability.

The voltinism of H. azteca could change with climate.

Butler (1982) describes a 7 year life cycle for two Alaskan species

of Chironomus, and changes in voltinism with latitude and altitude

are also known in the Odonata (Ingram and Jenner, 1976; Deacon, 1979).

Also, a small proportion of the population could differ in voltinism

from the rest. A population of the odonate Enallagma aspersum was

found to be 8% bivoltine, 92% univoltine (Ingram and Jenner, 1976).

The unavailability of an emergence curve makes it difficult to determine

such a pattern from the size frequency data for H. azteca, since

animals of different ages merge into the same size classes. If a

small portion of the Dock Lake population was bivoltine, or if

the average life span was less than 365 days, the production estimates

and P/B̄ ratios in Tables 4 and 5 were slightly underestimated.

Reproduction

In Dock Lake, individuals born early in the season bred

during their first summer. The data from this study, and from

West Blue Lake (Biette, 1969) suggest that H. azteca may mature

and breed in its first summer, and breed again in its second summer

if it survives the winter. The similarity of early spring and late

fall size frequency and density data (Appendix B, and Figure 5)

supports the hypothesis that the overwintering population is very

stable, with minimal mortality (Cooper, 1965).

Comparison of data from four studies of H. azteca (Table 7)

shows that the onset of reproduction, as indicated by the first

appearance of eggs in marsupiae, corresponds closely with 16°C ;
the critical threshold temperature reported by de March (1977) for
reproduction in this animal. The 12L-12D daylength which induces
and terminates reproduction at this temperature begins in mid-
March and ends in late September at the latitude of Dock Lake
(Bracken, 1982).

If the latitudinal difference of approximately 10° between
Sugarloaf Lake and West Blue Lake can be assumed to make little
difference in the date of 12L-12D daylength, then north temperate
populations of H. azteca are prevented from early spring breeding
only by the temperature threshold, since the photoperiod threshold
is reached while the lakes are still ice covered. Termination of
breeding may depend on slightly different thresholds. In all four
studies, cessation of breeding occurred at about the same time as
temperature dropped below 18°C. At this point, daylength had
decreased to less than 14 hours of light. An age-specific factor
may be involved as well, since young animals that matured late in
the season did not breed, while older animals were still ovigerous.

Hence, both temperature and photoperiod must be in the
optimal ranges of over 12 hours of light and at least 16°C (de March,
1977) for reproduction to occur. In the tropics, where there is
little variation in daylength, temperature and/or some other parameter
such as food may control reproduction. Sixteen hours of daylight
induces reproduction at temperatures below 16°C (de March, 1977).

This may be of crucial importance to far northern populations of H. azteca.

Production

Production estimates for Hyalella azteca range from 1.2 to 1.9 g/m^2 (Table 7). Production estimates for larger littoral zone amphipods are higher, ranging from 2.9 (Marchant and Hynes, 1981) to a maximum of 27.1 g/m^2 (Waters and Hokenstrom, 1980) for Gammarus pseudolimnaeus, and from 3.8 (Iversen and Jessen, 1977) to 12.9 g/m^2 (Welton, 1979) for G. pulex. Differences in annual production within a species may be due more to differences in population densities and recruitment rates than to growth rates of individuals (Marchant and Hynes, 1981). The difference in population density among the three shores in Dock Lake (Figure 5) is reflected in the variability in biomass, production and P/$\bar{B}$ ratios (Tables 4 and 6).

The P/$\bar{B}$ ratios listed in Table 7 suggest divergence between cohort G and the P/$\bar{B}$ ratio for H. azteca. The higher values for the cohort and daily G methods as compared to the size frequency method in Tables 4 and 6 support this hypothesis. Therefore, the production estimate for West Blue Lake may be an overestimate, as the cohort G of 4.6 from the Dock Lake data was used to calculate it. This was deemed applicable to the West Blue population because the size frequency histograms in Biette (1969) indicated a maximum

size similar to the Dock Lake population.

The close agreement between annual production and $P/\bar{B}$ ratios for 1980, 1981 and the 1980 cohort values (Tables 4 and 6) supports the hypothesis that H. azteca is univoltine, since the annual and cohort $P/\bar{B}$ ratios are the same. In a bivoltine species, the annual $P/\bar{B}$ ratio is twice as high as the cohort value (Waters, 1979). In addition, this agreement further validates the accuracy and usefulness of the size frequency method in analyzing populations with overlapping cohorts.

Several error factors may have contributed to the greater production value for 1981 than 1980, despite the warmer temperature regime of the latter year. Considerable biomass may have been lost in the sugar flotation of early 1980 Typha samples, which would contribute to low weighted mean production. In both years, the earliest samples were slightly lower than subsequent ones despite the fact that no reproduction had occurred. This suggests that in spring, there is a gradual onshore movement of animals. The second sample captured more animals than the first, and as a result, biomass was underestimated twice in 1980 (early spring 1980 and 1981; the estimates are calculated from ice-out to ice-out) and only once in 1981 (since the spring 1982 "sample" is an approximation); thus the 1981 production estimate would be larger than the 1980 estimate.

These error factors are slight when compared to the

effects of sampling error. Standard errors of the mean numbers

of adults and juveniles per sample usually ranged from one half

to one and one half times the mean. Hence differences between

1980 and 1981 are probably attributable to sampling error, which

is normally the largest error factor in any production estimate

(Marchant and Hynes, 1981; Waters, 1979).

Temperature is an important factor in the life history of

benthic invertebrates (see Hynes, 1970; Lehmkuhl, 1979), because

it influences features such as growth, voltinism and length of

aquatic life, which are all critical to secondary production

(Waters, 1979). Hyalella azteca is very temperature sensitive

(Geisler, 1944; Cooper, 1965; de March, 1978). Table 7 compares

annual production, biomass, and P/B̄ ratios of four populations of

this amphipod. Figure 7 illustrates the relationship of temperature

to these production and biomass data in two ways; the number of

days that the water temperature of the habitat being sampled is above

$10^{o}C$ (D10) and $20^{o}C$ (D20). The former is an interaction of climate

and lake morphometry, and is a factor limiting the geographic

range of H. azteca (Bousfield, 1958). The latter temperature

range measures the length of optimal growth conditions for this

amphipod (Cooper, 1965; de March, 1978). Table 8 lists the

regression equations and correlation coefficients for Figure 7.

In both Marion Lake and West Blue Lake, temperatures

exceed $20^{o}C$ during less than two weeks of the year. Production

values of just over 1 g/m^2 have been reported for both lakes (Mathias,

TABLE 7: Comparison of dry mass annual production (P), annual biomass ($\bar{B}$) in grams per square meter, and P/$\bar{B}$ ratios for four populations of Hyalella azteca. The asterisk indicates an extrapolation from the wet weight mean annual biomass given in Biette (1969). This value was divided by 6 to convert to dry weight (Waters, 1977), then multiplied by the cohort G (= P/$\bar{B}$) of 4.6 obtained in this study.

Location	P	$\bar{B}$	P/$\bar{B}$	Reference
Dock Lake, Ontario	1.23	0.32	3.9	Cooper (1965) IN Waters (1977)
Sugarloaf Lake, Michigan	1.93	0.40	4.8	Mathias (1971)
Marion Lake, British Columbia	1.15	0.27	4.2	
West Blue Lake, Manitoba	1.20*	0.26	(4.6)	Biette (1969)*
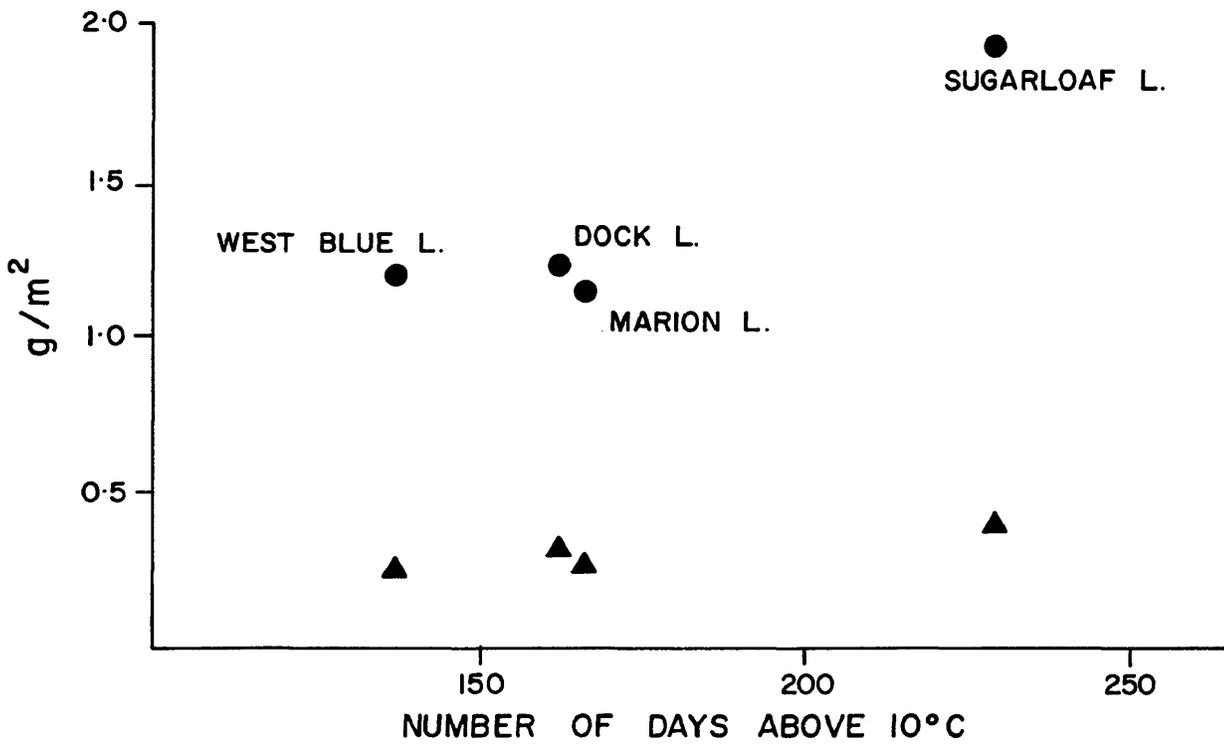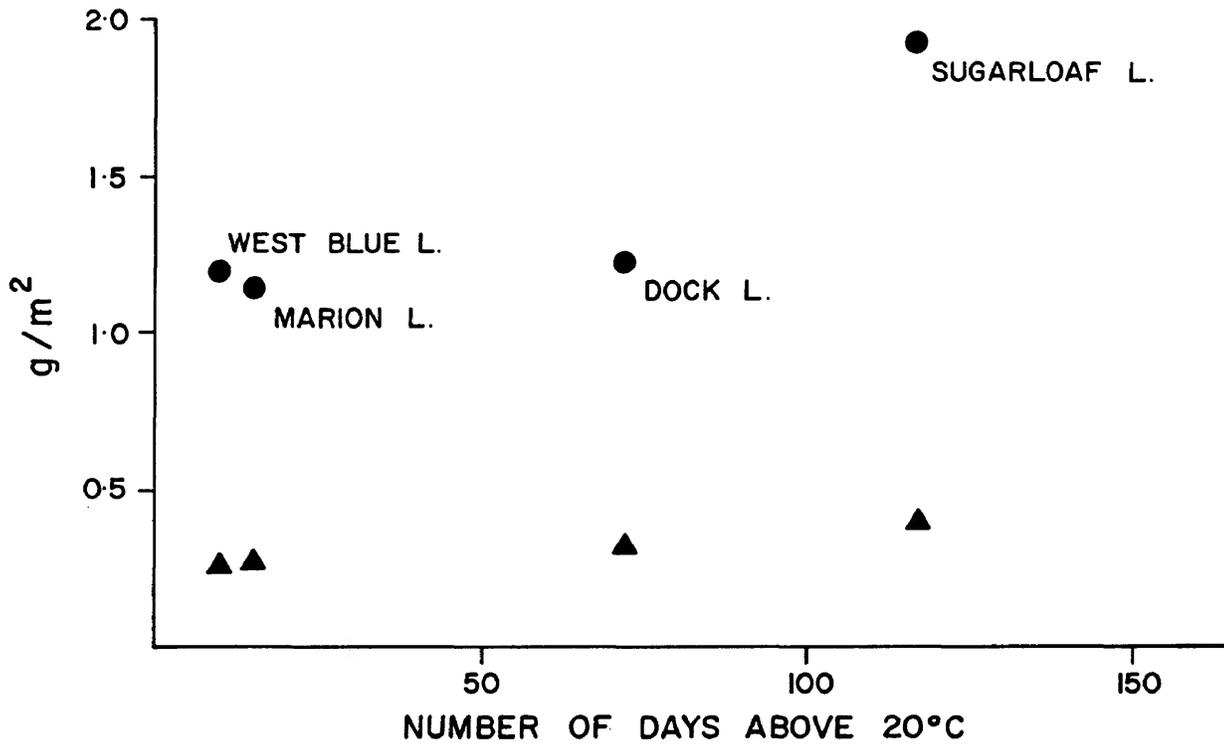
FIGURE 7: Interaction of climate with production (circles)

and biomass (triangles) in g/m^2 dry weight of

Hyalella azteca in four temperate zone lakes.

Number of days above 20°C reflects optimal growth

conditions; number of days above 10°C is an

interaction of climate and lake morphometry.

TABLE 8: Regression equations and correlation coefficients for the effect of climate on production and biomass of Hyalella azteca in four lakes. The variables are: annual production (P), and mean annual biomass ($\bar{B}$) in g/m^2 dry weight. D10 and D20 are the number of days the sampled habitat experiences temperatures exceeding 10°C and 20°C respectively. These latter figures are estimated from the temperature data included in the four studies of H. azteca.

REGRESSION

CORRELATION COEFFICIENTS

Number	Variables	Equation	Pearson	Kendal	Spearman
.	P,D10	P = -0.151 + 0.009 D10	0.93	0.33	0.40
2	P,D20	P = 1.040 + 0.006 D20	0.87	0.67	0.80
3	$\bar{B}$,D10	$\bar{B}$ = 0.048 + 0.002 D10	0.93	0.67	0.80
4	$\bar{B}$,D20	$\bar{B}$ = 0.246 + 0.001 D20	0.98	1.00	1.00

1971; Biette, 1969); the intercept of equation 2 (D20 = 0),ie, no optimal growth time, predicts production of approximately 1 g/m^2. The intercept of equation 1 (the D10 regression) is just below zero. No growth of young occurs at 10°C (Cooper, 1965), supporting the hypothesis that H. azteca cannot tolerate habitats with temperature regimes below 10°C. The effect of temperature could modify voltinism; arctic individuals probably require several years to complete development (see Butler, 1982), whereas tropical individuals could be multivoltine.

Brylinsky (1980) states that although biomass may be the same in lakes with long and short growing seasons (ie, in low and high latitudes), the number of generations produced, and therefore the amount of production per unit of biomass, increases with the length of growing season. Figure 7 supports this concept, with biomass remaining relatively constant in the four lakes, while production varies with season length. Biomass, however, seems strongly related to habitat quality (particularly the amount and type of food) within the lake. Mean annual biomass differed noticeably among the three shores in Dock Lake (Table 4), despite almost identical temperature regimes (Figure 2). In H. azteca, biomass is apparently temperature independent, while production is temperature dependent.

Comparison of Methods

Each method used in this study (Table 6) had characteristics

that recommended its use for comparison to the others. The size

frequency method is applicable where cohorts cannot readily be

distinguished (Waters, 1977). The removal summation method

apparently gives the most accurate estimates for a variety of

growth curves and sampling regimes (Cushman, Shugart, Hildebrand

and Elwood, 1978). The cohort G is the simplest, and provides a

check on the P/$\bar{B}$ ratio (Waters, 1981). Daily G is a graphical

method, useful when field and/or lab growth measurements are not

available, and can illustrate voltinism (see Hall, Waters and

Cook, 1980). The instantaneous growth method, and its graphical

equivalent, the Allen curve, are used for populations with

identifiable cohorts (Waters, 1977; Benke and Waide, 1977).

Gillespie and Benke (1979) recommend use of a hand-smoothed Allen

curve when sampling error is large (as in this study), and show

that removal summation and increment summation equations are equal

to an Allen curve estimate made by connecting the data points

with straight lines. The difference between the removal summation

and straight-line Allen curve estimates in Table 6 are probably due

to sampling variability and overlapping broods.

Waters (1981) justifies the use of the size frequency

method as a standard in the study of G. pseudolimnaeus. As H. azteca

is also a univoltine benthic amphipod with continuous reproduction

over the optimal growth season, these same criteria apply. In

studies which use more than one method, the size frequency estimate

generally gives a slightly higher result than the Allen curve, instantaneous growth or removal summation methods (see Waters and Hokenstrom, 1980; Wildish and Peer, 1981). However, the cohort G and daily G methods compare with or even exceed size frequency estimates (see Waters, 1981; and Table 6). This may be due to deviations of cohort G from the cohort P/$\bar{B}$ ratio, caused by variations in growth patterns and population densities (Waters, 1969).

In the comparison of cohort production by seven methods (Table 6), the lowest value is given by the instantaneous growth method. Cushman et al (1978) state that when the assumption of exponential growth is violated, production is underestimated by this method. Since the growth curve for H. azteca (Figure 6) is more or less linear, this may be the case in this study. The removal summation and size frequency methods assume linear growth, and may therefore be more accurate for this amphipod. The effect of prolonged recruitment is evident in Appendix D: 8; the Allen curves do not exhibit the expected smooth decline from high density/low mean weight to low density/high mean weight (Waters, 1969).

The extended presence of newly hatched animals in the population, and mortality of large adults before smaller ones of the same age, lower the mean weights calculated from the samples, and result in a great many negative values within the instantaneous growth and removal summation calculations (see Appendix D). The

size frequency method is not affected by this, since weights are
calculated from the length-weight regression rather than field data;
however it is subject, as are all other methods, to the effect
of sampling error on mean numbers. The variety of methods avail-
able, and their differing applications, suggest that if the data
are available, several methods of production estimation should
be used. For Hyalella azteca, the size frequency and removal
summation methods are probably the most useful and accurate.

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APPENDIX

Appendix A: 1   Relationship of antennal segment count
to total length (top) and head length
(bottom) for Hyalella azteca in Dock
Lake. In both, n = 358.   (73)

          2   Relationship of head length (mm x 10^{-2})
to total length (mm) of Hyalella azteca
in Dock Lake.   (75)

          3   Relationship of female total length (mm)
to brood count of Hyalella azteca in
Dock Lake.   (77)

Appendix B: 1   Size frequency histograms for Hyalella
azteca on the Carex shore of Dock Lake
in 1980 and 1981. Eleven of the 24
samples from 1980 are so arranged that
the dates corresponded as closely as
possible with the 1981 samples, for
comparison. Vertical scale: size classes
1 - 13, horizontal scale: 1 mm = 5%.   (79)

          2   Size frequency histograms for Hyalella
azteca on the Typha shore of Dock Lake
in 1980 and 1981. As in B: 1.   (81)

          3   Size frequency histograms for Hyalella
azteca on the Gravel shore of Dock
Lake in 1980 and 1981. As in B: 1.   (83)

Appendix C: 1   Size frequency estimate of annual pro-
duction for Hyalella azteca on the Carex
shore of Dock Lake (1980). The times
loss factor has been reduced from 13 to
12 to compensate for the minimal con-
tribution by size class 13. These
calculations are from May 1980 to May 1981. (85)

APPENDIX (Continued)

Appendix C: 2   Size frequency estimate of annual
production for $\underline{H}$. $\underline{azteca}$ on the $\underline{Typha}$
shore of Dock Lake (1980). As in C: 1.   (86)

                3   Size frequency estimate of annual
production for $\underline{H}$. $\underline{azteca}$ on the Gravel
shore of Dock Lake (1980). As in C: 1.   (87)

                4   Size frequency estimate of annual
production for $\underline{H}$. $\underline{azteca}$ on the $\underline{Carex}$
shore of Dock Lake (1981). These
calculations are from May 1981 to an
estimated sample for May, 1982.   (88)

                5   Size frequency estimate of annual
production for $\underline{H}$. $\underline{azteca}$ on the $\underline{Typha}$
shore of Dock Lake (1981). As in C: 4.   (89)

                6   Size frequency estimate of annual
production for $\underline{H}$. $\underline{azteca}$ on the Gravel
shore of Dock Lake (1981). As in C: 4.   (90)

Appendix D: 1   Calculation of production of $\underline{Hyalella}$
$\underline{azteca}$ on the $\underline{Carex}$ shore, Dock Lake,
by the instantaneous growth method.
G = instantaneous rate of growth, B =
standing crop, < B > = mean standing
crop over interval, P = production over
interval between successive sampling dates.
Values are rounded from the full number
of decimal places carried in the original
calculations.   (91)

                2   Calculation of production of $\underline{H}$. $\underline{azteca}$ on
the $\underline{Typha}$ shore, Dock Lake, by the
instantaneous growth method. Calculated
as in Table D: 1.   (92)

APPENDIX (Continued)

Appendix D: 3 Calculation of production of $\underline{H}$. $\underline{azteca}$
on the Gravel shore, Dock Lake, by the
instantaneous growth method. Calculated
as in Table D: 1.   (93)

4 Calculation of production of $\underline{Hyalella}$
$\underline{azteca}$ on the $\underline{Carex}$ shore, Dock Lake
(1980 cohort) by the removal summation
method. B = standing crop for each
sample, Weight at loss is the geometric
mean of the mean weights of two con-
secutive samples.   (94)

5 Calculation of production of $\underline{Hyalella}$
$\underline{azteca}$ on the $\underline{Typha}$ shore, Dock Lake
(1980 cohort) by the removal summation
method. As in Appendix D: 4.   (95)

6 Calculation of production of $\underline{Hyalella}$
$\underline{azteca}$ on the Gravel shore, Dock Lake
(1980 cohort) by the removal summation
method. As in Appendix D: 4.   (96)

7 Cohort production for $\underline{Hyalella}$ $\underline{azteca}$
on three shores in Dock Lake, by the
daily growth method.   (97)

8 Cohort production for $\underline{Hyalella}$ $\underline{azteca}$
on three shores in Dock Lake, by the
Allen curve method. Each Allen curve
was constructed two ways; a hand drawn
smoothed line (solid line) and straight
lines between data (dotted line).   (99)
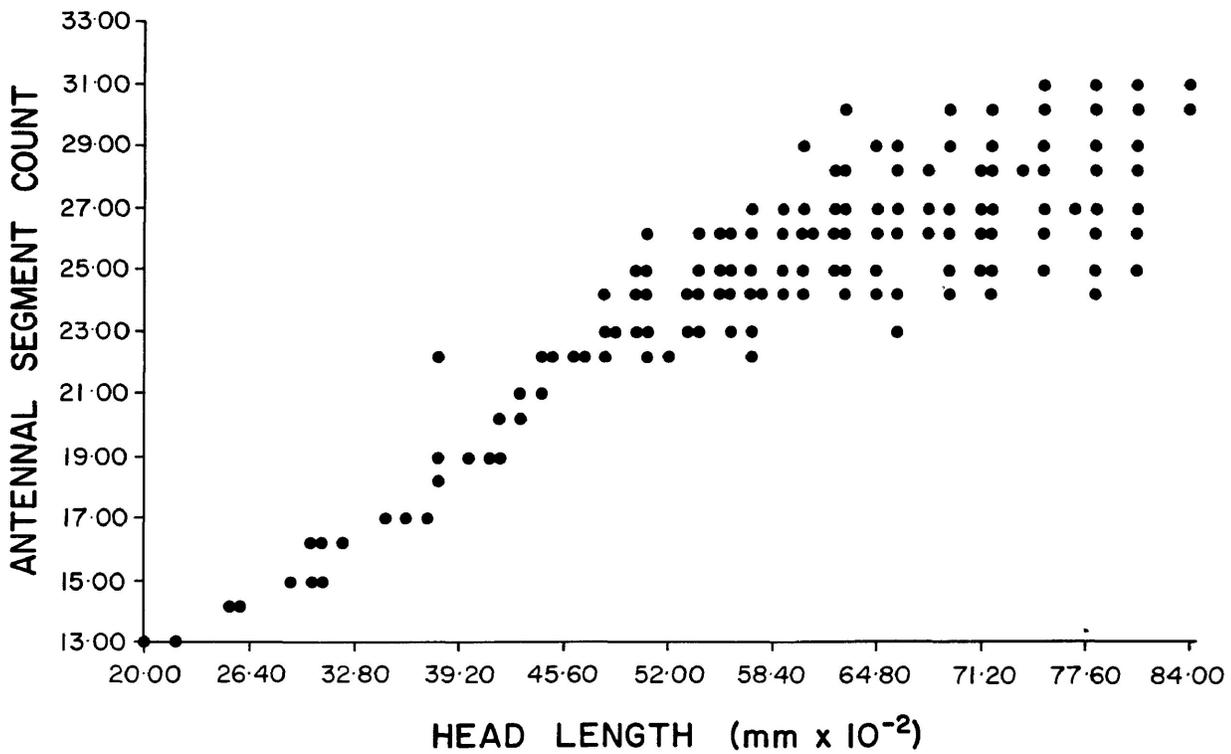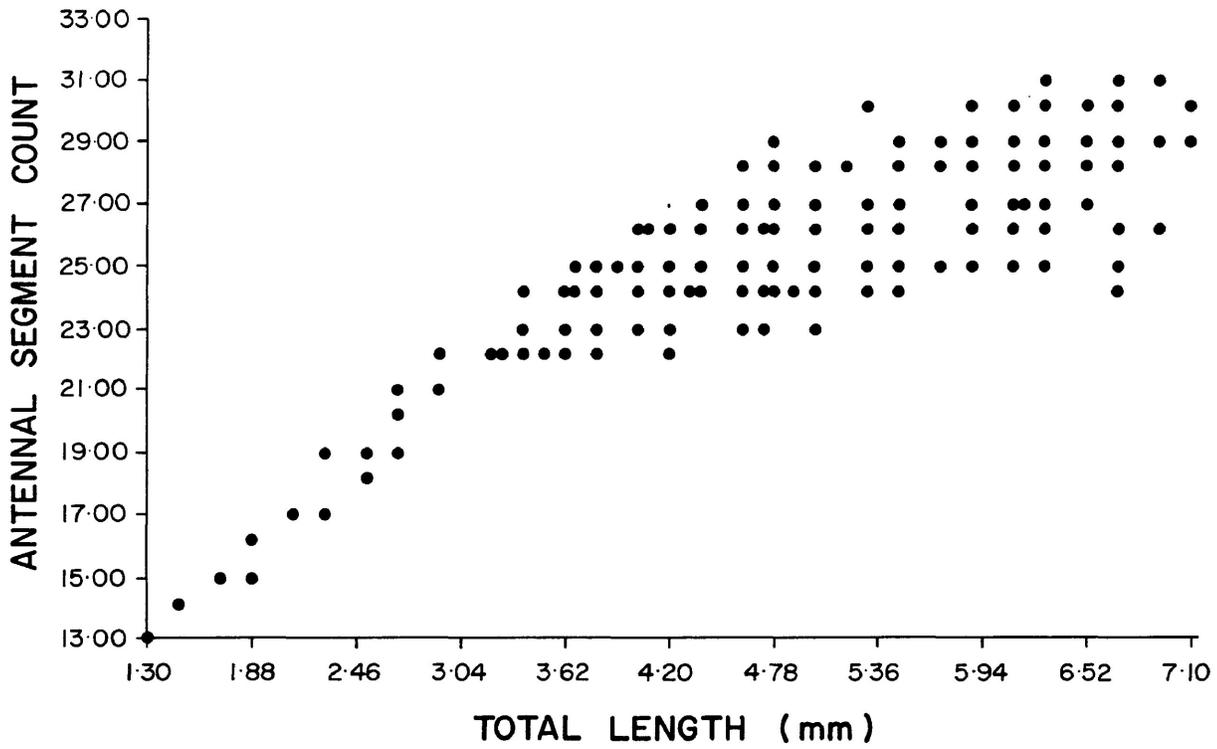
APPENDIX A: 1 Relationship of antennal segment count to

total length (top) and head length (bottom)

for _Hyalella_ _azteca_ in Dock Lake. In both,

n = 358.

HEAD LENGTH (mm x 10⁻²) vs TOTAL LENGTH (mm)

APPENDIX A: 2 Relationship of head length (mm x 10^{-2}) to total length (mm) of <u>Hyalella</u> <u>azteca</u> in Dock Lake.
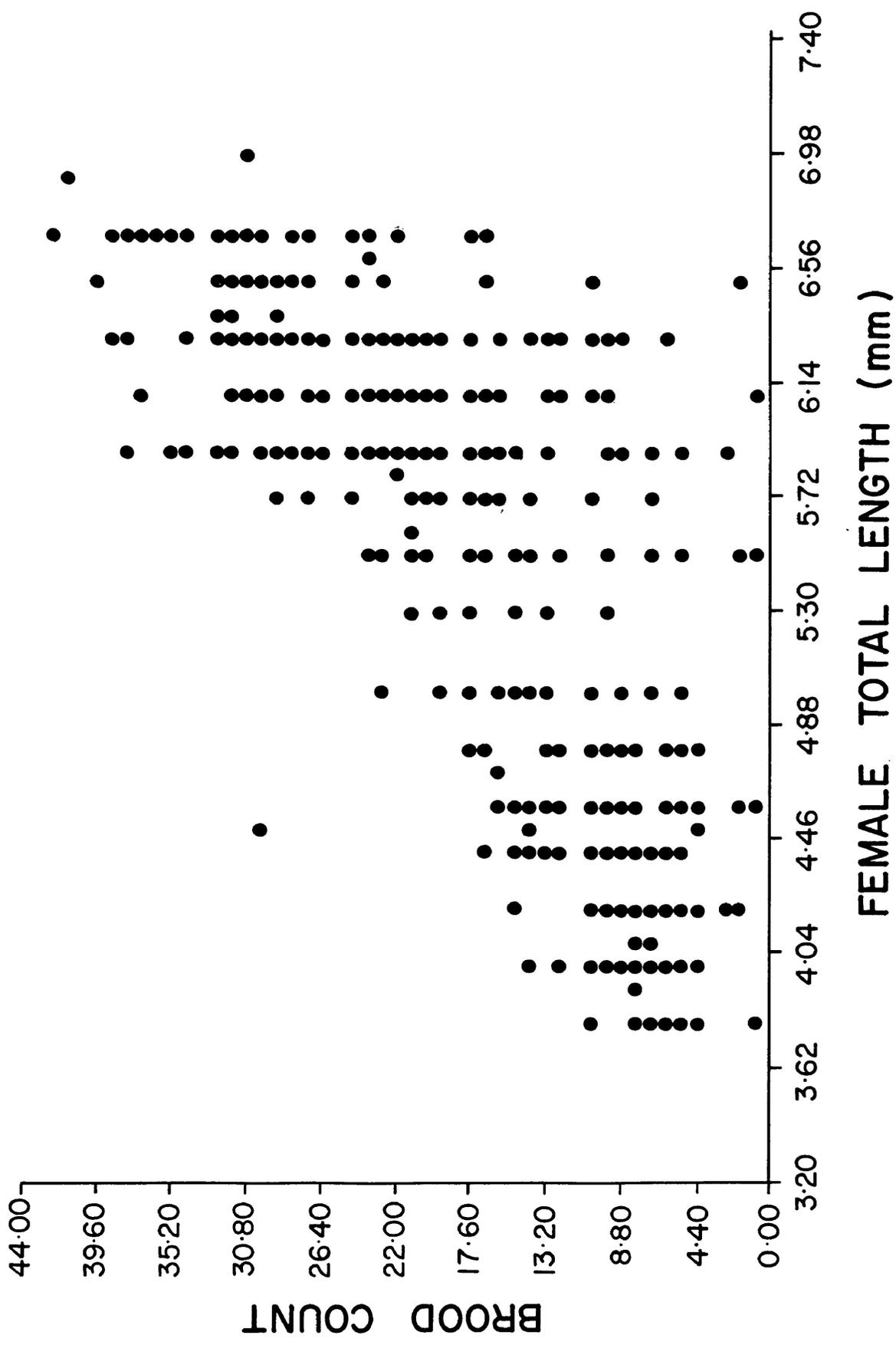
APPENDIX A: 3 Relationship of female total length (mm)

to brood count of <u>Hyalella</u> <u>azteca</u> in

Dock Lake.

CAREX 1980
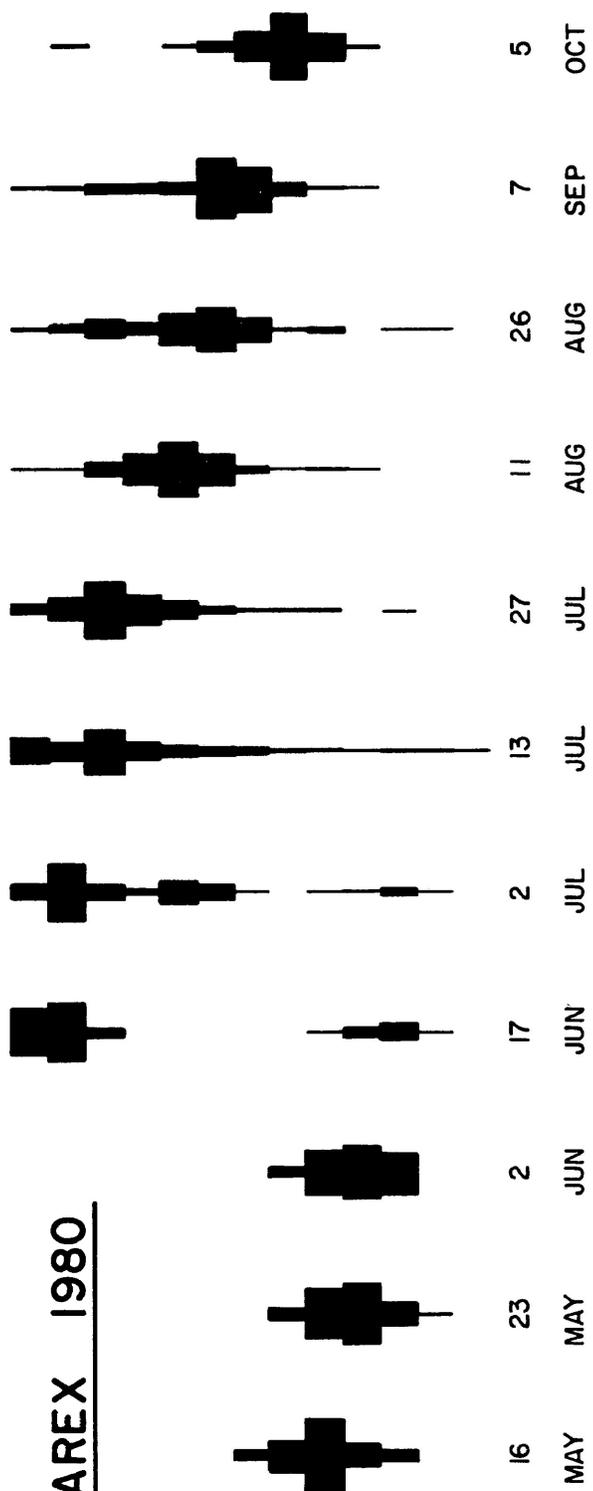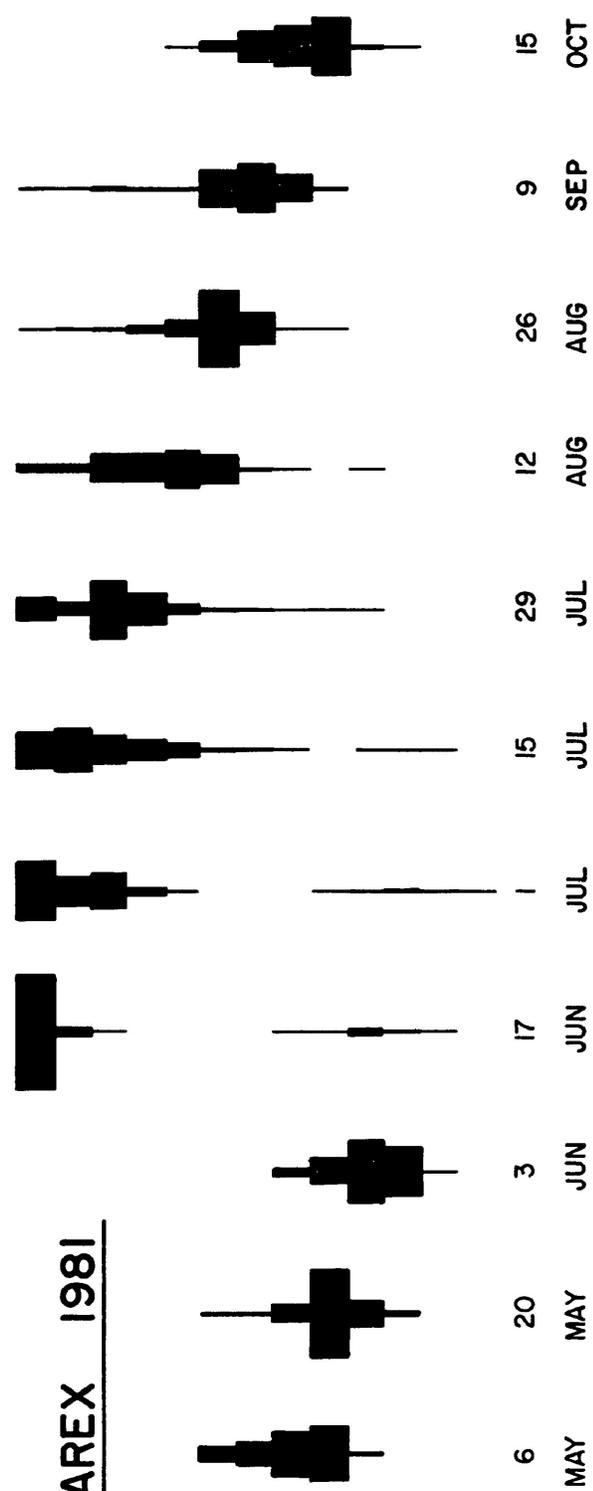
MAY 16 | MAY 23 | JUN 2 | JUN 17 | JUL 2 | JUL 13 | JUL 27 | AUG 11 | AUG 26 | SEP 7 | OCT 5

CAREX 1981

MAY 6 | MAY 20 | JUN 3 | JUN 17 | JUL 1 | JUL 15 | JUL 29 | AUG 12 | AUG 26 | SEP 9 | OCT 15

APPENDIX B: 1 Size frequency histograms for <u>Hyalella</u> <u>azteca</u> on the <u>Carex</u> shore of Dock Lake in 1980 and 1981. Eleven of the 24 samples from 1980 are so arranged that the dates corresponded as closely as possible with the 1981 samples, for comparison. Vertical scale: size classes 1 - 13, horizontal scale: 1 mm = 5%.

TYPHA 1980

16 MAY 23 MAY 2 JUN 17 JUN 2 JUL 13 JUL 27 JUL 11 AUG 26 AUG 7 SEP 5 OCT

TYPHA 1981

6 MAY 20 MAY 3 JUN 17 JUN 1 JUL 15 JUL 29 JUL 12 AUG 26 AUG 9 SEP 15 OCT
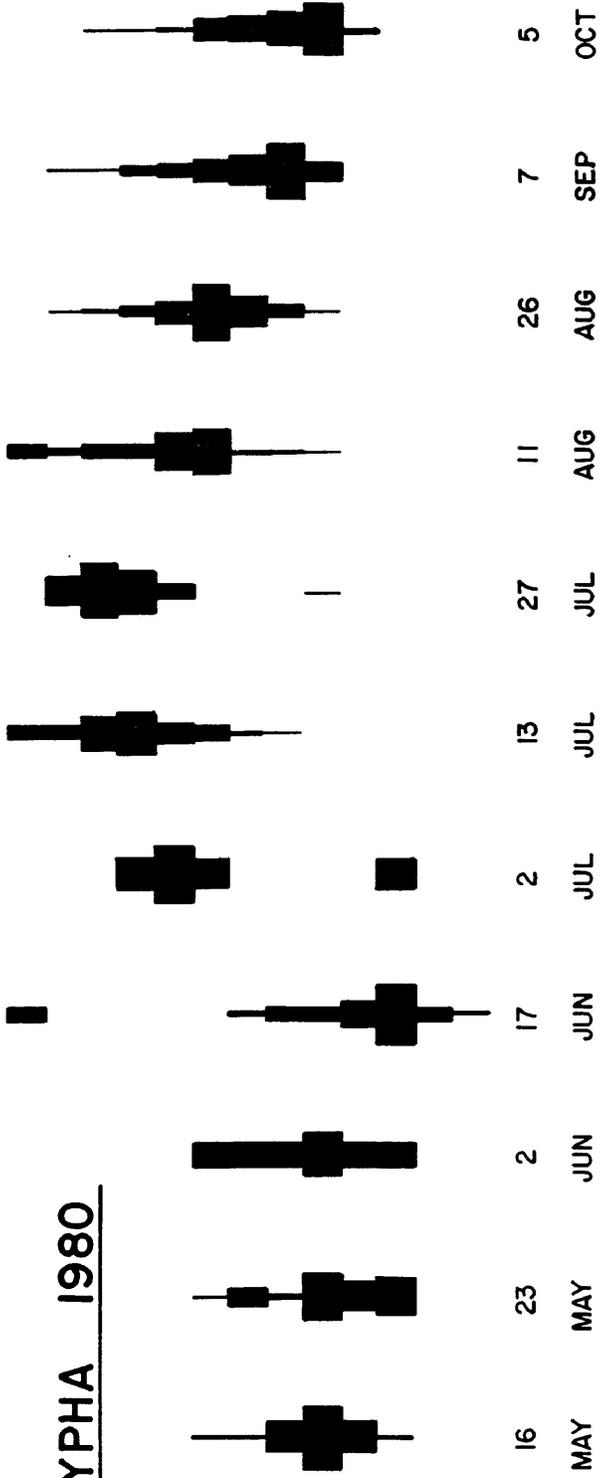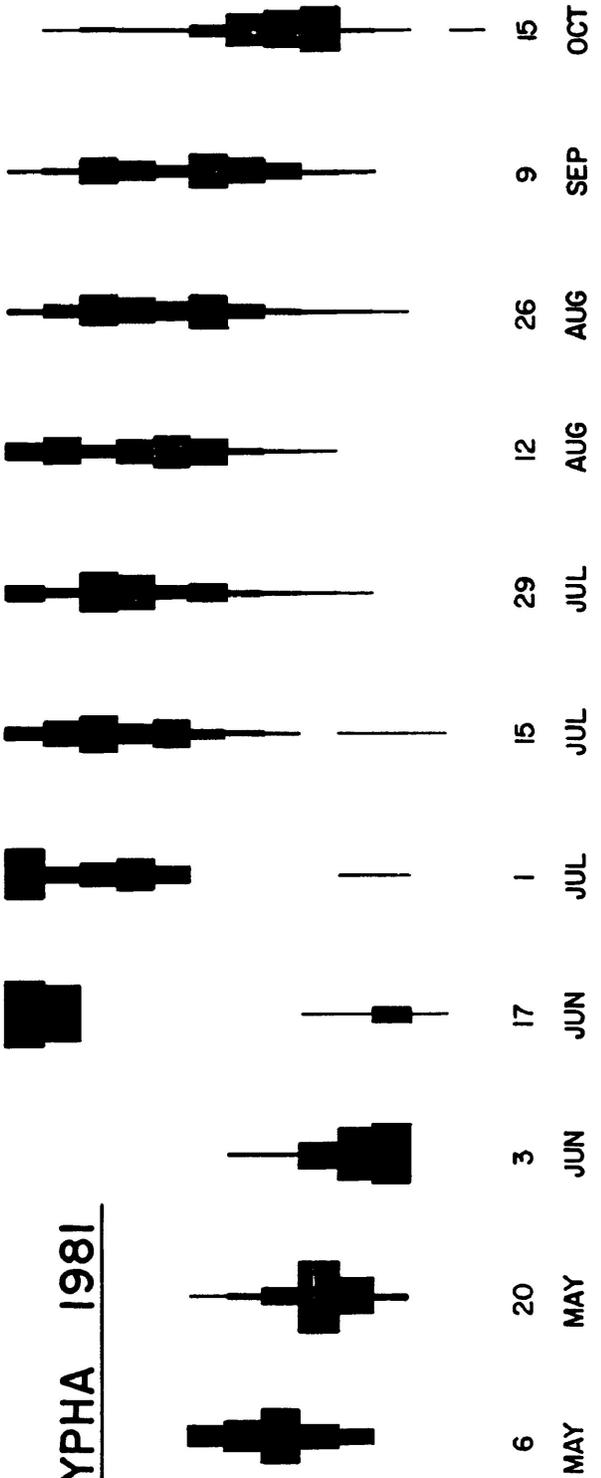
APPENDIX B: 2 Size frequency histograms for <u>Hyalella</u> <u>azteca</u>

on the <u>Typha</u> shore of Dock Lake in 1980 and

1981. As in B: 1.

GRAVEL 1980

16 MAY · 23 MAY · 2 JUN · 17 JUN · 2 JUL · 13 JUL · 27 JUL · 11 AUG · 26 AUG · 7 SEP · 5 OCT

GRAVEL 1981

6 MAY · 20 MAY · 3 JUN · 17 JUN · 1 JUL · 15 JUL · 29 JUL · 12 AUG · 26 AUG · 9 SEP · 15 OCT
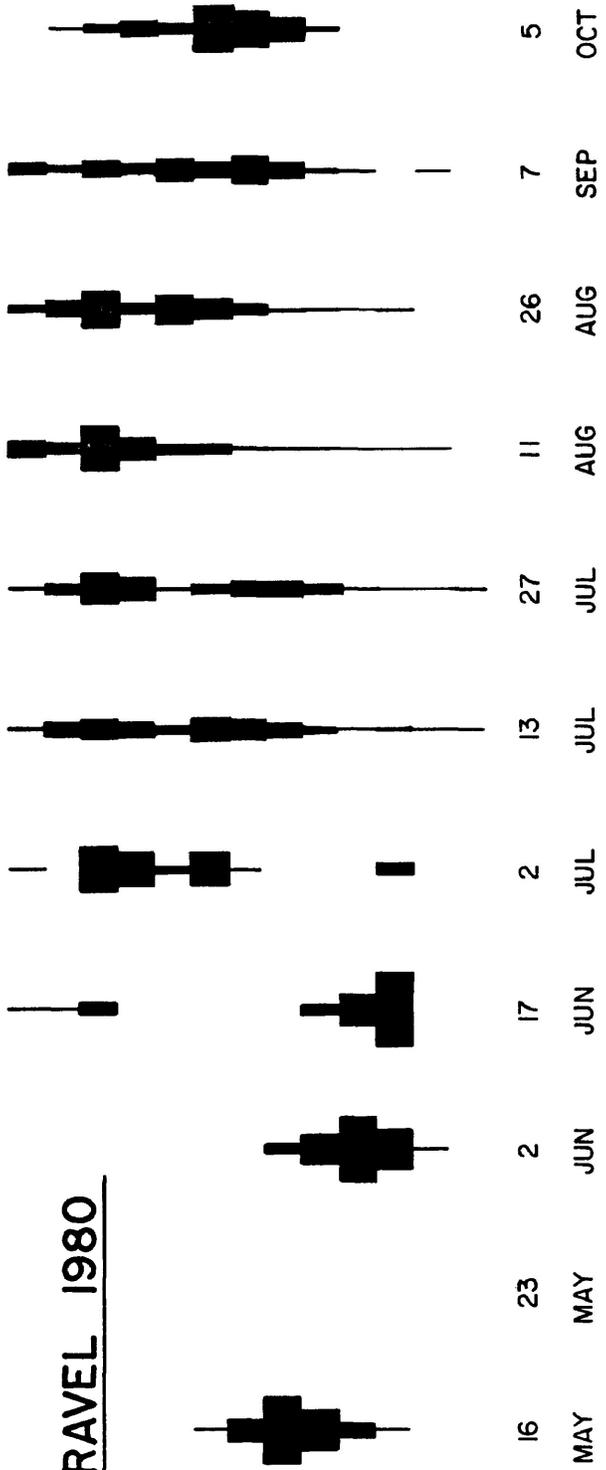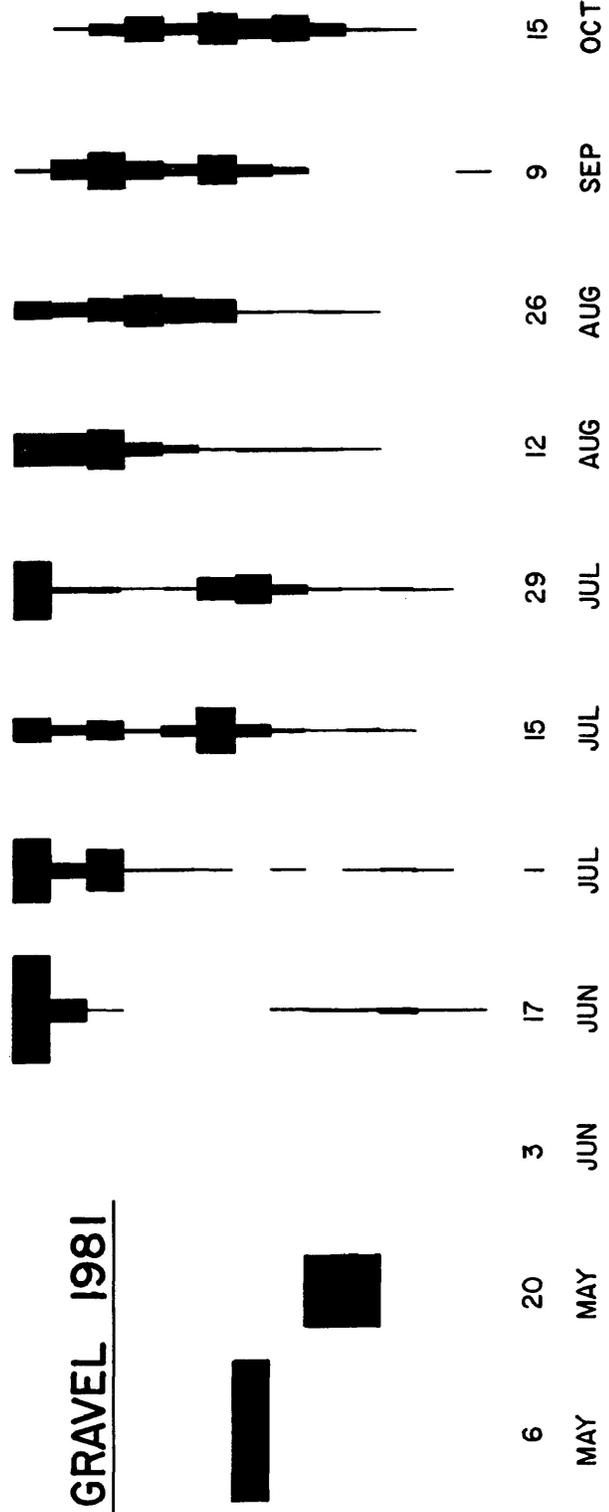
APPENDIX B: 3 Size frequency histograms for <u>Hyalella azteca</u>

on the Gravel shore of Dock Lake in 1980 and

1981. As in B: 1.

APPENDIX C: 1 Size frequency estimate of annual production for Hyalella azteca on the Carex shore of Dock Lake (1980). The times loss factor has been reduced from 13 to 12 to compensate for the minimal contribution by size class 13. These calculations are from May 1980 to May 1981.

SIZE CLASS	ANNUAL AV. NO. PER M²	NUMBER LOST	MEAN WEIGHT (G/INDIVIDUAL)	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION (G/M²/YEAR)
1	149.405	-16.436	0.000015	0.000023	-0.000377	
2	165.841	-60.017	0.000035	0.000049	-0.002949	
3	225.858	38.554	0.000069	0.000091	0.003494	
4	187.304	-91.915	0.000119	0.000150	-0.013748	
5	279.220	51.295	0.000188	0.000229	0.011769	
6	227.924	83.495	0.000280	0.000330	0.027556	
7	144.429	23.279	0.000389	0.000460	0.010718	
8	121.150	21.643	0.000545	0.000628	0.013595	
9	99.508	60.527	0.000724	0.000825	0.049906	
10	38.981	-0.312	0.000939	0.001058	-0.000330	
11	39.293	32.671	0.001192	0.001331	0.043497	
12	6.622	5.432	0.001487	0.001648	0.008953	
13	1.190	1.190	0.001827	0.001827	0.002174	
TOTAL					0.154257	

FINAL CALCULATIONS   12. x 365./365. x 0.154257 = 1.851

APPENDIX C: 2 Size frequency estimate of annual production for H. azteca on the Typha shore of Dock Lake (1980). As in C: 1.

SIZE CLASS	ANNUAL AV. NO. PER M^2	NUMBER LOST	MEAN WEIGHT (G/INDIVIDUAL)	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION ($G/M^2/YEAR$)
1	6.692	-2.954	0.000015	0.000023	-0.000068	
2	9.647	-7.885	0.000035	0.000049	-0.000387	
3	17.531	-7.643	0.000069	0.000091	-0.000693	
4	25.175	-17.068	0.000119	0.000150	-0.002553	
5	42.243	-73.430	0.000188	0.000229	-0.016847	
6	115.672	8.961	0.000280	0.000330	0.002957	
7	106.711	5.118	0.000389	0.000460	0.002357	
8	101.593	-23.996	0.000545	0.000628	-0.015073	
9	125.589	99.935	0.000724	0.000825	0.082398	
10	25.654	20.841	0.000939	0.001058	0.022049	
11	4.813	4.266	0.001192	0.001331	0.005680	
12	0.546	0.448	0.001487	0.001648	0.000738	
13	0.099	0.099	0.001827	0.001827	0.000181	
TOTAL					0.080739	

FINAL CALCULATIONS   12. × 365./365. × 0.080739 = 0.969

APPENDIX C: 3 Size frequency estimate of annual production for H. azteca on the Gravel shore of Dock Lake (1980). As In C: 1.

SIZE CLASS	ANNUAL AV. NO. PER M2	MEAN WEIGHT (G/INDIVIDUAL)	NUMBER LOST	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION (G/M2/YEAR)
1	27.683	0.000015	-4.199	0.000023	-0.000096	
2	31.882	0.000035	-36.642	0.000049	-0.001801	
3	68.524	0.000069	2.186	0.000091	0.000198	
4	66.338	0.000119	10.053	0.000150	0.001504	
5	56.285	0.000188	-83.014	0.000229	-0.019046	
6	139.300	0.000280	17.113	0.000330	0.005648	
7	122.187	0.000389	35.291	0.000460	0.016249	
8	86.896	0.000545	60.252	0.000628	0.037848	
9	26.644	0.000724	15.088	0.000825	0.012441	
10	11.556	0.000939	0.827	0.001058	0.000875	
11	10.729	0.001192	8.386	0.001331	0.011164	
12	2.343	0.001487	1.346	0.001648	0.002219	
13	0.997	0.001827	0.997	0.001827	0.001822	
TOTAL					0.069023	

FINAL CALCULATIONS   12. x 365./365. x 0.069023 = 0.828

APPENDIX C: 4 Size frequency estimate of annual production for H. azteca on the Carex shore of Dock Lake (1981). These calculations are from May 1981 to an estimated sample for May, 1982.

SIZE CLASS	ANNUAL AV. NO. PER M²	NUMBER LOST	MEAN WEIGHT (G/INDIVIDUAL)	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION (G/M²/YEAR)
1	379.797	195.255	0.000015	0.000023	0.004474	
2	184.543	-149.120	0.000035	0.000049	-0.007328	
3	333.663	143.551	0.000069	0.000091	0.013008	
4	190.112	46.910	0.000119	0.000150	0.007016	
5	143.202	-79.932	0.000188	0.000229	-0.018339	
6	223.134	-18.221	0.000280	0.000330	-0.006014	
7	241.355	18.465	0.000389	0.000460	0.008502	
8	222.890	-70.828	0.000545	0.000628	-0.044491	
9	293.718	246.416	0.000724	0.000825	0.203175	
10	47.302	21.556	0.000939	0.001058	0.022805	
11	25.746	22.228	0.001192	0.001331	0.029593	
12	3.518	2.923	0.001487	0.001648	0.004817	
13	0.595	0.595	0.001827	0.001827	0.001088	

TOTAL 0.218307

FINAL CALCULATIONS   12.   ×   365./365.   ×   0.218307   =   2.620

APPENDIX C: 5 Size frequency estimate of annual production for H. azteca on the Typha shore of Dock Lake (1981). As in C: 4.

SIZE CLASS	ANNUAL AV. NO. PER M²	NUMBER LOST	MEAN WEIGHT (G/INDIVIDUAL)	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION (G/M²/YEAR)
1	43.503	-3.569	0.000015	0.000023	-0.000082	
2	47.072	-34.288	0.000035	0.000049	-0.001685	
3	81.360	10.494	0.000069	0.000091	0.000951	
4	70.866	11.911	0.000119	0.000150	0.001782	
5	58.955	-23.246	0.000188	0.000229	-0.005333	
6	82.201	-10.547	0.000280	0.000330	-0.003481	
7	92.748	5.365	0.000389	0.000460	0.002470	
8	87.382	-16.616	0.000545	0.000628	-0.010437	
9	103.998	92.008	0.000724	0.000825	0.075862	
10	11.990	6.508	0.000939	0.001058	0.006886	
11	5.482	5.179	0.001192	0.001331	0.006895	
12	0.303	-0.872	0.001487	0.001648	-0.001438	
13	1.175	1.175	0.001827	0.001827	0.002148	
TOTAL					0.074537	
FINAL CALCULATIONS				12. × 365./365. ×	0.074537	0.894

APPENDIX C: 6   Size frequency estimate of annual production for H. azteca on the Gravel shore of
Dock Lake (1981). As in C: 4.

SIZE CLASS	ANNUAL AV. NO. PER M²	NUMBER LOST	MEAN WEIGHT (G/INDIVIDUAL)	WEIGHT AT LOSS	TOTAL WEIGHT AT LOSS	PRODUCTION (G/M²/YEAR)
1	207.187	140.621	0.000015	0.000023	0.003222	
2	66.566	-19.612	0.000035	0.000049	-0.000964	
3	86.178	35.925	0.000069	0.000091	0.003255	
4	50.252	20.326	0.000119	0.000150	0.003040	
5	29.927	-44.575	0.000188	0.000229	-0.010227	
6	74.502	31.368	0.000280	0.000330	0.010352	
7	43.133	2.166	0.000389	0.000460	0.000997	
8	40.967	20.330	0.000545	0.000628	0.012770	
9	20.638	8.541	0.000724	0.000825	0.007043	
10	12.096	2.354	0.000939	0.001058	0.002490	
11	9.742	8.926	0.001192	0.001331	0.011883	
12	0.817	0.428	0.001487	0.001648	0.000705	
13	0.389	0.389	0.001827	0.001827	0.000710	
TOTAL					0.045278	

FINAL CALCULATIONS   12.   ×   365./365.   ×   0.045278   =   0.543

APPENDIX D: 1 Calculation of production of <u>Hyalella</u> <u>azteca</u> on the <u>Carex</u>
shore, Dock Lake, by the instantaneous growth method. G =
instantaneous rate of growth, B = standing crop, < B > =
mean standing crop over interval, P = production over
interval between successive sampling dates. Values below
are rounded from the full number of decimal places carried
in the original calculations.

DATE	Av.No./m^2	B (g/m^2)	Mean Weight (micrograms)	G	< B > (g/m^2)	P (g/m^2)
Jun 6/80	. 2089.0	0.0453	21.7			
				0.3172	0.0720	0.0228
Jun 17	3311.5	0.0987	29.8			
				0.5701	0.1069	0.0610
Jun 22	2183.2	0.1151	52.7			
				0.8492	0.3566	0.3029
Jun 27	4854.4	0.5982	123.2			
				-0.1908	0.4988	-0.0952
Jul 2	3923.0	0.3993	101.8			
				0.2013	0.3197	0.0644
Jul 7	1927.4	0.2400	124.5			
				-0.0596	0.4286	-0.0255
Jul 13	5261.5	0.6172	117.3			
				-0.3092	0.4410	-0.1364
Jul 17	3074.9	0.2649	86.1			
				0.4250	0.3615	0.1536
Jul 22	3479.4	0.4582	131.7			
				-0.1184	0.4939	-0.0585
Jul 27	4528.8	0.5297	117.0			
				0.2194	0.8621	0.1891
Aug 1	8199.3	1.1944	145.7			
				0.0715	1.9621	0.1403
Aug 6	17438.8	2.7298	156.5			
				0.2215	1.9018	0.4212
Aug 11	5498.0	1.0738	195.3			
				-0.0113	1.2230	-0.0138
Aug 16	7106.5	1.3722	193.1			
				0.1701	1.6606	0.2825
Aug 21	8514.9	1.9490	228.9			
				0.0854	1.6978	0.1450
Aug 26	5803.0	1.4465	249.3			
				0.1918	1.0069	0.1931
Aug 31	1878.6	0.5673	302.0			
				0.0386	0.7823	0.0302
Sep 7	3177.0	0.9974	313.9			
				0.0668	0.9003	0.0601
Sep 14	2393.8	0.8033	335.6			
				0.2486	0.6932	0.1723
Sep 21	1355.0	0.5831	430.3			
				0.1928	0.4268	0.0823
Oct 5	518.6	0.2706	521.8			
				0.0786	0.3042	0.0239
May 6/81	598.4	0.3378	564.5			
				0.2696	0.6934	0.1869
May 20	1419.1	1.0490	739.2			
				0.2824	0.8569	0.2420
Jun 3	678.2	0.6649	980.4			
				0.0414	0.5566	0.0230˙
Jun 17	438.8	0.4484	1021.8			
				0.1678	0.4258	0.0714
Jul 1	333.6	0.4032	1280.5			
				-0.0081	0.2106	-0.0017
Jul 15	15.1	0.0181	1198.7			
				-0.2394	0.0134	-0.0032
Jul 29	9.2	0.0087	943.5			
				-0.2648	0.0043	-0.0012
			724.0*			

Total Production = 2.5327

* estimated from length-weight regression

APPENDIX D: 2 Calculation of production of <u>H. azteca</u> on the <u>Typha</u> shore, Dock Lake, by the instantaneous growth method. Calculated as in Table D: 1.

DATE	Av.No./m²	B (g/m²)	Mean Weight (micrograms)	G	< B > (g/m²)	P (g/m²)
Jun 6/80	18.1	0.0004	23.2			
				-0.4314	0.0003	-0.0001
Jun 17	7.3	0.0001	15.1			
				1.2701	0.0067	0.0085
Jun 22	246.7	0.0132	53.7			
				0.3077	0.0179	0.0055
Jun 27	308.3	0.0225	73.0			
				0.9762	0.0127	0.0124
Jul 2	14.5	0.0028	193.8			
				-0.0256	0.0017	-0.0000
Jul 7	3.6	0.0007	188.9			
				-0.3412	0.0232	-0.0079
Jul 13	340.9	0.0458	134.3			
				0.0551	0.0270	0.0015
Jul 17	58.0	0.0082	141.9			
				-0.1510	0.0183	-0.0028
Jul 22	232.2	0.0283	122.0			
				-0.0952	0.0200	-0.0019
Jul 27	105.2	0.0117	110.9			
				0.3872	0.1768	0.0684
Aug 1	2092.5	0.3419	163.4			
				0.2854	0.3120	0.0891
Aug 6	1298.4	0.2822	217.4			
				-0.0589	0.1853	-0.0109
Aug 11	431.5	0.0884	204.9			
				0.1408	0.1371	0.0193
Aug 16	787.1	0.1857	235.9			
				0.0078	0.1907	0.0015
Aug 21	823.3	0.1957	237.8			
				0.2082	0.2359	0.0491
Aug 26	942.8	0.2760	292.8			
				0.0697	0.5251	0.0366
Aug 31	2466.1	0.7741	313.9			
				0.3507	0.4808	0.1686
Sep 7	420.7	0.1875	445.8			
				-0.0902	0.6182	-0.0558
Sep 14	2575.1	1.0488	407.3			
				0.1024	0.9189	0.0941
Sep 21	1748.6	0.7890	451.2			
				0.1914	0.8265	0.1582
Oct 5	1581.4	0.8640	546.4			
				-0.0114	0.4506	-0.0051
May 6/81	68.9	0.0372	540.2			
				0.3689	0.1683	0.0621
May 20	383.2	0.2994	781.2			
				0.2179	0.2096	0.0457
Jun 3	123.3	0.1198	971.4			
				0.1216	0.0837	0.0102
Jun 17	43.5	0.0477	1097.0			
				-0.0354	0.0277	-0.0010
Jul 1	7.3	0.0077	1058.9			
				0.1329	0.0116	0.0015
Jul 15	12.8	0.0155	1209.4			
				-0.2610	0.0095	-0.0025
Jul 29	3.8	0.0035	931.6			
				0.0079	0.0018	0.0000
			939.0*			

Total Production = 0.7442

*estimated from length-weight regression

APPENDIX D: 3 Calculation of production of $\underline{H}$. $\underline{azteca}$ on the Gravel shore,
Dock Lake, by the instantaneous growth method. Calculated
as in Table D: 1.·

DATE	Av.No./m²	B (g/m²)	Mean Weight (micrograms)	G	< B >	P (g/m²)
Jun 6/80	127.0	0.0027	20.9			
				0.8083	0.0017	0.0013
Jun 17	14.5	0.0007	46.9			
				0.4520	0.0249	0.0113
Jun 22	667.3	0.0492	73.7			
				0.5024	0.0712	0.0358
Jun 27	765.2	0.0932	121.8			
				0.2577	0.0553	0.0143
Jul 2	110.9	0.0175	157.6			
				0.3850	0.0684	0.0263
Jul 7	515.0	0.1193	231.6			
				0.0868	0.1475	0.0128
Jul 13	696.0	0.1758	252.6			
				0.2446	0.1628	0.0398
Jul 17	464.2	0.1498	322.6			
				-0.3594	0.1414	-0.0508
Jul 22	591.1	0.1331	225.2			
				0.1367	0.2337	0.0320
Jul 27	1294.5	0.3342	258.2			
				-0.3597	0.3248	-0.1168
Aug 1	1749.7	0.3153	180.2			
				0.2578	0.2388	0.0616
Aug 6	696.4	0.1624	233.2			
				-0.4540	0.2243	-0.1018
Aug 11	1932.9	0.2863	148.1			
				0.2969	0.4041	0.1200
Aug 16	2618.5	0.5220	199.3			
				-0.1756	0.3022	-0.0531
Aug 21	493.1	0.0824	167.2			
				0.0765	0.2006	0.0154
Aug 26	1766.2	0.3188	180.5			
				-0.0022	0.1934	-0.0004
Aug 31	377.2	0.0679	180.1			
				0.4438	0.1353	0.0601
Sep 7	722.3	0.2028	280.7			
				-0.0456	0.1218	-0.0055
Sep 14	152.4	0.0409	268.2			
				0.4838	0.1051	0.0508
Sep 21	389.1	0.1693	435.1			
				-0.2635	0.4241	-0.1118
Oct 5	2031.0	0.6790	334.3			
				0.1585	0.3402	0.0539
May 6/81	3.6	0.0014	391.7			
				0.7507	0.0098	0.0073
May 20	21.8	0.0181	829.8			
				0.1236	0.0090	0.0011
Jun 3	0.0	0.0000	939.0*			
				0.1086	0.1536	0.0167
Jun 17	293.6	0.3073	1046.7			
				0.1108	0.2004	0.0222
Jul 1	80.0	0.0936	1169.4			
				-0.1541	0.0552	-0.0085
Jul 15	16.9	0.0169	1002.4			
				0.1514	0.0254	0.0038
Jul 29	29.0	0.0338	1166.2			
				0.0219	0.0169	0.0004
			1192.0*			

Total Production   =   0.1380

*estimated from length-weight regression

APPENDIX D: 4 Calculation of production of Hyalella azteca on the Carex
shore, Dock Lake (1980 cohort) by the removal summation
method. B = standing crop for each sample, Weight at loss is
the geometric mean of the mean weights of two consecutive
samples.

DATE	Av.No./m^2	B (g/m^2)	Mean Weight (micrograms)	Number Lost (per m^2)	Weight at loss ($g \times 10^{-4}$)	Weight Loss (g/m^2)
Jun 6/80	2089.0	0.0453	21.7			
				-1222.5	0.0254	-0.0311
Jun 17	3311.5	0.0987	29.8			
				1128.3	0.0396	0.0447
Jun 22	2183.2	0.1151	52.7			
				-2671.2	0.0806	-0.2152
Jun 27	4854.4	0.5982	123.2			
				931.4	1.1199	0.1043
Jul 2	3923.0	0.3993	101.8			
				1995.6	1.1258	0.2247
Jul 7	1927.4	0.2400	124.5			
				-3334.1	1.2085	-0.4029
Jul 13	5261.5	0.6172	117.3			
				2186.6	1.0050	0.2197
Jul 17	3074.9	0.2649	86.1			
				-404.5	1.0649	-0.0431
Jul 22	3479.4	0.4582	131.7			
				-1049.4	1.2413	-0.1303
Jul 27	4528.8	0.5297	117.0			
				-3670.5	1.3056	-0.4792
Aug 1	8199.3	1.1944	145.7			
				-9239.5	1.5100	-1.3952
Aug 6	17438.8	2.7298	156.5			
				11940.8	1.7483	2.0876
Aug 11	5498.0	1.0738	195.3			
				-1608.5	1.9420	-0.3124
Aug 16	7106.5	1.3722	193.1			
				-1408.4	2.1024	-0.2961
Aug 21	8514.9	1.9490	228.9			
				2711.9	2.3888	0.6478
Aug 26	5803.0	1.4465	249.3			
				3924.4	2.7439	1.0768
Aug 31	1878.6	0.5673	302.0			
				-1298.4	3.0789	-0.3998
Sep 7	3177.0	0.9974	313.9			
				783.2	3.2457	0.2542
Sep 14	2393.8	0.8033	335.6			
				1038.8	3.8001	0.3948
Sep 21	1355.0	0.5831	430.3			
				836.4	4.7385	0.3963
Oct 5	518.6	0.2706	521.8			
				-79.8	5.4273	-0.0433
May 6/81	598.4	0.3378	564.5			
				-820.7	6.4597	-0.5302
May 20	1419.1	1.0490	739.2			
				740.9	8.5130	0.6307
Jun 3	678.2	0.6649	980.4			
				239.4	10.0088	0.2396
Jun 17	438.8	0.4484	1021.8			
				105.2	11.1124	0.1169
Jul 1	333.6	0.4032	1280.5			
				318.5	12.0359	0.3833
Jul 15	15.1	0.0181	1198.7			
				5.9	10.6347	0.0063
Jul 29	9.2	0.0087	943.5			
				9.2	8.2650	0.0076
			724.0*			

Total Production = 2.5567

*estimated from length-weight

APPENDIX D: 5 Calculation of production of Hyalella azteca on the Typha shore, Dock Lake (1980 cohort) by the removal summation method. As in Appendix D: 4.

DATE	Av.No./m²	B (g/m²)	Mean Weight (micrograms)	Number Lost (per m²)	Weight at Loss (g x 10⁻⁴)	Weight Loss (g/m²)
Jun 6/80	18.1	0.0004	23.2			
Jun 17	7.3	0.0001	15.1	10.8	0.1870	0.0002
Jun 22	246.7	0.0132	53.7	-239.4	0.2844	-0.0068
Jun 27	308.3	0.0225	73.0	-61.6	0.6260	-0.0038
Jul 2	14.5	0.0028	193.8	293.8	1.1895	0.0349
Jul 7	3.6	0.0007	188.9	10.9	1.9132	0.0021
Jul 13	340.9	0.0458	134.3	-337.3	1.5927	-0.0537
Jul 17	58.0	0.0082	141.9	282.9	1.3804	0.0391
Jul 22	232.2	0.0283	122.0	-174.2	1.3158	-0.0229
Jul 27	105.2	0.0117	110.9	127.0	1.1634	0.0148
Aug 1	2092.5	0.3419	163.4	-1987.3	1.3462	-0.2675
Aug 6	1298.4	0.2822	217.4	794.1	1.8844	0.1496
Aug 11	431.5	0.0884	204.9	866.9	2.1104	0.1829
Aug 16	787.1	0.1857	235.9	-355.6	2.1986	-0.0782
Aug 21	823.3	0.1957	237.8	-36.2	2.3682	-0.0086
Aug 26	942.8	0.2760	292.8	-119.5	2.6383	-0.0315
Aug 31	2466.1	0.7741	313.9	-1523.3	3.0316	-0.4618
Sep 7	420.7	0.1875	445.8	2045.4	3.7407	0.7651
Sep 14	2575.1	1.0488	407.3	-2154.4	4.2609	-0.9180
Sep 21	1748.6	0.7890	451.2	826.5	4.2868	0.3543
Oct 5	1581.4	0.8640	546.4	167.2	4.9651	0.0830
May 6/81	68.9	0.0372	540.2	1512.5	5.4328	0.8217
May 20	383.2	0.2994	781.2	-314.3	6.4961	-0.2042
Jun 3	123.3	0.1198	971.4	259.9	8.7049	0.2262
Jun 17	43.5	0.0477	1097.0	79.8	10.3228	0.0824
Jul 1	7.3	0.0077	1058.9	36.2	10.7779	0.0390
Jul 15	12.8	0.0155	1209.4	-5.5	11.3164	-0.0062
Jul 29	3.8	0.0035	931.6	9.0	10.6143	0.0096
			939.0*	3.8	9.3528	0.0036

*estimated from length-weight

Total Production = 0.7452

APPENDIX D: 6 Calculation of production of <u>Hyalella</u> <u>azteca</u> on the Gravel
shore, Dock Lake (1980 cohort) by the removal summation method.
As in Appendix D: 4.

DATE	Av. No./m²	B (g/m²)	Mean Weight (micrograms)	Number Lost (per m²)	Weight at Loss (g × 10⁻⁴)	Weight Loss (g/m²)
Jun 6/80	127.0	0.0027	20.9			
				112.5	0.3131	0.0035
Jun 17	14.5	0.0007	46.9			
				-652.8	0.5879	-0.0384
Jun 22	667.3	0.0492	73.7			
				-97.9	0.9474	-0.0093
Jun 27	765.2	0.0932	121.8			
				654.3	1.3855	0.0906
Jul 2	110.9	0.0175	157.6			
				-404.1	1.9105	-0.0772
Jul 7	515.0	0.1193	231.6			
				-181.0	2.4187	-0.0438
Jul 13	696.0	0.1758	252.6			
				231.8	2.8546	0.0662
Jul 17	464.2	0.1498	322.6			
				-126.9	2.6954	-0.0342
Jul 22	591.1	0.1331	225.2			
				-703.4	2.4114	-0.1696
Jul 27	1294.5	0.3342	258.2			
				-455.2	2.1570	-0.0982
Aug 1	1749.7	0.3153	180.2			
				1053.3	2.0499	0.2159
Aug 6	696.4	0.1624	233.2			
				-1236.5	1.8584	-0.2298
Aug 11	1932.9	0.2863	148.1			
				-685.6	1.7180	-0.1178
Aug 16	2618.5	0.5220	199.3			
				2125.4	1.8255	0.3880
Aug 21	493.1	0.0824	167.2			
				-1273.1	1.7372	-0.2212
Aug 26	1766.2	0.3188	180.5			
				1389.0	1.8030	0.2504
Aug 31	377.2	0.0679	180.1			
				-345.1	2.2484	-0.0776
Sep 7	722.3	0.2028	280.7			
				569.9	2.7438	0.1564
Sep 14	152.4	0.0409	268.2			
				-236.7	3.4161	-0.0809
Sep 21	389.1	0.1693	435.1			
				-1641.9	3.8138	-0.6262
Oct 5	2031.0	0.6790	334.3			
				2027.4	3.6186	0.7336
May 6/81	3.6	0.0014	391.7			
				-18.2	5.7012	-0.0104
May 20	21.8	0.0181	829.8			
				21.8	8.8271	0.0192
Jun 3	0.0	0.0000	939.0*			
				-293.6	9.9139	-0.2911
Jun 17	293.6	0.3073	1046.7			
				213.6	11.0635	0.2363
Jul 1	80.0	0.0936	1169.4			
				63.1	10.8268	0.0683
Jul 15	16.9	0.0169	1002.4			
				-12.1	10.8120	-0.0131
Jul 29	29.0	0.0338	1166.2			
				29.0	11.7903	0.0342
			1192.0*			

Total Production = 0.1242

*estimated from length-weight

CAREX SHORE
P = 2.979 g/m²

TYPHA SHORE
P = 0.931 g/m²

GRAVEL SHORE
P = 0.651 g/m²
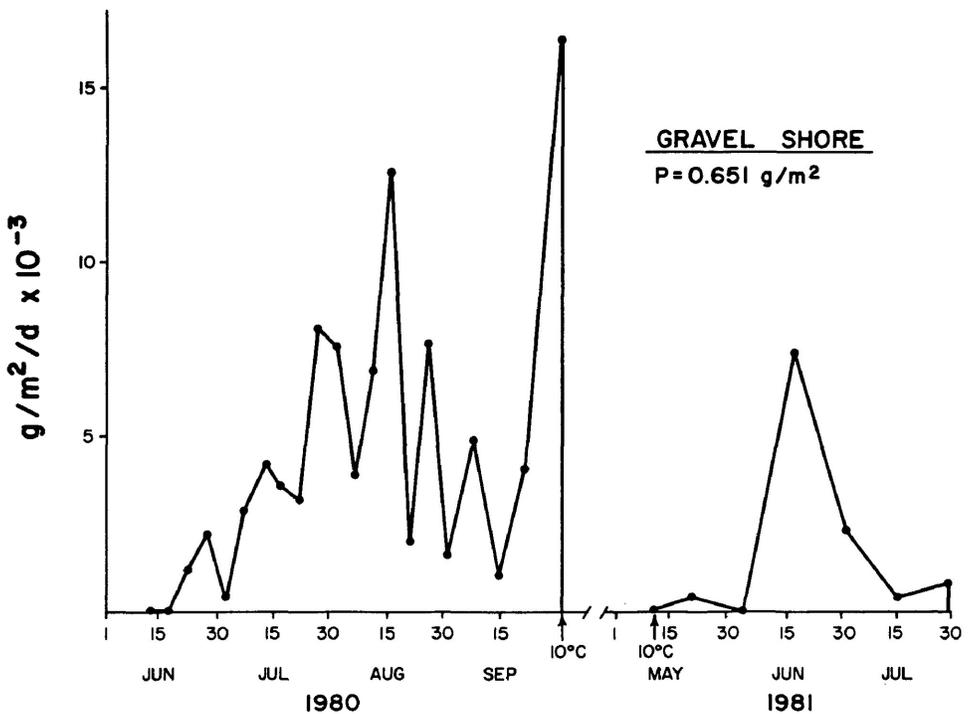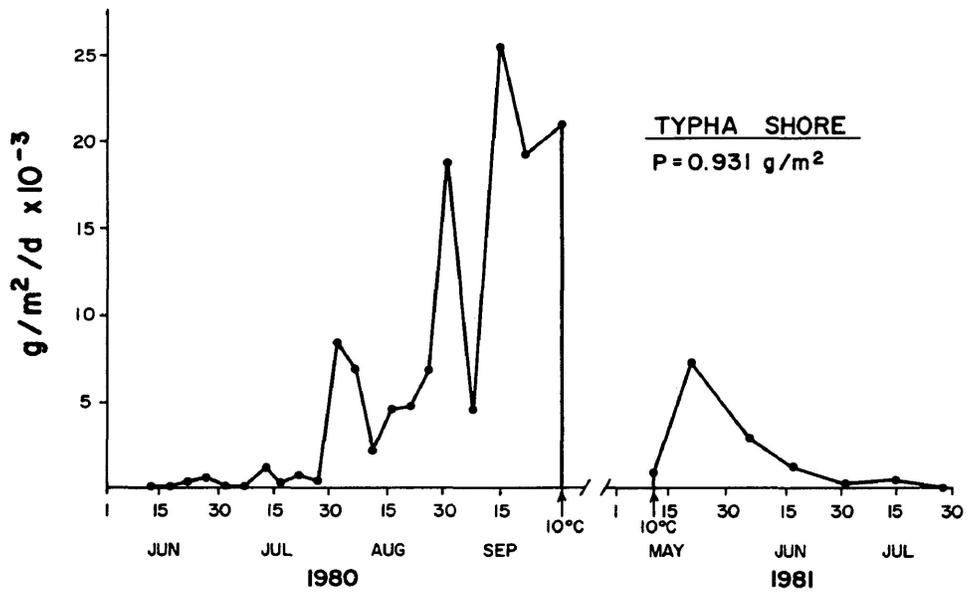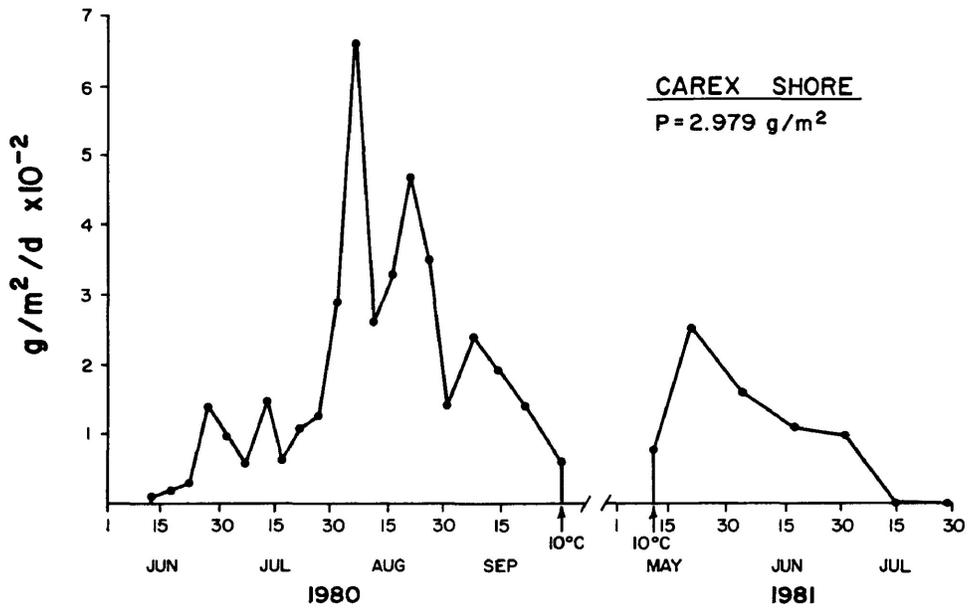
APPENDIX D: 7 Cohort production for <u>Hyalella</u> <u>azteca</u> on
              three shores in Dock Lake, by the daily
              growth method.

CAREX SHORE
COHORT ALLEN CURVE

TYPHA SHORE
COHORT ALLEN CURVE

GRAVEL SHORE
COHORT ALLEN CURVE
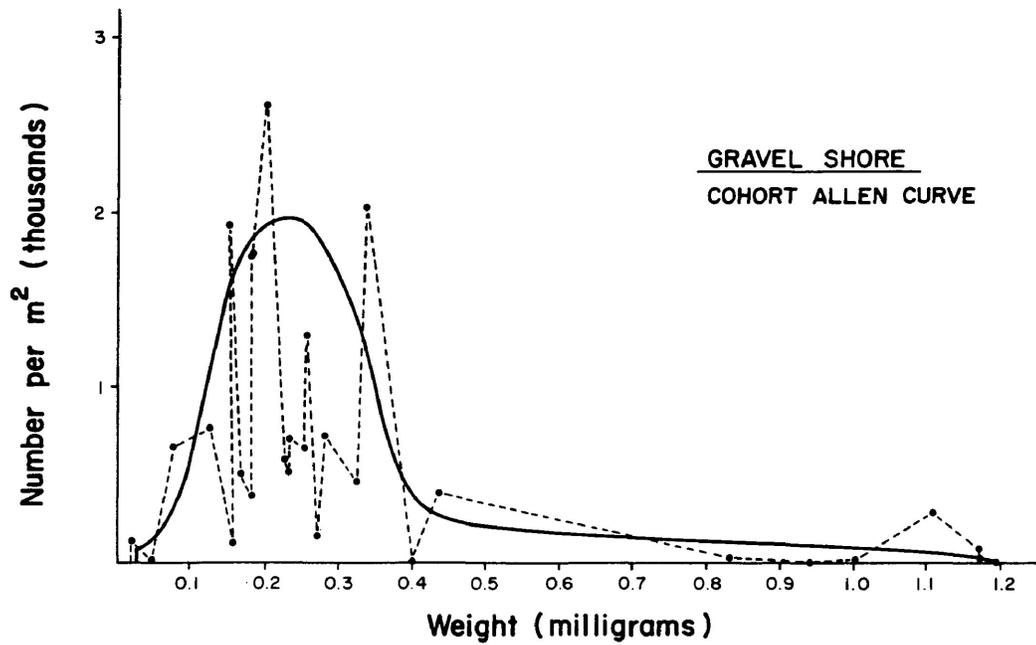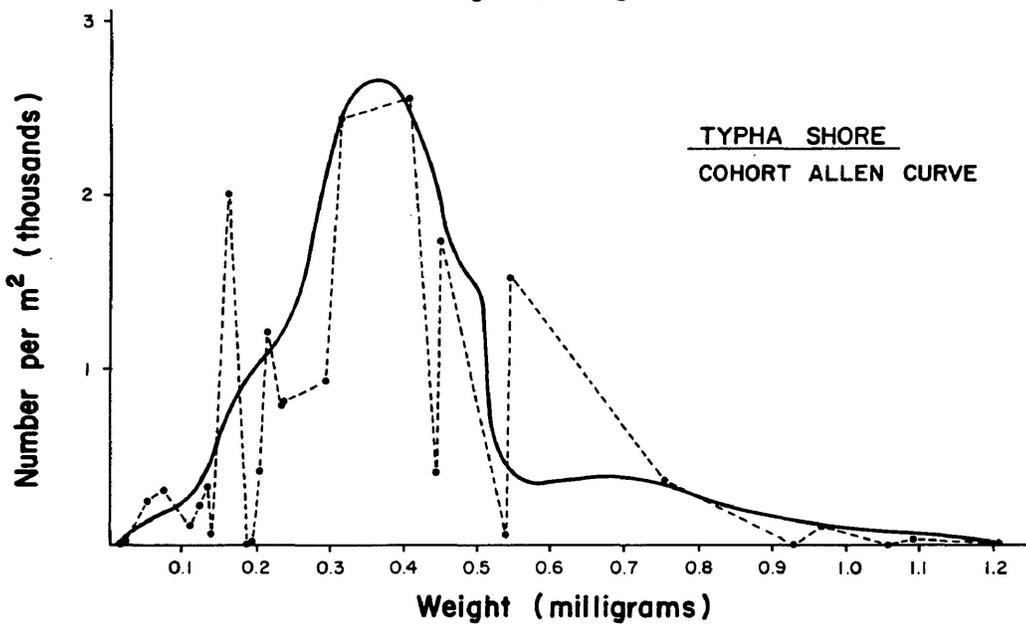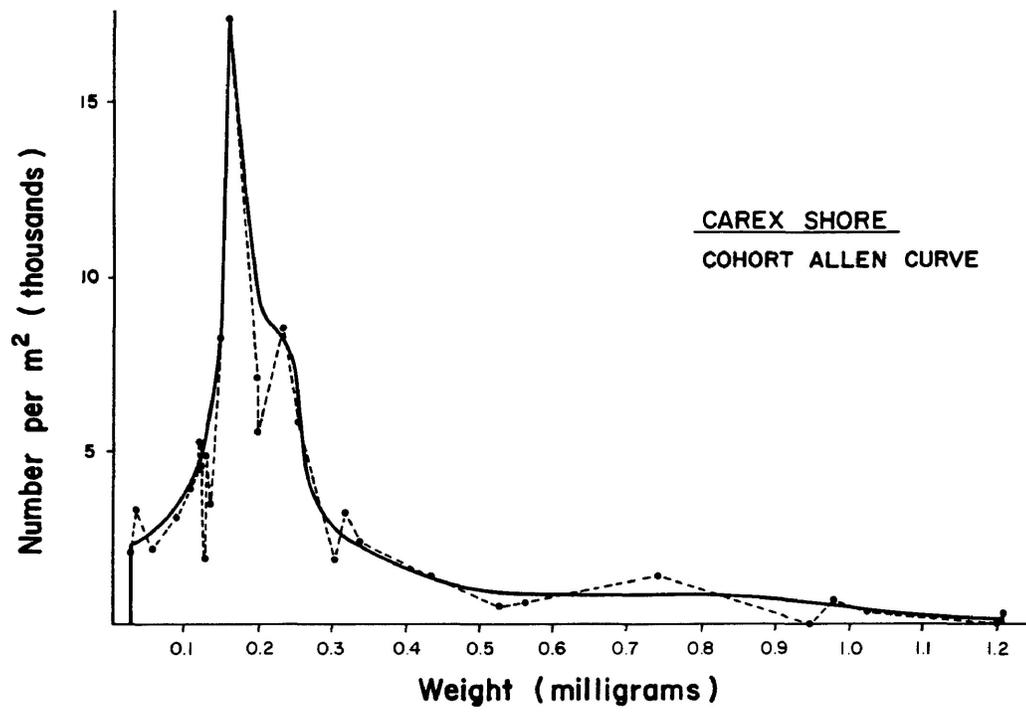
APPENDIX D: 8 Cohort production for <u>Hyalella</u> <u>azteca</u> on

three shores in Dock Lake, by the Allen

curve method. Each Allen curve was constructed

two ways; a hand drawn smoothed line (solid

line) and straight lines between data (dotted

line).