# LIFE HISTORY AND HABITAT DIFFERENCES BETWEEN GAMMARUS LACUSTRIS LACUSTRIS SARS AND HYALELLA AZTECA (SAUSSURE) IN WEST BLUE LAKE, MANITOBA

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# ABSTRACT

A year-round study of differences in characteristics of fundamental niches between *Gammarus lacustris lacustris* Sars and *Hyalella azteca* (Saussure) in the north end of West Blue Lake, Manitoba was begun in June 1967. Differences in relative abundance, size, in time when young were released, age at which reproduction first occurred, mortality rates, and periods of maximum growth are described. The reproductive periods were staggered with *Gammarus* releasing its young a month before *Hyalella*. Adult *Gammarus* had a greater mortality rate than that applying to adult *Hyalella*. Conversely, immature *Hyalella* was subject to a greater mortality rate than was immature *Gammarus*. *Gammarus* grew in winter whereas *Hyalella* did not.

Physiological differences were investigated by determining seasonal changes in rate of oxygen uptake. At low water temperatures the rate of oxygen uptake of *Gammarus* was apparently greater than that of *Hyalella*.

Habitat dissimilarities were evaluated by comparing relative abundance with different conditions of substrate, macrophyte species and depth. *Gammarus* was apparently associated with *Chara* and deeper water, whereas *Hyalella* was associated with *Potamogeton* and shallow water.

Differences in depth distribution, in hydrophyte, substrate and temperature preferences, and in oxygen requirements may maintain *Gammarus* and *Hyalella* spatially isolated. Staggering of reproductive

periods may provide temporal isolation of potentially competing life history stages. Differences in body size of the two species may enable them to utilize the same resource or portion of it in a different way. Since *Gammarus* and *Hyalella* probably do not have the same fundamental niche requirements, competition between them may be limited.

# INTRODUCTION

The research objective at West Blue Lake is to describe in quantitative terms energy exchanges and pathways in this circumscribed aquatic ecosystem. To attain this objective detailed information on community ecology is required, i.e. one must describe the organisms inhabiting a common environment and interacting with each other. One method is to define characteristics of a "fundamental niche", the cumulative abiotic and biotic factors permitting survival of a species (Hutchinson, 1957).

Two of the most abundant benthic species in the lake are *Gammarus lacustris lacustris* Sars and *Hyalella azteca* (Saussure). Glenn and Ward (1968) found that they are an important food item for Walleye, *Stizostedion vitreum vitreum*. In addition, they probably play an important role in converting detritus into fish flesh.

The present study was undertaken to investigate fundamental niche characteristics of *Gammarus lacustris lacustris* and *Hyalella azteca*. The approach was to sample the amphipod population at the north end of West Blue Lake and observe differences between the two species.

The objectives were: (1) to compare their relative abundance over a year, (2) to examine differences in reproduction, mortality and growth, (3) to investigate physiological differences by comparing their rate of oxygen uptake, and (4) to investigate habitat divergence that might minimize competition between the two coexisting species. The information obtained may help explain the complex community ecology of G.l. lacustris and H. azteca.

# LITERATURE REVIEW

## General Biology of North American Freshwater Amphipods

Members of the order Amphipoda are chiefly marine crustaceans with only a few North American freshwater species. Weckel (1907) listed 16 but Pennak (1953) stated that there are about 50 freshwater species. Bousfield (1958) described 30 species and subspecies present in glaciated North America and placed them into five families. Three of these, Corophidae, Talitridae, and Haustoridae contain only one species; Corophium spinicorne (Stimpson), Hyalella azteca (Saussure), and Pontoporeia affinis (Lindstrom), respectively. The family Pontogenidae contains one genus Paramoera with two species. All remaining species belong to the family Gammaridae.

Bousfield (1958) grouped the species of glaciated North America on the basis of their probable origin as follows: (1) those of ancient fresh-water lineage having no morphologically close marine origin. Bousfield (1958) placed the Crangonyx section of the Gammaridae in the first group. The second group was subdivided on the basis of whether or not the species were stenohaline or euryhaline. He suggested that on the Pacific coast the euryhaline species were represented by Anisogammarus sp (Eogammarus), Paramaoera sp and Corophium spinicorne, in the subarctic-boreal region by Pontoporeia affinis, and on the Atlantic coast by the Gammarus tigrinus -G. fasciatus complex. Included in Bousfield's stenohaline group were the holarctic Rivulogammarus complex (only G. duebeni was euryhaline) and the neotropical genus Hyalella which he suggested may have become ecologically separated from its' marine-littoral relatives (Hyale, Allorchestes) as early as the Mesozoic.

Rivulogammarus, Anisogammarus, Paramoera, Pontopereia, and members of the Crangonyx section live in bodies of water that are cold in summer, breed in winter and spring when water temperatures are low (5-15 C) and produce only one brood per year (Bousfield, 1958). In contrast, Gammarus tigrinus and G. fasciatus, Hyalella, few Crangonyx and Corophium live apparently in bodies of water that are warm in summer, breed in late spring and summer and may produce several broods per year (Bousfield, 1958).

Amphipods are an important food source for fishes since they are usually an abundant organism of the macrobenthos and are relatively abundant all year long as opposed to the largely seasonal distribution of the insect fauna (e.g., Clemens, 1950; Cooper, 1965; Keast, 1965). In addition aquatic birds and predacious insect larvae feed on amphipods (e.g., Jackson, 1912).

On the basis of morphology, adult Gammarus lacustris lacustris can be distinguished from adult Hyalella azteca by the following characteristics: the first antenna of Gammarus is longer than the second and contains an accessory flagellum of two-four segments, the telson is clefted, uropod three is biramous, and dorsal spines on abdominal segment one and two are absent; whereas the first antennae of Hyalella is shorter than the second and bears no accessory flagellum, The telson is entire, uropod three is uniramous, and dorsal spines on abdominal segments one and two are present (Bousfield, 1958).

## Biology of *Gammarus lacustris lacustris* Sars

Johansen (1920) stated that two gammarid species, *Gammarus fasciatus* and *G. limnaeus* were found in Canada, with the latter having the widest distribution. Subsequently, Shoemaker (1955) synonymized *G. limnaeus* with *G. lacustris*. Bousfield (1958) established two subspecies under *G. lacustris*, *G. lacustris lacustris* and *G. lacustris limnaeus*. In Canada, the former has a wider distribution than the latter. *G.l. lacustris* is found in provinces of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, and Quebec: while *G.l. limnaeus* is restricted to the St. Lawrence drainage basin from western Ontario to eastern Quebec and Newfoundland (Bousfield, 1958).

Until 1950 the knowledge of the life history of gammarids in North America was limited, except for Embody (1912) who described reproduction in *G. fasciatus* in New York, to brief descriptions of morphology and distribution lists of Weckel (1907), Huntsman (1915), Johansen (1920), Hubricht and Mackin (1940), and Shoemaker (1942). However, Clemens (1950) made a detailed study of the life cycle of *G. fasciatus* in Lake Erie and Menon (1966) investigated the life history of *G.l. lacustris* in Big Island Lake, Alberta.

The life cycle of *G.l. lacustris* was annual (Menon, 1966). A brief summary follows (Menon, 1966): Pairing of the sexes (precopula) occurred in early spring preparatory to ovulation, copulation and fertilization. The ova were carried by the females in the ventral brood pouch. In Big Island Lake most females had only a single brood, the size of which varied in direct relation to body length. Most females died after release of the first brood, while a few surviving females reproduced a second time. The incubation period was temperature specific with higher water temperatures favouring a more rapid completion of incubation. At mean water temperatures of 14.9 C and 22 C, the incubation time was four and two weeks, respectively. During summer and fall new recruits underwent a period of rapid growth, but in winter growth was slow. The annual life cycle was completed during the subsequent spring (Menon, 1966).

G. lacustris has a broad spectrum of ecological requirements. G. limnaeus was present in spring-fed lakes and streams in Ontario and absent from lakes whose maximum summer temperature was greater than 16 C (Pentland, 1930). Bousfield (1958) described the habitat of G.l. lacustris as being cold lakes, tundra ponds, sloughs and overflows that are cool and cold in summer. G. lacustris was more abundant in warm southern eutrophic lakes in Saskatchewan than in northern oligotrophic ones (Ali, 1960). In these northern lakes Pontopereia affinis was more abundant than G. lacustris with the latter restricted to shallow muddy regions (Ali, 1960). In Big Island Lake, Alberta (summer maximum 25.9 C), G.l. lacustris was abundant over a two year study (Menon, 1966). Krog (1954) reported, from laboratory experiments, the summer and winter upper lethal temperatures of

*G. limnaeus* captured from Goose Lake, Alberta as 30-32 C and 26 C respectively.

*G. limnaeus* was frequently present with *Chara*, *Elodea* and dead leaves (Embody, 1912; Pentland, 1930). Ali (1960) observed that both *G. lacustris* and *Hyalella azteca* were more numerous in regions of aquatic vegetation than in non-vegetated ones. *G.l. lacustris* was more abundant in samples taken from shoreline cattail regions than in those from mud shore, sandy shore, *Potamogeton* and lake regions (Menon, 1966). Menon (1966) concluded that the preferred habitat of *G.l. lacustris* was *Typha latifolia*, *Bromus erectus*, *Phragmites* sp. and *Spharagnum* sp.

Titcomb (1927) found *G. limnaeus* only in streams of high alkalinity (141-185 ppm of calcium carbonate), while Pentland (1930) after examining a number of ponds, streams and small lakes in various parts of Ontario concluded that alkalinity did not appear to control its distribution. *G.l. lacustris* in Big Island Lake, Alberta, tolerated a pH of 7.0-9.4 and dissolved oxygen concentration of 7.7 cc/liter (100% saturation) in spring and fall to no measurable amounts of oxygen during one winter month.

Embody (1912) reported that the food preference of *G. limnaeus* did not differ from that of *G. fasciatus*, *Hyalella azteca* and *Eucrangonyx gracilis* and their diet consisted of plants and animal carcasses. Hynes (1955) described the diet of gammarids as green algae, annelids, insects, dead leaves, cyclops and daphnids. The intestines of *G. lacustris* contained planktonic Protococcales and benthic and planktonic Diatomaceae, whereas the plankton samples indicated greater abundance of Cyanophyceae than Protoccales or Diatomaceae (Ermolaeva, 1962). Menon (1966) observed *G.l. lacustris* in winter months feeding on chironomid larvae.

Principal predators of *G. lacustris* and *G. limnaeus* were fish, aquatic birds, and carnivorous insect larvae (Embody, 1912; Ali, 1960; Menon, 1966). Stalked ciliates such as *Vorticella*, *Epistylis*, *Carchesium*, and *Zoothamnium* were main epibionts and cystacanths of acanthocephalans and cysticerci of cestodes were chief parasites of *G.l. lacustris* (Menon, 1966).

## Biology of *Hyalella azteca* (Saussure)

Wienert (1950) and Bousfield (1958) listed the following synonyms of *Hyalella azteca*: *Amphithoe aztecus* Saussure, 1858; *Allorchestes knickerbockeri* Bate, 1862; *Hyalella dentata* Smith, 1874; *Lockningtonia fluvialis* Harford, 1877; *Hyalella knickerbockeri* Weckel, 1907 and *Hyalella azteca* Stebbing, 1906.

Throughout North America, *Hyalella* inhabits most permanent bodies of water in which the monthly mean summer temperature exceeds 10 C (Bousfield, 1958).

Pairing of the sexes (precopula) occurred during the warmer months of the year preparatory to ovulation, copulation and fertilization (Jackson, 1912; Wienert, 1950). After an incubation period, dependent on temperature, young as miniature adults were recruited into the population. Bovee (1951) reported that the average incubation periods in the laboratory were 7 and 18 days at temperatures of 26-28 C and 20-22 C, respectively. At constant temperatures, Cooper (1965) observed average incubation periods of 26.5, 12.7, and 9.3 days at 15, 20, and 25 C, respectively.

The frequency of moulting was dependent on temperature. At a constant temperature of 15 C maturity was obtained in 98 days, while at 20 and 25 C 36 and 33 days were required, respectively (Cooper, 1965). Bovee (1951) observed average incubation periods of 34 and 60 days at temperatures of 26-28 C and 20-22 C respectively.

After the sixth instar the second gnathopod in females was similar in size and shape to the first, whereas in males it was larger and convex (Geisler, 1944). If mean field temperatures were high, newly recruited young matured and reproduced during their first summer (Embody, 1912; Wienert, 1950; Cooper, 1965). On the other hand, new recruits in Marion Lake, British Columbia, did not reproduce until their second summer (Mathias, 1967).

Fecundity was postively correlated with female body size (Cooper, 1965). Cooper (1965) and Mathias (1967) suggested that most females die after the release of the first brood with only a few surviving females reproducing a second time. On the other hand, Embody (1912) reported that one pair had the potential of producing an average of 18 eggs 15 times in 152 days.

Hyalella showed a wide spectrum in its preferences for most measurable environmental factors. Hyalella was found in shallow waters varying widely in temperature from warm partially stagnant marshy pools to cold running streams (Wienert, 1950). Bovee (1949) reported that the time required to produce thermal death varied from more than 11 hours at 33 C to less than one second at 50 C. Sprague (1963) estimated the highest 24-hour lethal temperature which could be obtained by raising acclimation as 33.2 C.

Hyalella occurred in lakes and ponds wherever there was an accumulation of living or dead vegetation (Embody, 1912). Jackson (1912) observed Hyalella to be abundant where Potamogeton was present. Wienert (1950) suggested that Hyalella preferred Chara, Nitella, Myriophyllum, and Ceratophyllum over Potamogeton, Typha, and Ranunculus. Hyalella was abundant in Typha, Potamogeton, and Bromus regions in Big Island Lake, Alberta (Menon, 1966). Hyalella has been found associated with a wide range of substrates including gravel, sand, and mud (Wienert, 1950). A concentration of oxygen of 0.7 mg/l caused 50% mortality in 24 hours at a temperature of 20 C (Sprague, 1963).

Hyalella feed on protozoa, unicellular algae, filamentous algae, and dead animal and plant material (Cooper, 1965). Efford (personal communication) suggested that bacteria are a major food source. Predators included fishes, birds and predaceous insects (Embody, 1912; Wienert, 1950; Cooper, 1965).

Hyalella is strongly thigmotactic (Holmes, 1901). In addition, Hyalella is negatively phototrophic both to intensity and direction of light rays (Phipps, 1915).

In experimental jars, Wilder (1940) showed that population density influenced growth, reproduction and mortality.

## Respiration

Internal respiration is defined as the sum total of all physical and chemical processes by which organisms utilize organic materials as sources of energy and heat (Prosser and Brown, 1961). Metabolism is expressed in terms of oxygen consumed, heat produced or carbon dioxide liberated. Ecologists measure the rate of oxygen uptake of an organism to define the relationship between physiological mechanisms and habitat distribution and to provide an indirect measure of food assimilated. This present review falls into the former category. First, sources of experimental error that could occur in measuring rate of oxygen uptake will be discussed.

### Experimental error

In comparative studies, rate of oxygen uptake of related organisms treated under identical experimental conditions are measured. The differences in the rates of oxygen uptake of closely related species are usually of small magnitude (Berg, Lumbye, and Ockelman, 1958). In addition, the rate of oxygen uptake of most poikilotherms is easily influenced by experimental conditions such as: temperature, quantity of oxygen available, time of day, season, activity, nutrition, life history, and size (Prosser and Brown, 1961.

With every 10 C changes in temperature, the metabolic rate of poikilotherms changes about two and one-half times. For example, Fry (1947) and Fry and Hart (1948) showed that standard metabolism of fish increased continuously with temperature up to lethal levels. The rate of oxygen uptake of _Gammarus_ _pulex_ _pulex_ increased with increasing temperature, but the rate of increase was less at lower temperatures than at higher temperatures (Wautier and Troiani, 1960). The rate of oxygen uptake of Trichoptera larvae, _Polycentropus_, _Plectrocnemia_ and _Limnophilus_, was not constant over the range of temperatures investigated. The rate was constant within the 4-10 C range, increased slightly from 10-20 C and increased sharply above 22 C (Collardeau, 1961).

In most experiments temperature is controlled precisely. However, if poikilotherms are kept at altered temperatures for several days, their rate of oxygen usually shows some adjustment to the new temperature (Hoar, 1966). If they are then returned to the original temperature, their rate of oxygen uptake does not usually return to the original level but rather to a higher or lower level depending on the direction of the adjustment (Hoar, 1966). For example, Edward and Irving (1943) observed that rate of oxygen uptake in the sand crab _Emerita_ _talpoidea_, was greater in winter than in summer. Similarily, Berg (1952) found that the limpet, _Ancylus_ _fluviatillis_, had a greater rate of oxygen uptake in winter than in summer. In contrast, Krog (1954) reported that the rate of oxygen uptake of _Gammarus_ _limnaeus_ was less in winter than in summer. The winter decrease in oxygen uptake was correlated with low oxygen concentrations of Goose Lake (Krog, _ibid_).

Berg, Jónasson and Ockelman (1962) found three types of relationships among the rate of oxygen uptake and availability of oxygen in the benthic organisms that they investigated. (1) The rate of oxygen uptake from 100%-1.5% level of oxygen saturation was constant, but below this level the rate decreased sharply. *Tubifex tubifex*, *Tubifex barbatus*, *Ilyodrilus hammoniensis* and *Chironomus anthracinus* followed this pattern. (2) The rate of oxygen uptake from 100%-4% level of oxygen saturation decreased followed by a greater change in decrease at lower levels. *Lumbricillus rivalis*, *Procladius*, and *Pisidium casertanum* followed this pattern. (3) The rate of oxygen uptake of *Corethra flavicans* decreased at a constant rate from 100% saturation to the lowest levels. Similar to this third pattern, Fox, Wingfield and Simmonds (1937) found that the rate of oxygen uptake of *Ephemera vulgata* was directly correlated with levels of environmental oxygen concentration.

Organisms in their natural physical environments possess rhythms which are adaptively adjusted to various activities. This is in turn reflected in their metabolic rate (Harker, 1958). Periodic patterns tend to persist even under constant laboratory conditions (Webb and Brown, 1959). Consequently, the effect of rhythms are a source of experimental error in measuring oxygen uptake of animals (Prosser and Brown, 1961).

A small animal in terms of grams of body weight has a higher metabolic rate than a larger one (Prosser and Brown, 1961). The relationship between rate of oxygen uptake and size is complicated by temperature (e.g. Berg and Ockelman, 1959; Vernberg, 1959; Armitage, 1962).

The metabolic rate of a species may vary with sex and life history stage (Wolvekamp and Waterman, 1960). In order to make valid comparisons, comparable animals should be tested (Prosser and Brown, 1961).

Muscular activity of an animal is one of the most difficult factors to control in measuring its rate of oxygen consumption (Wolvekamp and Waterman, 1960). Prosser and Brown (1961) defined basal metabolism as the oxygen uptake required just for body maintenance, standard metabolism as oxygen uptake measured with minimal motor activity, and active metabolism as oxygen uptake measured at some fixed or forced level of activity. Actual measurements usually fell between standard and active metabolism (e.g. Krogh, 1954; Wiens and Armitage, 1961; Mathias, 1967).

The presence or absence of food as well as the kinds of foods may influence the rate of oxygen uptake of animals (Prosser and Brown, 1961). For example, Berg, *et al*. (1962) reported that starvation did not immediately depress the rate of oxygen consumption of oligochaetes, *Lumbricillus ravalis*, *Tubifex tubifex*, *Tubifex barbatus*, and *Ilyodrilus hammoniensis* nor of insect larvae *Corethra flavicans*, *Procladius* sp, and *Chirnonomus anthracinus*; but did reduce slightly the rate of oxygen uptake of the pelecypod, *Pisidium casertanum*.

## Oxygen uptake of animals from different latitudes

Krogh (1916) hypothesized that the rate of respiration of related species inhabiting localities with extremely different temperatures would not differ as much as the temperature difference would ordinarily imply. Several investigators have found evidence that supports this hypothesis (e.g. Fox, 1936; Fox 1939; Scholander *et al*. 1953). In general, the rate of oxygen uptake of aquatic poikilotherms measured at natural habitat temperatures was less for cold-water animals than for warm-water ones, but at any given temperature animals acclimatized to low temperatures tended to have higher metabolic rates than those of related species acclimatized to high temperatures.

## Oxygen uptake of animals from different habitats

Fox, Simmonds, and Washbourn (1935) observed that ephemerid nymphs from a swift stream had higher oxygen uptakes than related species from slow flowing streams. Similarily, Washbourn (1936) showed that oxygen uptake of trout fry reared in swiftly flowing water was greater than for those reared in slow running water. In contrast, Berg, (1952) observed similar oxygen uptake between a stream snail, *Ancylus fluviatilis*, and a comparable stagnant water snail, *Acroloxus lacustris*.

The rate of oxygen consumption of two subspecies of gammarids, *G. pulex pulex* and *G. pulex fossarm* sampled from different habitats was not significantly different (Wautier and Troiani, 1960).

The rate of oxygen consumption of members of the crayfish, *Orconectes immunis* and *Orconectes nais*, was not significantly different at moderate temperatures and concentrations of oxygen, but it was significantly different at high temperatures and low levels of oxygen concentrations. The difference in rate appeared to be due to failure of *O. nais* to regulate as well as *O. immunis* under extreme conditions. This was linked to the absence of *O. nais* in the roadside ditch habitat of *O. immunis* (Wiens and Armitage, 1961).

Mathias (1967) observed that the rate of oxygen uptake of *Hyalella azteca* decreased considerably at low temperatures, whereas the rate of oxygen uptake of *Crangonyx richmondensis occidentalis* remained relatively constant from 10-24 C. Since *Crangonyx* was more abundant in deeper water than in shallow water and *Hyalella* was more abundant in shallow water than in deeper water, Mathias (1967) suggested that *Crangonyx* was better adapted to colder water than *Hyalella*.

Roux and Roux (1967) compared the rate of oxygen consumption of sympatric species, *Gammarus pulex*, *G. fossarum*, and *G. wautiera*. *G. pulex* had a greater rate of oxygen uptake at higher temperatures than at lower temperatures and a greater stability in its' rate at intermediate temperatures (15-20 C). On the other hand, the rate of oxygen uptake of *G. fossarum* was less than *G. pulex* at all temperatures and dropped rapidly at temperatures above 20 C. Roux and Roux (*ibid.*) suggested that *G. pulex* was adapted to intermediate temperatures

(15-20 C), while G. fossarum was adapted to lower temperatures and correlated these temperature adaptations with their distributions in the field.

# DESCRIPTION OF THE AREA

West Blue Lake, located in Duck Mountain Provincial Park in western Manitoba, is a "channel" lake, a variant kettle type. The basin occupies a former melt-water channel that was re-occupied by ice and drift. Re-occupation and subsequent melting resulted in a multi-basin configuration (Klassen, personal communication).

The principal morphometric features relative to this study are the high mean depth, the steeply sloped shores, and the multiple basin configuration which have tended to limit and isolate the littoral zones.

There is a variety of fauna and flora in West Blue Lake. The most common fishes are: Walleye, Stizostedion vitreum vitreum; Yellow Perch, Perca fluviatilus; Lake Trout, Salvelinus namaycush; Northern Pike, Esox lucius; Five-spined Stickleback, Culaea inconstans; and Fathead Minnow, Pimephales promelas.

The following birds are transitory residents of the lake: Common Loon, Gavia immer; Franklin's gull, Larus pipixan; Mallard, Anas platyrhynchos platyrhynchos; Golden-eye, Glaucionetta sp. and Merganser, Mergus sp.

Zooplankton consists of Rotatoria, Cladocera, Copepoda and Chaoborus. Fernando (personal communication) identified the rotifers Keratella cochlearis, K. quadrata, Felinia longiseta and Asplanchna sp as well as the copepods Diaptomus siciloides and Cyclops biscuspidatus. Patalas (personal communication) identified the cladoceran Daphnia

Table I. Partial list of benthic fauna of West Blue Lake.

| Phylum | Class, Order etc. | Scientific Name | Identified by |
|---|---|---|---|
| Platyhelminthes | Turbellaria | *Dugesia* | Cober, J., 1966 |
| Aschelminthes | Nematoda | | " " " |
| Annelida | Oligochaeta | | " " " |
| | Hirudinea | *Erobdella* | " " " |
| Mollusca | Pelecypoda | *Musculium*, *Sphaerium*, | " " " |
| | | *Pisidium* | " " " |
| | Gastropoda | *Physa* | " " " |
| Arthropoda | Amphipoda | *Gammarus lacustris lacustris* | Bousfield, E.L., 1967 |
| | | *Hyalella azteca* | " " " " |
| | Decapoda | *Orconectes virilis* | Bell, R., Biette, R., 1968 |
| | Ephemeroptera | *Ephemera* | " " " " " |
| | Odonata | *Aeschna* | " " " " " |
| | Trichoptera | *Phryganea* | Cober, J., 1966 |
| | Coleoptera | *Haliplus* | " " " |
| | Tendipedidae | *Procladius* | Cober, J., 1966, Hamilton, A.L., 1967 |
| | | *Pentaneura* | Cober, J., 1966, Hamilton, A.L., 1967 |
| | | *Anatopynia* | Cober, J., 1966, Hamilton, A.L., 1967 |
| | | *Harnischia* | Hamilton, A.L., 1967 |
| | | *Cryptochironomus* | " " " |
| | | *Tendipes* = *Chironomus* | " " " |
| | | *Chironomus* = *Tendipes* | |

*pulex* and copepods *Epischura lacustris* and *Mesocyclops edax*. The cladoceran *Bosmina* sp was identified by Ward (personal communication).

The benthos is rich both in numbers and kinds of fauna. All benthic organisms have not been identified. Table I summarizes the chief components identified to date.

Partial list of summer phytoplankton is: Cyanophyta, *Anabaena*; Chlorophyta, *Zygnema* and *Spirogyra*; Chrysophyta, *Asterionella*, *Stephanodiscus* and *Dinobryon*; and Phytomastigina, *Ceratium.*

Principal hydrophytes are: *Chara* sp, *Ranunculus circinatus*, *Potamogeton pectinatus*, and *Potamogeton richardsoni*.

# METHODS AND MATERIALS

## Sampling Area

Sampling was conducted in the littoral zone at the north end of the lake (Figure 1). This region had an area of 4,400 $m^2$, a mean depth of 1.14 m and a maximum depth of 3.8 m. This compact area faciliated sampling and it was accessible in winter. Furthermore, it was separated from other extensive littoral zones thus limiting immigration and emigration.

## Sampling

Numbered sampling units were located along 11 parallel transects arranged at 90° to the north shore (Figure 1). Transects extended from the shorelines to the sublittoral zone which was defined as that portion of the lake between the lakeward limit of rooted aquatics and the upper limit of the hypolimnion. During each sampling period (Table 11), 10 random samples with replacement were taken. A 0.25 $m^2$ metal frame was lowered into each sample unit and the substrate within the frame was removed with a dip net (mesh size 500 micron) and placed in polyethylene bags (18" x 32"). In shallow water ($< 1$ m) samples were taken by standing directly over the sampling frame. SCUBA (self-contained underwater breathing apparatus) was used at depths greater than 1 m. Wood (1963) outlines the techniques of adapting SCUBA to limnology. SCUBA was not used in winter. A hole was chopped through the ice at each sample unit, the frame was

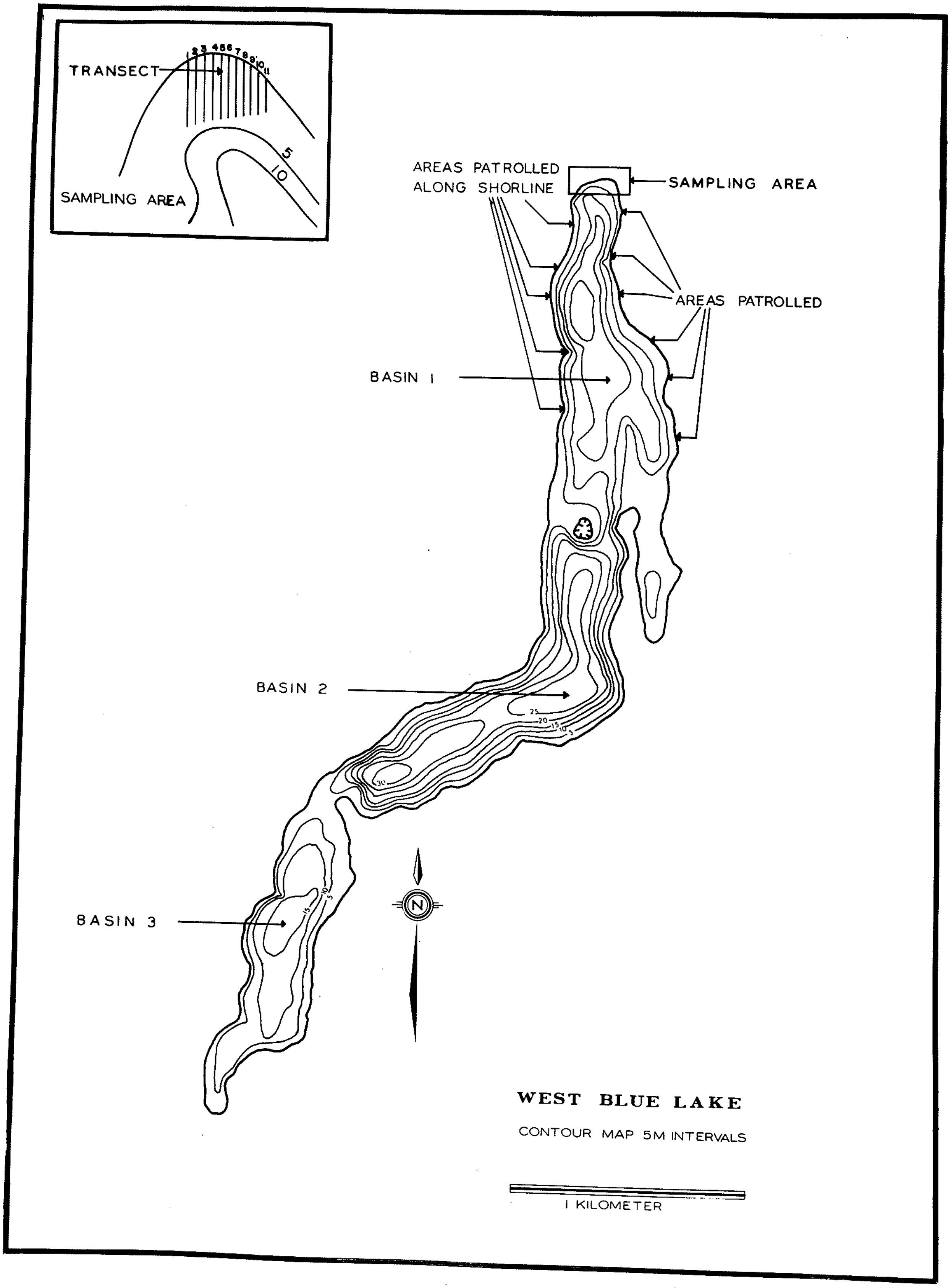

Figure 1. Bathymetric map of West Blue Lake showing sampling region and areas patrolled along shoreline.

Table II. The dates and seasons of sampling.

| | Date | | Season |
|---|---|---|---|
| 1. | June | 12, 1967 | spring-late |
| 2. | " | 26 | " " |
| 3. | July | 7 | summer |
| 4. | " | 17 | " |
| 5. | " | 28 | " |
| 6. | August | 9 | " |
| 7. | " | 21 | " |
| 8. | September | 2 | " |
| 9. | " | 28 | fall |
| 10. | October | 26 | " |
| 11. | November | 25 | " |
| 12. | December | 27 | winter |
| 13. | January | 27, 1968 | " |
| 14. | February | 23 | " |
| 15. | March | 25 | " |
| 16. | May | 12 | spring |
| 17. | June | 18 | " |

lowered, and the substrate was sampled.

Sampling was based on two assumptions:

(1) amphipods were restricted to the littoral zone,

(2) the north end of West Blue Lake (Figure 1) was sufficiently isolated from the other extensive littoral zones so that immigration and emigration was minimal. These assumptions were examined by observing depth distribution and migration along the shores.

Seasonal depth distribution, was investigated by taking a series of Ekman dredge samples on: 15 June, 1967, 11 August, 1967, 8 September, 1967, 16 May, 1968, and 20 June, 1968. Using a 0.24 m x 0.24 m Ekman dredge, samples were taken along extended transects 3, 5 and 9 (Figure 1) at depths of 1, 2, 3, 4, 6, 8, 10, and 12 m. In the laboratory amphipods from each depth were identified to species and counted.

In addition, depth distribution over a 24 hour period was examined for evidence of diel inshore-offshore movements. On 18 and 19 June, 1968 samples were taken at the following times: (1) 1 hour before sunset, (2) sunset, (3) darkness, (4) 1 hour before sunrise, (5) sunrise, (6) 1 hour after sunrise, (7) noon and (8) mid-afternoon. For each time period, sampling was conducted along transects 3, 5, and 9 (Figure 1) at depths 0.25, 1.5, 2.5, and 4 m. At each depth the 0.25 $m^2$ sampling frame was lowered and the substrate within the frame was removed with the dip net. In the laboratory amphipods from each depth were identified to species and counted.

Amphipods could migrate along the shoreline from the sampling region to the extensive littoral zone separating basin 1 and 2 (Figure 1). On 14 May, 1968 observations were made along both shores during day and night to detect horizontal movements of amphipods.

## Treatment of Samples

The samples were sieved through a nest of monofilament screens (aperture opening 2630-500 micron) constructed on wooden frames. During this process amphipods trap air bubbles under their body segments making them less dense than water. Animals were then floated from the sediment by placing the screens in water. Sediments were sorted by hand to ensure that all specimens were extracted. The amphipods were preserved in 5% formalin.

In the laboratory 10,538 amphipods were identified to species, measured, sexed, divided into life history stages and counted. Amphipod density was expressed as mean number per square metre.

Lengths were measured to the nearest 0.1mm using a dissecting microscope fitted with a measuring eye piece and stage micrometer. Measurement was from the base of first antennae to the tip of telson. To facilitate this measurement specimens were placed in water for 12 hours. This made bodies less rigid, so that curled animals could be extended for more accurate measuring. For both species the samples were divided into 8 size classes based on total body measurement.

Eggs were removed and counted with the aid of dissecting microscope from each female bearing a brood. Fecundity was defined as the number of eggs observed per female.

Sex of adult Gammarus was determined by presence of calceoli on the flagellum of second antennae in males and presence of öostegites in females. Presence of the large subchelate propodus of second gnathopod defined a male Hyalella, whereas a female was defined by presence of öostegites.

Samples were divided into the following life history stages: immatures, pre-reproductive, reproductive and post-reproductive adults. Amphipods with well developed sexual characters, in precopula and females bearing ovaries or brood were defined as reproductive adults. Those with rudimentary sexual characters, not in precopula and females not possessing ovaries or brood were defined as pre-reproductive or post-reproductive adults depending on size and time of year. Sex ratios at appropriate sizes were used to determine number of males present in these life history stages. Immature animals were defined as those with no observed sexual characteristics.

## Measurement of Environmental Factors

During each sampling period an electric thermometer was used to record water temperature. Using a Cambridge pocket meter, pH was recorded. Habitat dissolved oxygen levels were measured by the modified Winkler technique. Seasonal sediment-water interface values for pH, mg/l of dissolved oxygen, and water temperatures are shown in Figure 2. For each quadrat sampled, depth, hydrophyte, and substrate present were recorded.

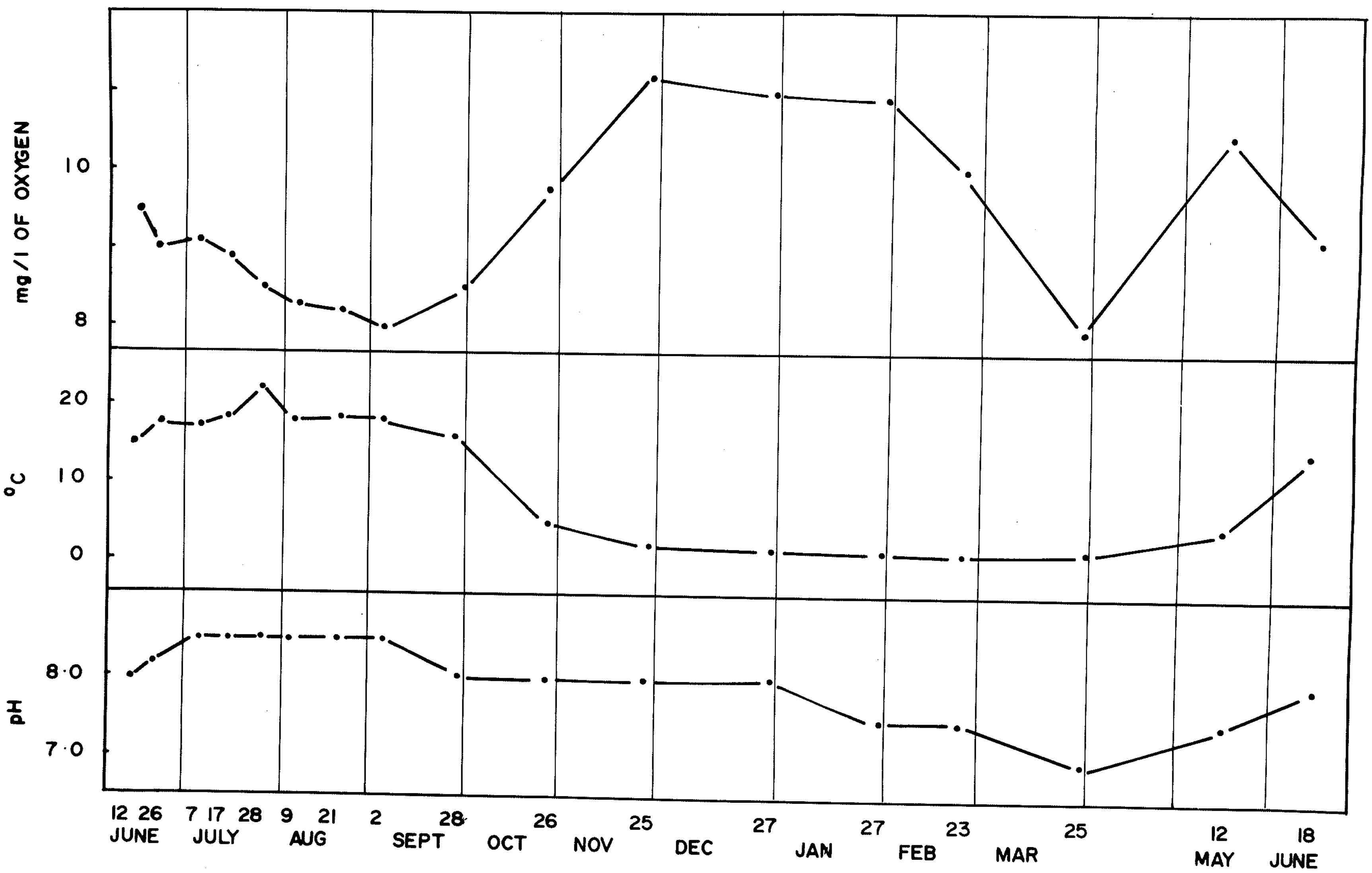

Figure 2. Distribution of pH, temperature, and mg/l of dissolved oxygen at the sediment-water interface in sampling region during June 1967 to June 1968.

## Mortality

One of the simplest assumptions of mortality is that a constant fraction of animals present die per unit time. Numerical representation of this relationship is (Ricker, 1958):

$$N_t = N_o e^{-it}$$

where

$N_o$ = initial number of animals present

$N_t$ = number of animals present at time t

e = base of natural logarithms

i = instantaneous mortality rate

t = any period in time

Expressing this relation in the natural logarithmic form:

$$\ln N_t = \ln N_o - it$$

the instantaneous mortality rates for reproductive adults and juvenile animals were estimated by method of least squares.

Spring samples of reproductive adults of Gammarus contained gravid females with well developed eggs as well as new eggs, whereas spring samples of Hyalella did not contain eggs and thus were not in comparable life history stage. To compare mortality rates of reproductive adults of both species, relative abundance of Gammarus adults collected during June 12 to July 28 were compared with relative abundance of Hyalella adults collected from July 7 to September 2. Non-overwintering adults of Hyalella were not included.

Mortality rates of juvenile animals of both species were estimated from cessation of recruitment in 1967 to prior to first appearance of reproductive adults in 1968. For Gammarus, this period was from July 28 to March 25, and for Hyalella from September 2 to May 12. Juvenile individuals were defined as new recruits of 1967. After September 2, juvenile animals of Hyalella consisted entirely of pre-reproductive adults. Juvenile individuals of Gammarus consisted of both immature animals and pre-reproductive adults from July 28 to December 27, but consisted of only pre-reproductive adults after December 27.

If reproduction was highly synchronized, i.e. all females became gravid at the same time, released their eggs at the same time and died, there would be a relatively short period of overlap between presence of eggs in the population and presence of young. Thus, in a relatively short time, the standing crop of eggs released would become the standing crop of immature animals. In the absence of mortality between egg and immature life history stage, the two standing crops should be numerically equal; thus any difference between the two would reflect a real mortality effect.

Since fecundity was determined for each gravid female sampled, the number of eggs per square metre was calculated for each sampling period. If there were no gravid female mortality, if all eggs counted were viable, and if all females became gravid in a relatively short period of time, then the density of eggs observed at the beginning of recruitment would be an estimate of the number of new recruits expected to enter the population.

The reproductive adults, however, were characterized by an exponential rate of decline. Consequently, density of eggs observed were corrected for number of eggs lost due to female mortality. The difference between the number of young expected to enter the population and the actual mean standing crop of young after cessation of recruitment indicated the number of animals lost during this period. Instantaneous mortality rates were calculated using the above formulae.

### Growth

Mean body lengths were calculated on each sampling date for immature animals, pre-reproductive and reproductive adults of *Gammarus* and *Hyalella*. Mean body lengths of reproductive adults of *Hyalella* were calculated from July 7 until September 2. During this period, reproductive adults of *Hyalella* were comparable to those of *Gammarus*. Non-overwintering reproductive adults were not included in the calculations. Since there was a size difference between male and female gammarids, mean lengths of the sexes of pre-reproductive adults were calculated separately.

### Respiration

Rate of oxygen uptake per male amphipod was measured with a Scholander Model VR-300, respirometer, (Scholander *et al.*, 1952) at temperatures 1, 2, 5, 7, 13, 19, and 20 C.

Before a test period, specimens were collected from the field and sorted by species, sex and life history stage. The constant temperature water bath was set equal to habitat water temperature. For each species two to four animals were placed into the respiratory vials with 5 ml of screened lake water. During fall and winter, pre-reproductive adults were measured at 5, 7, and 1, 2 C respectively. Reproductive adults were measured at 19 and 20 C in summer. In spring (13 C) pre-reproductive *Hyalella* was compared with reproductive *Gammarus*. The method outlined by Scholander *et al*. (1952) was used for carbon dioxide absorption. To obtain volume stability, 1 hour thermoequilibration was allowed. The shaking rate of the manometer rack was adjusted so specimens would not be trapped in the surface film. Oxygen uptake was measured every hour for two hours. Specimens were removed from the vial, dried of excess water on filter paper and weighed. Rate of oxygen uptake was recorded as cubic centimeters of oxygen consumed per gram wet weight per hour.

In winter, animals were transported from the field station to the university laboratory. During transportation and sorting, animals were exposed to higher than habitat temperatures. Animals were acclimated to 1 and 2 C for 70 hours. After acclimation, the procedure was identical with the above.

## Habitat Preference

It seemed by observation that *Gammarus* preferred deeper water and *Chara* beds, whereas *Hyalella* preferred shallow water where

*Potamogeton* was the dominant hydrophyte. To test this hypothesis the following variables were recorded for each of the 145 sampling units: depth of the water column, water temperature, number of *Gammarus* and *Hyalella*, substrate type (one of gravel, sand, silt, or mud), hydrophyte type (either *Chara* sp, *Potamogeton pectinatus*, *P. richardsoni*, *Ranunculus cirinatis*; or any combination depending on what ones were present). The object was to determine whether the distribution of *Gammarus* and *Hyalella* were correlated with depth, hydrophyte cover, substrate, and temperature.

In the analysis the following problems were encountered:

(1) All variables were intercorrelated. This problem will be discussed.

(2) Both quantitative and qualitative variables were recorded. Hence, the variables were analyzed in a stepwise fashion with the qualitative variables being analyzed first and then the quantitative variables were introduced.

(3) Since any one of the four hydrophyte species could either be present or absent from any one sampling unit, 16 different combinations were possible. In order to test the hypothesis it was desirable to divide the hydrophyte samples into groups of samples which were as different from each other in floral composition as possible. The hydrophyte data were analyzed by an association analysis method of Williams and Lambert (1959).

In this technique data consisting of presence and absence of each of S species in each of N samples ($N > S$), were analyzed by determining the species whose presence and absence best divides the N samples into two groups in which the differences between groups were maximized and those within groups minimized. This procedure was repeated on both of the two groups of samples thus produced, and so on, resulting in a hierarchy of groups of samples defined by species presences or absences.

(4) Since the numbers of Gammarus and Hyalella in each sampling unit were 'contagious' (few quadrats contained a moderate number of animals and many quadrats contained none or very few animals), the frequency distribution was skewed. To reduce the skewness a natural logarithmic transformation was performed. To overcome the difficulties with zero counts in logarithmic transformations a constant one was added to the original count (x); i.e. $X_{Trans.} = \ln (x + 1)$.

(5) Since water temperature was the same for each sample quadrat on any sampling date, it was excluded from the analysis.

To test the independence of substrate type from the groups of hydrophyte samples in which the within-group heterogeneity was minimized, a chi-square analysis was conducted. A 4x3 contingency table was used. The two variables of classification were homogeneous hydrophyte groups with three categories and substrate type with four categories. The null hypothesis was that substrate type and homogeneous hydrophyte groups were independent.

To determine whether significant differences in mean number of Gammarus, Hyalella, and depth occurred in the homogeneous hydrophyte samples, one-way analysis of variances, using the completely random design, were applied to the data.

The statistical test and the "F" table used are given in Steele and Torrie (1960).

# RESULTS

## Sampling

The samples collected with the Ekman dredge (Figure 3) indicated that the depth distribution of Gammarus and Hyalella remained relatively constant during all seasons with few individuals of either species occurring at depths greater than the maximum transect depth of (3.8 m). Similarly, diel variations in distribution were not apparent (Figure 4). Regardless of hour, again few animals were captured beyond the maximum transect depth.

Observations along the shore made at 11 AM and 11 PM on 12 May, 1968 indicated the presence of amphipods in isolated areas. However, few animals were present in these areas and there was no evidence for diel variation in abundance or movement.

## Relative Abundance and Density

Amphipods collected from 12 June, 1967 to 18 June, 1968 (10,538) were 33% Gammarus and 67% Hyalella (Table III). Gammarus was less abundant than Hyalella in all but the 26 June, 1967 and 18 June, 1968 samples.

In the first sample (12 June, 1967) there were about 80 Gammarus per $m^2$ (Figure 5), but by June 26 density had increased to the seasonal maximum ($223/m^2$). After mid-July density decreased gradually, reaching the seasonal minimum ($32/m^2$) on 12 May, 1968.

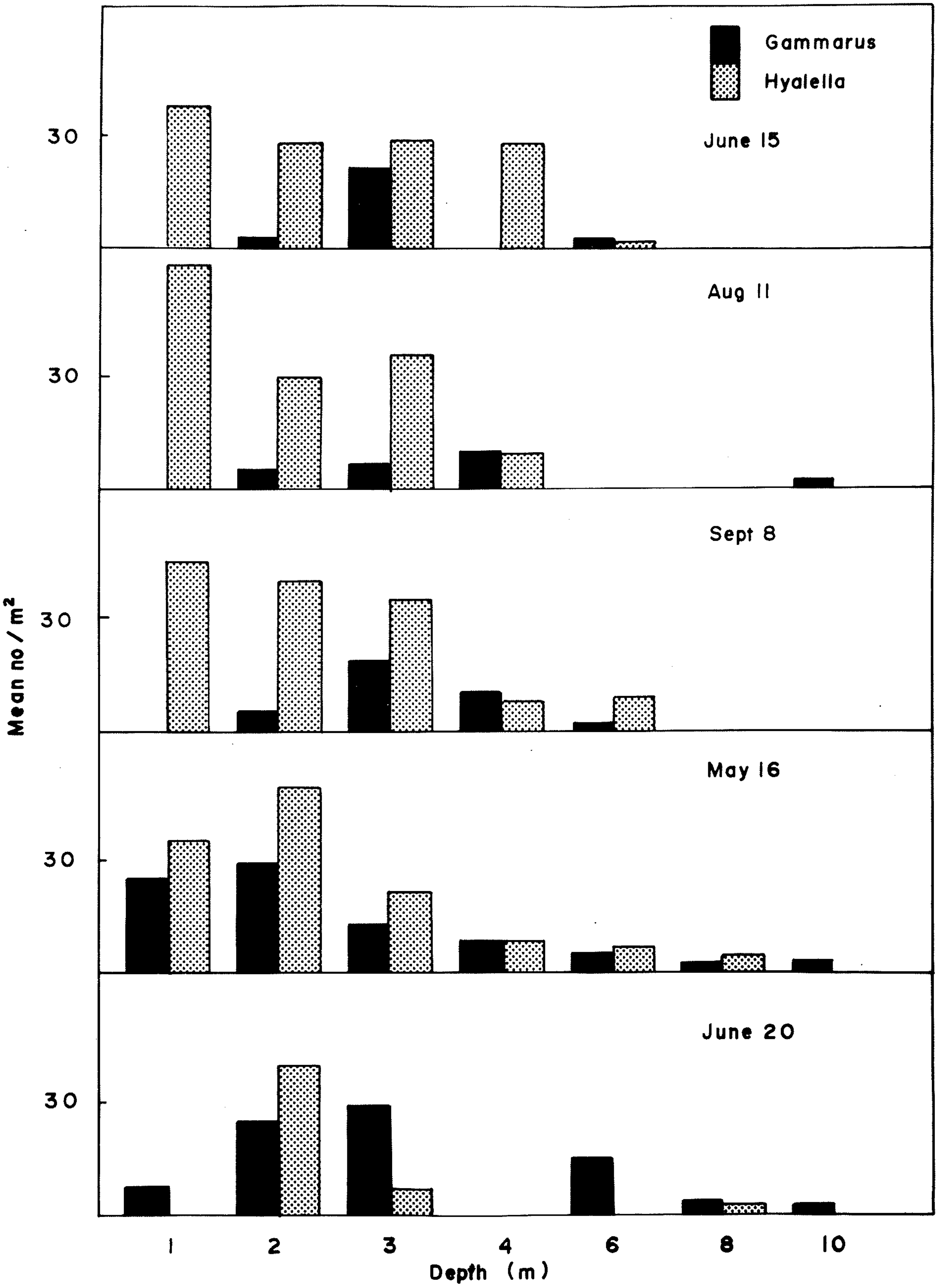

Figure 3. Depth distribution of Gammarus and Hyalella.

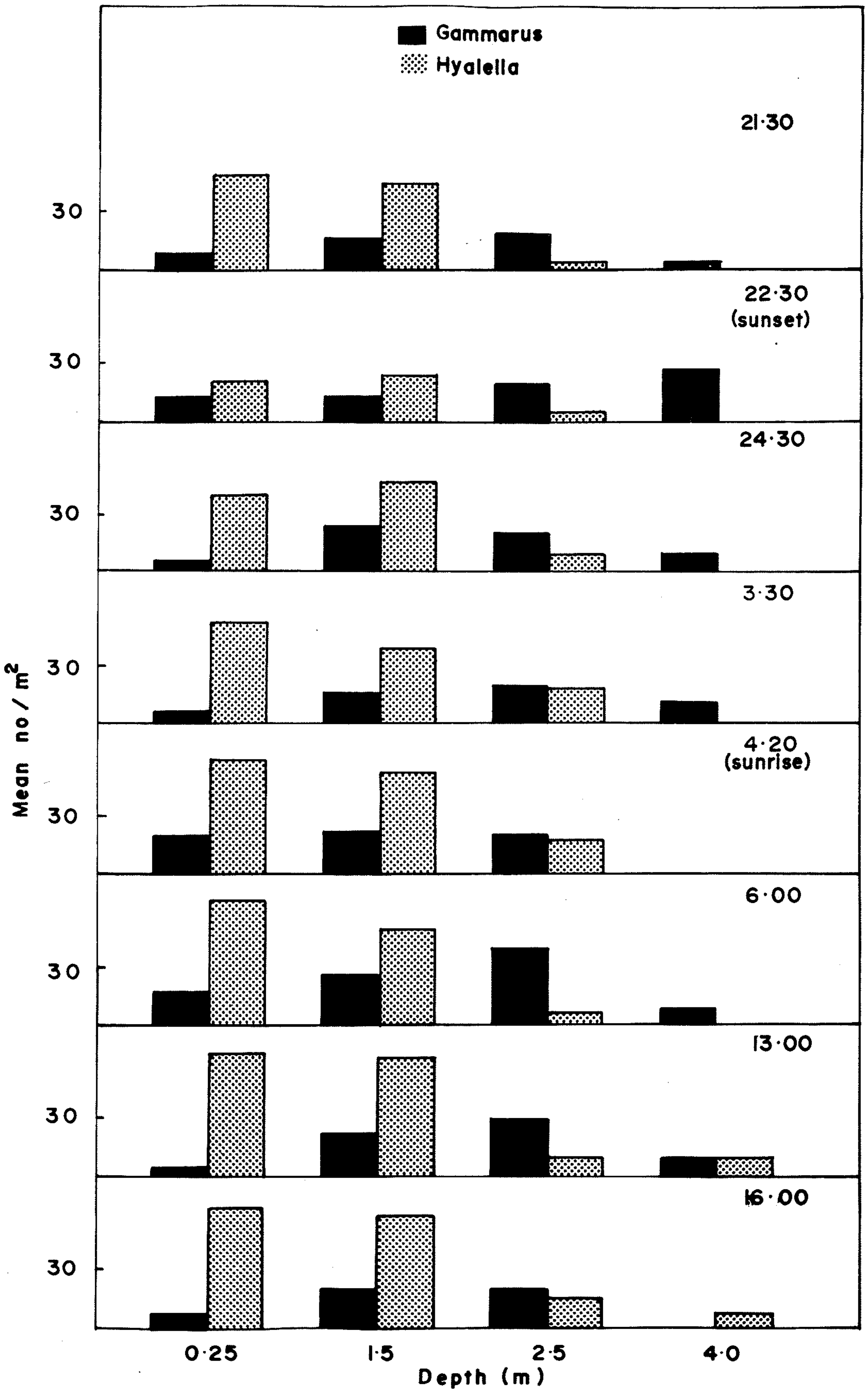

Figure 4. Diel variations in distribution of *Gammarus* and *Hyalella*.

Table III. Number of *Gammarus* and *Hyalella* sampled and their abundance relative to each other during the sampling periods.

| | Number | | | Percent | |
|---|---|---|---|---|---|
| Date | *Gammarus* | *Hyalella* | Total | *Gammarus* | *Hyalella* |
| June 12 | 179 | 439 | 618 | 28.96 | 71.04 |
| 26 | 502 | 391 | 893 | 56.22 | 43.78 |
| July 7 | 307 | 432 | 739 | 41.54 | 58.46 |
| 17 | 371 | 646 | 1017 | 36.48 | 63.52 |
| 28 | 321 | 751 | 1072 | 29.94 | 70.06 |
| Aug. 9 | 253 | 554 | 807 | 31.35 | 68.65 |
| 21 | 189 | 486 | 675 | 28.00 | 72.00 |
| Sept. 2 | 161 | 384 | 545 | 29.54 | 70.46 |
| 28 | 145 | 378 | 523 | 27.72 | 72.28 |
| Oct. 26 | 137 | 320 | 457 | 29.98 | 70.02 |
| Nov. 25 | 135 | 351 | 486 | 27.78 | 72.22 |
| Dec. 27 | 145 | 370 | 515 | 28.16 | 71.84 |
| Jan. 27 | 92 | 261 | 353 | 26.06 | 73.94 |
| Feb. 23 | 72 | 216 | 288 | 25.00 | 75.00 |
| March 25 | 72 | 227 | 299 | 24.08 | 75.92 |
| May 12 | 68 | 378 | 446 | 15.25 | 84.75 |
| June 18 | 535 | 270 | 805 | 66.46 | 33.54 |
| Total | 3684 | 6854 | 10,538 | Mean 32.50 | 67.50 |

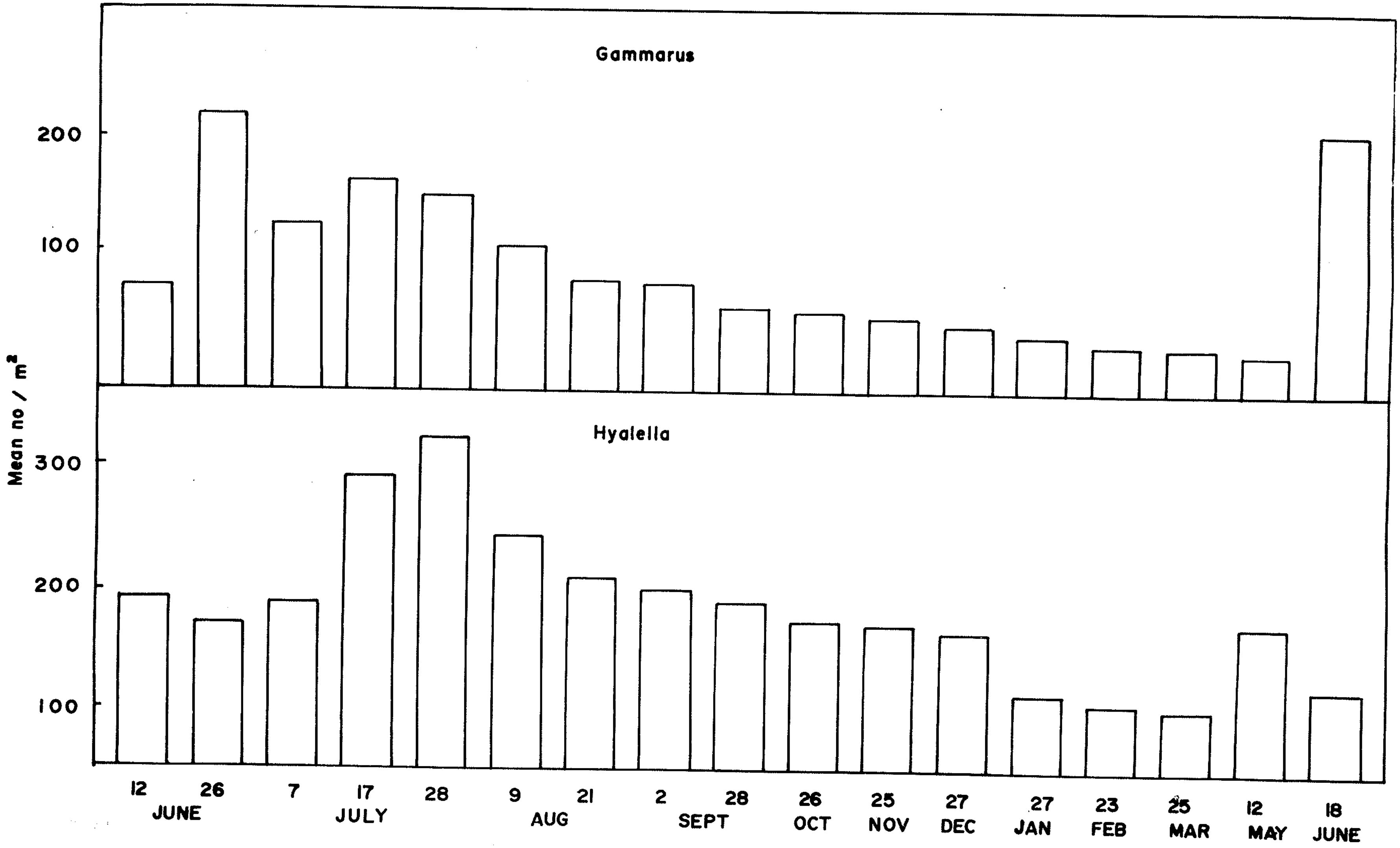

Figure 5. Mean number of <u>Gammarus</u> and <u>Hyalella</u> per square metre during June 1967 to June 1968.

Relative abundance on 18 June, 1968 was similar to that observed previously on 26 June, 1967 (Figure 5).

In Hyalella samples, the seasonal maximum ($334/m^2$) was obtained on July 28 (Figure 5). After this date the sample density decreased and reached a seasonal minimum ($101/m^2$) on 25 March, 1968.

## Biomass

Biomass estimates were made for immature animals, pre-reproductive and reproductive adults of both species from estimated mean wet weights of 20 average-sized individuals in each life history stage. The weights for reproductive and immature animals were based on individuals collected on 1967, July 17, while those for pre-reproductive adults were based on individuals collected on 27 January, 1968. These weights were then multiplied by mean number of animals per square metre present on these dates (Table IV).

Table IV. Biomass estimates for each life history stage.

| Life history stage | Gammarus | | Hyalella | |
|---|---|---|---|---|
| | Mean wt.(g) | $g/m^2$ | Mean wt.(g) | $g/m^2$ |
| Reproductive adults | 0.0954 | 3.49 | 0.0167 | 1.75 |
| Immature animals | 0.0071 | 1.03 | 0.0038 | 0.64 |
| Pre-reproductive adults | 0.00711 | 2.91 | 0.0197 | 2.29 |

## Population Structure

Gammarus collected on 12 June, 1967 were entirely reproductive adults (Figure 6), however they had virtually disappeared from the samples by July 17. Throughout the summer and fall, about 3% of all Gammarus sampled were post-reproductive adults. In summer, immature animals made up 85% of Gammarus in the samples. These immature individuals gradually developed into pre-reproductive adults. Pre-reproductive adults formed 77% and 98% of the total individuals in the fall and winter samples (Table II). By 12 May, 1968 pre-reproductive Gammarus had developed into sexually mature adults with their newly released young making up 81% of the total individuals collected on June 18.

In the first sample (12 June, 1967) there were 53% and 47% reproductive and pre-reproductive Hyalella, respectively (Figure 6). Pre-reproductive adults matured rapidly into reproductive individuals. Reproductive adults were present all summer, but the size distribution in the samples of August 9 and August 21 were composed of both large and small reproductive animals (Figure 7). The smaller reproductive animals were interpreted as non-overwintering adults that had developed into reproductive individuals in their first summer. In winter and spring the samples consisted entirely of pre-reproductive adults. Population structure in June, 1968 was similar to that observed previously in June, 1967 (Figure 6).

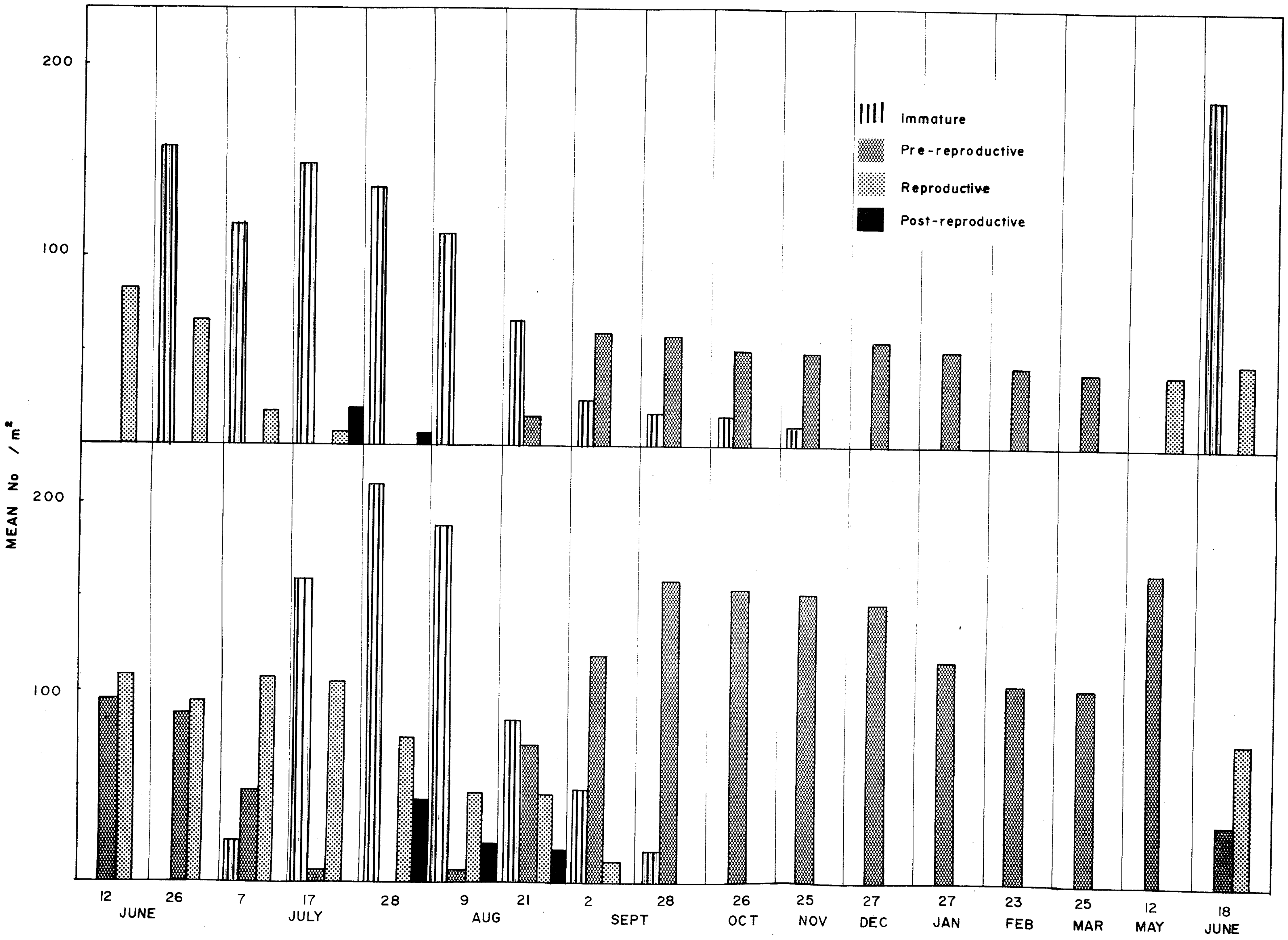

Figure 6. Population structure of Gammarus and Hyalella during June 1967 to June 1968.

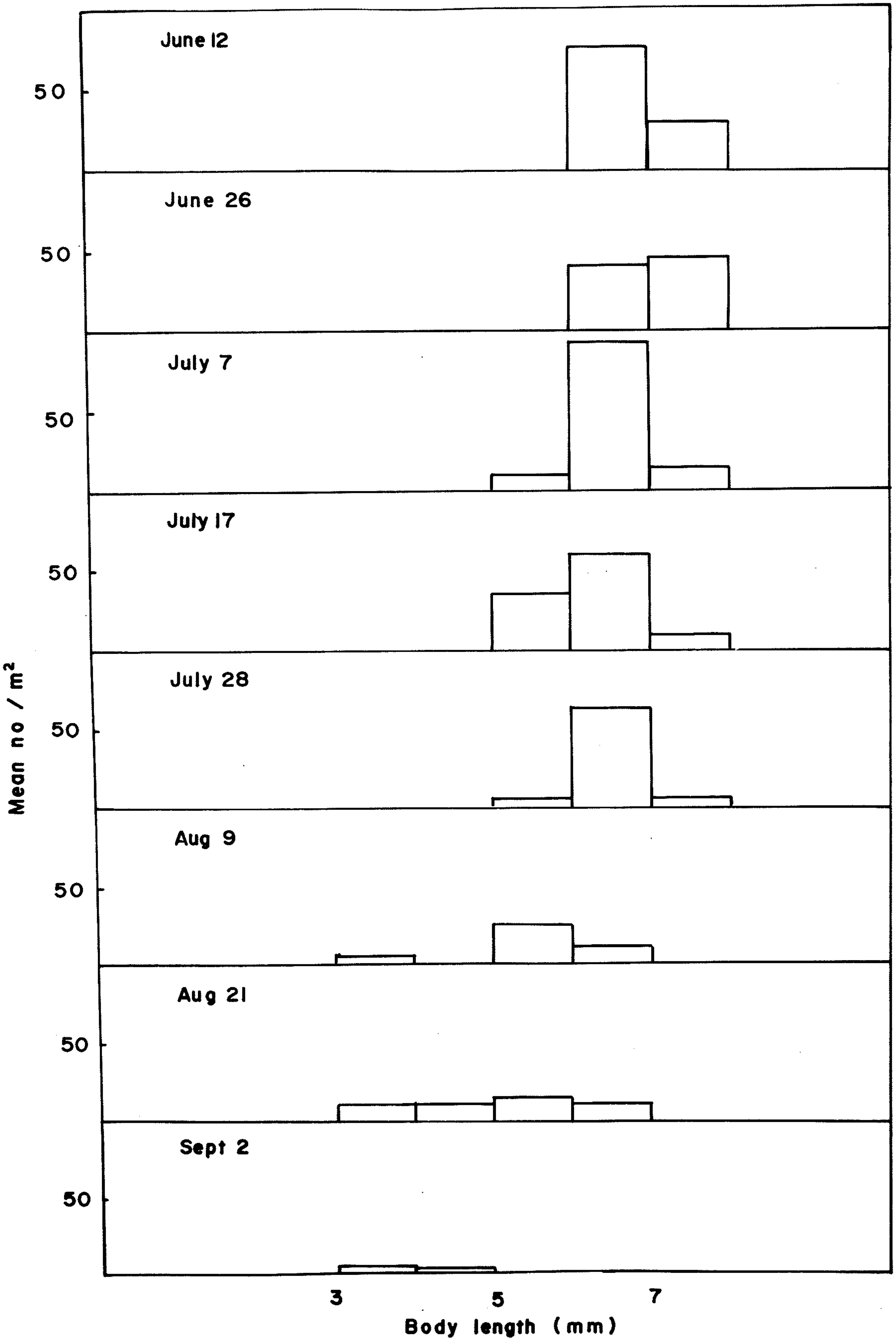

Figure 7. Length distribution of reproductive adults of *Hyalella* during 1967.

## Size Classes

The length frequency distribution of Gammarus from June 26 to August 9 was bimodal with reproductive and post-reproductive adults forming the modal group of larger individuals (10-17 mm) and immature individuals (2-7 mm) making up the second (Figure 8). During this period, the smaller individuals gradually increased in size as the larger individuals were eliminated from the samples. From August 21 to June 18 the mode of the distribution gradually shifted to the right as immature individuals increased in size becoming pre-reproductive and reproductive adults. On 18 June, 1968 the size frequency distribution was similar to that observed on June, 1967 (Figure 8).

June, 1967 samples of Hyalella consisted of large reproductive adults (5.8-7.9 mm) and smaller pre-reproductive adults (4.0-6.1 mm) (Figure 8). Throughout the summer large reproductive adults, before being eliminated from samples, gave rise to small (0.5-0.9) immature individuals, while pre-reproductive animals increased in size as they matured. After June 26 small animals (0.5-0.9 mm) were evident in the samples and their rise through the size classes could be followed (Figure 8).

For comparable life history stages Gammarus was larger than Hyalella (Table V).

Figure 8. Length distribution of Gammarus and Hyalella during June 1967 to June 1968.

Table V. Mean length and size ratios of Hyalella to Gammarus for the life history stages during 1967 and 1968.

| Life history | Mean length mm | | Ratio | |
|---|---|---|---|---|
| | Gammarus | Hyalella | Hyalella: | Gammarus |
| Immature | 4.37 | 1.76 | 1 : | 2.48 |
| Pre-reproductive | 11.05 | 5.19 | 1 : | 2.13 |
| Reproductive | 14.11 | 6.06 | 1 : | 2.33 |

Reproduction

Gravid females of Gammarus were present in 1967 from June 12 to July 17 and did not occur until 11 months later on 12 May, 1968 (Figure 9). All immature individuals overwintered before reproducing (Figure 6). Since immature animals first appeared in the samples on 26 June, 1967 and reproductive adults did not occur until 12 May, 1968, the age when reproduction first occurred was estimated as 11 months (Figure 6).

In the 1967 samples of Hyalella gravid females were present from June 26 until September 2 with a maximum number occurring on July 17 (Figure 9). On the basis of body length reproductive adults were divided into overwintering and non-overwintering adults (Figure 7). Non-overwintering adults appeared (August 9) one month after newly released young where first observed (July 7). The majority of immature animals overwintered before becoming reproductive adults, but a few animals matured in their first summer (Figure 7).

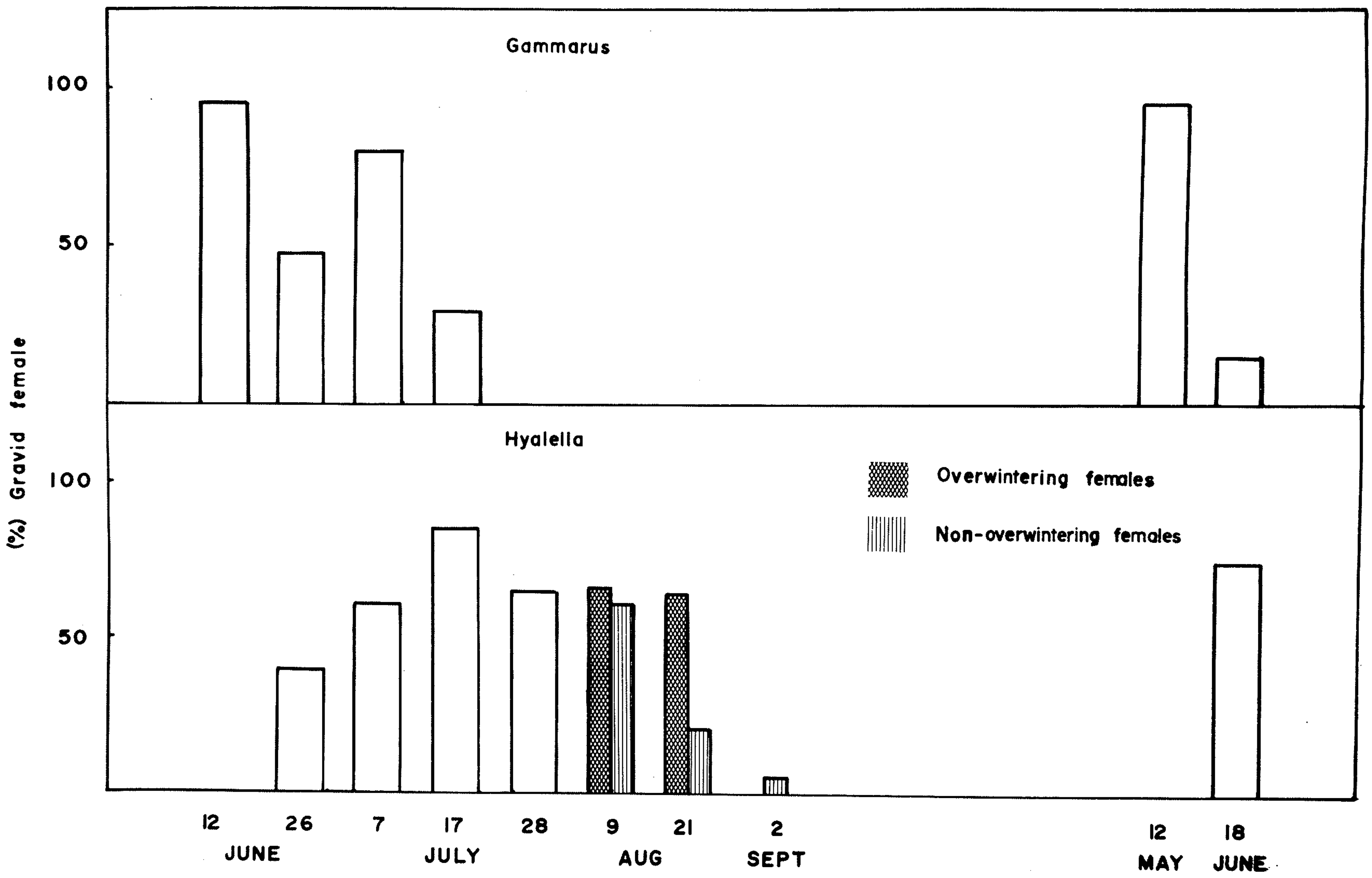

Figure 9. Distribution of percent gravid females of Gammarus and Hyalella during June 1967 to June 1968.

For both species gravid females were divided into size groups on the basis of body length and mean fecundities were determined (Table VI). Fecundity was positively correlated with female body length (Figure 10).

There was no apparent difference in the sex ratio between the two species (Table VII). Prior to reproduction the sex ratio of both species approached 1 : 1. whereas females were more abundant during the reproductive period. This might indicate that males, which were more active during precopula, had a shorter life span or that predation was selecting the larger males over the smaller females. When pre-reproductive adults first appeared in the 1967 samples of Gammarus (August 22), males were more numerous (Table VII), indicating perhaps that males matured earlier than females.

## Mortality

Instantaneous mortality rates for reproductive adults, juvenile animals after recruitment had terminated, and immature animals which occurred during recruitment are tabulated in Table VIII.

Table VIII. Instantaneous mortality rates per unit time.

| Life history | Per unit time (months) | Gammarus | Per unit time (months) | Hyalella |
|---|---|---|---|---|
| Reproductive adults | 1 | 0.044 | 1 | 0.020 |
| Juvenile animals (after recruitment) | 10 | 0.0065 | 10 | 0.0018 |
| Immature animals (during recruitment) | 1 | 1.20 | 1 | 1.30 |

Table VI. Mean fecundity per female and confidence intervals (P = 0.95) of Hyalella and Gammarus.

| Length of body (mm) | Mean fecundity | 95% Confidence interval |
|---|---|---|
| | Hyalella | |
| 3.2 | 7.0 | 4.5 - 9.5 |
| 3.7 | 9.3 | 7.0 - 11.6 |
| 4.2 | 8.9 | 5.3 - 12.5 |
| 4.7 | 8.5 | 4.8 - 12.2 |
| 5.2 | 9.3 | 4.6 - 14.0 |
| 5.7 | 14.3 | 8.7 - 19.9 |
| 6.2 | 19.5 | 18.2 - 20.8 |
| 6.7 | 21.8 | 18.6 - 25.0 |
| 7.2 | 25.9 | 22.2 - 29.6 |
| 7.7 | 26.0 | 21.7 - 30.3 |
| | Gammarus | |
| 9 | 15.4 | 11.2 - 19.6 |
| 10 | 16.2 | 10.7 - 21.7 |
| 11 | 19.0 | 13.9 - 24.1 |
| 12 | 22.7 | 16.7 - 28.7 |
| 13 | 23.3 | 17.1 - 29.5 |
| 14 | 25.8 | 18.0 - 33.6 |

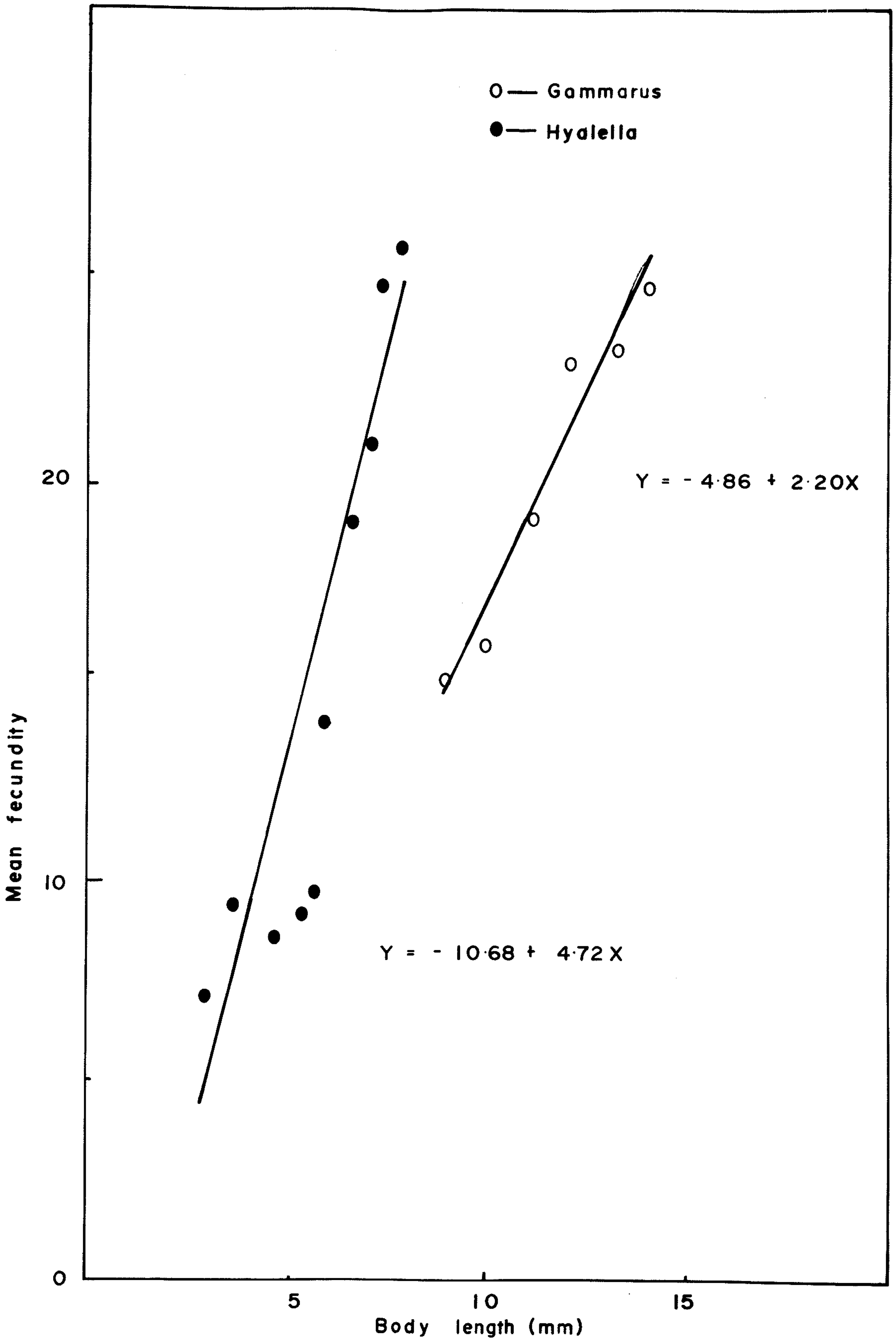

Figure 10. Female length correlated with mean fecundity.

Table VII. Number of males and females and ratios of males to females for <u>Gammarus</u> and <u>Hyalella</u> sampled during 1967 and 1968.

| Sampling date | | Gammarus | | | Hyalella | |
|---|---|---|---|---|---|---|
| | Male | Female | Ratio | Male | Female | Ratio |
| June 12 | 79 | 100 | 1 : 1.27 | 196 | 244 | 1 : 1.24 |
| 26 | 59 | 81 | 1 : 1.37 | 165 | 210 | 1 : 1.27 |
| July 7 | 20 | 27 | 1 : 1.35 | 191 | 185 | 1 : 0.97 |
| 17 | 15 | 26 | 1 : 1.73 | 119 | 151 | 1 : 1.27 |
| 28 | 3 | 4 | 1 : 1.33 | 111 | 134 | 1 : 1.21 |
| Aug. 9 | - | 2 | - | 59 | 83 | 1 : 1.41 |
| 21 | 27 | 6 | 1 : 0.22 | 149 | 145 | 1 : 0.97 |
| Sept. 2 | 58 | 60 | 1 : 1.03 | 122 | 164 | 1 : 1.34 |
| 28 | 52 | 62 | 1 : 1.19 | 120 | 173 | 1 : 1.44 |
| Oct. 26 | 57 | 54 | 1 : 0.95 | 180 | 140 | 1 : 0.78 |
| Nov. 25 | 52 | 60 | 1 : 1.15 | 210 | 141 | 1 : 0.67 |
| Dec. 27 | 69 | 69 | 1 : 1.00 | 207 | 163 | 1 : 0.79 |
| Jan. 27 | 45 | 47 | 1 : 1.04 | 140 | 121 | 1 : 0.86 |
| Feb. 23 | 34 | 38 | 1 : 1.12 | 108 | 108 | 1 : 1.00 |
| Mar. 25 | 37 | 35 | 1 : 0.95 | 110 | 117 | 1 : 1.06 |
| May 12 | 25 | 43 | 1 : 1.72 | 150 | 228 | 1 : 1.52 |
| June 18 | 20 | 82 | 1 : 4.10 | 99 | 171 | 1 : 1.73 |

Regression lines fitted by method of least squares are shown for reproductive adults and juvenile animals of both species (Figure 11). Detailed calculations for all three life history stages are included in Appendix A, Tables A-I and A-II.

## Growth

Data in Figure 12 revealed that neither the linear additive model nor the exponential model of growth would give a reasonable description of the growth pattern of immature and pre-reproductive individuals. Consequently, a smooth curve was drawn through the points by eye (Figure 12). Linear growth curves for reproductive adults were fitted by eye (Figure 12).

## Respiration

Table IX shows the mean rates of oxygen uptake of males of *Gammarus* and *Hyalella*. The rate of oxygen uptake of *Gammarus* at low water temperature was apparently greater than that of *Hyalella*, while at higher temperatures the rate of *Hyalella* was apparently greater than that of *Gammarus* (Figure 13).

An experiment was conducted to investigate the effect of acclimation on rate of oxygen uptake of *Gammarus* and *Hyalella*. Oxygen uptake was measured for animals taken directly from the field (temperature 13 C) and compared to oxygen uptake of similar sized animals that were subjected to a period of upwards acclimation to 18 C for three days followed by a period of downwards acclimation to 13 C for 70 hours. This one experiment indicated no significant difference between animals subject to upwards and downwards acclimation

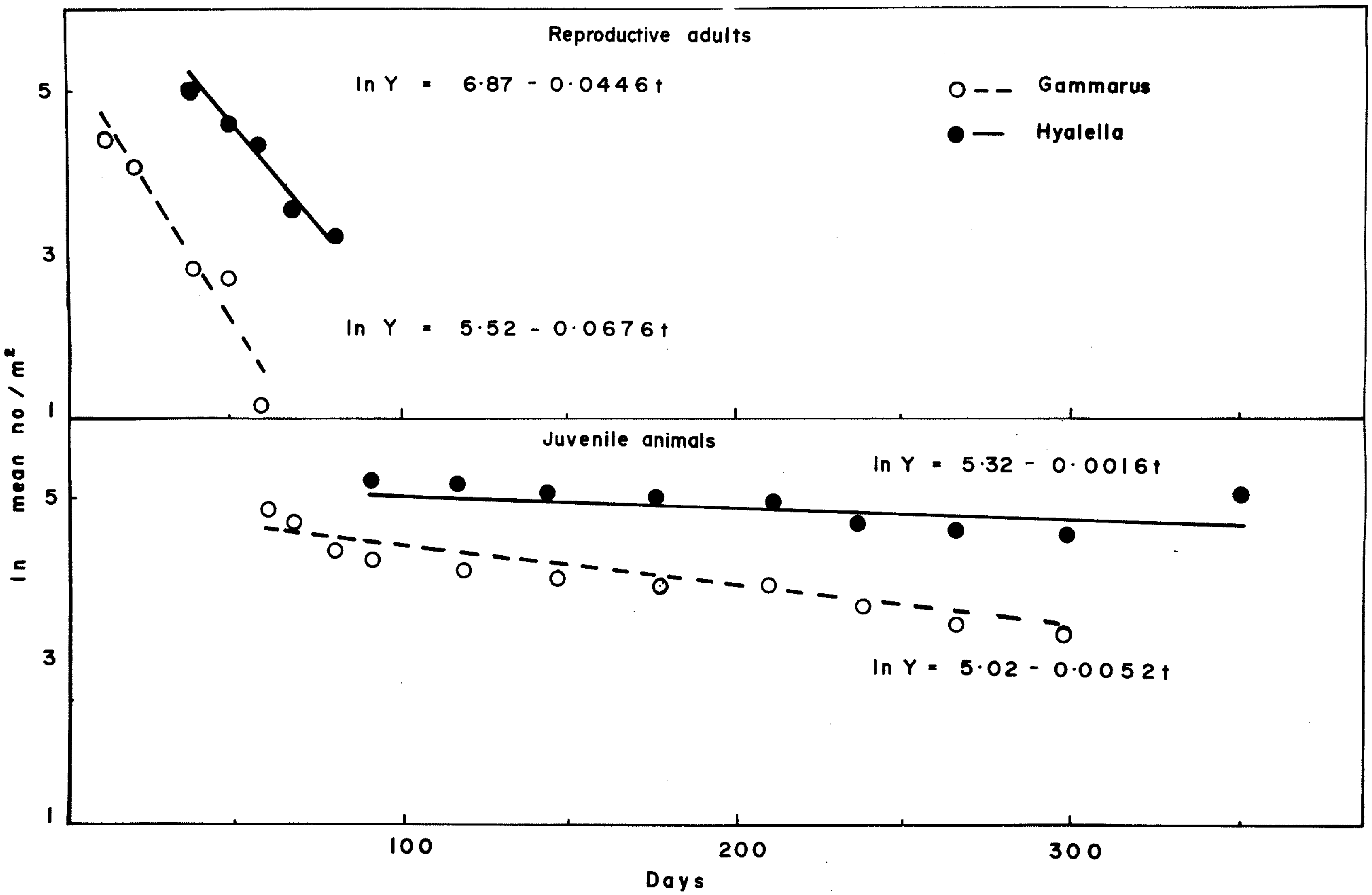

Figure 11. Natural logarithms of numbers per square metre of juvenile and reproductive Gammarus and Hyalella related to time.

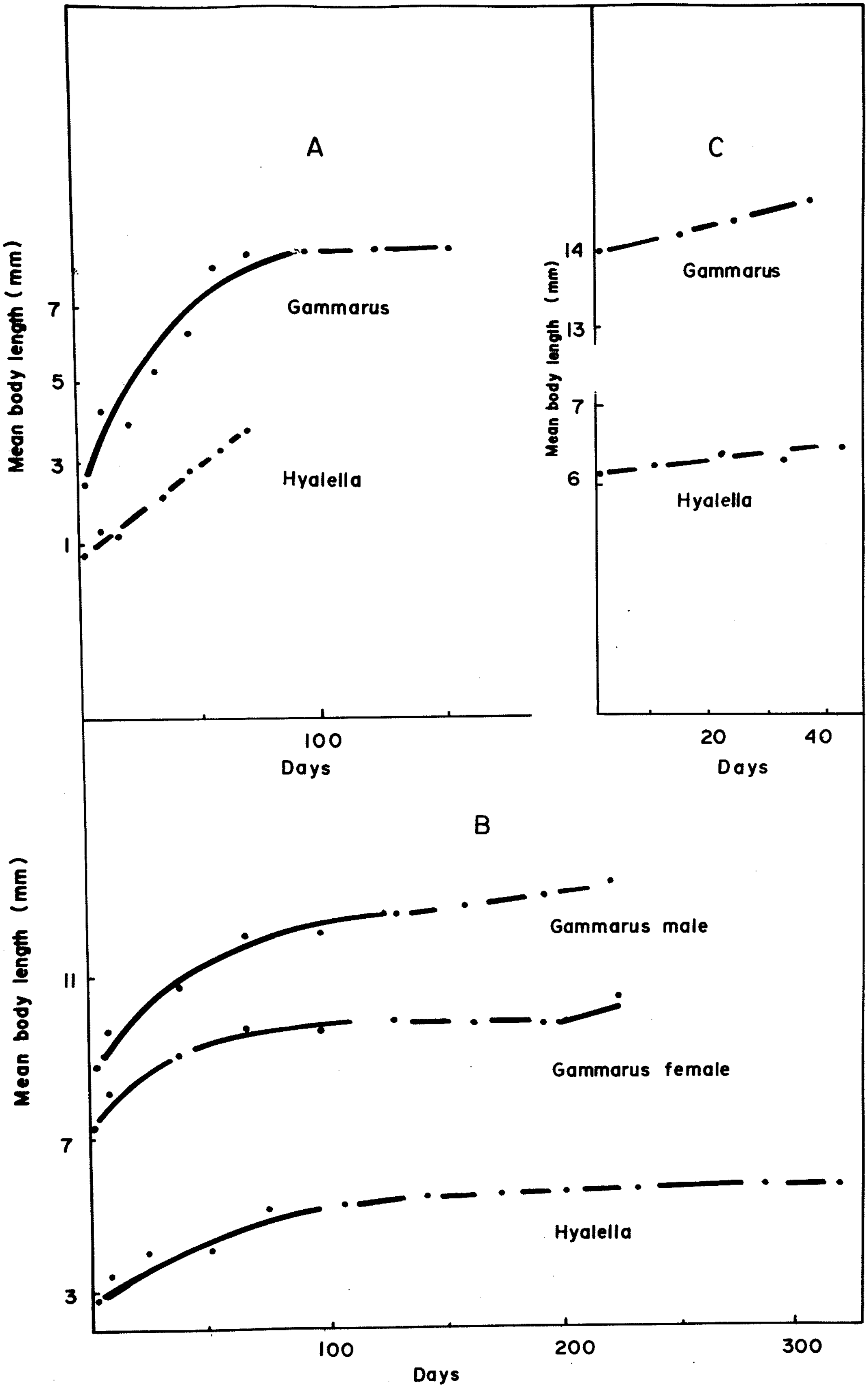

Figure 12. Growth in mean length of immature(A), juvenile(B), and reproductive(C) animals of *Gammarus* and *Hyalella* during June 1967 to June 1968.

Table IX. Mean rate of oxygen uptake and confidence intervals (P = 0.95) about the mean of <u>Gammarus</u> and <u>Hyalella</u>. The values given are in cc of oxygen consumed/gram wet wt./1 hr. N = number of animals tested at each temperature.

| Temp. | Gammarus | | Hyalella | |
|---|---|---|---|---|
| C | N | Mean<br>CI | N | Mean<br>CI |
| 1 | 21 | 0.263<br>(0.237, 0.289) | 19 | 0.074<br>(0.062, 0.086) |
| 2 | 14 | 0.271<br>(0.228, 0.314) | 16 | 0.098<br>(0.071, 0.125) |
| 5 | 15 | 0.350<br>(0.315, 0.385) | 15 | 0.215<br>(0.152, 0.278) |
| 7 | 10 | 0.364<br>(0.327, 0.401) | 12 | 0.176<br>(0.125, 0.227) |
| 13 | 5 | 0.556<br>(0.529, 0.583) | 5 | 0.538<br>(0.515, 0.560) |
| 19 | 18 | 0.573<br>(0.532, 0.614) | 10 | 0.877<br>(0.834, 0.920) |
| 20 | 9 | 0.566<br>(0.528, 0.604) | 7 | 1.069<br>(1.046, 1.088) |

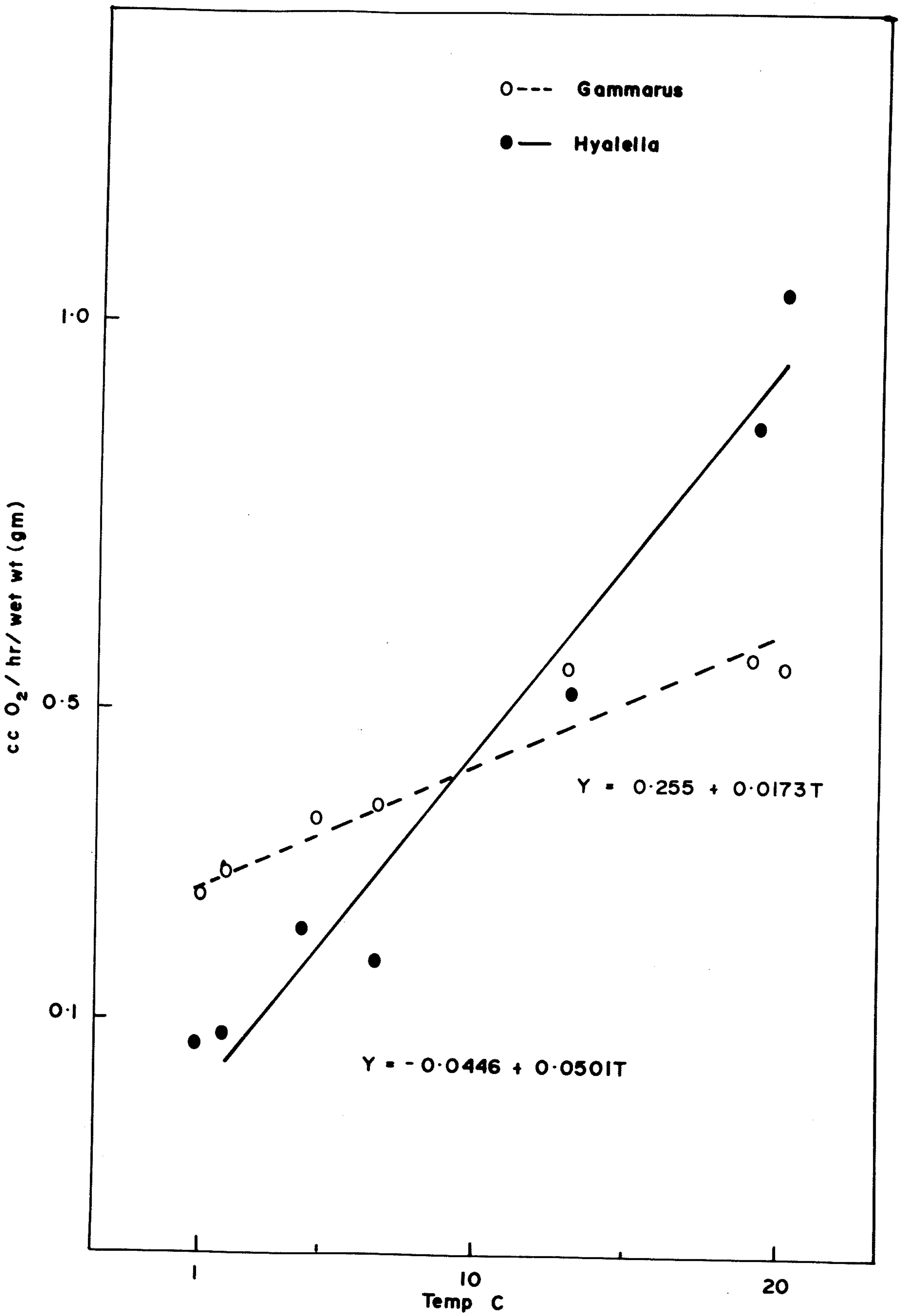

Figure 13. Rate of oxygen uptake of Gammarus and Hyalella as a function of temperature.

and those not (Table X).

## Habitat Preference

The association analysis method of Williams and Lambert (1959) produced three groups of samples for which the floral differences among groups were maximized and those within groups minimized. These homogeneous groups were Chara, Ranunculus, and Potamogeton. Complete calculations for these results are included in Appendix B, Tables B-I.

Table XI shows that substrate type (gravel, sand, silt, or mud) was not independent of the three homogeneous floral groups ($\chi^2_{6,.05} =$ 24.81, $P < 0.05$).

The results of analysis of variance calculations designed to test for significant differences in mean number of Gammarus and Hyalella and mean depth within the three homogeneous hydrophyte groups are summarized in Table XII. Complete calculations for these tests are included in Appendix C, Tables C-I.

Table XII. Results of one-way analysis of variance designed to test for significant mean number of Gammarus and Hyalella and mean depth in each of the three homogeneous hydrophyte groups.

| | F | Critical value | P 0.05 |
|---|---|---|---|
| Gammarus | 54.29 | 3.06 | * |
| Hyalella | 7.18 | 3.06 | * |
| Depth | 7.16 | 3.06 | * |

Table X. Results of the effect of introduced acclimation on mean rate of oxygen uptake of _Gammarus_ and _Hyalella_.

| | No introduced acclimation | Introduced acclimation |
|---|---|---|
| | _Gammarus_ | |
| No. of animals | 5 | 5 |
| Mean oxygen uptake (cc/hr./gm. wet wt.) | 0.456 | 0.478 |
| Confidence interval (P = 0.95) | (0.429, 0.483) | (0.445, 0.515) |
| | _Hyalella_ | |
| No. of animals | 5 | 5 |
| Mean oxygen uptake (cc/hr./gm. wet wt.) | 0.438 | 0.453 |
| Confidence interval (P = 0.95) | (0.415, 0.460) | (0.419, 0.487) |

Table XI. Chi-square 4x3 contingency table. The null hypothesis was that the three homogeneous hydrophyte groups were independent of the substrate type.

| | | Gravel | Sand | Silt | Mud | Total |
|---|---|---|---|---|---|---|
| *Chara* | Observed | 13 | 23 | 7 | 11 | 54 |
| | Expected | 8.19 | 13.03 | 16.39 | 16.39 | 54 |
| | (Obs.)$^2$/Exp. | 20.63 | 40.60 | 2.99 | 7.38 | 71.50 |
| *Ranunculus* | Observed | 6 | 6 | 6 | 0 | 18 |
| | Expected | 2.73 | 4.34 | 5.46 | 5.46 | 18 |
| | (Obs.)$^2$/Exp. | 1.32 | 0.83 | 0.66 | 0 | 2.81 |
| *Potamogeton* | Observed | 3 | 6 | 31 | 33 | 73 |
| | Expected | 11.08 | 17.62 | 22.15 | 22.15 | 73 |
| | (Obs.)$^2$/Exp. | 0.81 | 2.04 | 43.39 | 49.16 | 95.40 |
| Total | Observed | 22 | 35 | 44 | 44 | 145 |
| | Expected | 22 | 35 | 44 | 44 | 145 |
| | (Obs.)$^2$/Exp. | 22.76 | 43.47 | 47.04 | 56.54 | 169.81 |

$$\chi^2_{6,.05} = 12.6$$

$$\chi^2_{6,.05} = \Sigma\Sigma(\text{Obs.})^2/\text{Exp.} - N$$

$$\chi^2_{6,.05} = 169.81 - 145$$

$$\chi^2_{6,.05} = 24.81^*$$

The calculated "F" value of 54.29 exceeded the critical value of 3.06, $P < 0.05$ (Table XII). Hence, the null hypothesis that there was no significant difference in mean number of Gammarus within the three homogeneous hydrophyte groups was not accepted.

Similarily, there was a significant difference in mean number of Hyalella and mean depth within the three hydrophyte groups. The calculated "F" value of 7.18 for Hyalella exceeded the critical value of 3.06, $P < 0.05$, whereas for depth the calculated "F" value of 7.16 exceeded the critical value of 3.06, $P < 0.05$ (Table XII).

# DISCUSSION

The co-occurrence of <u>Gammarus</u> and <u>Hyalella</u> at the north end of West Blue Lake suggested a possible competitive relationship, contradicting Gause's contention (Gause, 1934). Odum and Odum (1953) stated that competition occurs between species wherever niches overlap. When there is considerable overlap of niches, one species will eventually displace the other (Wallace and Srb, 1964). Consequences of competition between two species inhabiting very similar spatially overlapping niches are, first, one species may eliminate the other and second, if the niches are sufficiently dissimilar both species could coexist. In the latter case, continued selection might lead to divergence and consequently, greater use of and reliance on the dissimilar aspects of the niches.

The main focus of the present study of the fundamental niches of <u>Gammarus</u> and <u>Hyalella</u> was on differences in relative abundance and life histories. However, preliminary observations were made on physiological and habitat differences.

## Population Dynamics

Since both species are essentially univoltine a repetition of annual patterns can be expected with peaks of abundance occurring at intervals of about one year (Figure 5). The highest level of population density of <u>Gammarus</u> (223/m$^2$) was observed on 26 June, 1967. At this time about 72% of the samples were composed of newly recruited immature animals. After this peak, the decreasing phase of the population density began. When the water temperatures were high and the samples contained a large precent of immatures, the downward slope of the density curve was steep. There was a slower rate of decline in fall and winter when water temperatures were low and the samples consisted almost entirely of moderately large pre-reproductive adults. The population density on 12 May, 1968 was $30/m^2$ with reproductive adults making up 100% of the samples. On June 18 the population density had increased to $214/m^2$.

The population density of Hyalella reached a maximum ($334/m^2$) on July 28, one month after the maximum numerical abundance of Gammarus. The decreasing phase was similar to the one observed for Gammarus. During fall, winter, and spring, the samples consisted of only pre-reproductive adults. There was a sudden increase in population density on 12 May, 1968 that could not be explained by reproduction as all samples observed were overwintering pre-reproductive adults (to be discussed).

The population density patterns for both species were similar except for two differences. First, Hyalella was consistently more abundant than Gammarus and secondly, the time of numerical maximum abundance was staggered by one month. Gammarus reached maximum relative abundance on June 26, while Hyalella was most abundant on July 28.

## Sampling

The above changes in population density in samples could have been caused by variability in sampling efficiency and by immigration to the north end of the lake and emigration from the north end of the lake. In fact there was evidence that the assumptions of the sampling design were satisfied. (1) Data shown in Figure 3 suggested that seasonal migrations did not occur. (2) Diel variations in distribution were not apparent on 18 and 19 June, 1968 (Figure 4). (3) Observations along the shore made on 12 May, 1968 revealed no evidence for diel variation of movement. (4) Population density patterns of both species, with the exception of May 12 samples of <u>Hyalella</u>, showed an decreasing trend after recruitment (Figure 5). (5) Population density patterns, population life history stages, and size classes indicated that samples were consistent from sampling period to sampling period. This suggested that one population of each species was being investigated.

There was, however, some evidence that migration could have occurred. (1) During the spring of 1968 amphipods were observed actively swimming at night in the open lake surface. (2) The sudden increase in population density in May 12 samples of <u>Hyalella</u> could not be explained on the basis of reproduction.

Both seasonal and diel movements have been reported for several benthic organisms. For example, Wodsedalek (1912) reported that <u>Heptagenia</u> <u>interpunctata</u> (may-fly nymph) migrated out of the littoral zone in autumn and returned to shore in spring. Similarily, Eggleton (1931) observed seasonal differences in distribution for *Chaoborus*, *Chironomus*, *Limnodrilus*, *Pisidium* and nematodes. Moon (1940) reported diel variations in distributions of *Gammarus pulex*, *Sigara* nymphs, and the mite *Hygrobates naicus*. Jónasson (1955), however, questioned some reports of seasonal migrations and suggested that in some cases the apparent seasonal variations in numbers of a species are artifacts that arise as the result of the mesh gauge employed and size of the life history stage. Mundie (1959) observed on the basis of several nights sampling in Lac La Ronge, Saskatchewan, that both *Hyalella azteca* and *Pontoporeia affinis* underwent vertical diel migrations. Similarily, Marzolf (1965) observed that adults of *Pontoporeia affinis* underwent vertical diel migrations. He suggested that migrations facilitated genetic continuity between otherwise isolated benthic populations.

It seems probable that during spring of 1968 at West Blue Lake there was a period during which *Hyalella* underwent migration. This migration apparently did not occur during sampling periods of 1967.

## Reproduction

The reproductive cycles of *Gammarus* and *Hyalella* were different. *Gammarus* reproduced in spring and early summer, while *Hyalella* reproduced in summer. Samples of *Gammarus* collected 12 June, 1967, 17 days after the lake was free from ice, contained

Similarily, gravid females were first present in samples collected 12 May, 1968, about 14 days after ice had disappeared from the lake surface (Figure 9). Since precopula was not observed in the March 25 samples, mating and copulation probably would have occurred between March 25 and May 12.

Reproductive adults of Gammarus were not present in 28 July, 1967 samples, and hence reproduction had terminated by this date (Figure 6). Consequently, new recruits of Gammarus were released into the population in 1967 between June 12 and July 28 with the majority of gammarids being released by June 26 (Figure 6).

In contrast, Hyalella was observed in precopula on 12 June, 1967 and on 18 June, 1968. Gravid females were not present in samples of Hyalella until 26 June, 1967 (Figure 9). Since reproductive adults were not present in samples after September 2, reproduction apparently terminated between September 2 and September 28. In 1967 new recruits were released into the population between June 26 and September 28 (Figure 6). However, the majority of young were released by July 28, one month after Gammarus had released the majority of its young (Figure 6).

Age at which reproduction first occurred for Gammarus was estimated as 11 months (Figure 6). A similar age was estimated for the majority of new recruits of Hyalella. Early summer recruits of Hyalella, however, matured the same summer (Figure 7). Newly released young were first observed in samples of July 7, and by August 9 samples contained newly recruited adults. Hence, age at which reproduction first occurred was about one month. The average mud-water interface temperature during this period was 19.4 C.

The results concerning the reproduction of <u>Gammarus</u> agree with those of Clemens (1950) and Menon (1966), whereas the results of <u>Hyalella</u> do not agree completely with what other investigators have found. Bovee (1951), in the laboratory, observed that at 20-22 C maturation occurred on the average in 60 days. Cooper (1965) reported that majority of young obtained maturity in their first summer in Sugarloaf Lake. In this lake water temperature rises to 20 C by mid-May and varies between 22 C and 27 C until the first of August. In addition, Cooper (1965) observed that at a constant temperature of 20 C maturation occurred in 36 days, while at 25 C it occurred in 33 days. Mathias (1967) reported that at an average summer and mud-water interface temperature of about 18 C maturation did not occur until the following summer.

It is apparent that water temperature is important in determining age of maturation. The average summer water temperature at the north end of West Blue Lake was intermediate between Sugarloaf Lake (Cooper, 1965) and Marion Lake (Mathias, 1967). Probably as a consequence of this, the time required to reach maturity was somewhat intermediate to that reported by Cooper (1965) and Mathias (1967).

## Mortality

Figure 12 suggested that reproductive adults and juvenile animals of both species are characterized by an exponential rate of decline, therefore the assumption of the mathematical expression was satisfied. Reproductive adults and juveniles of Gammarus had a higher mortality rate than those of Hyalella (Table VIII).

It is interesting to note the low mortality rates of juvenile animals of both species. Cooper (1965) reported low mortality rates for overwintering juveniles of Hyalella.

To estimate mortality that occurred during recruitment phase of life history, an estimate of number of young recruits entering the population should be made. The number of estimated young recruits is a function of the age structure of the egg population, the mortality rates of the adult animals, and developmental rate of the eggs (Cooper, 1965).

Cooper (1965) used a mathematical model to estimate the proportion of eggs expected to hatch. This model assumed that rate of decline of adult animals was exponential, age distribution of eggs was stable, i.e. there was an equal number of young and mature eggs, all eggs counted were viable, and laboratory incubation times were equivalent to field conditions.

In this study, crude observations of the age distribution of eggs suggested that it was not stable. In addition, laboratory temperature-specific incubation rates might be significantly different from field conditions. Consequently, the assumptions of Cooper's model could not be fulfilled.

In Gammarus populations all females become gravid in a relatively short period of time, and after reproduction ceased females were eliminated (Figure 9). In addition, there was a relatively short period of overlap between presence of gravid females in the population and presence of young. Thus, in a relatively short time, the standing crop of eggs was released to become the standing crop of juveniles.

In Hyalella populations, unlike those of Gammarus, there was a longer period of overlap between presence of reproductive adults in the population and presence of young (Figure 6). However, the size distribution of reproductive adults (Figure 7) and age structure of eggs suggested that reproduction might have a synchronization similar to that of Gammarus, i.e. females became gravid in a short period of time and died after releasing their brood, but instead of essentially one reproductive period there were three. That is, large overwintering reproductive adults reproduced during early summer, smaller overwintering reproductive adults reproduced during mid-summer, and small nonwintering adults reproduced in late summer. Estimates of young recruits expected to enter the population were made for each size group of reproductive adults.

The estimates of mortality on the immature animals are at the very best rough estimates. Many factors such as, temperature specific incubation rates, age structure of eggs observed, duration of any instar at ambient temperatures, and viability of eggs counted, should be considered in estimating the number of new recruits expected to enter the population. In this study, however, the data did not permit the investigator to take into account these factors. Consequently the estimates of mortality on the immature animals are interesting only in terms of speculation.

With the above considerations immature animals of Hyalella appear to have a slightly higher rate of mortality than those of Gammarus. Since immature Hyalella are smaller (0.7 - 1.0 mm) than those of Gammarus (2.3 - 2.7 mm), there was a greater probability of losing the smaller individuals during the sorting process. Hence, the mortality rate of immature animals of Hyalella may be overestimated.

## Interaction of Reproduction and Mortality

Cole (1957) pointed out that "it is to be expected that natural selection will be influential in shaping life history patterns to correspond to efficient populations". Cole (1957) described the following ways a species might increase its intrinsic rate of natural increase: decrease in age when reproduction occurs, increase in brood size, increase in number of broods, increase in number of females, and increased survival to the end of reproductive life.

Using the above survivorship and fecundity data, estimates of intrinsic rate of natural increase (r) and net reproductive rates ($R_o$) were made for both species. Fecundity schedules

(Table XIII) were constructed with following columns (Southwood, 1966):

$x$ = pivotal age

$l_x$ = number females alive during given age interval

$m_x$ = number living females born per female in each age interval

$l_x m_x$ = total number of female births in each age interval

The assumptions were: (1) Mortality rates of female animals were equivalent to those observed for both males and females. (2) All eggs observed were viable. (3) Sex ratio was 50: 50.

Table. XIII. Fecundity schedule for _Gammarus_ and _Hyalella_.

| (months) | $l_x$ | $m_x$ | $l_x m_x$ |
|---|---|---|---|
| _Gammarus_ | | | |
| 0 | 1.00 | - | - |
| 1 | .16 | - | - |
| 11 | .16 | 10 | 1.60 |
| _Hyalella_ (do not mature during their first summer) | | | |
| 0 | 1.00 | - | - |
| 2 | .13 | - | - |
| 11 | .13 | 10 | 1.30 |
| _Hyalella_ (mature during their first summer) | | | |
| 0 | 1.00 | - | - |
| 1 | .02 | 3.5 | .07 |
| 11 | .02 | 10 | .20 |

The number of times a population will multiply per generation is described by the net reproductive rate $R_o$, which is (Southwood, 1966):

$$R_o = \int_0^\infty l_x m_x \; d_x$$

which was approximated by:

$$R_o = \Sigma \; l_x m_x$$

The net reproductive rate for Gammarus was estimated as 1.60 and for Hyalella as 1.30 and 0.27. Values in excess of one imply an increasing population (Southwood, 1966).

The growth rate of a population is (r) in the equation:

$$N_t = N_o e^{rt}$$

The parameter (r) describes population growth under conditions of an unlimited environment and with a stable age distribution this parameter becomes a constant (Southwood, 1966). This has generally been considered to represent the intrinsic rate of natural increase, the maximum value of (r) possible for the species under the given physical and biotic environment is denoted as $r_m$, and can be expressed as (Southwood, 1966):

$$\int_0^\infty e^{-r_m x} \; l_x m_x \; d_x = 1$$

The animals designated as 1 are the offspring of the breeding animals that reproduced in the interval (t). At time (t-1) there were $e^{-r_m}$ individuals of age 0 and 1, of these have survived to provide the $l_1 e^{-r_m}$ individuals of age 1 alive at time t. At time (t-2) there were $e^{-2r_m}$ individuals born and they are represented by $l_2 e^{-2r_m}$ individuals at time t. In general, at time (t-x) there were $e^{-r_m x}$ individuals born and at time (t) they are represented by $l_x e^{-r_m x}$ individuals. The number of individuals born to animals alive at time (t) is $\int_0^\infty l_x m_x e^{-r_m x}$ which equals 1 (Slobodkin, 1966).

The equation above can be approximated to:

$$\Sigma \; e^{-r_m x} \; l_x m_x = 1$$

The intinsic rate of increase ($r_m$) for Gammarus was estimated as 0.52 per year and for individuals of Hyalella that did not reproduce in their first summer as 0.29 per year and -0.132 per year for those individuals that did reproduce in their first summer.

When $R_o = 1$, $r = 0$; the population will be stationary. Gammarus population would be stationary, if there was a 6% increase in mortality of juvenile females and Hyalella population would be stationary if there was a 3% increase in mortality of juvenile females (not including those individuals that reproduced in their first summer).

The reproduction data and its interaction with mortality suggested that estimates of intrinsic rates of natural increase were slightly higher for Gammarus than for Hyalella. If net reproductive rates for both cohorts of Hyalella are summed (i.e. 1.30 + 0.27), then the value for Hyalella was similar to one for Gammarus.

Since the mortality estimates on immature animals enter into the calculations of fecundity schedules, the net reproductive rates and intrinsic rates of natural increase are interesting from the point of view of spectulation.

## Growth

Growth rates as revealed by Figure 12 were underestimated for immature and pre-reproductive life history stages, since smaller sized individuals were being recruited into these life history stages. This was especially true for immature animals of *Hyalella* and early pre-reproductive adults of *Gammarus*. Similarily, reproductive adult growth curves represent true growth rates only if mortality rates are equal for all adult size classes. No recruitment of adults occurs to depress the adult growth curves.

With the above consideration, the data suggests that pre-reproductive adults of *Gammarus* grew in winter, whereas pre-reproductive adults of *Hyalella* did not. It appears that *Hyalella* required warmer water temperatures for growth and subsequent maturation. This is important in terms of time when reproduction occurred. The above contention is supported by the following data concerning metabolism in the two species.

## Respiration

Data in Figure 13 suggests that the rate of oxygen uptake of *Gammarus* at low water temperatures was greater than that of *Hyalella*, while at higher temperatures the rate of Hyalella was greater than Gammarus. However, four sources of experimental error should be considered.

(1) Animals measured at 1 C and 2 C were initially exposed to higher water temperatures (about 5 C) for two to three days, and then acclimated down to 1 C and 2 C for 70 hours. Sprague (personal communication) pointed out that amphipods like most animals acclimate upwards quickly but downwards very slowly. This might mean that test animals measured at 1 C and 2 C were actually acclimated to slightly higher temperatures.

An experiment was conducted to investigate the effect of introduced acclimation on the rate of oxygen uptake of Gammarus and Hyalella. The results indicated no significant difference between animals subjected to upwards and downwards acclimation and those not subjected to any acclimation. (Table X). Since both species were treated similarily, a comparison could be made. However, the difference in rates of oxygen uptake might not be a temperature response, but a difference in response to acclimation. Difference in their rate of oxygen uptake at 5 C and 7 C, however, suggested a temperature response.

(2) Muscular activity of the experimental animals was not controlled. Animals placed in test chambers were initially very active, but their activity decreased with time. All measurements were made one hour after placing animals in test chambers. During the test period their activity was variable.

(3) Presence or absence of food in the gastro-intestinal tract of experimental animals was not controlled. Animals were taken directly from the sampling area or acclimation jars and placed in test chambers.

(4) *Gammarus* was larger than *Hyalella*. Since small animals have a higher rate of oxygen uptake per gram of body weight than larger ones, difference in their rate of oxygen uptake might be attributed to a size difference. On the basis of size alone, one would expect the rate of oxygen uptake of *Hyalella* to be greater than that of *Gammarus*. During fall, winter, and spring, the data indicated the opposite. If these data were adjusted for size, the difference between the species might be greater. In summer, the rate of oxygen uptake of *Hyalella* was apparently greater than that of *Gammarus*. Since *Hyalella* is smaller than *Gammarus*, this difference that occurred in summer might be explained on the basis of size. Consequently, the summer data were suspect.

With these considerations, the data suggest that there is a distinct difference in the rate of oxygen uptake of *Gammarus* and *Hyalella*. *Gammarus* was apparently better adapted to low water temperatures than *Hyalella*.

## Niche Diversity

Mayr (1963) discussed ways in which coexisting species have either reduced or avoided competition. These factors are discussed here in relation to *Hyalella* and *Gammarus*.

Habitat preference minimizes competition. The results indicated that *Gammarus* showed an apparent habitat preference for *Chara* in deeper waters and that *Hyalella*, on the other hand, seemed to prefer *Potamogeton* in shallower water (Table XII).

Both species display a wide spectum of hydrophyte preferences (e.g. Jackson, 1912; Wienert, 1950; Ali, 1960; Cooper, 1965). Menon (1966) observed that both *Hyalella* and *Gammarus* had similar habitat preferences. Mathias (1967) reported that *Hyalella* was more abundant in shallow water than in deeper water where *Crangonyx* was more numerous.

Hydrophyte groups were not independent of particle size of substrate (Table XI). Consequently, substrate may influence the distribution of *Gammarus* and *Hyalella*. In this study an attempt was made to investigate the relation between substrate and the distribution of *Gammarus* and *Hyalella*. The sediments were categorized crudely to particle size as gravel, sand, silt, and ooze. There was a greater number of coarse sediments observed in *Chara* group than in *Potamogeton* group, and a greater number of fine sediments in *Potamogeton* group than in *Chara* group (Table XI). Substrate relationships should be investigated further.

Marzolf (1963) reported that the distribution of *Pontoporeia affinis* in the mouth of Grand Traverse Bay in Lake Michigan was not correlated with depth, particle size, or organic matter, but with number of bacteria in sediments. Croker (1967) showed in the laboratory that the intertidal amphipods, *Neohaustorius schmitzi* and

*Haustorius* sp., preferred cleaner substrate over a silty one and correlated this substrate preference with their distribution in the field.

Figure 3 suggested that *Gammarus* lives in deeper waters whereas *Hyalella* lives in shallower waters. In addition, Bousfield (1958) reported that *Hyalella* is restricted in distribution to bodies of water that reach a monthly mean summer temperature of 10 C, while *Gammarus* is found in bodies of water that are cool to cold in summer.

The respiration experiments suggested that *Gammarus* was better adapted to low water temperatures than *Hyalella* (Figure 13). Data shown in Figure 12 supported this suggestion. *Gammarus* grew in winter, whereas *Hyalella* did not.

Depth distributions, hydrophyte cover, substrate, temperature, and oxygen were all intercorrelated factors. For example, depth distribution probably reflects temperature and oxygen concentration tolerances and preferences. The fact that a greater number of *Gammarus* was observed in *Chara* beds in deeper waters does not necessarily mean that *Chara* and depth are the important factors in the distribution of *Gammarus*, since these factors may be correlated with other factors that were not included in this investigation. For example, important factors might be epiphytic growths on *Chara* or number of bacteria in substrate which is in turn correlated with depth and hydrophyte present.

The data suggested that Gammarus lives in deeper waters with Chara sp and lower water temperatures whereas, Hyalella lives in shallower waters with Potamogeton and higher water temperatures. This niche difference might ameliorate competition between Gammarus and Hyalella.

The most obvious dissimilarity between the two species was their difference in size (Table V). Size differences may be accompanied by differences in the type of food utilized by the two species which would therefore reduce competition. According to Hutchinson (1951) niche diversification might be on the basis of a size difference. There are examples in the literature that supports his hypothesis. For example, calanoids, Diatomus laticeps Sars and D. gracilis Sars, coexisted in the plankton of Lake Windermere. They were distinguished by a size difference which was correlated with differences in food taken; D. laticeps the larger species, feeding chiefly on Melosira and D. gracilis on minute algal particles (Fryer, 1954). Differences were found in feeding habitats of two coexisting species of Coregonus (Nilsson, 1958). The smaller species with numerous gillrakers (C. peled) fed mainly on Entomostracans (mostly Bosmina), while C. pidschian fed on larger invertebrates such as Mollusca, Trichoptera, and Chironomidae. It was, however, also shown that there was no simple relationship, as the food eaten varied annually and seasonally and there were large deviations within the species (Nilsson, 1958). Croker (1967), in the laboratory, showed that larger intertidal amphipods, Haustorius sp, ingested larger sized particles than the smaller Neohaustorius schmitzi.

Hutchinson (1959) collected together a number of skull measurements in mammals and culmen lengths in birds. He showed that where species co-occurred the ratio of their skull size of culmen length ranged from 1: 1.2 to 1: 1.4 with a mean ratio of about 1: 1.3. He suggested that this latter figure may tentatively be used as an indication of the kind of difference necessary to permit two species to co-occur in different niches but at the same trophic level. In this study measurements were not made of mouth parts or head regions. Ratios for mean body lengths of the three life history stages of Gammarus and Hyalella ranged from 1: 2.1 to 1: 2.5, and averaged 1: 2.3 for the year (Table V). These ratios might be an indication of the kinds of size differences permitting the coexistence of Gammarus and Hyalella at the same trophic level. Further work is required to study the size of particles ingested by the various life history stages.

Maintenance of size differences and ratios was supported by the staggering of reproductive peaks. For birds or mammals, where the growth period is short compared with life span, Hutchinson (1959) postulated that niche separation may be possible simply through genetic size differences, while in insects with relatively longer growth periods, a seasonal difference in reproduction might be important. For the maintenance of size ratios, the larger species must never breed later than the smaller one (Hutchinson, 1959). Figure 6 supported this hypothesis, i.e. Gammarus reproduced earlier than

Hyalella. In addition, competition is probably reduced through the temporal isolation of potentially competing life history stages by staggering of the reproductive periods.

There are probably other dissimilarities not investigated in this study that might limit competition. Differences in behavioural mechanisms such as migration activity, swimming ability, and physical and chemical responses might exist. Experiments should be conducted on these mechanisms.

Importance and operation of differences is probably related to environmental factors and population densities. There was some evidence for this. Menon (1966) working in Big Island Lake reported that Gammarus was relatively more abundant than Hyalella. At the north end of West Blue Lake, Gammarus was less numerous than Hyalella. Big Island Lake, in terms of physical, chemical, and biological factors was very different from West Blue Lake. Big Island Lake was shallow (maximum depth 2.5 m) eutrophic, and hydrogen sulphide gas present in winter, and did not have a fish population.

In West Blue Lake, amphipods were an important item for Walleye (Glenn and Ward, 1968). Fish predation might be actively selecting for the larger Gammarus over Hyalella. Cooper (1965) reported that Yellow perch (Perca flavescens) actively selected for larger sized Hyalella over smaller ones. In addition, the deeper water preference of Gammarus might influence fish predation. Fish predation in West Blue Lake may influence relative numbers of Gammarus and Hyalella.

In terms of numbers, Hyalella was more abundant than Gammarus. However, the body size of Gammarus was much larger than that of Hyalella (Figure 8). Crude biomass estimates were calculated on the basis of mean weights of averaged sized individuals in each life history stage (Table IV). Gammarus had a mean biomass of 2.17 $g/m^2$ while Hyalella had 1.56 $g/m^2$.

Differences between Gammarus and Hyalella probably have varying degrees of importance in reducing or avoiding competition. Competition is probably reduced by the staggering of the reproductive periods through the temporal isolation of potentially competing life stages. Size differences between the two species may be correlated with differences in the type of food utilized. Hence, niche diversification may be on the basis of a size difference. Niche diversification may be on the basis of habitat divergence since differences in depth distribution, hydrophyte, substrate, and temperature preferences, and oxygen requirements may aid in maintaining Gammarus and Hyalella spatially isolated.

Mechanisms, such as capacity for utilizing alternative resources, habitat differences, behavioural, and structural specializations, are probably operating that tend to direct Gammarus and Hyalella into different ways of life.

Gammarus and Hyalella may not have the same fundamental niche requirements. Differences in these requirements may allow these two coexisting species to live in the north end of West Blue Lake without entering into severe competition for those resources of the environment essential for their existence.

# SUMMARY AND CONCLUSIONS

Differences in fundamental niche characteristics of _Gammarus lacustris lacustris_ Sars and _Hyalella azteca_ (Saussure) were studied in the littoral zone at the north end of West Blue Lake, Manitoba. The approach was to sample the amphipod population quantitatively at regular intervals comparing differences in relative abundance, reproduction, mortality, growth, and habitat preferences.

From June 1967 to June 1968, 10,538 amphipods were sampled. _Gammarus_ formed 33% of the total samples, while _Hyalella_ made up 67%. _Hyalella_ was consistently more abundant than _Gammarus_ except for the June samples. However, throughout the year _Gammarus_ had an estimated mean biomass of 2.17 $g/m^2$, while _Hyalella_ had 1.56 $g/m^2$.

For both species the samples were divided into immature, pre-reproductive, reproductive, and post-reproductive individuals, and into size classes based on total body length. Ratios of mean body lengths of _Hyalella_ to _Gammarus_ for all life history stages averaged 1: 2.3 for the year.

_Gammarus_ reproduced in spring and early summer, whereas _Hyalella_ reproduced throughout the entire summer. _Gammarus_ released its young a month before _Hyalella_. Eight percent of the total gravid _Hyalella_ reached maturity within the same summer. The majority of new recruits of _Hyalella_ obtained maturity the following summer. All new recruits of *Gammarus* overwintered before maturing. The mean length and brood size of gravid *Hyalella* and *Gammarus* were 6.2 mm, 11.5 mm, and 19.1 eggs, 20.4 eggs respectively.

Estimates of instantaneous mortality rates were made for immature and juvenile animals, and for reproductive adults. For both species, mortality rates were higher for immature animals than for juvenile individuals and reproductive adults. Both juvenile individuals and reproductive adults of *Gammarus* had a greater mortality rate than those of *Hyalella*, but immature *Hyalella* had a greater rate than those of *Gammarus*.

Changes in mean body length were followed for immature, pre-reproductive, and reproductive individuals of *Gammarus* and *Hyalella*. *Gammarus* grew in winter whereas *Hyalella* did not.

Using a Scholander respirometer, the rate of oxygen uptake of *Gammarus* and *Hyalella* were compared at seasonal habitat temperatures. At low water temperatures, the rate of oxygen uptake was apparently greater for *Gammarus* than *Hyalella*.

Habitat preference was investigated by comparing relative abundance with different conditions of macrophyte species, and depth. *Gammarus* showed an apparent preference for *Chara* and deeper waters, while *Hyalella* apparently preferred *Potamogeton* and shallower waters.

*Gammarus* and *Hyalella* probably do not have the same fundamental niche requirements. Habitat divergence suggested by differences in depth distribution, hydrophyte, substrate and temperature preferences, and oxygen requirements may allow *Gammarus* and *Hyalella* to coexist in the study area without entering into severe competition for those resources of the environment essential for their existence. Differences in body size between *Gammarus* and *Hyalella* may indicate a niche diversification based on size. Consequently, competition between *Gammarus* and *Hyalella* is probably ameliorated.

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## APPENDIX A

Instantaneous Mortality Rates

Simple

Table A-I. Sample linear regression analysis of natural logarithms of numbers per square metre of juvenile and reproductive Gammarus and Hyalella. The instantaneous mortality rate (i) is slope of line $\ln N_t = \ln N_o - it$.

GAMMARUS REPRODUCTIVES

| Sampling date | | Numbers /$m^2$ | ln N /$m^2$ | Predicted ln N/$m^2$ | ln $N_o$ | -i |
|---|---|---|---|---|---|---|
| June | 12 | 79 | 4.37 | 4.71 | 5.52 | 0.0676 |
| | 26 | 62 | 4.13 | 3.77 | | |
| July | 7 | 21 | 2.92 | 3.02 | | |
| | 17 | 19 | 2.90 | 2.34 | | |
| | 28 | 3 | 1.12 | 1.60 | | |

HYALELLA REPRODUCTIVES

| Sampling date | | Numbers /$m^2$ | ln N /$m^2$ | Predicted ln N/$m^2$ | ln $N_o$ | -i |
|---|---|---|---|---|---|---|
| July | 7 | 163 | 5.09 | 5.22 | 6.87 | 0.0446 |
| | 17 | 114 | 4.74 | 4.77 | | |
| | 28 | 108 | 4.68 | 4.28 | | |
| Aug. | 9 | 36 | 3.58 | 3.79 | | |
| | 21 | 25 | 3.22 | 3.26 | | |

Table A-I. (continued)

GAMMARUS JUVENILES

| Sampling date | | Numbers /m$^2$ | ln N /m$^2$ | Predicted ln N/m$^2$ | ln $N_o$ | -i |
|---|---|---|---|---|---|---|
| July | 28 | 139 | 4.96 | 4.72 | 5.02 | 0.0052 |
| Aug. | 9 | 111 | 4.72 | 4.66 | | |
| | 21 | 83 | 4.43 | 4.60 | | |
| Sept. | 2 | 80 | 4.39 | 4.53 | | |
| | 28 | 70 | 4.28 | 4.40 | | |
| Oct. | 26 | 68 | 4.23 | 4.25 | | |
| Nov. | 25 | 60 | 4.09 | 4.10 | | |
| Dec. | 27 | 58 | 4.06 | 3.93 | | |
| Jan. | 27 | 41 | 3.71 | 3.76 | | |
| Feb. | 23 | 36 | 3.58 | 3.62 | | |
| Mar. | 25 | 32 | 3.47 | 3.47 | | |

HYALELLA JUVENILES

| Sampling date | | Numbers /m$^2$ | ln N /m$^2$ | Predicted ln N/m$^2$ | ln $N_o$ | -i |
|---|---|---|---|---|---|---|
| Sept. | 2 | 184 | 5.21 | 5.17 | 5.32 | 0.0015 |
| | 28 | 185 | 5.22 | 5.13 | | |
| Oct. | 26 | 160 | 5.08 | 5.09 | | |
| Nov. | 25 | 156 | 5.05 | 5.04 | | |
| Dec. | 27 | 148 | 5.00 | 5.32 | | |
| Jan. | 27 | 116 | 4.75 | 4.94 | | |
| Feb. | 23 | 108 | 4.68 | 4.89 | | |
| Mar. | 25 | 101 | 4.62 | 4.84 | | |
| May | 12 | 168 | 5.10 | 4.77 | | |

Table A-II. Estimations of the number of immature animals lost during recruitment.

| | Gammarus | Hyalella |
|---|---|---|
| No. of eggs observed at beginning of recruitment. | $940/m^2$ | $2216/m^2$ |
| No. of eggs lost due to female mortality. | $63/m^2$ | $96/m^2$ |
| No. of new recruits expected. | $877/m^2$ | $2120/m^2$ |
| No. of new recruits (all instars) observed. | $139/m^2$ | $175/m^2$ |
| No. of recruits lost. | $738/m^2$ | $1945/m^2$ |
| Instantaneous mortality rate (per month) ($N_t = N_o e^{-it}$) | 1.20 | 1.31 |

# APPENDIX B

Williams and Lambert (1959). Association Analysis.

Table B-I. Values of $\chi^2$ ($\chi^2$ uncorrected) for association between pairs of hydrophyte species. Significant values based on corrected, are indicated by (*) and imply that something other than random variation is causing the pair of species to occur in quadrats if the sign is negative and not to occur if the sign is positive.

ALL HYDROPHYTES PRESENT
N = 145

| | Chara | P. pectinatus | P. richardsoni | Ranunculus |
|---|---|---|---|---|
| Chara | | 0.2282* | 0.1935* | -0.0195 |
| P. pectinatus | 0.2282* | | -0.0778 | -0.0644 |
| P. richardsoni | 0.1935* | -0.0778 | | -0.0763 |
| Ranunculus | -0.0195 | -0.0644 | 0.0763 | |
| Total | 0.4412 | 0.3704 | 0.3476 | 0.1602 |

CHARA PRESENT
N = 56

| | P. pectinatus | P. richardsoni | Ranunculus |
|---|---|---|---|
| P. pectinatus | | 0.0357 | -0.1786 |
| P. richardsoni | 0.0357 | | 0.0178 |
| Ranunculus | -0.1786 | 0.0178 | |
| Total | 0.2143 | 0.0535 | 0.1964 |

Table B-I. (continued)

CHARA ABSENT
N = 89

| | P. pectinatus | P. richardsoni | Ranunculus |
|---|---|---|---|
| P. pectinatus | | -0.0106 | -0.1751 |
| P. richardsoni | -0.0106 | | -0.2819* |
| Ranunculus | -0.1751 | -0.2819* | |
| Total | 0.1857 | 0.2925 | 0.4570 |

CHARA ABSENT AND RANUNCULUS PRESENT
N = 16

| | P. pectinatus | P. richardsoni |
|---|---|---|
| P. pectinatus | | 0.0962 |
| P. richardsoni | 0.0962 | |

CHARA AND RANUNCULUS ABSENT
N = 73

| | P. pectinatus | P. richardsoni |
|---|---|---|
| P. pectinatus | | -0.0528 |
| P. richardsoni | -0.0528 | |

# APPENDIX C

## Analysis of Variance Data

Table C-I. Analysis of variance values for the mean number of *Gammarus* and *Hyalella* and mean depth per 0.25 m in each of the three homogeneous hydrophyte groups. Count data was transformed to ln(x + 1). Significant $F_{2,142,05}$ 3.06

MEAN NUMBER *GAMMARUS*

| Source of variation | df. | ss. | ms. | f |
|---|---|---|---|---|
| Between | 2 | 143.44 | 71.72 | 54.29* |
| Within | 142 | 187.60 | 1.32 | |
| Total | 144 | 331.04 | | |

MEAN NUMBER *HYALELLA*

| Source of variation | df. | ss. | ms. | f |
|---|---|---|---|---|
| Between | 2 | 11.53 | 5.76 | 7.18* |
| Within | 142 | 114.07 | 0.80 | |
| Total | 144 | 125.60 | | |

MEAN DEPTH

| Source of variation | df. | ss. | ms. | f |
|---|---|---|---|---|
| Between | 2 | 94,032.65 | 47,016.33 | 7.16* |
| Within | 142 | 932,775.14 | 6,568.84 | |
| Total | 144 | 1,026,807.79 | | |