THE ECOLOGY OF THREE SPECIES OF AMPHIPODS IN SASKATCHEWAN

A Thesis Submitted to the Faculty of Graduate Studies in Partial Fulfilment of the Requirements for the Degree of Master of Science in the Department of Biology University of Saskatchewan

by

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Saskatoon, Saskatchewan June, 1960

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INTRODUCTION

The purpose of this investigation was to study the ecology, life history and economic importance of the three species of amphipods found in Saskatchewan—_Pontoporeia affinis_ Lindström, _Hyalella azteca_ (Saussure), and _Gammarus lacustris_ Sars. They are abundant in the bottom fauna of many lakes of Saskatchewan and are used as food by many of the fish species.

_P. affinis_ is found in deep cold lakes of the north. Larkin (1948) studied the ecology and distribution of this species in Lake Athabaska, Great Slave Lake, and Great Bear Lake. Previous investigations in the lakes of North America reveal its occurrence as a major bottom organism. It has been reported by various authors (Huntsman, 1915; Adamstone, 1924; Eggleton, 1936-37; and Rawson, 1930-59). Birge and Juday (1914, 1921, 1927) were the first to study its life history and ecology in North America. Ricker (1959) has shown its importance as a glacial relict of Pleistocene glaciation in North America. In Europe, _P. affinis_ has been widely discussed as a glacial relict and contributions by Samter and Weltner (1902, 1904), Ekman (1918, 1920) and Thienemann (1926, 1928) are the main sources of our knowledge. Mathieson (1953) studied its life cycle in European lakes.
H. azteca has a wide distribution in the province. In North America its distribution was studied by Weckel (1907), Shoemaker (1930) and Saunders (1933). Embody (1910), Wilder (1940) and Giesler (1944) studied different aspects of its life history and ecology.

G. lacustris occurs widely in North America. Its distribution has been mentioned by Shoemaker (1920, 1955), Saunders (1933) and Rawson (various papers). Though the contributions on the life cycle and ecology of the family Gammaridae are numerous and some species have been extensively studied, there is still a paucity of material available on G. lacustris. Dahl (1915) studied its life cycle in Norway, and Berg (1938) investigated it in Denmark. In Britain, Hynes (1955) studied the reproductive cycle of G. lacustris and investigated its distribution in the British Isles.

The field work for the present study was carried out at Lac la Ronge, Saskatchewan, in July 1958 and during a four-month period in the summer of 1959. However, the materials available for analyses had been collected from lakes throughout Saskatchewan over a period of about 15 years.

METHODS AND MATERIAL

Several methods were used in the collection of
amphipods. A fine-mesh dipnet was used for the qualitative sampling in shallow water and an Ekman dredge was used for sampling in deep water with soft bottom. A Peterson dredge was used where the bottom consisted of stones or gravel. Samples from each dredging were washed through graduated screens. The specimens were then preserved in formalin or alcohol. A very large number of dredgings had been taken by Dr. Rawson in the course of his investigations of many lakes in northern Saskatchewan. These were made available for examination by the writer.

At Lac la Ronge, sampling was carried on at three selected stations for habitat distribution studies and the amphipods collected were used for numerical, growth and sex analyses. Each specimen was measured from rostrum to the base of the telson to determine the body length. A thin glass slide with an etched millimeter scale was used for this measurement.

Sexual condition was determined and recorded in the following classes: (i) Male; (ii) Female; (iii) Female with eggs or young; (iv) Female with developed oostegites; (v) Juvenile. The number of eggs from egg-bearing females was recorded and the developmental stages were observed. Parasites from specimens were preserved and the rate of infestation was recorded. For food analysis, shrimps were killed
in about 10% alcohol. The contents of the gut were squeezed out on a slide and the food eaten during the period of sampling was identified for the three species.

DESCRIPTION OF THE AREA

The province of Saskatchewan, Figure 1, lies between latitudes 49° and 60°, and includes parts of two main physiographic regions. The northern half, which is on the Laurentian Plateau, is covered with boreal forest and dominated by white spruce. The largest freshwater lakes lie in this region. The southern half is part of the Interior Continental Plain. It includes the parkland, having aspen groves alternating with tall grass, and farther south is the prairie or grassland area. In the parkland and grassland areas are found both freshwater and saline lakes. Altitudes in the province range from 700 to 4000 feet. The highest part in the province is in Cypress Hills in the southwest of Saskatchewan. From this point elevations tend to decrease towards the northeast.

There are four distinct geological regions. More than one third of the north is of Precambrian rocks. Innumerable lakes lie in this region. Many of these lakes are deep, clear and cold. A narrow band of Palaeozoic limestone lies between the Precambrian and the large area
Figure 1. Map of Saskatchewan showing lakes referred to in this study.
of Cretaceous deposits to the south. In the southeast corner of the province there is a small area of tertiary deposits. Edmunds (unpublished manuscript) describes the geology and glacial history of the province.

Waters of the province drain in three directions. The northern part drains through the Athabaska and Mackenzie rivers into the Arctic Ocean. A smaller drainage is in the south which begins on the slopes of the Cypress Hills and Wood Mountain regions and drains into the Missouri and thence to the Mississippi River. The third drainage empties into Hudson Bay through the Churchill River in the north and the Saskatchewan River in the central region.

In northern Saskatchewan low temperatures prevail during the winter. Precipitation is in the form of snow, and low temperatures prevail for about seven months. The southern part of the province has a semi-arid climate with a longer summer season. Lakes in the north are frozen for approximately six months, from mid-November to mid-May. The southern lakes have at least one month less duration of ice cover than the northern lakes.

LIMNOLOGICAL STUDIES OF SASKATCHEWAN LAKES

A considerable number of lakes in Saskatchewan have been subjected to limnological investigations since 1928.
The following brief account, and Table I, have been assembled from pertinent publications to illustrate the important limnological features of the lakes from which the amphipods examined in the study were collected.

The majority of the lakes concerned lie in the northern half of the province. The largest lakes of this Precambrian region are Athabaska, Wollaston, Cree, Reindeer, and La Ronge. The largest two of these are Athabaska and Reindeer, with surface areas of 3050 square miles and 2150 square miles respectively; both cut across the boundaries of the province. Lac la Ronge on the southern margin of the Precambrian Shield has a surface area of 500 square miles. These lakes are deep and cold, and have about a six-month open-water period. Most of these lakes show a moderate thermal stratification. Lake Athabaska is only slightly stratified, possibly because of great exposure and heavy winds. Selected limnological data are given in Table I for comparison. Lake Athabaska is considered to be an oligotrophic lake. Reindeer Lake is slightly warmer than Athabaska, having well oxygenated surface and bottom water. The mean depth and bottom conformation place the lake in the range of mesotrophic condition. Cree Lake, which is situated in the centre of northern Saskatchewan, has been investigated by Rawson (1959). A deficiency in the mineral content, evidently, is the main cause of its
<table>
<thead>
<tr>
<th>Lake</th>
<th>Area (square miles)</th>
<th>Mean Depth (m.)</th>
<th>Highest Mean Temp. °C.</th>
<th>Average Bottom O₂ mg/l.</th>
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<td>11.1</td>
<td>18.3</td>
<td>2.9</td>
</tr>
<tr>
<td>Sturgeon</td>
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<td>21.4</td>
<td>4.0</td>
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<tr>
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<td>4.9</td>
<td>17.7</td>
<td>5.5</td>
</tr>
<tr>
<td>Bigstone</td>
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<td>3.1</td>
<td>19.9</td>
<td>5.5</td>
</tr>
<tr>
<td>Wakaw</td>
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<td>4.7</td>
<td>18.4</td>
<td>6.2</td>
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<tr>
<td>Redberry</td>
<td>27.0</td>
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<td>17.4</td>
<td>3.0</td>
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<td>13.2</td>
<td>0.5</td>
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</table>
low productivity. Wollaston Lake has higher surface temperatures than Cree Lake. The surface temperature of the water in shallow bays was above 17°C. Stratification occurs in July and August and there is a complete circulation by September. However, there is no deficiency of dissolved oxygen in the bottom water. Lac la Ronge is divided into two natural regions, the open water to the south, and the northern Islands Region. Hunter Bay is isolated by a small narrows in the northeast of the Islands Region. Thermal stratification is prominent in the main lake, but in Hunter Bay it is of lesser intensity. Maximum mid-summer surface temperature in the main lake was recorded as 20.5°C. and in Hunter Bay 18.8°C. in 1953. Lac la Ronge is considered to be mesotrophic and Hunter Bay as oligotrophic.

An investigation on the limnology of the lakes lying in the Churchill Valley has been made by Rawson (1957). These lakes, Frobisher, Big Peter Pond, Little Peter Pond and Ile à la Crosse, vary in size, are of moderate depth, and have fairly high surface temperatures. The highest mean temperature ranges from 16°C. to 21°C. and there is no marked thermal stratification. The mineral content is high in all the lakes except Frobisher, which lies on the Precambrian Shield and tends to be somewhat dystrophic.

Lakes in the south are smaller in size and vary
from freshwater to saline. Three lakes of varying degrees of salinity from this southern area have been selected for examination of their amphipod fauna. The most saline is Redberry, Wakaw is intermediate, and Last Mountain Lake is of low salinity. In Montreal and Bigstone lakes no thermal stratification occurs, but Sturgeon Lake stratifies. Most of the lakes have complete circulation, but the deepest water in Wakaw and Sturgeon lakes has low dissolved oxygen which indicates incomplete circulation. Last Mountain Lake showed a maximum surface temperature of $21.4^\circ C$. It is a eutrophic lake showing a very short period of thermal stratification. Redberry is one of the highly saline lakes of the province, having a salinity of about 15,000 p.p.m. It is thermally stratified and its dissolved oxygen content is very low. It is classified as a eutrophic lake (Rawson and Moore, 1944).

**TAXONOMY OF THE THREE SPECIES**

The amphipod crustaceans are distinguished by the specific characters of their numerous appendages, which are modified for various purposes. The Canadian freshwater amphipods may be classified into two main groups according to Bousfield (1958). The first group belongs to freshwater lineage and shows little relation to the second group, which has originated recently from marine stock; the first group is
more numerous and it is believed that its distribution in Canada occurred during Mesozoic and Cenozoic periods.

The freshwater amphipods are further classified into three families: Gammaridae, Talitridae and Haustoriidae, and each family is represented by one species in Saskatchewan. *Gammarus lacustris* Sars is a representative of the Gammaridae; *Hyalella azteca* (Saussure) represents the Talitridae; and *Pontoporeia affinis* Lindström belongs to the Haustoriidae.

**Gammarus lacustris**, G.O. Sars.

This species (Fig. 2) has characters similar to those of *G. limnaeus* which occurs in northwestern Europe (Bousfield, 1958). The first antenna is longer than the second and has a short accessory flagellum (2-4 segments). Pereiopods three to five are slender in shape, and the fourth is slightly longer than the fifth. The third uropod has a short setose terminal segment of the outer ramus. The eyes are placed slightly inside of the anterior margin of the head. The limbs of the female are shorter than those of the male. The abdominal side plates are well developed and used as a distinguishing character.

**Hyalella azteca** (Saussure), Figure 3.

In *Hyalella*, the first antenna is shorter than the second and does not possess an accessory flagellum. The
Figure 2. *Gammarus lacustris* G. O. Sars. ×10
Figure 3. *Hyal*ella *azteca* (Saussure). ×14
telson is entire and the third uropod is uniramous. The
typical dorsal abdominal carination is found in both
sexes (Fig. 3). In females, the second gnathopod is
inconspicuous. The brood plates are large and triangular,
and their margins are armed with numerous hooked bristles
which interlock with neighbouring plates.

**Pontoporeia affinis**, Lindström. (Fig. 4)

In this species the first antenna is shorter than
the second. A small accessory flagellum is present on
segments three and four. Pereiopods three to five are
unlike in structure and size. The fourth is the largest
and the basal joint of the fifth is greatly expanded.
The gnathopods are also unlike, small and typically sub-
chelate. In the female, the first antenna is very short,
a convenient character for distinguishing females from
males. The specimens of **Pontoporeia** collected in North
America were originally considered to be a different species.
In 1937 Segerstråle, in his taxonomic review, concluded
that all the specimens found in North American lakes are
identical to **P. affinis** which occurs in glaciated lakes
of Europe.

A detailed account of the taxonomy of the species
has been presented by Bousfield (1958).
Figure 4. Pontoporeia affinis Lindström. X14
DISTRIBUTION IN SASKATCHEWAN LAKES

Table II shows the relative abundance of amphipods in representative lakes of Saskatchewan. In general the lakes lying in the Precambrian region show a greater abundance, with the exception of Cree Lake, where only *Hyalella* is present, and in small numbers. *Pontoporeia* is dominant in the large lakes of northern Saskatchewan. It is a major species in Athabaska, Wollaston, Reindeer and Hunter Bay. In Lake Athabaska, *Gammarus lacustris* is present but *Hyalella* was not found. *Hyalella* is the dominant amphipod in Frobisher Lake. As described previously, this lake is dystrophic and has large areas of shallow warm water. In Wollaston and Reindeer lakes, *Hyalella* contributes a very small percentage of the total number of amphipods. *Pontoporeia* is abundant in Wollaston Lake. *Gammarus lacustris* is sparsely distributed in these lakes and appears to be absent from Reindeer Lake and Hunter Bay. In Wollaston and Frobisher it is restricted to shallow water. Lakes of the Buffalo Narrows region have all three species. *Pontoporeia* is dominant in Big Peter Pond and Ile à la Crosse. *Gammarus* and *Hyalella* are present in all the lakes but only in small numbers.

Lac la Ronge and Amisk, both of which lie across the border of the Precambrian Shield, have all three species of amphipods. Dredgings taken during 1948 and 1949 in
<table>
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<th>Lake</th>
<th>Species Present</th>
<th>Numerical % of Amphipods in Bottom Fauna</th>
<th>Major Species</th>
</tr>
</thead>
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<tr>
<td>Athabaska</td>
<td>+ + +</td>
<td>60.0</td>
<td>Pontoporeia</td>
</tr>
<tr>
<td>Wollaston</td>
<td>+ + +</td>
<td>70.5</td>
<td>Pontoporeia</td>
</tr>
<tr>
<td>Cree</td>
<td>+ +</td>
<td>1.3</td>
<td>Hyalella</td>
</tr>
<tr>
<td>Reindeer</td>
<td>+ + +</td>
<td>71.9</td>
<td>Pontoporeia</td>
</tr>
<tr>
<td>Frobisher</td>
<td>+ +</td>
<td>43.0</td>
<td>Hyalella</td>
</tr>
<tr>
<td>Churchill</td>
<td>+ + ?</td>
<td>23.2</td>
<td>Pontoporeia</td>
</tr>
<tr>
<td>Big Peter</td>
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<td>21.1</td>
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</tr>
<tr>
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</tr>
<tr>
<td>Ile à la Crosse</td>
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</tr>
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<td>Drope</td>
<td>+ +</td>
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<tr>
<td>Nistowiak</td>
<td>+ +</td>
<td>12.6</td>
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</tr>
<tr>
<td>Drinking</td>
<td>+ +</td>
<td>72.0</td>
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<tr>
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<tr>
<td>Hunter Bay</td>
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<td>17.0</td>
<td>Hyalella</td>
</tr>
<tr>
<td>Amisk</td>
<td>+ +</td>
<td>60.0</td>
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<tr>
<td>Waskesiu</td>
<td>+ +</td>
<td>58.9</td>
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<tr>
<td>Sturgeon</td>
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<td>14.3</td>
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<td>Montreal</td>
<td>+ +</td>
<td>9.6</td>
<td>Hyalella</td>
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<tr>
<td>Bigstone</td>
<td>+ +</td>
<td>65.9</td>
<td>Hyalella</td>
</tr>
<tr>
<td>Wakaw</td>
<td>+ +</td>
<td>42.0</td>
<td>Hyalella</td>
</tr>
<tr>
<td>Redberry</td>
<td>+ +</td>
<td>16.0</td>
<td>Hyalella</td>
</tr>
<tr>
<td>Last Mountain</td>
<td>+ +</td>
<td>5.2</td>
<td>Hyalella</td>
</tr>
</tbody>
</table>

@Only in littoral region and few in numbers.
Lac la Ronge (Fig. 5) show the highest concentration of Pontoporeia between 10-15 metres' depth in the island region and a dense population between 0-5 metres' depth in the open water region. In Hunter Bay the concentration zones extend from depths of 15 to 40 metres. The island region shows Pontoporeia dominating 10-15 metre depth zone. The distribution of Pontoporeia in Amisk Lake is similar to the island region except that the concentration is in 15-20 metres of water. No Hyalella was found in the open water region of Lac la Ronge nor in Hunter Bay, but in the island region it comprises sixty per cent of the population.

In the lakes of the Stanley Mission area P. affinis is a major species. Hyalella is found in Otter and Nistowiak lakes and Gammarus only in Mountain Lake. Hyalella has not been collected so far from Drinking Lake, but in Drope Lake it comprises more than forty per cent of the population. Figure 6 illustrates the distribution of Pontoporeia and Hyalella in the lakes of the Stanley Mission area. Otter Lake has Pontoporeia dominating 0-10 metres and 10-20 metres of water, but diminishes in 20-30 metre depth zone. Both Otter and Mountain lakes have shallow bays which might be the cause of low population of Pontoporeia. Drope, with a total area of about four square miles, has the smallest number of amphipods among these lakes. The
Figure 5. Depth distribution of *P. affinis*, Lac la Ronge, 1948-49.
Figure 5. Depth distribution of *P. affinis*, Lac la Ronge, 1948-49.
Figure 6. Distribution of *H. azteca* and *P. affinis* in the lakes of Stanley Mission area.
largest concentration in Nistowiak and Drinking lakes is in deep water.

Pontoporeia is not found in any of the lakes lying in the parkland and grasslands regions. This is presumably due to the high temperatures and shallow waters. Sturgeon and Bigstone have both Gammarus and Hyalella present in thickly vegetated areas. Gammarus was not collected from Montreal Lake. Large areas of shallow water provide suitable habitat for the amphipods in Bigstone Lake.

The three saline lakes, Wakaw, Last Mountain and Redberry, have both Gammarus and Hyalella. Redberry has the highest salinity among the three lakes, but both species are more abundant there than in Last Mountain Lake, which is less saline.

The larger abundance of amphipods in the lakes of the Precambrian Shield is due to the presence of the glacial relict Pontoporeia. It is believed that the Pleistocene glaciation in North America was responsible for the present distribution of this species (Ricker, 1959). Ekman (1915) and Thienemann (1926, 1928) investigated northern European lakes and found that the temperature and oxygen concentration were the important factors limiting the distribution of Pontoporeia. Thienemann (1928) observed that in northern German lakes Pontoporeia was forced to occupy cold and deep water when the temperature was greater than 14.5°C. It is
suggested (Rawson, 1930) that Pontoporeia may have inhabited Lake Simcoe, Ontario, but due to the warming of the lake since glaciation, it does not exist. Larkin (1948) states that the greater abundance of Pontoporeia in shallow water in the northern lakes is due to the lower temperatures and shorter summer season. Rawson (1960) observes that a high percentage of amphipods is found in oligotrophic lakes. The oligotrophic lakes on the Precambrian Shield are cold and deep, supporting large populations of Pontoporeia. Besides the temperature and shorter open water season, area and depth may possibly be the additional factors limiting the distribution of Pontoporeia in northern lakes. In the lakes across the margin, Pontoporeia is present, although it is not dominant. Even the shallow and warm lakes on the Precambrian Shield do not show the presence of this species. The distribution of Gammarus and Hyalella in large northern lakes is scanty. The unfavourable factors of deep and cold water and short summer period probably reduce the rate of reproduction. In the lakes south of the Precambrian Shield Hyalella becomes a dominant species. The lakes in the south tend also to be eutrophic. Pontoporeia is absent from these lakes.
THE ENVIRONMENT AND HABITS

*Gammarus lacustris* is the largest of the three amphipods and is found in both lentic and lotic waters. The length of the reproducing adults is between 10.5 and 18.0 mm. (Saunders, 1933). Their colour is usually yellowish, but sometimes brown or greenish *Gammarus* have also been collected. They swim freely and are often observed crawling in the muddy places where the water is a few inches deep. The pereiopods are used for crawling and walking and the gnathopods, which bear claws, function for seizing and grasping the prey and also for holding the female during mating. In aquaria, they often hide in the vegetation or lie on one side of their bodies under a centimeter or two of mud.

*Hyalella azteca* is an active swimmer, occasionally lives in the same habitat with *Gammarus* and shows similar habits. When swimming, *Hyalella* does not show any peculiarity, but in air, it will cling to a plant branch and walk in an upright position which, according to Bousfield (1958), indicates its semiterrestrial ancestry.

*Pontoporeia affinis* occurs only in deep, cold waters. The body is colourless with no modification of the first two pereiopods into gnathopods. It does not show any habit of clinging and grasping. In aquaria, it walks
swiftly in the oozy matter, searching for food.

_Gammarus limnaeus_ appears to be resistant to higher temperatures than _G. lacustris_. Pentland (1930) found _G. limnaeus_ fairly abundant in Ontario lakes where maximum summer temperatures were above 18° and 20°C. _G. lacustris_ is resistant to low oxygen and general stagnant conditions (Hynes, 1955). Bousfield (1956) suggests that _Hyaella_ is found in all freshwaters reaching a monthly mean summer temperature of more than 10°C. Observations in Saskatchewan lakes agree with this generalization. _Pontoporeia_ occurs in waters where temperature is usually less than 10°C., although it is occasionally found in warm waters. _Pontoporeia_ in Saskatchewan is abundant only in deep cold lakes, as was indicated in Table II above, but in these lakes it may come into shallow warm water in considerable numbers. Samter and Weltner (1904) have collected _Pontoporeia_ from fairly warm lakes. It could be found in abundance at places where oxygen concentration fell to 2.3 cc. per litre at a depth of 65 metres (Birge and Juday, 1927), while Pennak (1953) noted its presence in the water of less than seven per cent saturation.

In general, the amphipods are considered negatively phototrophic since they move away from the source of light (Clemens, 1950). They are found hidden in vegetation or clinging under the leaves. _Pontoporeia_ generally concentrate
in greater depths of water where the light penetration is low. It is believed that the water movements affect the distribution of amphipods. Clemens (1950) observed the effect of wind in the fluctuation of *Gammarus* population in Lake Erie. The nature of the bottom material limits the distribution of the various species of amphipods. *Gammarus* prefers soft bottom with woody detritus and ooze, though it also occurs on sandy bottom. *Pontoporeia* has been collected mainly from the cozy bottoms of the lakes.

Pentland (1930) in his investigation on *Gammarus* found that the mineral content of the water did not control the distribution of individual species. Similar observations on *G. limnaeus* were made by Saunders (1933) on Vancouver Island.

Amphipods are not restricted to any single type of vegetation. Clemens (1950) found greater numbers of *Gammarus* in vegetated than in non-vegetated areas. *Gammarus* is often abundant in the aquatic vegetation such as *Chara* but this association is not assumed to be a major factor in the distribution. Rosine (1955) related the plant surface areas with the density of invertebrates and found that two *Hyalella* were present for 100 square centimetres of *Chara* surface during the mid-season in the Muskeg Lake, Colorado. *Pontoporeia*, a typically deep
water species, is not associated with any type of vegetation.

The food of the three species includes small protozoa and diatoms. They also consume almost all kinds of dead plant and animal matter. Food analyses made by the writer at Lac la Ronge showed that *Gammarus* and *Hyalella* eat similar food. The animals seemed to prefer algae and the genera identified mostly were *Ulothrix*, *Navicula*, *Synedra*, *Pinnularia*, and *Pediastrum*. In a few specimens appendages of zooplankters were recognizable. Dahl (1915) found in Norway that *G. lacustris* fed mainly on plant detritus, and that it often destroyed fish nets. The destruction of fish nets was also observed in several small northern lakes of Saskatchewan (Rawson personal communication). *Pontoporeia* appears to feed mostly on the diatoms and bacteria. *Sphaerocystis*, *Tribonema* and *Amphora* were recognized in few specimens. Larkin (1948) states that organic debris and diatoms are the main food for *Pontoporeia* in deep water.

Most of the amphipods living in shallow water are affected by wave action. Humus material, woody detritus, objects such as small stones, and submerged plants provide shelter for gammarids. Hynes (1955) found large numbers of *G. lacustris* hidden under large loose stones. Protective behaviour of *Gammarus* has been observed in aquaria by
the writer. The animals clung to the wood fragments on the surface of the water and remained holding to the underside of these until they reached the bottom. When disturbed, they tended to swim against the current and tried to cling to any object near to them or to dig into the sandy bottom of the aquaria. In Lac la Ronge amphipods are more densely distributed on the vegetated muddy bottom of the shallow water than on the mud or rocky bottom of the deeper water. In the sandy bottom, they would be more exposed to predation.

Both Pontoporeia and Hyalella make diurnal migrations. Mundie (1959) collected large numbers of Pontoporeia at the surface of Lac la Ronge to which they migrate during the night. Hyalella also showed diurnal migration, but with no definite mode. Observations made by Larkin (1948) revealed that Pontoporeia move upwards to the surface at night. Some specimens were collected at the surface at 10 p.m.; heavy concentration was noticed at midnight, and then a gradual decline in numbers until dawn.

LIFE HISTORIES

The female organs of reproduction include a pair of ovaries situated ventral to the heart. They extend
from the second segment to the fifth, opening into the oviducts, which lead back to the genital pores at the base of the sixth coxal plates. The male has a pair of testes occupying a place in the body similar to that of ovaries, i.e., from the second to the fifth or sixth segments, opening into short vasa deferentia which then open exteriorly on the ventral side through two short papillae.

The breeding period is known to occur between April and October, but the exact time differs from species to species and depends largely on the temperature of the water.

Specimens of the three species, *G. lacustris*, *H. azteca* and *P. affinis*, were kept in shallow glass dishes in the laboratory at Lac la Ronge for observation. Eight pairs of adult Gammarus were studied under captivity for comparison with the life history in the field. The method of mating in *G. lacustris* was similar to that of *G. limnaeus* described by Clemens (1950). The females which became ovigerous for the first time laid a smaller number of eggs (4-8). Large females (average size 10-12 mm.) bred normally producing large numbers of young. Female *G. lacustris* produced an average of 20 eggs before dying. The mean number of eggs was higher in July than in the later season. This was due to the large-sized females in early season, while the number decreased in mid-August when a few newly-matured females were carrying a small number of eggs. In
the laboratory it took 20-22 days for the incubation of eggs when the water temperature varied between 18°C and 22°C. During the investigation the males died quite often and were replaced by males of the same size.

Six pairs of adult *Hyalella* were kept in the laboratory and observations on mating, development of eggs and hatching were made. After a week in captivity the females showed green ovaries. During mating the females were found constantly moving their pleopods to pass the sperm into the brood pouches for fertilization. After fertilization the females were found still in the bottoms of the dishes. When disturbed they moved slowly, always pressing their brood pouches with pleopods. Incubation took six to eight days and the young were released in succession from the brood pouches. Some males were observed mating even when the females had young in the brood pouches.

*Pontoporeia affinis* were kept in the laboratory to observe the rate of growth but they died, probably because of the high temperatures since no refrigerator was available for such purpose.

The males of *Gammarus* copulate first when they are in their ninth instar (Clemens, 1950). In *Gammarus* and *Hyalella* the male carries the female on his back, keeping the body closer with the help of the gnathopods. They swim in this manner for about seven days, after which the female
begins to moult. Clemens (1950) observed that the male had a desire to pair only prior to mouling and ovulation. While the female moults, the male remains separate. The following description on the copulation in G. fasciatus is given by Clemens (1950). The male attaches the posterior side of his body around the ventral side of the female. The female flexes her pleon while arching and bringing her body in close contact with the papillae of the male. Finally, the male takes a position so as to place his pleopods over the openings of the oviducts into the brood pouch. The sperms then start moving into the marsupium and the female with her pleopods continuously pushes them into her brood pouch. Copulation takes less than a minute and the process is repeated several times. The female then separates and releases the eggs from the oviducts into the marsupium where they are fertilized. The writer has observed that the number of eggs passed by the female depends on her size, her age, and the temperature of the water, and also differs with the species. In Hyalella, the number of eggs released varied from eight to 25. This is similar to Pennak’s (1953) observation on this species.

The act of mating in Hyalella differs from that of Gammarus (Gaylor, 1922). The male Hyalella extends the posterior part of the body around the ventral side of the female without changing his hold and uses his uropod to
penetrate the marsupium of the female. Unlike *Gammarus*,
the female *Hyalella* does not arch her body backwards, nor
does the male use his antenna to hold the female firmly.

The eggs in the marsupium are protected by stiff
hairs of oostegites plates. Incubation periods vary ac­
cording to the species and the hatching period depends mainly
on the temperature. *Hyalella* takes about six days for incu­
bation (Wilder, 1940). *Gammarus fasciatus* under laboratory
conditions required 16 days at a mean temperature of 16°C.
and the young matured in 13 weeks (Clemens, 1950).

In *Pontoporeia* reproduction occurs during winter
months at all depths. Juday and Birge (1927) observed that
90 per cent of the sexually mature females were carrying
eggs in their brood chambers in January. These eggs were
approximately in the same stage of development.

*Pontoporeia* produces a single brood in the life cycle.
*Hyalella* has an average of 15 broods in 152 days (Embody,
1910), and *G. lacustris* produces three or more broods with
an average of 22 eggs before the female dies (Hynes, 1955).
Sometimes the females in *Hyalella* pair even before emptying
the marsupium. A minimum of nine instars has been observed
in the life cycle of *H. azteca* (Giesler, 1944). The develop­
ment is direct and the young show all the characteristic
appendages of the adult. In the first five instars, it is
difficult to distinguish the sexes, but the sixth and
seventh instars show an adult appearance and the sexes can be differentiated. The males have conspicuous gnathopods, while in the females these become inconspicuous and typical in structure. Mating occurs in the eighth and ninth instars and continues in the subsequent instars of the adult phase.

The process of moulting is similar in all three species. In gammarids the cuticle splits between the head and the paraeon, which helps the animal in pulling out the head and antenna first, and the remaining body and exoskeleton of the appendages later (Clemens, 1950). The time taken in moulting is less than half an hour. The period between successive moultings ranges from three to 40 days, depending on the temperature, food condition and the species. In immature amphipods, the moulting occurs at much shorter intervals than in adults.

The life cycle varies in the three species. In *P. affinis*, the females are ovigerous between December and April, the period of life cycle is about 30 months, and the young are released from the brood pouch during the spring. Breeding in *H. azteca* commences in spring and continues throughout the summer. The life cycle is of more than two years. The females of *G. lacustris* become ovigerous in late spring and in early summer, and the life cycle is of 15 months (Bousfield, 1958). The life cycle of *G. lacustris* is strictly annual in Denmark (Berg, 1938), but Dahl (1915)
suggested that in a few specimens it extended up to two years.

LIFE HISTORIES, DISTRIBUTION AND POPULATION IN LAC LA RONGE

Lac la Ronge was selected to study the habitats and the population changes. Weekly samples of five to seven dredgings were collected from each of the three stations from June to August in the summer of 1959. The location of these stations is indicated in the sketch map (Fig. 7). The data obtained are summarized in Table III, and the description of the habitats represented by each station follows.

Station I.

This was located at a depth of two and a half metres close to the mouth of the Montreal River. The bottom was muddy, with much dead vegetation and wood detritus. Sparse vegetation consisting of Potamogeton and Ceratophyllum was observed during May and June; but the vegetation increased as the water warmed and by the first week of August it became quite dense with Potamogeton, Ceratophyllum, Myriophyllum and Lemna. The water temperature by this time was 18°C.

Station II.

This station was located at a depth of about three metres, in a more exposed region, about 200 yards from the shore and 300 yards from Station I. The bottom material consisted mainly of mud, dead leaves of Lemna and mollusc
Figure 7. Map of a part of Lac la Ronge showing locations of three stations.
TABLE III

SUMMARY OF AMPHIPODS COLLECTED FROM THREE STATIONS AT LAC LA RONGE, JUNE TO AUGUST
June to August, 1959

<table>
<thead>
<tr>
<th></th>
<th>All Species</th>
<th>Gammarus</th>
<th>Hyalella</th>
<th>Pontoporeia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Station I</td>
<td>648.0</td>
<td>44.0</td>
<td>604.0</td>
<td>-</td>
</tr>
<tr>
<td>Station II</td>
<td>405.6</td>
<td>0.60</td>
<td>405.0</td>
<td>-</td>
</tr>
<tr>
<td>Station III</td>
<td>1182.0</td>
<td>-</td>
<td>293.4</td>
<td>888.6</td>
</tr>
</tbody>
</table>
shells. There was no vegetation in the beginning of the summer, but with the change of weather in early July, aquatic vegetation, mainly Ceratophyllum and Myriophyllum, appeared.

**Station III.**

This was situated in a small bay in the Freeman's Island region. The depth of the water was three metres and the bottom was of brown mud with a thick surface layer of organic ooze. No growth of vegetation was observed in this habitat and the bay was surrounded by bare rocky shores. A slight change was noticed in July when some Ceratophyllum drifted into the region.

A fourth station might have been selected in a depth of at least 20 metres where Pontoporeia would be the only amphipod present. This was not necessary since dredging on Lac la Ronde had provided plenty of material from this habitat.

Gammarus and Hyalella were present at Stations I and II. Hyalella was collected in very large numbers from both stations. Station III was inhabited by Pontoporeia and Hyalella, with Pontoporeia as the major species. No Gammarus were found at Station III during the sampling period.

Daily fluctuation in the population density of amphipods was observed in a small heavily-vegetated bay west of the laboratory at Lac la Ronde for four periods of one week each. Samples taken in the non-vegetated period (mid-May to mid-June) showed small numbers of Gammarus and Hyalella,
with Hyalella outnumbering *Gammarus* by 4:1. In the vegetated period (mid-June to mid-July) the samples taken showed similar numbers and proportion of the two species.

In order to draw conclusions as to the habitat selection and population changes, it is now necessary to examine the data for each species separately.

*Gammarus lacustris*, as stated previously, was collected from Station I and Station II. This shrimp occurs in shallow water where it was difficult to sample with the Ekman dredge and thus a dipnet (non-quantitative) was used at Station I to obtain sufficient numbers of *Gammarus* for study.

A total of 128 *G. lacustris* was collected during the sampling period from the two stations, out of which only two specimens were collected from Station II. Those taken in June were of large size. The males had an average size of 14.0 mm., and the females 13.2 mm. The sex ratio in the last sample, on August 20, was one male to 1.3 females. The average sized males of this population were 8.50 mm., and the females 8.29 mm. Smaller *Gammarus* of average size 6.0 mm. made about 40 per cent of the population. The bi-weekly qualitative samplings gave similar results.

The mating in *Gammarus* commenced about three weeks after the melting of ice when the temperature of the water was 16°C. The population of July 10 included no young
individuals. The average size of individuals in this population was 8.5 mm., suggesting that they had overwintered as mature Gammarus. The females outnumbered the males by 2:1. About 50 per cent of the population showed precopulation (pairing but not mating) in the middle of July. More than 60 per cent of the females were carrying eggs in their brood pouches on July 20 when the temperature of the water was 20°C. This indicates that the breeding commenced between July 10 and July 20. Samples taken on July 25 had fewer Gammarus; this was believed to be due to mortality and predation. About 25 per cent of the overwintered population was surviving on August 9. However, an increase was noticed on this date when the new generation began to appear. The average size of the young Gammarus ranged from 4.0 mm. to 5.80 mm. Two weeks later, on August 24, only two per cent of the overwintered population was surviving. At this time a new group of young individuals of 5 mm. average length were dominant. No breeding female was collected after August 20, showing that the breeding stopped as the cooling of the water began after this date. The population of August 20 was, therefore, of two generations, the first reaching a size large enough for capture between July 25 and August 9 and a second following two or three weeks later. It is assumed that both groups reach maturity to breed in the next summer.
Clemens (1950) studied the life cycle and ecology of *G. fasciatus* in the region of Lake Erie. Hynes (1955) observed that the males of *G. lacustris* died before the females, the breeding period was short, and the young appeared in April and May. The males were over 16 mm., and the females over 14 mm. Dahl (1915) investigated the life cycle and ecology of *G. lacustris* in Norway. He noticed abundant population of ovigerous females in June and small-sized population in July and August. He further believed that the growth to maturity in this species takes two years, but Hynes (1955) does not agree. The main period of production of young in Norway was July and August. In Denmark (Berg, 1938) the main season of production of young was May and June. The males and females collected from southern Norway were of larger size than the males and females of the north of Norway. Hynes (1955) suggested that the length of *G. lacustris* could vary inversely with the latitude or temperature. He further stated that the species shows a slow growth with no resting period and has a very short breeding period.

The population of *H. azteca* at the three stations is shown in Figure 8. It was highest in the beginning of the season at Station I and Station II and then reduced by July 24. A similar reduction was noticed at Station III on July 30. The cause of this decrease could be the
Figure 8. Seasonal changes in numbers of H. azteca at the three stations, Lac la Ronge, 1959.
mortality of overwintered population and heavy predation. A repopulation began after July 24 at Station I, and later at Station II and Station III.

The sex ratio and average size of Hyalella on each date of sampling is shown in Table IV. The females outnumbered the males by 3.6:1 at Station I on July 24. Since the females on this date are considerably smaller than the males, it is suggested that the high ratio is due to the entrance of a new brood of females into the population. By July 30 the average size of the males had decreased and the ratio was restored to almost equal numbers of males and females, indicating that a new brood of males had entered the population. The ratio at Station II was highest on August 20, when the females outnumbered the males by 5:1. It would seem, therefore, that the number of females has increased due to the entry of the young females. Station III presented a different trend, with females outnumbering males by 3.6:1 from the beginning of the season and with a decrease in sex ratio later. This may possibly be explained by postulating that the overwintered population had large numbers of females and small numbers of males. There would have been slow growth in the population because of cold water under the ice. The influence of higher water temperatures on the new brood could possibly be a factor determining the sex of the individuals as suggested by Kinne (1959) for G. duebeni. Perhaps the high temperatures of the water at the close of the summer would have resulted
TABLE IV

THE SEX RATIO AND SIZE GROUP ANALYSES OF
ADULT POPULATION OF HYALELLA
AT THREE STATIONS
Lac la Ronge, 1959

| Date      | Average size (mm.) | Sex ratio | STATION I | Male Female | Male Female | STATION II | Male Female | Male Female | STATION III | Male Female |
|-----------|--------------------|-----------|-----------|-------------|-------------|------------|-------------|-------------|-------------|-------------|-------------|
| 16 June   | 5.83 : 5.49        | 1 : 2.2   | 5.14 : 5.47 | 1 : 1.4     | 4.70 : 4.13 | 1 : 3.0    |
| 20 June   |                    |           |           |             |             |            |             |             |             |             |
| 26 June   | 5.38 : 5.21        | 1 : 1.1   | 5.03 : 4.89 | 1 : 1.6     | 4.40 : 4.42 | 1 : 3.6    |
| 2 July    | 5.40 : 4.94        | 1 : 1.6   | 5.07 : 5.02 | 1 : 1.6     | 4.43 : 4.35 | 1 : 2.6    |
| 9 July    | 5.52 : 4.88        | 1 : 0.9   | 5.50 : 5.04 | 1 : 2.0     | 4.50 : 4.50 | 1 : 1.8    |
| 16 July   | 5.51 : 5.21        | 1 : 1.2   | 5.41 : 5.16 | 1 : 1.2     | 5.18 : 4.78 | 1 : 1.6    |
| 24 July   | 6.27 : 3.55        | 1 : 3.6   | 5.92 : 5.48 | 1 : 3.1     | 5.33 : 4.97 | 1 : 1.3    |
| 30 July   | 4.77 : 4.42        | 1 : 1.2   | 5.61 : 5.40 | 1 : 2.0     | 5.47 : 5.20 | 1 : 1.7    |
| 6 August  | 5.04 : 4.086       | 1 : 2.2   | 5.12 : 4.92 | 1 : 1       | 5.70 : 4.89 | 1 : 0.70   |
| 13 August | 4.03 : 3.81        | 1 : 1.4   | 4.87 : 4.44 | 1 : 2.2     | 6.15 : 5.58 | 1 : 2.8    |
| 20 August | 4.49 : 4.27        | 1 : 2.0   | 4.49 : 4.12 | 1 : 5.0     | 5.94 : 5.39 | 1 : 1.8    |
in more females in the young population.

The numbers of egg-bearing females represent the potential population of a species. The seasonal abundance of breeding females at the three stations is presented in Figure 9. Station I had the highest percentage of breeding females on July 2, when the temperature of the water was 18°C. After this date a gradual decline was noticed up to August 6 and then the breeding stopped. At Station II, the percentage of breeding females was highest on July 16, when the temperature of water was 20.0°C. The disturbed condition of the water in the beginning of the season could have prevented breeding. However, after July 16, there was a decrease up to the last date of sampling. Station III was typical in its breeding population in having maximum egg-bearing individuals on August 6. It then showed decline though the breeding continued up to the last sampling day, August 20.

It would seem, therefore, that the breeding of Hyalella at the three stations depended on the temperature of water. The new-born population was observed first at Station I in mid-July and a week later at Station II. They appeared a month later (August 20) in the sample at Station III. The slow breeding, the late hatching and a very short period of warm water could possibly be the cause of small population of Hyalella at Station III. The females, of
Figure 9. Seasonal abundance of breeding females of *H. azteca* at three stations, Lac la Bonge, 1959.
average size 5.48 mm., were collected from Station II in
the end of July. The average size of smallest breeding
females was 3.85 mm. These females were observed when the
temperature of the water was 20°C. It would appear (Fig.
10) that the larger-sized females bore larger numbers of
eggs, though this was not true of a few large females which
carried small numbers of eggs in the beginning of the sum-
mer when the temperature was low.

*Pontoporeia affinis* occurred only at Station III
with *Hyalella*. The seasonal changes in the population of
the two species is shown in Table V. The average ratio
between *Pontoporeia* and *Hyalella* was 3:1. *Pontoporeia*
outnumbered *Hyalella* by 5:1 on July 16 and August 6. No
explanation could be given of the large numbers of *Ponto-
poreia* on these dates, but it seems that on July 16 a
large group of *Pontoporeia* must have entered the station
and on August 6 the mortality of large-sized *Hyalella* may
have decreased the population. The population of *Ponto-
poreia* (Fig. 11) at Station III showed two distinct maxima,
on June 26 and on July 24. The first concentration was
noticed when the average size of the specimens was 3.70 mm.,
and the second when the average size was 5.12 mm. The col-
lection in the sample of August 6 had small numbers of *Ponto-
poreia*. The high temperature of the water on this date may
have caused the emigration of this size group. The growth curve
Figure 10. Relation of number of eggs to average size in *H. azteca*, Lac la Ronge, 1959.
TABLE V

SEASONAL CHANGES IN THE POPULATION OF HYALELLA AND PONTOPOREIA AT STATION III Lac la Ronge, 1959

<table>
<thead>
<tr>
<th>Date</th>
<th>Number of Specimens Examined</th>
<th>Species Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hyalella : Pontoporeia</td>
</tr>
<tr>
<td>20 June</td>
<td>462</td>
<td>1 : 3.35</td>
</tr>
<tr>
<td>26 June</td>
<td>253</td>
<td>1 : 3.0</td>
</tr>
<tr>
<td>2 July</td>
<td>253</td>
<td>1 : 3.36</td>
</tr>
<tr>
<td>9 July</td>
<td>474</td>
<td>1 : 2.51</td>
</tr>
<tr>
<td>16 July</td>
<td>334</td>
<td>1 : 4.96</td>
</tr>
<tr>
<td>24 July</td>
<td>485</td>
<td>1 : 2.75</td>
</tr>
<tr>
<td>30 July</td>
<td>529</td>
<td>1 : 3.04</td>
</tr>
<tr>
<td>6 August</td>
<td>99</td>
<td>1 : 5.19</td>
</tr>
<tr>
<td>13 August</td>
<td>161</td>
<td>1 : 3.87</td>
</tr>
<tr>
<td>20 August</td>
<td>340</td>
<td>1 : 2.40</td>
</tr>
</tbody>
</table>
Figure 11. Population fluctuation and size-group distribution of *P. affinis* at Station III, Lac la Ronge, 1957.
(Fig. 12) indicates the increase in size throughout the period of observation. It was slightly faster in the early season but as the water became warmer, a slow and fairly uniform growth was observed. The specimens remained unsexable throughout the sampling period. A slight scattering of dark pigmentation of the eyes was noticed in the large-sized Pontoporeia at the end of the summer. Larkin (1948) has interpreted this as evidence of senescence.

**GROWTH AND MIGRATION OF PONTOPOREIA IN WOLLASTON LAKE**

The growth and migration of Pontoporeia in Wollaston Lake was studied from the collections made by Dr. D. S. Rawson in 1956. The data regarding physical and chemical conditions are recorded from Rawson (1959). The surface temperature at the time of the first sampling in mid-June was 4°C. and the bottom 3.8°C.

The size-group distribution during the months of June, July and August in different depths of the lake is shown in Figure 13. In June, young-of-the-year, mostly two mm. long, are abundant in shallow water (0-10 metres), suggesting that they have migrated to shallow water after being released from the females. Adults of the previous year, mostly five to six mm. long, are common in all depth zones but more abundant in depths of 10-20 metres. It is believed that the largest size group, those of seven to nine mm. length, are two years old, as was found in Great Slave Lake by
Figure 12. Rate of growth of P. affinis at Station III, Lac la Ronge, 1959.
Figure 13. Depth and size frequency distribution of *P. affinis* in Wollaston Lake, 1956.
Larkin (1948). Presumably these die after raising their second brood or undergo predation.

In July the distribution shows an abundance of the three mm. group in 0-10 metres of water. These are the individuals which formed the two mm. size group in the month of June. The young-of-the-year in this month make up one third of the population in 0-10 metres depth zone. Some of the two-year-olds are also present in 20-30 metres of water, but practically none from the depths of 30-40 metres. The thermal conditions of the lake in July are quite different from those in June. There is a distinct thermocline below five metres and the bottom temperatures are 5.6°-6.8°C.

In August, the present brood reaches an average size of four mm. and is dominant in the population in depths of 0-10 metres. The one- and two-year-old groups are fewer in 0-10 metres depth zone, but in 10-20 metres of water they are dominant. These two-year-olds, present in small numbers in all depths during the three months of sampling, show senescent characters. No sampling was made from the depths of 20-30 metres. In deeper water, 30-75 metres, the young-of-the-year are present in large numbers, showing their migration from shallow water to deep water which remains cold and unmixed in August. The increase in size with increasing depth shows that the smaller ones in these depths grow rapidly until they overlap in size with the last year's individuals.
Measurements were made on 25 females collected in early June from 10-20 metres of water. The length averaged eight mm. Five of these females were carrying 1-15 eggs in their brood pouches. One of these was carrying a single egg in the last stage of development. In 10-20 metres, only one female was found with a developed brood pouch containing six eggs. It is possible that the females migrate towards shallow water to release the young, after breeding in deep water.

Samter/Weltner (1904) and Ekman (1915) observed that the reproductive period in Pontoporeia occurs in winter in European lakes. A similar observation was made by Birge and Juday (1927) in Green Lake, Wisconsin. Samter and Weltner (1904) found that temperatures greater than 7°C prevent egg production in Pontoporeia. Larkin (1948) studied the distribution and life cycle of Pontoporeia in Athabaska, Great Slave and Great Bear lakes. He observed that the summer population of Pontoporeia in Athabaska was of a mixed population, the larger-sized one-year-olds were confined to deeper water, and the smaller-sized, the young-of-the-year, were found in 0-10 metre depth zone.

PARASITES

Parasites from the bodies of amphipods were kindly
identified by Dr. L. G. Saunders of the Department of Biology, University of Saskatchewan. *Hyalella azteca* and *G. lacustris* were infested by the coloured larvae of an echinorhynchid worm. The larvae in *Hyalella* occupy the dorsal region of the second and third segment. *Hyalella* has been found infested also by a microsporidian parasite which appeared as opaque white patches in the abdomen (Saunders, 1933), but no such specimens were collected at Lac la Ronge.

The infested specimens of both species were measured and their sex determined. The average of infestation throughout the summer was about five per cent (Fig. 14). The females of *Hyalella*, with average size 4.85 mm., were more heavily parasitized in early summer. Few parasitized females of 3.5 mm. were present in the collection during mid-season. No gravid females had parasites; however, a number of females with developed oostegites bore parasites. *Gammarus*, average size 8.50 mm., were lightly parasitized in May, more heavily in June, and lightly again in August. The larvae had grown to considerable size in the specimens collected at the end of the summer. It is not known whether the parasites continue to live in the bodies of the hosts during the winter.

A few infested specimens of *Gammarus*, average size 8.25 mm., were kept in the laboratory for observation. The
Figure 14. Echinorhyncid infestation in Gammarus and Hyalella, Lac la Ronge, 1959.
males showed no tendency to mate with infested females although they were mature. Females, however, developed costegites but with no indication of breeding. In Hyalella, the infested females were observed participating in pre-copulation activities, but no breeding was noticed.

_Pontoporeia affinis_ was not infested throughout the period of sampling at Lac la Ronge. However, in the collection of Wollaston Lake, four infested _Pontoporeia_, average size 6.1 mm., were present in the sample of the 30-40 metre depth zone. They were parasitized by the plerocercoid larvae of the tapeworm, _Cyathocephalus_ sp. In all the specimens the parasites were occupying the mid-portion of the body.

Saunders (1933) found _Gammarus_ and _Hyalella_ infested by the same two kinds of parasites in Vancouver Island. _Hyalella_ were 50 per cent infested by microsporidian larvae during August. Hynes (1955) found _G. lacustris_ infested by the roundworm, _Polymorphus minutus_, a common parasite of ducks in England. He observed multiple infection with a high rate of incidence in August and October and believed that the infestation affected the breeding and probably prevented it altogether. Larkin (1948) found _Pontoporeia_ parasitized by the plerocercoid larvae of _Cyathocephalus_ sp. in Great Slave Lake and Lake Athabaska. The parasitized
specimens were equally abundant in all depth zones of the lakes.

AMPHIPODS AS FISH FOOD

Examination of the stomach content of fish has revealed the importance of amphipods as fish food in Saskatchewan. The main species which consume amphipods are the whitefish, Coregonus clupeaformis; the white sucker, Catostomus commersoni; yellow perch, Perca flavescens; cisco, Leucichthys sp.; pike, Esox lucius; and burbot, Lota maculosa. The whitefish, which is commercially important, the white suckers and the ciscoes are the largest consumers of amphipods in Saskatchewan lakes. Pontoporeia is an important food available to whitefish at all depths in the deep and cold lakes of the north. In lakes Athabaska, Reindeer and Wollaston it formed 30-65 per cent of the stomach contents of the whitefish. The examination of fish taken from the lakes of the Upper Churchill Drainage indicated that whitefish, ciscoes, pickerel, pike and burbot feed on amphipods (Rawson, 1957). The per cent volume occupied by the three species of amphipods in the stomachs varied with the species and the season. The perch from Churchill and Big Peter Pond lakes had considerable numbers of amphipods in the stomach contents. The fish of Stanley Mission area showed the presence of about 20 per cent amphipod
remains in whitefish stomachs and frequent occurrence in stomachs of other fish in the area. Lakes in the parkland and the grassland have amphipods occurring only in the littoral and sub-littoral regions. Suckers, whitefish and ciscoes feed on Gammarus and Hyalella in Montreal and Bigstone lakes. The examination of whitefish stomachs from Hunter Bay for a period of five months revealed that in early summer, late May to mid-June, amphipods formed the main bulk of the stomach contents (Rawson and Atton, 1949). They were the dominant food in the stomachs of ciscoes at the end of August. In the main part of Lac la Ronge, amphipods made up a small percentage of the stomach contents of whitefish and had little importance in their diet.

Larkin (1948) found Pontoporeia to be the chief source of available food of whitefish at all depths in Lake Athabaska. The examination of the stomach contents of ciscoes in Green Lake, Wisconsin, during the summer showed Pontoporeia as the dominant food (Pearse, 1921). Novakowski (1955) found amphipods to be a major food item for longnose suckers and ciscoes in Reindeer Lake. Atton and Murray (1952) showed the importance of chironomids as food for whitefish in Last Mountain Lake.
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SUMMARY AND CONCLUSIONS

1. The literature on ecology and distribution of Gammarus lacustris, Hyalella azteca and Pontoporeia affinis is reviewed.

2. The physical, geographical and climatic features of Saskatchewan are outlined and the limnology of the lakes has been described briefly. The lakes in the north from which amphipods were collected are large, deep and cold, and have short open water periods, while the lakes in the south are small, have longer duration of open water, and vary from freshwater to saline.

3. In G. lacustris, the first antenna is longer than the second, the third uropod has a short setose terminal segment of the outer ramus, and the eyes are placed inside of the anterior margin of the head. H. azteca has a shorter first antenna, the telson is entire, and dorsal segments of the abdomen are carinated. As in H. azteca, the first antenna in P. affinis is shorter than the second, the pereiopods are unlike in structure and size, and the gnathopods are small and subchelate.

4. In many of the northern lakes of Saskatchewan, P. affinis is dominant, inhabiting the cold and deep waters. H. azteca constitutes a small per cent of the total population of amphipods and it lives in littoral regions. G. lacustris usually thrives in shallow, muddy places in
these northern lakes. It seems that the deep and cold waters and shorter summer period are responsible for their small population of *G. lacustris* and *H. azteca*. The southern lakes tend to be more shallow and warmer, thus *Pontoporeia affinis* is absent, but *H. azteca* and *G. lacustris* are present in large numbers.

5. *Gammarus lacustris* and *H. azteca* live in the same habitat and possess similar feeding habits. *P. affinis* does not show the habit of clinging and grasping, but is usually found moving swiftly over the substratum. The three species have somewhat different temperature requirements. They are considered negatively phototropic. *Gammarus* and *Hyalella* have been found hidden in vegetation and *Pontoporeia* concentrate in deep waters where the light penetration is low. Water movements and the nature of the bottom material are believed to affect the distribution of the three species.


7. Amphipods thrive on vegetated muddy or oozy bottoms of lakes, presumably because these provide food and protection from predators.

8. Observations were made on amphipods kept in captivity in the laboratory to compare with the life histories in the field. *G. lacustris* has a breeding period of about
two months as compared to three months for the other two species. The incubation time for *Gammarus* in the laboratory is about 22 days, but this is believed to be abnormally shortened by the high water temperatures which prevailed. *H. azteca* required six to eight days for incubation. The young of both *Hyalaelea* and *Gammarus* were released in succession from the brood pouch. *P. affinis*, though kept for observations, died, presumably because of high temperatures in the laboratory.

9. Three stations were selected at Lao la Ronge to study habitats and population changes in the three species. It was found that a larger number of amphipods was present in the stations situated in the shallow and protected regions than in the one located in a more exposed region.

10. *Gammarus lacustris* collected at Lao la Ronge in early summer were of large size. The females outnumbered the males in mid-July when the breeding was first observed. By August, the large overwintered individuals were decreasing and a new generation was entering the population. Two generations were observed in the period of sampling, and both of these are believed to reach maturity in the next summer.

11. The population of *H. azteca* at the three stations in Lao la Ronge varied during the summer. Breeding started early at Stations I and II and about two weeks later at
Station III. The smaller population of *H. azteca* at Station III is considered due to a short breeding period and late hatching which result from longer persistence of ice cover. Females, averaging 3.85 mm. in length, were observed breeding in mid-summer when the temperature of the water was 20°C.

12. *Pontoporeia affinis* outnumbered *H. azteca* at Station III, Lac la Ronge, throughout the season. On two occasions the number of *P. affinis* was five times that of *H. azteca*. The rate of growth of *P. affinis* was fairly uniform throughout the observation period of two months, during which time they grew from three mm. to six mm.

13. The growth and migration studies of *P. affinis* in Wollaston Lake showed the migration of the young-of-the-year (2 mm.) to shallow water in June. The adults of the previous year were abundant at all depths, but more concentrated in 10-20 metres of water. In July, the group which was two mm. long in June had grown to three mm., while in August they had reached the size of four mm., and were dominant in 10-20 metres depth zone. In August, the young-of-the-year migrated again to deep water, which was cold and unmixed. In this cold water they grew rapidly.

14. *Gammarus lacustris* and *H. azteca* in Lac la Ronge were found infested by the larvae of echinorhynchid worm. The average rate of infestation was about five per cent
during summer. Gammarus males showed no tendency to mate with the infested mature females. In Hyalella, infested females were found mating but no eggs were produced. A few Pontoporeia, infested by plerocercoid larvae of the tapeworm Cyathocephalus sp., were found in the samples of Wollaston Lake.

15. The importance of amphipods has been shown by the studies of stomach contents of fish found in the province. Pontoporeia is usually the chief food for whitefish in deep and cold northern lakes. Several species of fish in southern lakes consume Gammarus and Hyalella and these often form a major part of their diet.


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