SURVIVAL AND GROWTH OF YOUNG GAMMARUS LAWRENCIANUS BOUSFIELD AT DIFFERENT TEMPERATURES AND ON DIFFERENT DIETS IN NEWFOUNDLAND

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SURVIVAL AND GROWTH OF YOUNG GAMMARUS LAWRENCIANUS BOUSFIELD AT DIFFERENT TEMPERATURES AND ON DIFFERENT DIETS IN NEWFOUNDLAND

by

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Survival, growth and egg production of Gammarus lawrencianus was determined for newly released young kept without food and maintained on diets of TetraMin, the Blue Mussel(Mytilus edulis), and the algae Dictyosiphon foeniculaceus, Pilayella littoralis and Enteromorpha intestinalis, at 15° C. Similar experiments were performed on animals fed TetraMin at 5°, 10°, 12° and 15° C. Concurrent field collections were made at Witless Bay Pond and North Arm Holyrood, Newfoundland. The selectivity of immature and adult G. lawrencianus were also investigated and the energy and amino acid content of the diets determined.

Survival was inversely proportional and growth directly proportional to temperature. Temperature also significantly influenced fecundity and age at maturity, but not maturation size in the range of the temperatures tested. Higher temperatures reduced the maturation age and increased the number of eggs produced. Diet significantly influenced survival, growth, fecundity as well as size and age at maturation. Survival was enhanced by fine algae but growth, fecundity and age , and size at maturation were optimized on a diet of Mytilus. Size at maturity in the field was comparable to animals fed diets of TetraMin or Mytilus, but diets of filamentous algae produced a much larger maturation size. Maturation size in the field decreased as the summer progressed, probably due to changes in the quality of the available diet.

The total energy content of the food appeared to be an important variable in the quality of the diet. Texture probably had a large influence on the amount of energy actually available to the animals, especially when algae were a major part of the diet.

No obvious correlation between the quality or quantity of amino acids

in the diet and the growth, survival and fecundity was found except in the case of TetraMin. TetraMin was deficient in a great number of amino acids when compared to G. lawrencianus. Animals fed TetraMin had a very low survival rate when compared to the other diets, but growth and fecundity were similar to Mytilus, the diet that most closely corresponded to the amino acid makeup of G. lawrencianus.

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INTRODUCTION

Gammarus lawrencianus Bousfield is a common benthic crustacean which is endemic to the northwestern Atlantic (Steele and Steele 1974). It is found in large numbers during the summer at the upper reaches of estuaries (Steele and Steele 1970) from Labrador and Newfoundland south to Connecticut and Long Island Sound (Bousfield 1973). Steele and Steele (1970) discussed the biology of G. lawrencianus including the distribution and abundance, size at maturity, size of the embryos, life cycle, female reproductive cycle and fecundity.

G. lawrencianus was selected as the experimental animal primarily because of its ease of culture. MacKay and Vassallo (1977) cultured a number of the common shallow water amphipods found in the northwestern Atlantic including G. tigrinus Sexton, G. oceanicus Segerstrale, G. mucronatus Say and G. lawrencianus. G. lawrencianus survived best under culture conditions. Although its individual fecundity is low, the speed at which it matures and broods young results in a high reproductive potential. G. lawrencianus is an ideal experimental animal. It has a short generation time, can be sexed, measured and the number of eggs in the female brood pouch determined with minimal effort. It is easily collected in large numbers in intertidal and shallow waters.

Temperature has been previously identified as a major environmental factor affecting the biology of gammarids (Kinne 1959, 1960, 1961; Nilsson 1977; Steele and Steele 1970, 1972b, 1973). It influences growth rates (Kinne 1959; Nilsson 1977), survival (Kinne 1959; Nilsson 1977), molting frequency (Kinne 1959, 1960, 1961), duration and time for reproduction (Kinne 1959), mean maturation size (Steele and Steele 1970, 1972b) and duration of egg developement (Kinne 1959, 1960; Steele and

Steele 1973). Recently photoperiod has been found to be an important factor regulating the reproductive cycle (Steele 1967; Steele et al. 1977). Diet has largely been ignored in marine gammarids probably because of the difficulty in assessing its effects in the field. Diet has been shown to affect growth, survival and molting frequency in the freshwater amphipod G. pulex (L.) (Willoughby and Sutcliffe 1976). Other work on the feeding biology of freshwater gammarids has been carried out by Moore (1975, 1977), Anderson and Raasveldt (1974), Lubyanov and Zubchenko (1970) and Barlocher and Kendrick (1973, 1975). Ladle (1974) provides a thorough review of the subject.

There is little doubt that in gammarids a large number of biological processes are directly dependent on temperature such as the duration of egg development (Steele and Steele 1973). Other properties (eg. distribution, growth, brood size, age and size at maturation, etc.) could be significantly influenced by diet. This is the case in many Crustacea (Hall 1964; Willoughby and Sutcliffe 1976; Barlocher and Kendrick 1973, 1975; Wenner et al. 1974).

During a study of the economic potential of amphipods as a protein source for fish culture (MacKay and Vassallo 1977) a correlation was observed between the spring bloom of ephemeral brown algae and the release of young. Steele and Steele (1975) made similar observations and postulated that the resting stage (a period in the female reproductive cycle when no eggs are produced) was an adaptation for synchronizing the release of the young with optimum conditions, the spring algal bloom. Steele and Steele hypothesized that survival of the young was enhanced by the presence of these algae. To test this hypothesis and concurrently study the effect of various temperatures and dfets on a number of

ecologically significant parameters such as growth, survival, age and size at maturation and fecundity, experiments were conducted. During the course of the experiments it was observed that diet had an effect on growth rate and reproductive capacity. In an attempt to provide some insight into the reasons for this, the energy and amino acid content of the foods were analysed. Since feeding habits could have a profound effect on the types of food ingested food preferences were investigated. Populations in the field were also studied so as to be able to relate the experimental data to a natural situation.

Steele and Steele (1970) collected gammarid amphipods in a number of locations close to St. John's. In choosing appropriate sampling sites these localities were visited and North Arm Holyrood and Witless Bay Pond chosen for sampling. They harboured large populations of the experimental animal, G. lawrencianus, and represented highly different habitat types.

METHODS AND MATERIALS

Areas sampled

i) North Arm Holyrood

Sampling was carried out at North Arm Holyrood between March 15 and September 24, 1977. North Arm Holyrood is located approximately 50 km southwest of St. John's, Newfoundland, at the head of Conception Bay (Figure 1, Plates 1 and 2). Sampling was restricted to the shoreline or shallow shelf (less than 1 m in depth at low tide) at the mouth of the North Arm River (Figure 1). The shelf, produced by silt carried down the river, had a gradient of sediment types; at the mouth of the river large boulders and rocks, farther down this shelf coarse sand and gravel, followed by silt and mud. Eelgrass (Zostera marina L.) was not common but a small bed was found near the middle of the shelf. Fucus sp. was much more abundant but generally restricted to the intertidal flats and along the shoreline, although some plants did grow where rocks projected out of the mud. The subtidal part of the shelf was largely dominated by Dictyosiphon foeniculaceus (Huds.) Grev. which formed tangled masses 0.4 to 0.6 m deep. Another brown alga, Pilayella littoralis (L.) Kjellm., was dominant in intertidal areas as an epiphyte on Fucus sp. It was also the most common alga at the river mouth, where it was attached to rocks. Blue mussel (Mytilus edulis L.) was the most obvious invertebrate but most shells were empty. They littered the bottom of the subtidal Dictyosiphon zone. The dominant invertebrates were gammarid amphipods at all sampling sites.

In North Arm Holyrood four sampling sites were chosen to correspond to the major habitats (Figure 1). Site 1 was on the southeast side of the Bay about 1 m from shore and approximately 30 cm in depth at low tide. The substrate was mostly coarse sand with a rocky intertidal zone.

Figure 1. The North Arm Holyrood sampling area. The sites sampled are also included.

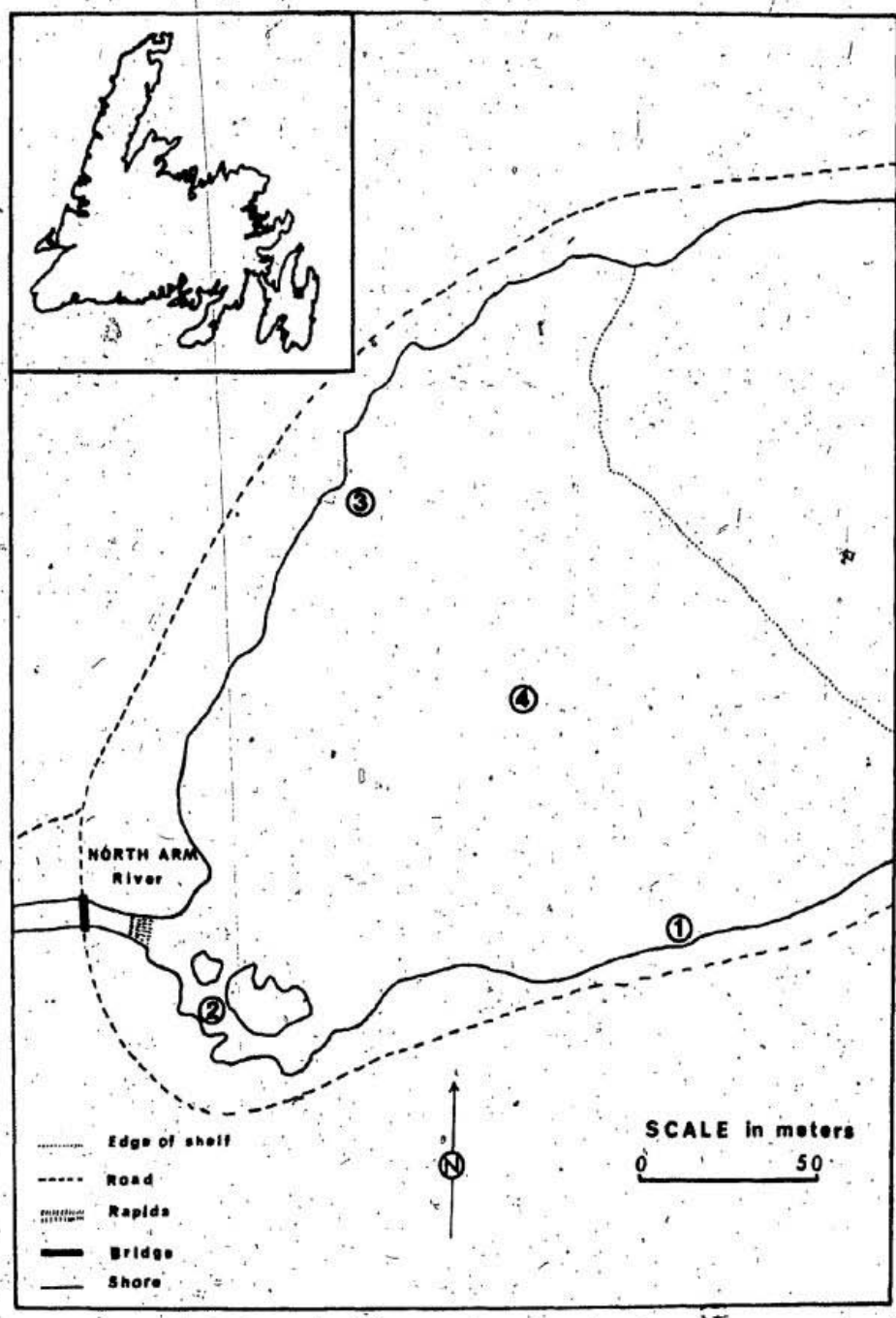

NORTH ARM
River
1
2
3
4
Edge of shelf
Road
Rapids
Bridge
Shore
N
SCALE in meters
0
50

Plate 1. North Arm Holyrood, High tide.

Plate 2. North Arm Holyrood, low tide.

The vegetation was dominated by Fucus sp. and Pilayella which formed a narrow band along the coastline. Site 2 was a small cove just south of the mouth of the North Arm River. This sampling site was approximately 30 cm in depth at low tide. A channel of the river flowed through the area. The site had no macroscopic vegetation although there was an Enteromorpha intestinalis(L.) Link bed about 3 m away. It did collect some detritus and dead squid. The substrate was essentially rock overlain with small stones. Site 3 was on the northwest side of the bay, about 1 m from shore and 50 cm in depth at low tide. The shoreline was more marine in nature. The substrate was solid rock which extended out about 4 m from the low water mark. It appeared to be the only site exposed to wave action. The site was dominated by Fucus and Pilayella but other algae were also present, eg. Chondrus crispus Stackhouse and Dictyosiphon. Site 4 was in the center of the shelf approximately 1 m in depth at low tide. The substrate consisted mostly of fine sand and silt. A small amount of Fucus grew where rocks projected out of the substrate. The dominant alga was Dictyosiphon which grew on the subtidal area of the shelf in mats up to 0.6 m deep.

ii) Witless Bay Pond

Witless Bay is located about 50 km south of StJohn's, Newfoundland (Figure 2, Plate 3). Sampling was restricted to a small saltwater pond between Witless Bay Brook and Witless Bay. It was inside a spit and modified by the construction of two bridges and the dredging of the harbour. Dredging had created a deep central trough but the perimeter is shallow with a sand bar along one side. The entrance to the bay is under the main highway bridge. It was very shallow and narrow (less than 0.6

Figure 2. The Witless Bay Pond sampling area. The sites sampled are also included.

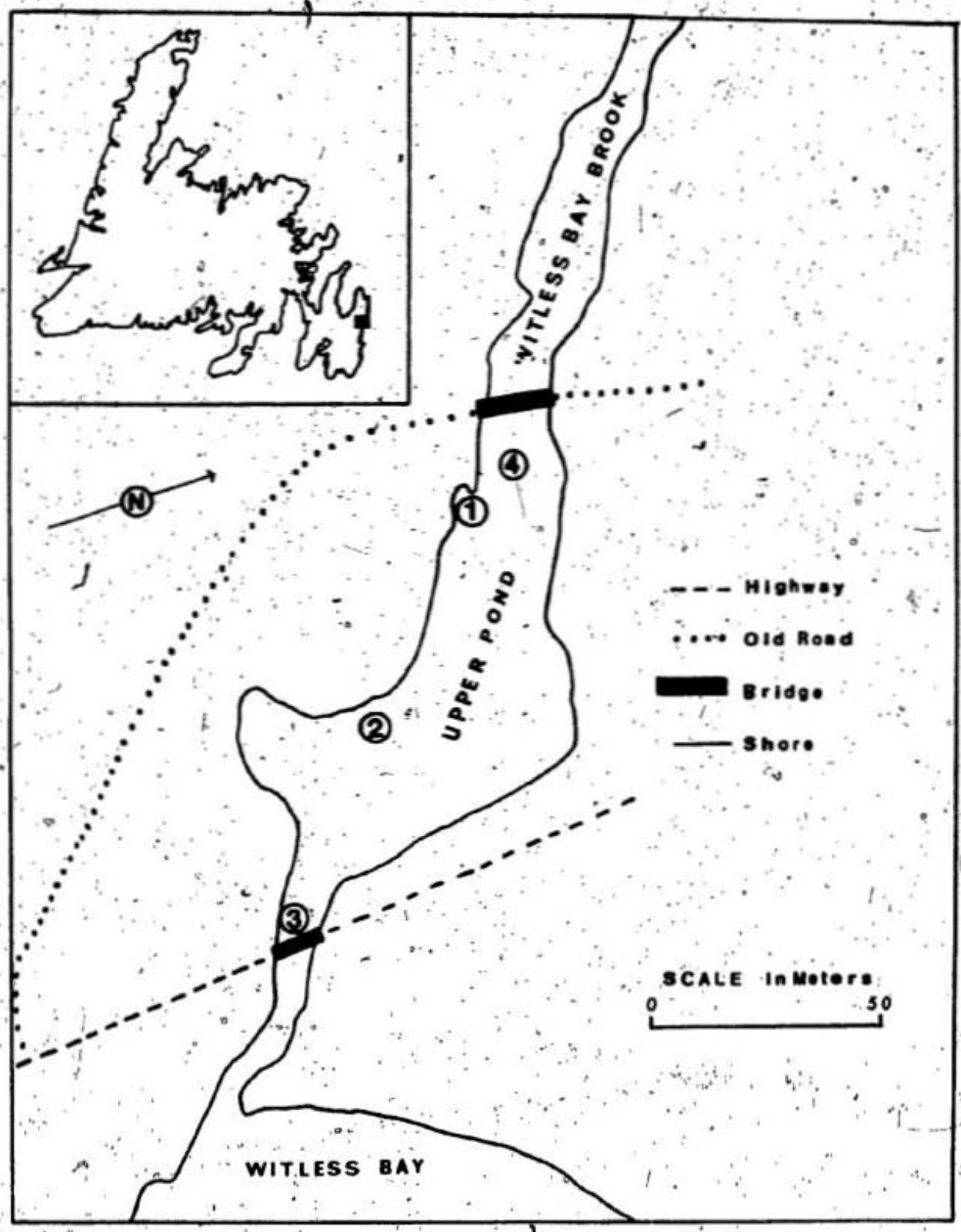

WITLESS BAY BROOK
UPPER POND
WITLESS BAY
N
1
2
3
4
Highway
Old Road
Bridge
Shore
SCALE in Meters
0
50

Plate 3. Witless Bay Pond.

m in depth and 3 m wide at low tide). Freshwater flowed down Witless Bay Brook under the old highway bridge and into the pond where it was mixed with seawater. Water flowed out of the pond on a falling tide with a reverse flow from Witless Bay on a rising tide. Flow down Witless Bay Brook was slow and dependent on rainfall. The substrate largely consisted of coarse sand and gravel with large rock faces protruding along the southwest side of the pond.

Macrophytic vegetation was sparse in Witless Bay Pond. Pilayella was the most common alga but it was generally restricted to the southwest side of the pond where there was a stable substrate of rock and small stones. Enteromorpha intestinalis was present but not abundant. The dominant invertebrate and in some samples the only one was Gammarus lawrencianus which was found throughout the pond during the sampling period. Detritus, both plant and animal, was common. Effluent from a fish plant as well as detached coastal algae were carried into the pond with a rising tide.

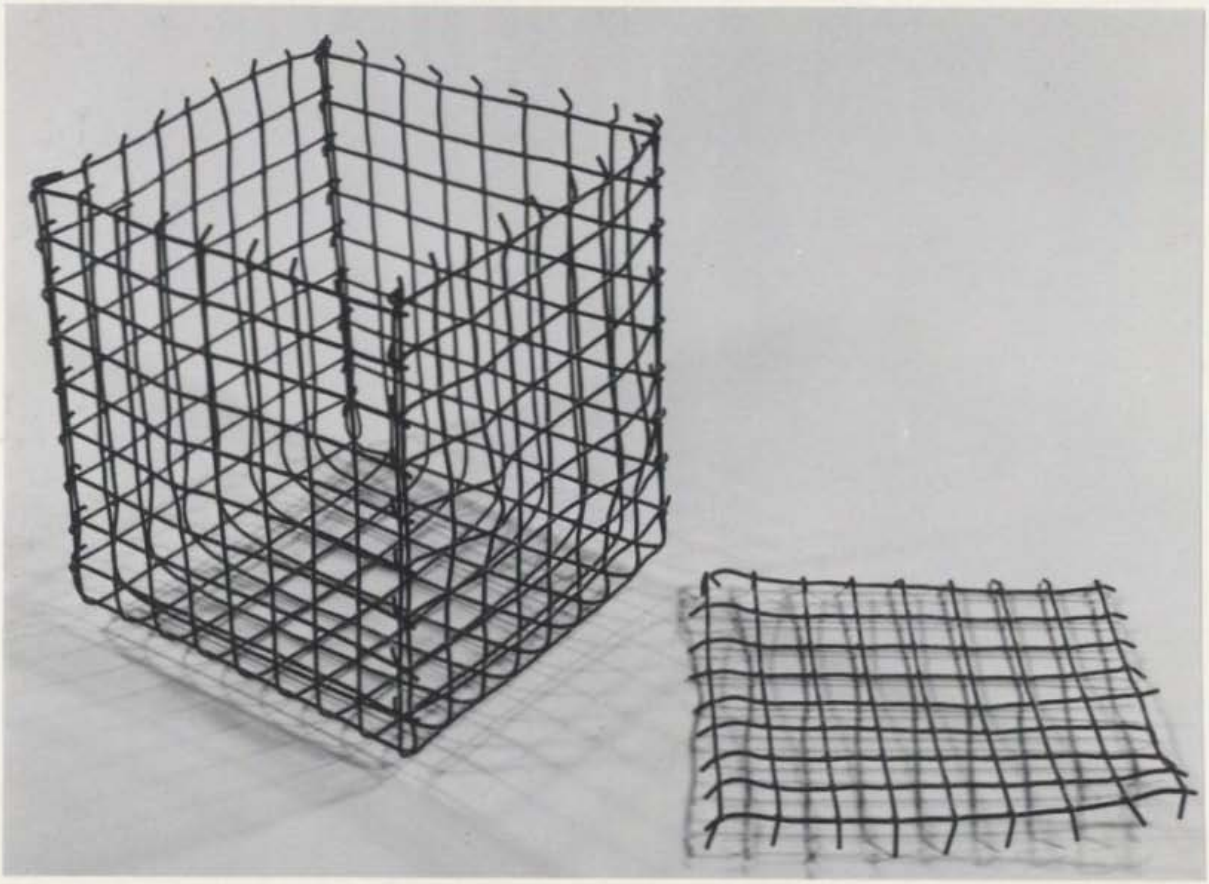
In Witless Bay Pond three main sampling sites were chosen (Figure 2). They were all on the southwest side of the pond because the northeast side was almost entirely sand, with few amphipods and no Pilayella. The sites were chosen according to three criteria; adult G. lawrencianus and Pilayella had to be pregent, and the sites had to represent a gradient from stream to bay. Site 1, a backwater area where the brook entered the pond, was covered by a large amount of brown Pilayella. The substrate was silt. One cm below the silt was black anaerobic mud. The site was approximately 50 cm from shore and 12-30 cm in depth at low tide. Site 2, just off a spit of land, had a patchy covering of Pilayella

with some Enteromorpha scattered throughout. The substrate consisted of a sandstone base with a light covering of small rocks and sand. The site was about 1 – 2 m from shore and approximately 10 - 40 cm in depth at low tide. Site 3, next to and on the south side of the main highway bridge, had a patchy covering of Pilayella and Enteromorpha. Large tufts of Pilayella were present along the shoreline and a small bed of Enteromorpha in deeper water. The substrate had a solid rock base with small rocks and sand scattered throughout. The site was approximately 50 cm from shore and 10 - 40 cm in depth at low tide. Only Pilayella samples were collected at site 3. A fourth site, the brook, was sampled when air supply permitted. The brook had no macroscopic vegetation. It had a mixed substrate of rocks, gravel and sand. It was shallow (less than 50 cm in depth) and the current was slow. Samples were collected in the center of the brook where it entered the pond. The site was approximately 1.5 m from shore and 30 cm in depth.

Sampling methods

To determine the distribution, abundance and life cycle of field populations, amphipods were collected by three main sampling techniques: basket traps (Levins 1976), air lift sampler (MacKey 1972) and collecting Pilayella with an aquarium net. Basket traps were used only at North Arm Holyrood. They were made from galvanized "bolting cloth" wire (Gauge #9) and constructed with dimensions of 10.5 cm by 10.0 cm with square mesh of 1.2 cm each side (Plate 4). Stakes were hammered into the substrate to support the cages where possible. On solid substrates the cages were tied to rocks and placed on the bottom.

Plate 4. Basket traps (½ actual size).



Initial experiments were carried out using the cage samplers to determine which type of substrate would collect G. lawrencianus. Six different substrates were tested: Fucus without macroscopic epiphytes, Fucus with macroscopic epiphytes (mostly Pilayella), Dictyosiphon, Pilayella, Dictyosiphon with Fucus placed in as a filler, and Pilayella with Fucus placed in as a filler. Fucus without epiphytes collected only G. oceanicus, Fucus with epiphytes collected large numbers of G. lawrencianus , but the supply of Fucus with epiphytes was limited and the amount of epiphytic growth varied greatly with location and season. Both Pilayella and Dictyosiphon, if not supported by Fucus, tended to float through the holes in the cages. Pilayella with Fucus tended to roll up in a ball and did not collect many amphipods. Only Dictyosiphon with Fucus as a filler provided consistent results.

Experiments were also conducted on the most efficient time period that the collectors should be left in the environment. Ten collectors were placed at site 4 at North Arm Holyrood and a pair were collected every 3 days until 15 days had elapsed. After 15 days, the number of G. lawrencianus found in the collectors was still increasing with over 150 animals per collector. It was decided that a 10 day interval was the most efficient time period that would provide an adequate sample size.

To set up a basket trap, two trips to the sampling area were necessary. On the first trip Fucus, free of macroscopic epiphytes and Dictyosiphon were collected with dip nets and by hand. The algae were thoroughly washed with tap water, patted dry with paper towels and weighed on a top loading Mettler balance (Model no. P-163) to the nearest 0.1g. Fucus and Dictyosiphon were divided into 200 g and 10 g

portions respectively. Each portion was placed in a separate container flooded with Logy Bay seawater (salinity 30 - 33 ‰) and kept at 10° C (± 1° C) for a maximum of two days. To fill the traps, approximately half the Fucus portion was placed in a basket, then the Dictyosiphon portion, followed by the rest of the Fucus. The Fucus acted as a filler to hold the Dictyosiphon in place. The baskets were then returned to the stake or bottom, approximately 30 - 40 cm below the low water level. After ten days the cages were removed with a dip net, emptied and the Dictyosiphon and Fucus placed in separate containers. To separate the the amphipods from the algae 5% formalin, prepared from water collected at the sampling site, was added to the containers. Most of the amphipods swam out of the algae and were transferred to a vial containing 5% formalin prepared with Logy Bay seawater. The algae was washed in freshwater and the remaining amphipods removed and transferred to a vial.

An air-lift sampler was used both in North Arm Holyrood and Witless Bay Pond, in areas where it was possible to collect relatively quantitative benthic samples. The air-lift sampler worked on the principle that compressed air, liberated in the submerged end of an open pipe will form an air-water mixture which will produce lift if there is sufficient pressure. An air-lift sampler was constructed from a 1 m length of plastic drainpipe of 7.9 cm internal diameter, producing a sampling area of approximately 0.005 m^2 (Plates 5 and 6). The Π - shaped upper end was built using a 30 cm length of drainpipe and two elbows. This allowed the flow of water to run into a bucket. Compressed air from a diving tank was fed through an air line down the side of the drainpipe and into a U- shaped brass feed pipe positioned so the exhaust was liberated in

Plate 5. Air-lift sampler.

Plate 6. Air-lift sampler in use.

the center of the bottom of the drainpipe. The diving tank had an "A" clamp with a valve to control the rate of air flow. Two people were necessary to properly use the sampler. The air tank was connected to the sampler by a long hose so the tank could be left on shore. The sampler was carried into the water and the sampling area chosen at random. It was lowered over the spot to be sampled and a bucket hung from the sampler to collect the sample (Plate 6). The air was turned on and when the substrate began to collect in the bucket the air was shut off. In this way an average of six samples could be collected per tank of air. The contents of the bucket were poured through an aquarium net, then transferred to containers and flooded with 5% formalin made from water collected at the sampling site. To separate the amphipods from the substrate forceps were used to pick out the larger ones. The smaller amphipods were floated out using a modified sugar flotation technique (Anderson 1959). This process involved draining the formalin from the sample and placing the solid contents into an enamel dissecting pan. The sample was flooded with a sugar solution of 1.12 specific gravity (approximately 0.3 kg of sugar per liter of solution). The fauna floated and were picked up with forceps or a piece of paper. The sample was drained, flooded with freshwater and allowed to sit for at least 20 minutes. The process was then repeated. This technique has been used on amphipods previously with separation efficiencies of 85 - 100% (Anderson 1959; Vassallo 1975). All invertebrates were preserved in 5% formalin made with Logy Bay seawater. Any animals under 1.5 mm were discarded because of the tendency of females to release their brood during the sampling and preservation procedure.

Both of the sampling techniques described above were biased towards adults as the young tend to cling to filamentous algae. To collect the young, Pilayella was collected with an aquarium net at a depth of 10 - 30 cm at low tide. A tuft of Pilayella was scooped up and placed in 5% formalin. Most of the young amphipods swam out of the Pilayella and were picked up with a medicine dropper and preserved in 5% formalin. The alga was washed thoroughly in freshwater to remove the remaining young. Any adults caught in the aquarium net were discarded. The alga was washed in distilled water, air dried on blotting paper or aluminum foil and ground to a powder using a mortar and pestle. The Pilayella was dried in an oven (100° C) for a minimum of 24 hours. The samples were kept in a desiccator until weighed on a Mettler pan balance (Model no. H-34) to ± 0.1 mg.

All sampling was carried out within one h of low tide. In both localities, temperatures were recorded and salinity samples collected at the surface and at the depth amphipod samples were taken. Temperatures were measured using a Celsius thermometer and salinity using a hydrometer in the field or a conductivity meter in the lab.

In North Arm Holyrood sampling was carried out approximately once a month from March 18 to September 24, 1977 as shown in Table 1. Initially from March 18 to May 21 all sampling was performed using basket traps and confined to site 4. Thereafter all sites were sampled. In June the Dictyosiphon in the baskets began to disappear, presumably being consumed by amphipods. To counteract this, the amount of Dictyosiphon in the baskets was increased, from 10 g to 20 g, after June 21 and the time the basket traps were left in the water reduced from 10 days to 5 days. At

Table 1. The number and type of samples collected in North Arm Holywood Bay at various sampling sites. (CS - cage samples; ALS - air-lift samples).

Date	Site 1		Site 2		Site 3		Site 4	
	CS	ALS	CS	ALS	CS	ALS	CS	ALS
March 18-29 1977	0	0	0	0	0	0	3	0
April 1-27 1977	0	0	0	0	0	0	5	0
May 7-21 1977	4	0	3	0	4	0	6	0
June 25 1977	3	0	0	2	3	0	3	0
July 23 1977	3	0	0	2	3	0	3	0
August 19 1977	3	0	0	2	3	0	3	0
September 24 1977	3	0	0	2	3	0	3	0

site 2 the basket traps had to be abandoned in favor of air -lift samples.

Other problems at North Arm Holyrood also reduced the effectiveness of the sampling program. The number of G. lawrencianus collected in the samples began to decline while the number of G. oceanicus was rising dramatically. It was found that quantitative sampling of amphipods in Dictyosiphon beds was not possible due to the patchiness of the alga and my inability to efficiently separate the amphipods from the algae collected.

Because of the problems encountered at North Arm Holyrood, Witless Bay Pond was sampled beginning on June 18. At sampling sites 1,2 and 4 air-lift samples were collected approximately once a month from June 18 to November 1 as shown in Table 2. At sampling sites 1,2 and 3 Pilayella samples were collected from June 18 to August 2 as presented in Table 2.

The initial sorting and identification of all amphipods was performed by eye or with a stereoscopic microscope. In small samples all amphipods were sexed where possible and measured to the nearest 0.1 mm using a stereoscopic microscope with an ocular micrometer. Where numbers were large a subsample was analyzed. All length measurements were from tip of the rostrum to the end of the telson (Steele and Steele 1969). Sex was determined by the presence of genital papillae on the males and oostegites on the females. The presence of hairs on the oostegites was used to determine maturity. Any amphipod possessing neither papillae nor oostegites were classed as unsexable (Steele and Steele 1969). The number of amphipods in the samples was determined by counting or where numbers were large, by an estimate. The latter was obtained in an enamel dissecting pan with 100 numbered squares on the bottom (Plate 3). The amphipods

Table 2. The number of samples collected in Witless Bay Pond at the various sampling sites (A- air-lift samples; B- Pilayella samples).

Date	Site 1	Site 2	Site 3	Site 4
	A			
June 18, 1977	2	2	0	2
July 9, 1977	2	1	0	2
August 2, 1977	3	3	0	0
August 31, 1977	2	2	0	1
September 25, 1977	0	2	0	2
November 1, 1977	1	2	0	2
	B			
June 18-23, 1977	2	2	4	0
July 9-19, 1977	5	3	4	0
August 2, 1977	2	2	2	0

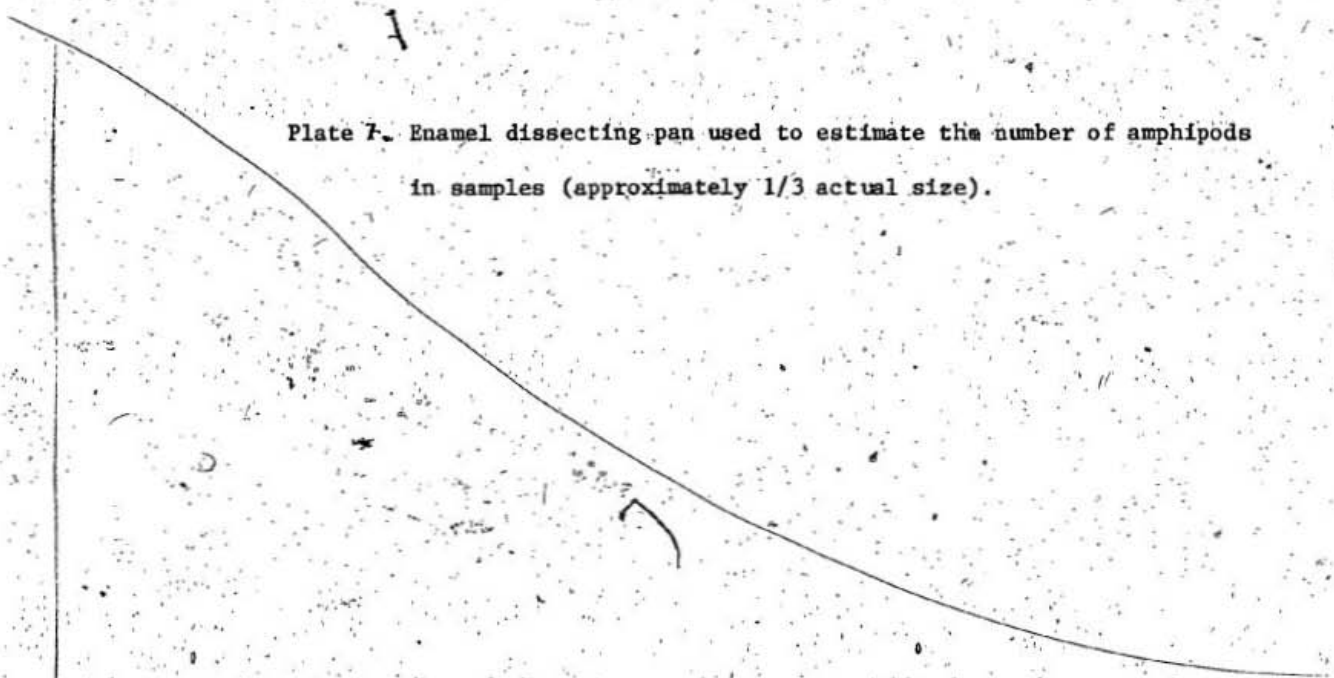


Plate 7. Enamel dissecting pan used to estimate the number of amphipods in samples (approximately 1/3 actual size).


10
20
30
40
50
60
70
80
90
100

were evenly spread out and about 25 - 30 squares selected using a table of random numbers (Rohlf and Sokal 1969). The number of amphipods in each of these squares was counted and the mean calculated. The mean was multiplied by 100 to obtain an estimate of the total number.

Growth, survival and egg production experiments

All experiments in which G. lawrencianus were studied had the same basic format. In all cases 500ml freezer containers (Plates 8 and 9) were used containing 300 ml of filtered Logy Bay seawater (salinity 30 - 33 ‰). Filtering was performed using a vacuum flask with a faucet attachment and a Buchner funnel containing #3 filter paper. A brood stock of overwintering adult G. lawrencianus was collected at North Arm Holyrood. They were kept in a cold room overnight (10° ± 1° C) and transferred the next day to containers. The amphipods were incubated in a Hot Pack incubator (Plate 10) at 15° C until the eggs in the brood pouch hatched. Young were removed from the containers or directly from the brood pouch with a medicine dropper. In this way 300 - 400 young were collected per trial. The young were left overnight in an incubator at the appropriate temperature for the experiment. To set up an experiment the young were moved 15 to a container, incubated in the dark at the appropriate temperature and supplied with food. Water was changed and food checked every 5 days. Food was provided in excess. It was collected at North Arm Holyrood before the beginning of each experiment and frozen. Any container showing signs of anaerobic conditions was discarded. Every 10 days the amphipods were counted and a container selected using a table of random numbers (Rohlf and Sokal 1969). The amphipods were

Plate 8. Freezer containers (approximately $\frac{2}{3}$ actual size).

Plate 9. Freezer containers with amphipods (actual size).

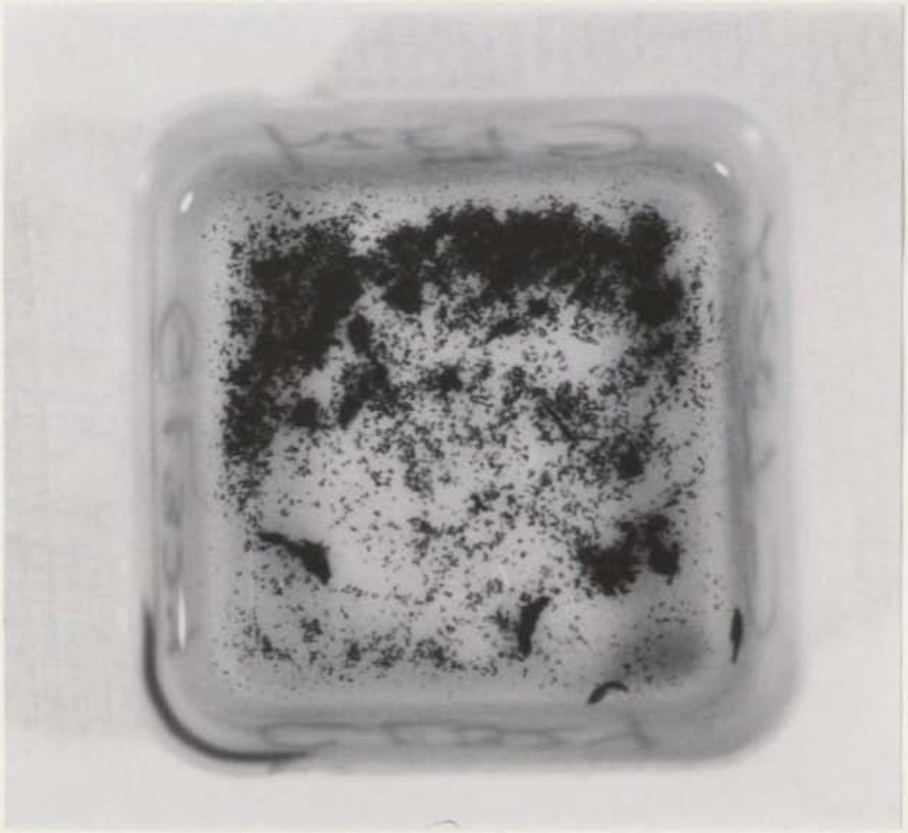


Plate 10 Hot Pack incubator (approximately 1/10 actual size).


GL324

preserved in 5% formalin for later analysis. This sampling procedure was repeated until no containers remained, the amphipods became large enough to measure live, approximately 4 - 6 mm, or the experiment was terminated. Preserved amphipods were measured in Petri dishes while submerged in 5% formalin. Those measured live were placed in dry Petri dishes where following an initial burst of activity they settled into a quiescent state. The amphipods could then be handled easily with fine forceps without injury. They were stretched out, measured and then returned to their container. Lengths of all amphipods were measured to the nearest 0.1 mm under a stereoscopic microscope fitted with an eyepiece micrometer. Length was measured from the tip of the rostrum to the end of the telson. Volumes were calculated using the equation $V \approx L^3$. When maturation occurred, defined in these experiments as the onset of precopula, the pair was measured and segregated into a separate container. When eggs were observed in the female's brood pouch, the pair was again measured and the eggs removed with a medicine dropper and counted. If the eggs had been present in the brood pouch for less than 24 hours, they were preserved and their average diameter $\left(\frac{\text{length} + \text{width}}{2}\right)$, measured under the stereoscopic microscope and egg volumes calculated using the equation $V = 4/3 \cdot \pi r^3$. This procedure was followed through multiple broods until the females died.

Two sets of experiments were set up using the above procedure. Both were designed to measure survival, growth, egg production and size of the female at maturation. The first set of experiments dealt with the effect of temperature on these variables and the second with the effect of diet. In the first set of experiments 15 containers were used in each experiment except for the 15° C experiment where 10 were used. TetraMin, a commercial fish food, was supplied as food and the containers were

incubated at 5°, 10°, 12° and 15° C. All containers were kept in Hot Pack incubators (± 2° C) except for the 10° C experiment. These were kept in a cold room (± 1° C). The 5°, 10°, 12° and 15° C experiments began on May 12, 9, 14 and June 9, 1977 respectively.

In the second set of experiments the diets included TetraMin, a commercial fish food containing plant and animal products, the fine algae Dictyosiphon foeniculaceus and Pilayella littoralis, the coarse green alga Enteromorpha intestinalis, the Blue Mussel Mytilus edulis and no food. All the algae tested were abundant in G. lawrencianus habitats. Another group of algae that would fit in this category are the Fucoids. They were not used in these experiments because G. lawrencianus does not feed on them (D.H. Steele, personal communication). The cultures were kept in a Hot Pack incubator at 15° C. The TetraMin experiment was set up on June 16, 1977. The no food, Mytilus and Dictyosiphon on June 20 and the Pilayella and Enteromorpha experiments on July 27, 1977.

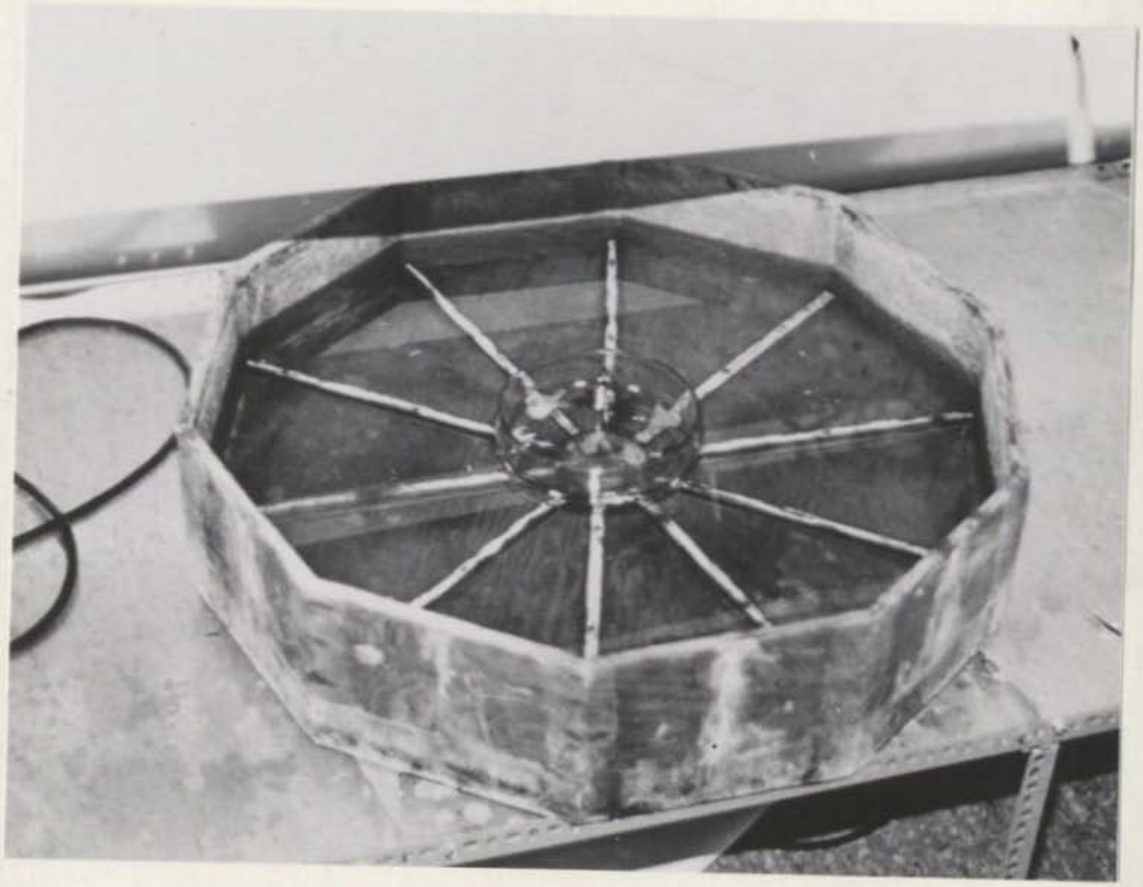
Selectivity

The selectivity experiments were designed to determine the food preference of adult and juvenile Gammarus lawrencianus. Adult G. lawrencianus were collected from North Arm Holyrood. Juveniles were obtained from adults cultured in growth and survival experiments reported previously. Logy Bay seawater (salinity 30 - 33‰) was used in all experiments. The amphipods were maintained in Hot Pack incubators at 12° C (± 2° C) before the start of the experiment (within 10 days of collection). All animals were starved for 24 hours prior to the start of all experiments. The experiments allowed the amphipods to select between five different foods

in the experiments using adults and five different substrates in the juvenile selectivity experiments. These included Pilayella, Dictyosiphon, Enteromorpha, the adductor muscle of Mytilus and no food in the juvenile experiment or Kimwipes (a commercial optical tissue paper) in the adult experiment. TetraMin was not used because of its flaky consistency and tendency to produce anaerobic conditions. The experimental chamber consisted of a large finger bowl 19 cm in diameter and 6 cm deep with a volume of approximately 1.75 l. The circumference of the container was divided into 10 equal sections numbered from 1 to 10. This allowed paired samples of the five foods. The food was measured by volume using a 10 ml graduated cylinder. Because of the different size and behaviour of the adult and juvenile G. lawrencianus, identical experimental techniques could not be used. The juveniles were too small (approximately 1.2 mm) to keep under continuous observation in the chamber. They also tended to be sedentary, keeping in close contact with the filamentous algae as reported by MacKay and Vassallo (1977). Adults were much larger (5 - 12 mm) and quite active. Feeding generally involved breaking off a piece of food and eating it while in motion. If left for any period of time with food they would distribute it throughout the chamber. This made a different type of selectivity experiment necessary.

In the adult selectivity experiment 0.2 ml of one of the five foods was placed in each of the numbered sections of the chamber (Plate 11) using a table of random numbers (Rohlf and Sokal 1969). Sixteen pre-copulating pairs were isolated for use in the adult selectivity experiment. The sexes were kept apart in separate containers. Each sex was tested in a separate chamber to prevent any bias due to pheromones. The experiments

Plate 11. Adult selectivity chamber (approximately 1/8 actual size).



were conducted at night with a fluorescent lamp (approximately 5000 lux) hanging overhead as the only light source. To maintain a relatively constant temperature (10° - 12° C) the chamber was placed in a water bath. An amphipod was introduced into the center of the chamber. The amount of time spent feeding at each station was recorded until 300 seconds of feeding time had expired. Feeding behaviour was defined as the ingestion of food, rapid beating of the pleopods while stationary and/or the manipulation of food by the gnathopods. This procedure was repeated until all 16 pairs had been tested.

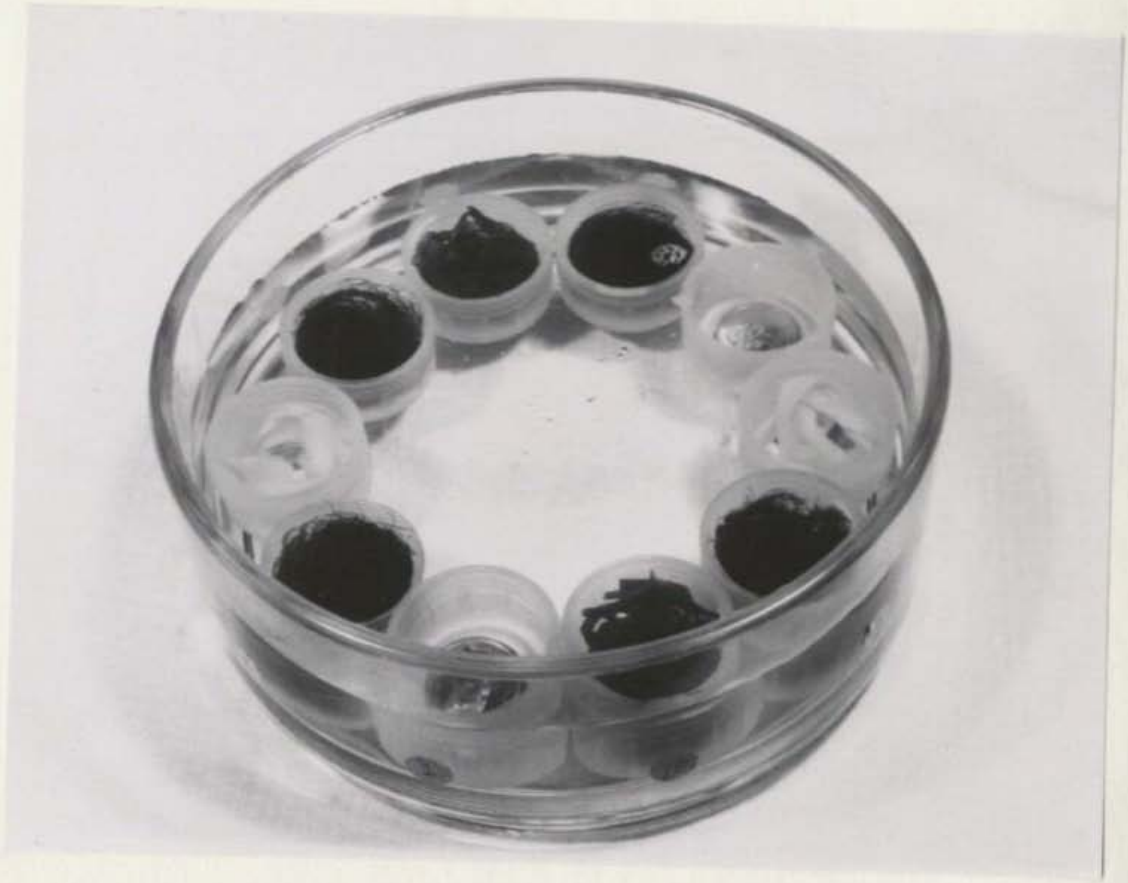
The juvenile selectivity experiment utilized the same basic chamber with 10 plastic cups 4.8 cm in diameter and 2.8 cm deep, having a volume of 30 ml. A cup was placed in each numbered section (Plate 12) and weighed down by two twenty-five cent pieces. Two ml of each food were placed in each cup using a table of random numbers as before. The chamber was placed in a Hot Pack incubator (12° C $\pm$ 2°C) and approximately 1 l of filtered Logy Bay seawater was added. 25 to 100 juvenile amphipods were then released into the center and left for 12 hours. To terminate a trial, the water was siphoned out of the chamber with a length of plastic hose. The number of amphipods found in each plastic cup were recorded. This was repeated for eight trials.

Food analysis

i) Energy content

Oxygen Bomb Calorimetry was performed on the amphipod Gammarus lawrencianus and the five foods used in growth and survival experiments: TetraMin, the adductor muscle of Mytilus edulis, Pilayella littoralis, Dictyosiphon foeniculaceus and Enteromorpha intestinalis. The material was

Plate 12. Juvenile selectivity chamber (approximately 1/3 actual size).



ground to a powder with a mortar and pestle and compressed to form a pellet which was weighed and then combusted in an isothermal oxygen bomb calorimeter. The process was repeated for each food and for the amphipod until two consecutive readings were obtained within 125.5 joules of each other (Parr Instrument Co. 1964).

ii) Amino acid analysis

Amino acid analysis was performed on the five foods used in growth and survival experiments and on the amphipod G. lawrencianus. The five foods were TetraMin, the adductor muscle of Mytilus edulis, Pilayella littoralis, Dictyosiphon foeniculaceus and Enteromorpha intestinalis. The material was rinsed in distilled water and homogenized in a blender with enough distilled water to complete the process. To remove any suspended matter, the homogenate was centrifuged at 3,000 rpm for 5 min and the supernatant filtered. To produce a constant volume the supernatant was freeze dried overnight and then dissolved in 20 ml of 20 % Trichloroacetic acid (TCA). This fluid was vortexed at 4° C for 15 min, then centrifuged in a refrigerated (4° C) Sorval Ultracentrifuge at 10,000 rpm for 10 min. The supernatant was discarded and the precipitate freeze dried overnight. The dry precipitate was ground to a powder with a mortar and pestle. Analysis of the amino acid constituents was performed via acid hydrolysis 6N HCL by the Analytical Ultracentrifuge Amino acid facility of the Department of Biochemistry, MUN. The quantitative analysis of the conjugated amino acids was performed by liquid chromatography.

Statistical anlysis

Probit analysis (Stanley 1963) was performed on the survival data from lab cultures and maturation size of field populations of Gammarus lawrencianus. The fifty percent value was calculated and its standard error determined. The final regression line was fitted and its goodness of fit determined using a chi-square test. If applicable a t-test was used to determine if a significant difference existed between two regression lines.

The 50% maturation sizes of G. lawrencianus collected at Witless Bay Pond on August 2 and August 31,1977 were compared using the t-test mentioned above. Survival data were compared by determining confidence limits around the 50% survival point (Stanley 1963).

Growth data for G.lawrencianus were first analyzed as suggested by Sokal and Rohlf (1969). Individual measurements were transformed into logarithms and confidence limits determined. This was sufficient for experiment 1,where temperature was the variable. There was no overlap in confidence limits. In experiment 2, where food was the variable, there was considerable overlap in confidence limits. The data were further analyzed using an analysis of variance computer program (Alberta Statistical Package, ANOVA-24).

All regression analysis was done using a Fisheries Board Statistical Package (A040 QQCV4). The program also analyzed the amount of covariance between two regression equations.

An arithmetic regression on the number of eggs in the brood pouch of female G. lawrencianus to the body length was done where the amounts of data were adequate,i.e. experiments using TetraMin (10° C and 15° C), Mytilus (15° C) and Dictyosiphon (15° C). Analysis of covariance was also

performed on the data. In the experiments using Mytilus (15° C) and Dictyosiphon (15° C) enough data were available to compare the volume of the brood to the volume of the female. A log-log regression was done and the two equations were compared by an analysis of covariance.

An arithmetic regression of the energy content of the various foods to the mean maturation of the amphipods fed those foods was also done. Two separate regression lines were obtained, one for dry weight energy content and the other for ash-free dry weight energy content.

Food preferences were analyzed by means of a G-test. First the paired results for each type of food item were combined. The null hypothesis that food selection was random was then tested for males, females and immature G. lawrencianus.

RESULTS

Field collections

1) Environment

Temperature

In Witless Bay Pond temperature varied little within and between the three main sampling sites on any one date (Figure 3, Appendix 1a) but large variations in temperature over short time periods were common. For example on June 18 the average temperature was 15.7° C but by June 27 it had dropped by approximately 5° C to 11.1° C. Similarly from August 2 to 12 the average temperature dropped from 21.2° C to 13.4° C.

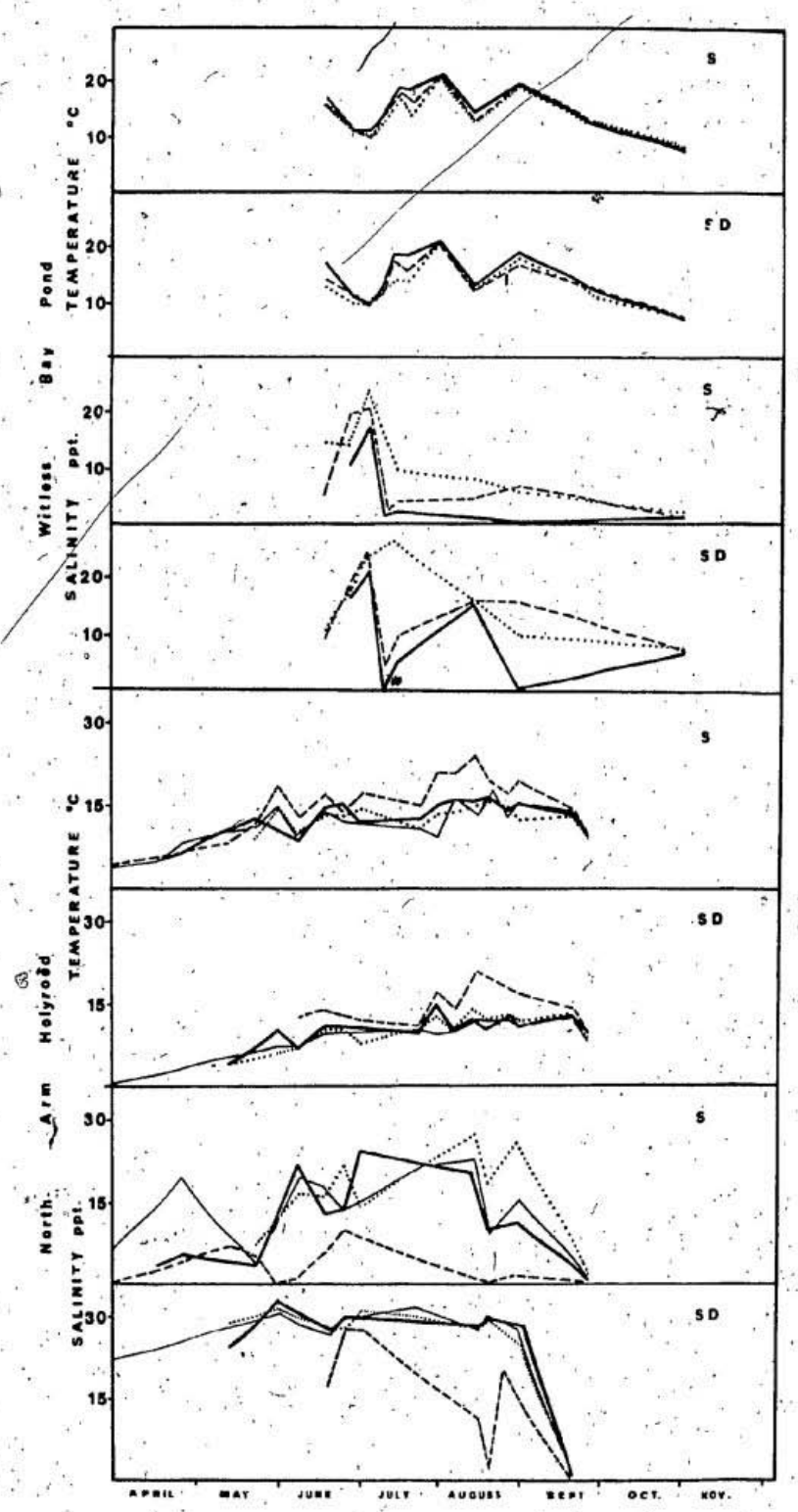
In North Arm Holyrood large variations in temperature occurred within and between sites (Figure 3, Appendix 1b). Temperatures at the sampling depth were on an average of 2.4° C lower than that at the surface as compared to 0.7° C at Witless Bay Pond. Temperatures at site 2 were much higher than at the other sites throughout the summer. It was closer to the source of the river and directly affected by the warm river water.

Salinity

In Witless Bay Pond salinity varied considerably within and between the sites sampled with a range of 0 to 27‰ (Figure 3, Appendix 1a). The average salinity at the surface was 8.2 ‰ and at the sampling depth 12.6‰. .

In North Arm Holyrood salinities were higher and more stable than at Witless Bay Pond(Figure 3, Appendix 1b). The average salinity at the surface was 10.6‰ and at the sampling depth 24.9‰ . At the sampling depth the average salinity varied the least with a range of 20.8‰ to 32.2‰ except for September 24, when following a violent rainstorm the

Figure 3. Temperature and salinity at the various sampling sites in North Arm Holyrood and Witless Bay Pond (S - surface, SD - sampling depth).


Pond
Bay
Witless
Arm
Holyrood
North-
TEMPERATURE °C
SALINITY ppt.
S
SD
20
10
30
15
APRIL
MAY
JUNE
JULY
AUGUST
SEPT
OCT.
NOV.

salinity fell to 1,3‰ . The average surface salinity varied from 0‰ to 21.7 ‰.

ii) Gammarus lawrencianus populations

Size composition

Figure 4 shows the size composition of the Witless Bay Pond and North Arm Holyrood populations of Gammarus lawrencianus (Appendices 2 and 3). The two populations had similar chronologies. There appeared to be at least two distinct cohorts, a summer and an overwintering one. The overwintering adults dominated the air-lift and cage samples until late July - early August. The disappearance of the overwintering adults from the populations appeared to correspond to the maturation of the summer cohort. Large numbers of dead adults were actually observed in Witless Bay Pond on August 2. The summer cohort, when they appeared in these samples, already showed signs of maturation (presence of oostegites in females and genital papillae in males). Immatures were generally only collected in Pilayella samples and not in the samplers.

The reduction in the mean length of the North Arm Holyrood population on September 24 and the Witless Bay Pond population on November 1 (Figure 4) would suggest a third, fall cohort, but continuous recruitment makes the identification of distinct cohorts difficult.

The mean length of the overwintering cohort of G. lawrencianus at North Arm Holyrood and Witless Bay Pond is presented in Table 3. The average length of the males was greater than that of the females. This size difference increased as the summer progressed and reached a peak of more than 2mm just before the cohort disappeared from the samples.

Figure 4. Size composition of Gammarus lawrencianus populations at Witless Bay Pond and North Arm Holyrood Bay. The number of animals examined is circled.

WITLESS BAY POND
NORTH ARM HOLYROOD
(Cage Samples)
LENGTH (mm)
% FREQUENCY
Trinyalla Samples
Air-lift Samples

Table 3. The mean length of overwintering populations of Gammarus lawrencianus. The confidence limits (95%) and number collected are shown in brackets. Collections were made at A - North Arm Holyrood, B - Witless Bay Pond.

MONTH	A		B	
	Mean length (mm)		Mean length (mm)	
	Males	Females	Males	Females
MARCH	6.9 (± 0.35) (35)	5.6 (± 0.22) (51)		
APRIL	7.5 (± 0.22) (76)	5.6 (± 0.12) (199)		
MAY	8.5 (± 0.16) (119)	6.6 (± 0.10) (203)		
JUNE	8.7 (± 0.33) (17)	6.8 (± 0.29) (18)	10.2 (± 0.19) (106)	7.9 (± 0.10) (220)
JULY	9.2 (± 0.24) (15)	6.9 (± 0.15) (73)	10.3 (± 0.19) (66)	8.2 (± 0.10) (184)

The average length of the populations differed. The animals at North Arm Holyrood were on average 1.2 to 1.3 mm smaller than those at Witless Bay Pond. Because of continuous recruitment the mean lengths of the summer cohorts were not compared.

Sex ratio

Females consistently outnumbered males, except in the September and November sampling periods at North Arm Holyrood and Witless Bay Pond respectively (Table 4). In the overwintering cohort females outnumbered males with an average ratio of 0.58. There were not enough individuals collected from the summer cohort in North Arm Holyrood to make accurate comparisons. In Witless Bay Pond the sex ratio was 0.85 as the summer cohort matured (August 2) but by August 31 the ratio was 0.47. In the fall samples it appeared that males outnumbered females. These samples were made up of small individuals and the apparent predominance of males could be due to the faster growth and therefore earlier maturation of males.

Distribution and abundance

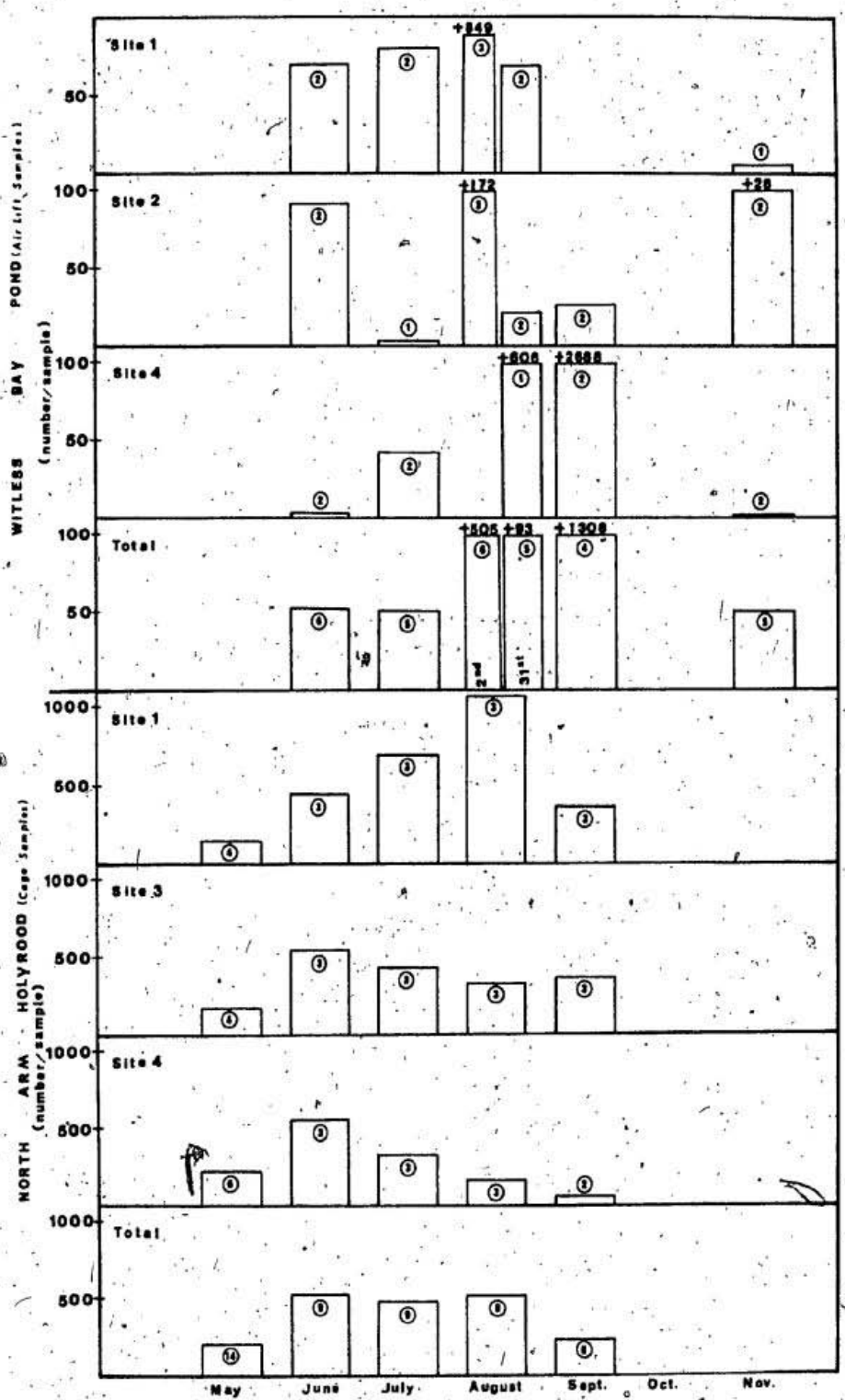
The average number of gammarid amphipods collected per sample at both Witless Bay Pond and North Arm Holyrood is presented in Figure 5 (Appendix 4). In North Arm Holyrood only small numbers of Gammarus lawrencianus were collected, the samples consisting mostly of G. oceanicus (Appendices 3a and 4b). In Witless Bay Pond G. lawrencianus was the only amphipod species collected.

Because of the small numbers of G. lawrencianus collected at North Arm Holyrood much of the data collected concern only G. oceanicus. G.

Table 4. Seasonal variation in Gammarus lawrencianus sex ratio. Column A reports the number of males collected, column B the number of females and column C the ratio $\frac{A}{B}$.

WITLESS BAY POND				NORTH ARM HOLYROOD			
MONTH	A	B	C	MONTH	A	B	C
JUNE	106	220	0.48	MARCH	35	51	0.69
JULY	66	184	0.36	APRIL	76	199	0.33
AUGUST 2	586	697	0.85	MAY	119	203	0.59
AUGUST 31	163	348	0.47	JUNE	17	18	0.94
SEPTEMBER	110	238	0.46	JULY	16	79	0.20
NOVEMBER	209	38	5.50	AUGUST	4	17	0.24
				SEPTEMBER	9	4	2.25

Figure 5. The mean number of gammarid amphipods collected per sample at the various sampling sites. The number of samples is circled.

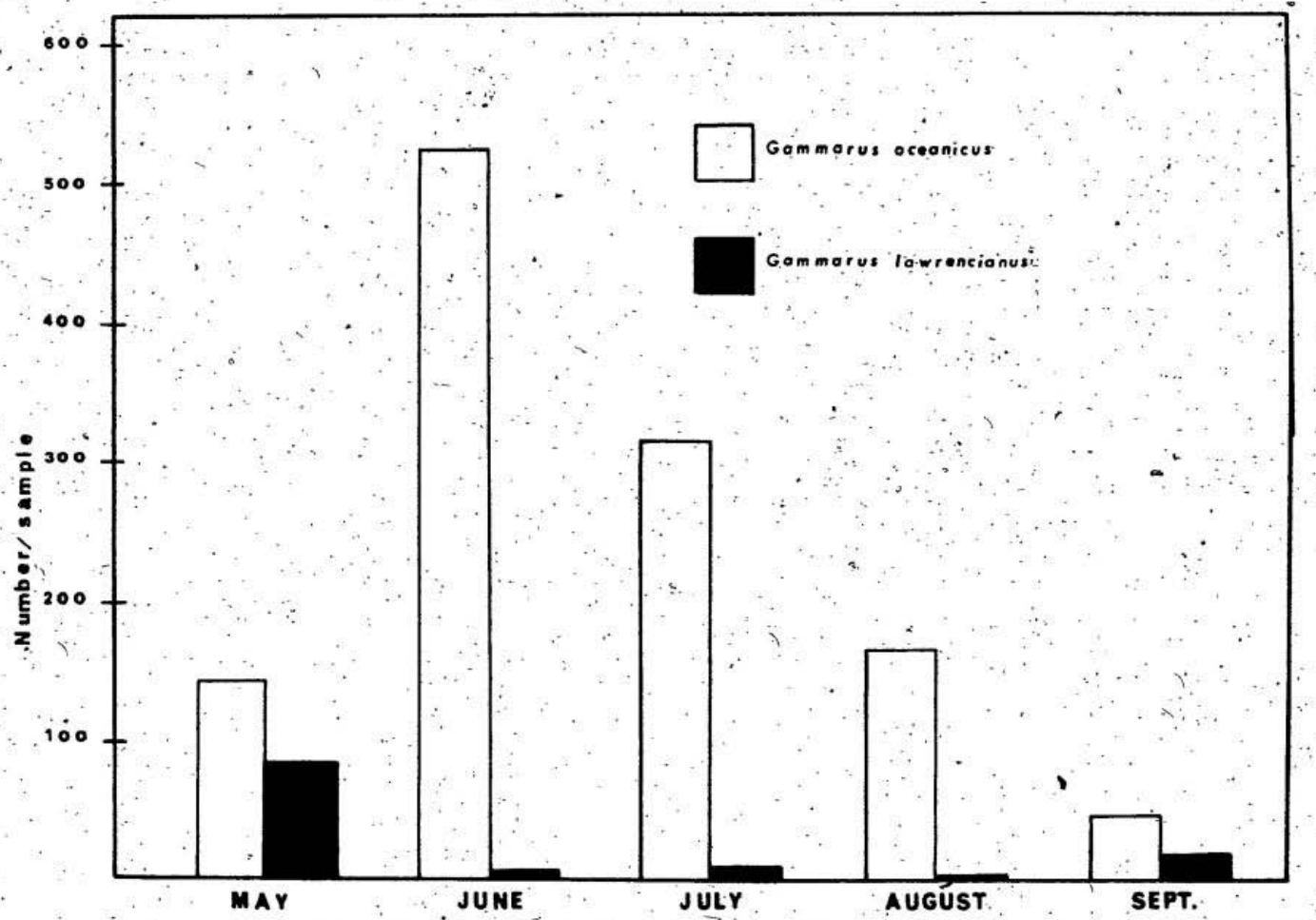

WITLESS BAY POND (Air Lift Samples)
(number/sample)
Site 1
Site 2
Site 4
Total
+849
+172
+28
+606
+2688
+505
+93
+1308
2nd
31st
NORTH ARM - HOLYROOD (Cage Samples)
(number/sample)
Site 1
Site 3
Site 4
Total
50
100
500
1000
May
June
July
August
Sept.
Oct.
Nov.

lawrencianus was consistently collected only at site 4. The numbers of G. lawrencianus and G. oceanicus collected per sample at site 4 are presented in Figure 6 (Appendix 5). As the density of G. oceanicus increased, the number of G. lawrencianus declined from over 86 per sample in May to 4 per sample in August. By September the number of amphipods per sample had risen to 19.5. The numbers of G. oceanicus had declined from a high of 527 per sample in June to 45.5 per sample in September.

In North Arm Holyrood there was a general increase in the density of gammarid amphipods (mostly G. oceanicus) in the spring, with a peak in June which was maintained over the summer. The population tended to decline in the fall to near its spring value (Figure 5). This overall trend was not as apparent at the individual sampling sites. In the most exposed site (Site 1) the spring increase in abundance tended to continue throughout the summer with a maximum density of over 1000 amphipods per sample in late August (Figure 5). At site 3 the peak was reached in June with the population density stabilizing throughout the summer. At site 4 the peak in June was followed by a general decline with less than 50 individuals collected per sample in September. The number of amphipods collected per sample at site 2 was not included in Figure 5, because problems with the sampling procedure mentioned previously made such comparisons meaningless.

In Witless Bay Pond the only apparent trend was a general increase in abundance as the summer progressed (Figure 5). Site 4 (the brook) accounted for much of this increase. There appears to be a shift in abundance from the outflow of Witless Bay Pond (Site 2) toward the brook

Figure 6. The mean number of Gammarus lawrencianus and G. oceanicus collected per sample at site 4 in North Arm Holyrood Bay.


600
500
400
300
200
100
Number/ sample
Gammarus oceanicus
Gammarus lawrencianus
MAY
JUNE
JULY
AUGUST
SEPT.

(Site 4). This appeared to be reversed in the fall.

The number of young G. lawrencianus per mg dry weight of Pilayella collected at Witless Bay Pond is reported in Appendix 2a. The abundance of G. lawrencianus appeared to decline as the young matured but this could be due to an increase in the amount of algae present.

Size at maturation

The 50% maturation size at Witless Bay Pond was calculated by probit analysis (Table 5). A t-test showed a significant difference in maturation size between August 2 and August 31 ($P < 0.01$). In the G. lawrencianus population at Witless Bay Pond maturation among females occurred at a smaller size (4.2 mm) on August 31 than on August 2 (5.1 mm).

Laboratory results

i) Survival

Temperature

Laboratory survival of newly released Gammarus lawrencianus at various temperatures is presented in Figure 7 (Appendix 6). The lines were fitted and 50% survival age calculated by probit analysis (Table 6). Temperature was inversely related to survival. All differences in survival at various temperatures tested were significant. This supported the hypothesis that higher temperatures decreased the survival rate.

Diet

Survival of newly released G. lawrencianus fed various diets is presented in Figure 8 (Appendix 7). The lines fitted and 50% survival age calculated by probit analysis (Table 7). The effect of various diets

Table 5. Size at which 50% of the sample females were mature at Witless Bay Pond.

DATE	50% MATURATION SIZE (mm)	NUMBER	95% CONFIDENCE LIMITS
August 2, 1977	5.1	432	0.20
August 31, 1977	4.2	182	0.20

Figure 7. Survival of Gammarus lawrencianus at various temperatures.

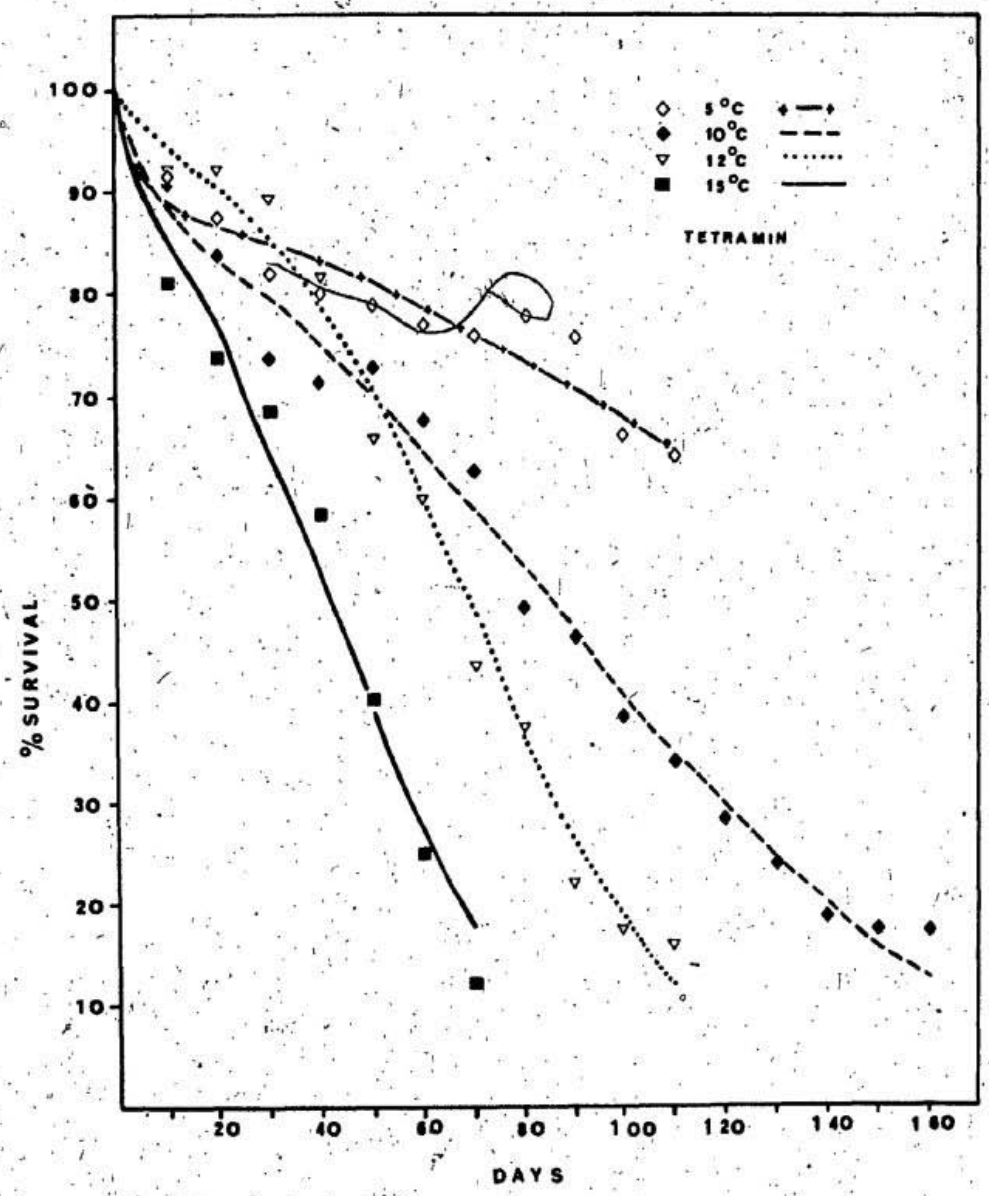

5 °C
10 °C
12 °C
15 °C
TETRAMIN
% SURVIVAL
100
90
80
70
60
50
40
30
20
10
20
40
60
80
100
120
140
160
DAYS

Table 6. Number of days 50% of Gammarus lawrencianus survived at various temperatures. TetraMin was supplied as food.

TEMPERATURE (°C)	50% SURVIVAL (days)	95% CONFIDENCE LIMITS
5	154.5	17.3
10	85.0	2.3
12	68.3	2.8
15	41.4	1.6

Figure 8. Survival of Gammarus lawrencianus fed various diets.

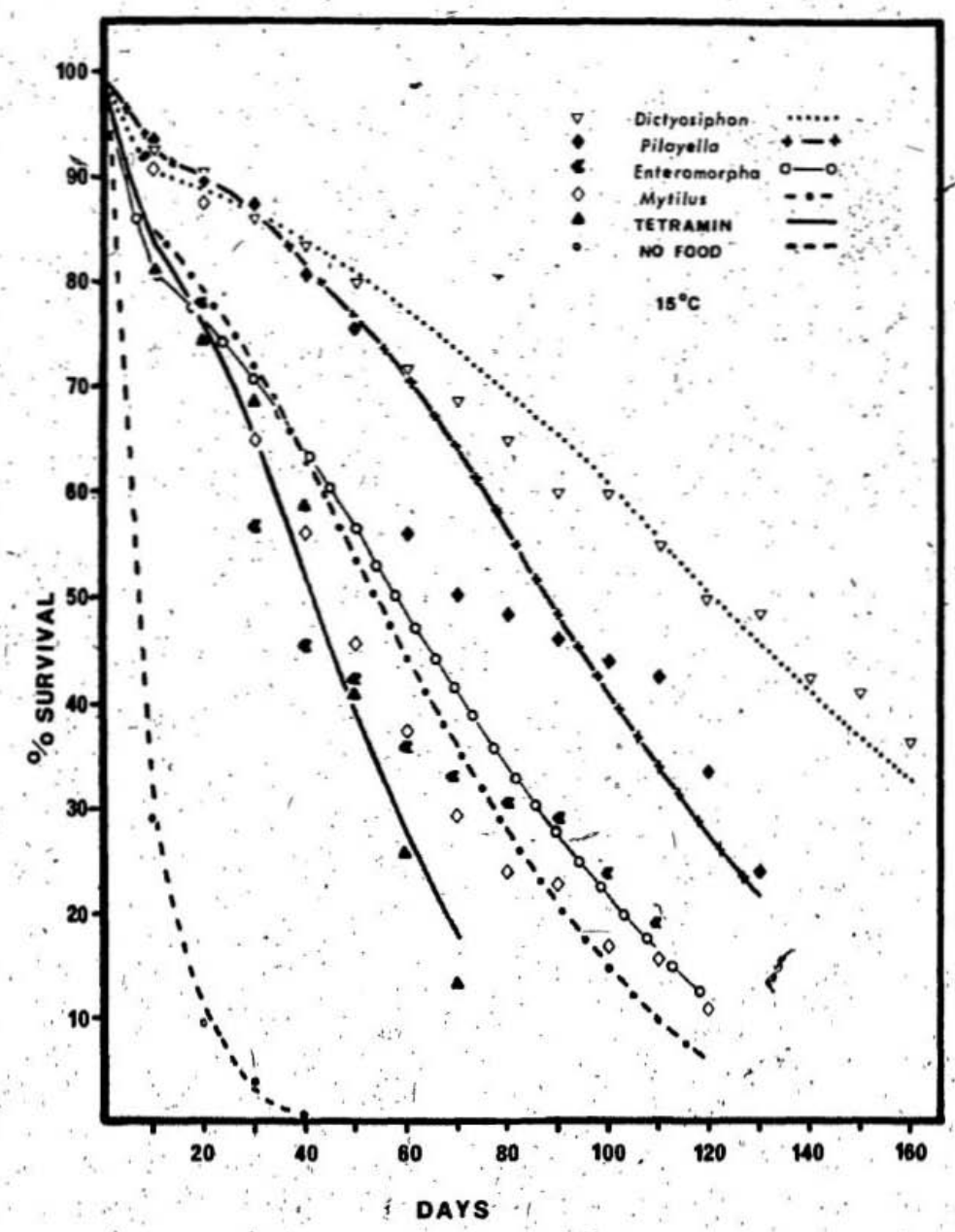

Dictyosiphon
Pilayella
Enteromorpha
Mytilus
TETRAMIN
NO FOOD
15°C
% SURVIVAL
DAYS
100
90
80
70
60
50
40
30
20
10
20
40
60
80
100
120
140
160

Table 7. Number of days 50% *Gammarus lawrencianus* survived on various diets.

DIET	50% SURVIVAL (Days)	95% CONFIDENCE LIMITS (Days)
NO FOOD	1.5	0.8
TETRAMIN	41.4	1.6
Mytilus	54.8	2.8
Enteromorpha	57.9	5.3
Pilayella	88.0	2.4
Dictyosiphon	122.9	0.4

on survival was analyzed by comparing them to the starved animals. Survival did vary with diet with all differences statistically significant except for Enteromorpha and Mytilus. Survival was best on the fine algae Dictyosiphon and Pilayella, intermediate on Enteromorpha and Mytilus and lowest on TetraMin. Fine algae increased the survival rate of G. lawrencianus compared to Mytilus, Enteromorpha or TetraMin.

Growth and maturation

Increases in length and sexual maturation at various temperatures and diets are shown in Figures 9 and 10 (Appendices 8 and 9). The arrows indicate the onset of sexual maturation defined in this experiment as the first precopula. Before maturation the sexes were combined. After maturation the males and females are shown separately if there were more than 9 measurements. However, with TetraMin at 12° C, where few females survived after first precopula, and Dictyosiphon where a great deal of variation was found in the size and age at maturation, the male and female growth data were combined. Amphipods fed Enteromorpha at 15° C or TetraMin at 5° C did not mature before termination of the experiments. The TetraMin at 5° C experiment only ran for 70 days because the small size of the animals precluded live measurements. The amphipods continued to be preserved for measurement until none remained. Anaerobic conditions in a number of bowls reduced the number of animals in this experiment.

Temperature had a direct effect on growth (Figure 9). With increasing temperature, the growth rate increased. This result was statistically significant over the range of the temperatures tested since there was no overlap in confidence limits (Appendix 8). There were also differences in

Figure 9. Growth in length and age at sexual maturation of Gammarus lawrencianus at various temperatures. TetraMin was provided as food.

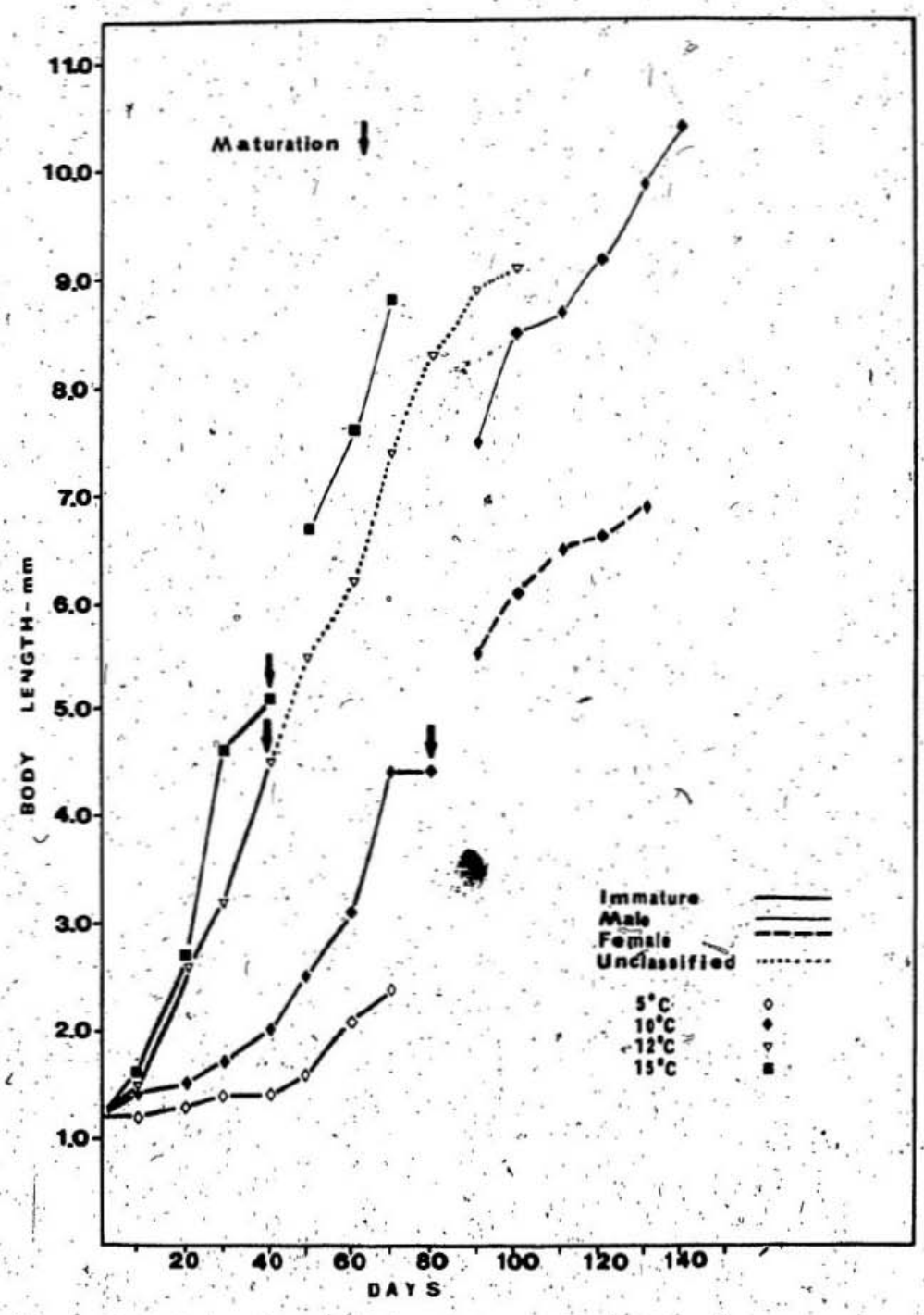
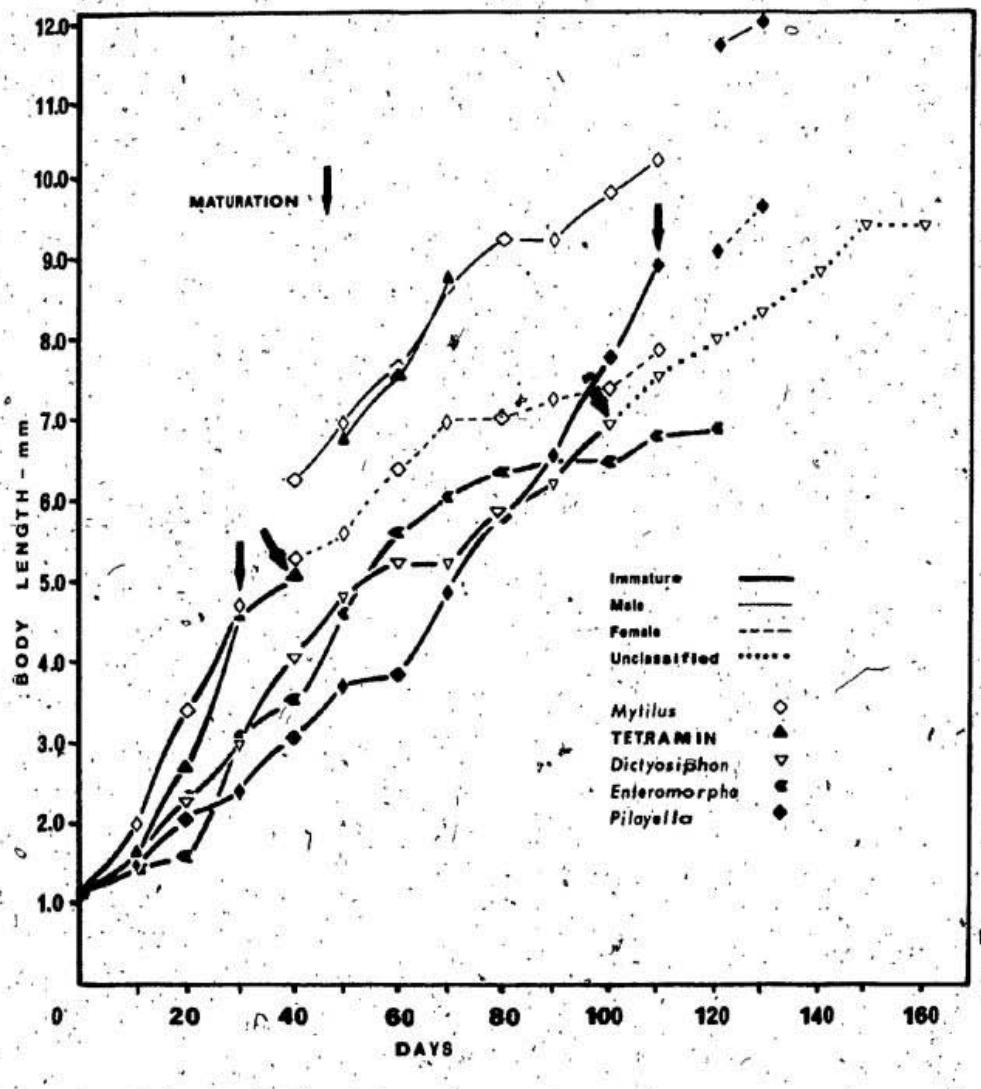

Maturation
BODY LENGTH - mm
DAYS
11.0
10.0
9.0
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
20
40
60
80
100
120
140
Immature
Male
Female
Unclassified
5°C
10°C
12°C
15°C

Figure 10. Growth in length and age at sexual maturation of Gammarus lawrencianus fed various diets. Temperature was maintained at 15° C.


MATURATION
BODY LENGTH - mm
DAYS
Immature
Male
Female
Unclassified
Mytilus
TETRAMIN
Dictyosiphon
Enteromorpha
Pilayella

the age at maturation. For cultures maintained at 12° C and 15° C, the animals matured at approximately 40 days of age. The animals kept at 10° C matured at approximately 80 days. There was no significant difference in the size at maturation of the females cultured at 10° and 15° C. The size at maturation was 5.4 mm and 5.6 mm respectively (Table 8). Not enough animals kept at 12° C matured to make accurate comparisons.

A great deal of variation was found in the effect of food on growth (Appendix 9). An analysis of variance was performed on the immature class up to 90 days of age and it was found that the effect of food on growth was highly significant ($P < 0.001$). Mytilus and TetraMin were most conducive to rapid growth of young G. lawrencianus and early maturation. Algae produced much slower growth and a later maturation. Because growth slows after maturation the animals fed algae tend to catch up to the earlier maturing ones. Food had a statistically significant effect on size at maturation (Table 9). Those fed TetraMin and Mytilus had a maturation size of 5.4 - 5.6 mm. Animals fed the fine algae Dictyosiphon and Pilayella matured at 7.6 mm and 9.3 mm respectively. As growth rate increased the age and size at maturation decreased.

ii) Fecundity

Temperature

The number of eggs produced by females at temperatures of 10° and 15° C is presented in Figure 11 (Appendix 10). Regression analysis produced equations of $y = 9.5\ L - 41.8$ for 10° C and $y = 7.4\ L - 25.6$ for 15° C. An analysis of covariance showed that the two regression lines were significantly different ($P = 0.049$). The low level of significance suggests that more data are necessary.

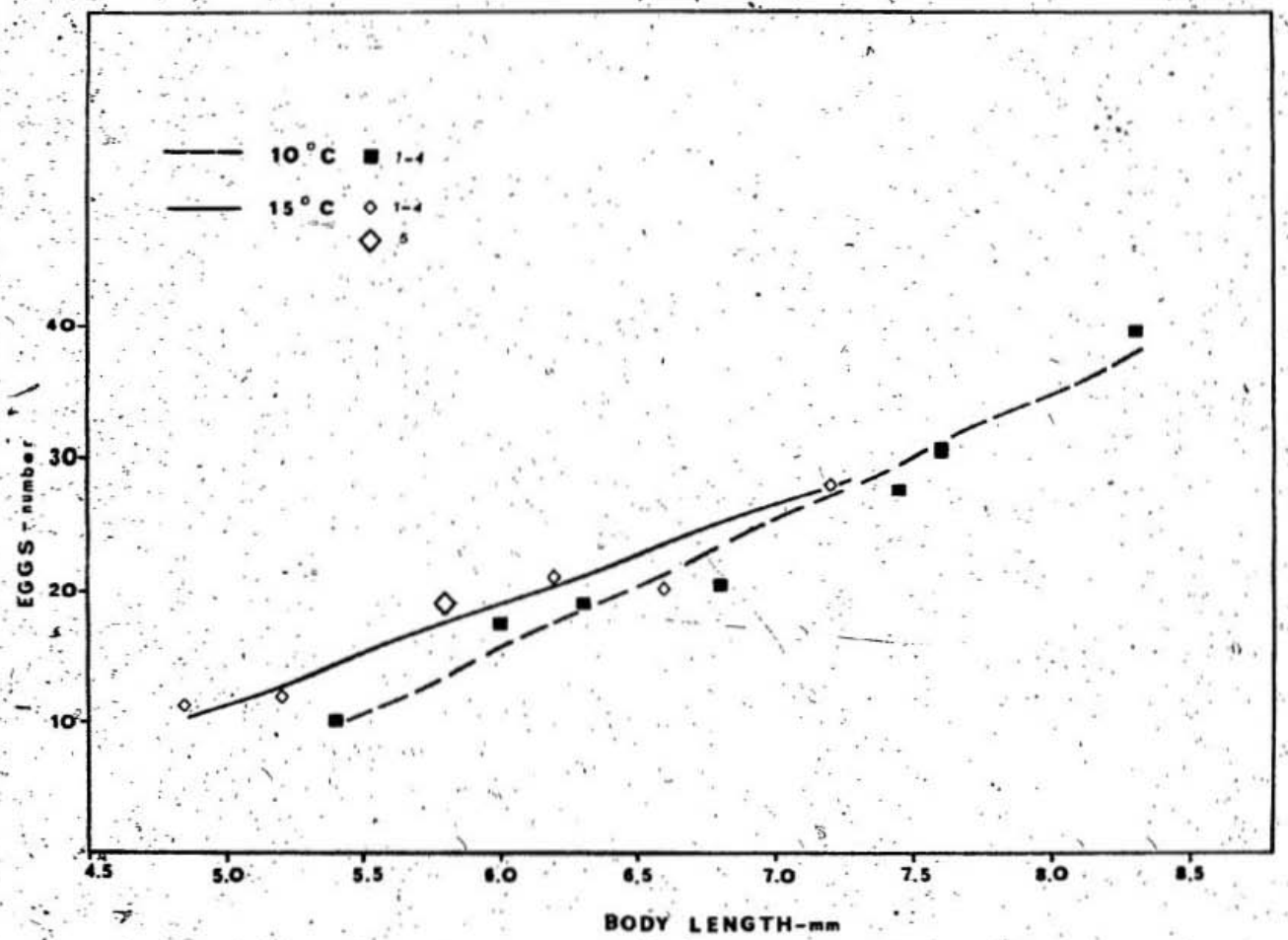
Table 8. Mean size at maturation of female Gammarus lawrencianus at various temperatures. TetraMin was supplied as food.

TEMPERATURE (°C)	MEAN MATURATION SIZE (mm)	NUMBER	95% CONFIDENCE LIMITS
10	5.4	8	0.42
15	5.6	14	0.28

Table 9. Mean size of maturation of female Gammarus lawrencianus on various diets.

DIET	MEAN MATURATION SIZE (mm)	NUMBER	95% CONFIDENCE LIMITS
TETRAMIN	5.6	14	.28
Mytilus	5.4	14	.28
Pilayella	9.3	8	.23
Dictyosiphon	7.6	8	1.00

Figure 11. The fecundity of female Gammarus lawrencianus at 10° C and 15° C. TetraMin was supplied as food.


10°C ■ 1-4
15°C ◇ 1-4
◇ 5
EGGS number
40
30
20
10
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
BODY LENGTH-mm

Diet

The egg production of females fed Mytilus, Dictyosiphon and TetraMin is presented in Figure 12 (Appendix 10). The regression equation for Mytilus was y = 8.1 L - 31.3 , Dictyosiphon y = 9.2 L - 51.5 and TetraMin y = 7.4 L - 25.6. The difference between Mytilus and Dictyosiphon was significant ($P < 0.001$) as it was between TetraMin and Mytilus ($P < 0.001$). Fewer eggs were produced by Dictyosiphon but they were larger than those produced by animals fed Mytilus. The mean diameter of 92 eggs produced by animals fed Dictyosiphon was 0.391 mm with a standard error of 0.002 mm whereas 72 eggs from animals fed Mytilus had a mean diameter of 0.348 mm with a standard error of 0.002 mm. No eggs less than 24 hours old were collected from TetraMin. The regression line for the comparison of the volume of the brood to that of the female was $\log V = 1.104 \log L^3 - 3.199$ for Dictyosiphon and $\log V = 0.918 \log L^3 - 2.585$ for Mytilus (Figure 13; Appendix 11). These two regression lines were not significantly different ($P = 0.053$) but the low probability makes this result inconclusive.

iii) Selectivity

The selection of various food items by Gammarus lawrencianus is presented in Figure 14 and Appendices 12, 13 and 14. A G-test (Sokal and Rohlf 1969) was used to test the hypothesis that animals selected randomly. The hypothesis was rejected in all cases ($P < 0.005$) so some degree of selectivity must be concluded.

Both adult males (Length 10-12 mm) and females (Length 6-8 mm) showed a marked preference for Mytilus. This choice accounted for 70-75 % of total feeding time of both sexes. The remaining 25 - 30 % was spread out over several food items with no one item dominating. In the

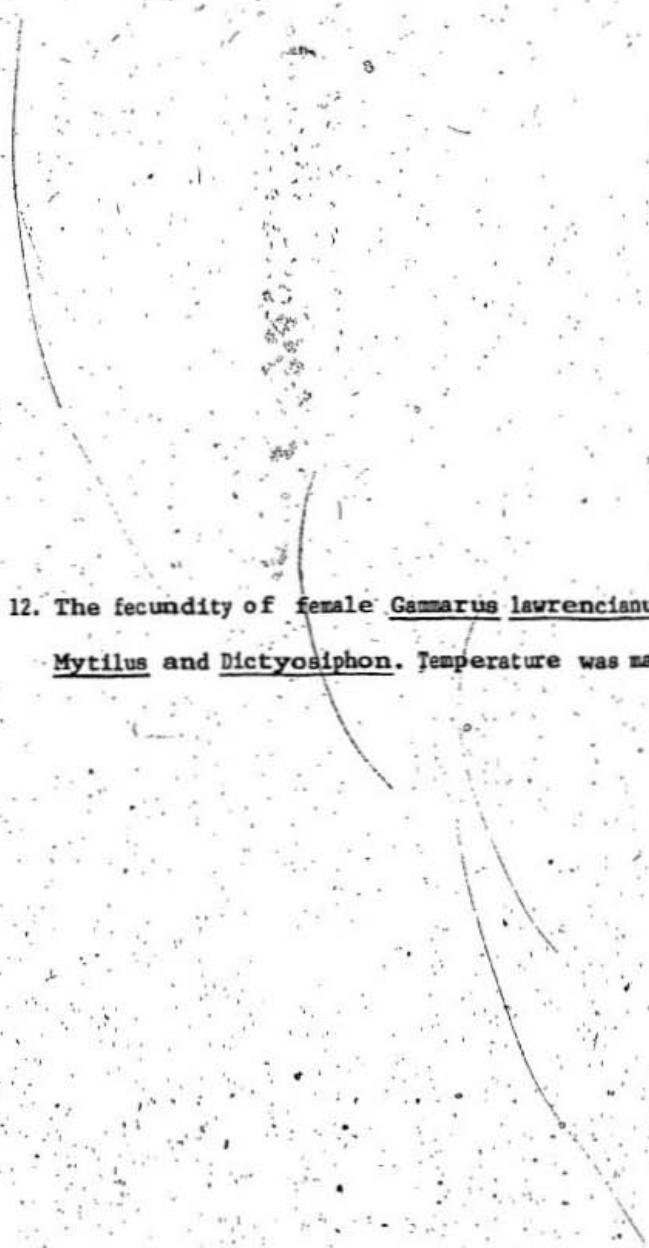


Figure 12. The fecundity of female Gammarus lawrencianus fed TetraMin, Mytilus and Dictyosiphon. Temperature was maintained at 15° C.

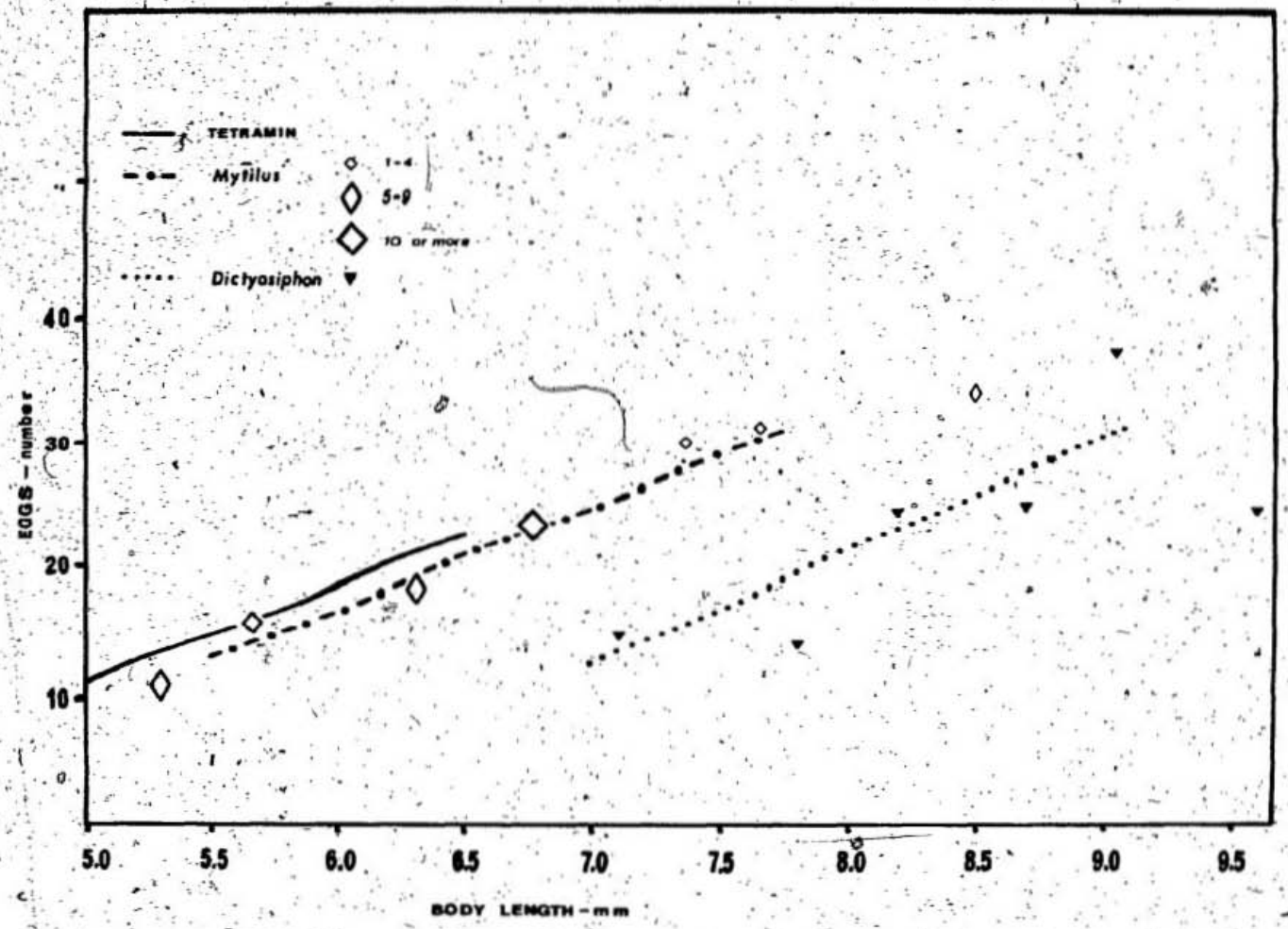

TETRAMIN
Mytilus
1-4
5-9
10 or more
Dictyosiphon
EGGS - number
0
10
20
30
40
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5
BODY LENGTH - mm

Figure 13. The volume of the brood compared to the volume of the female for Gammarus lawrencianus fed Mytilus and Dictyosiphon.

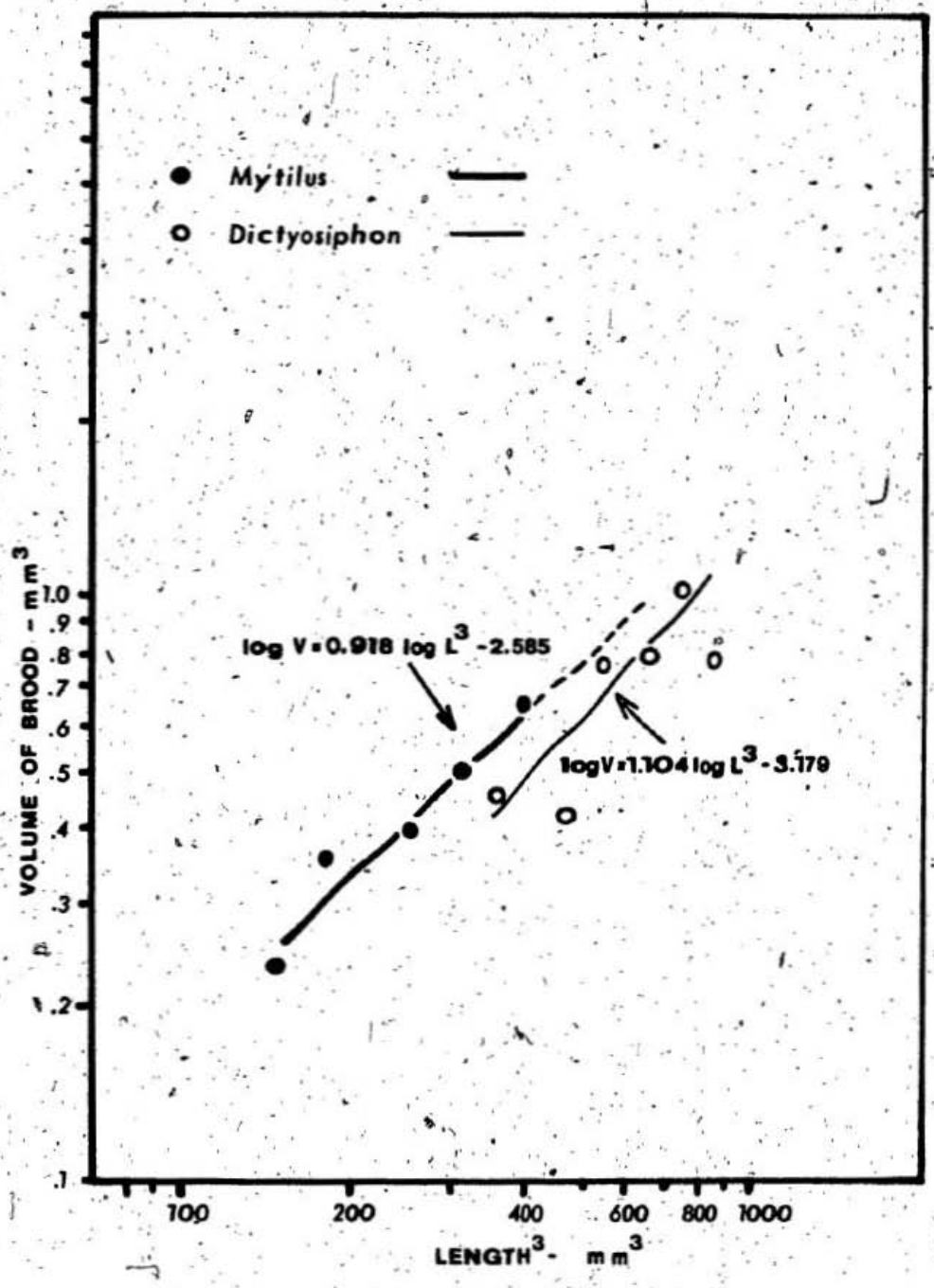
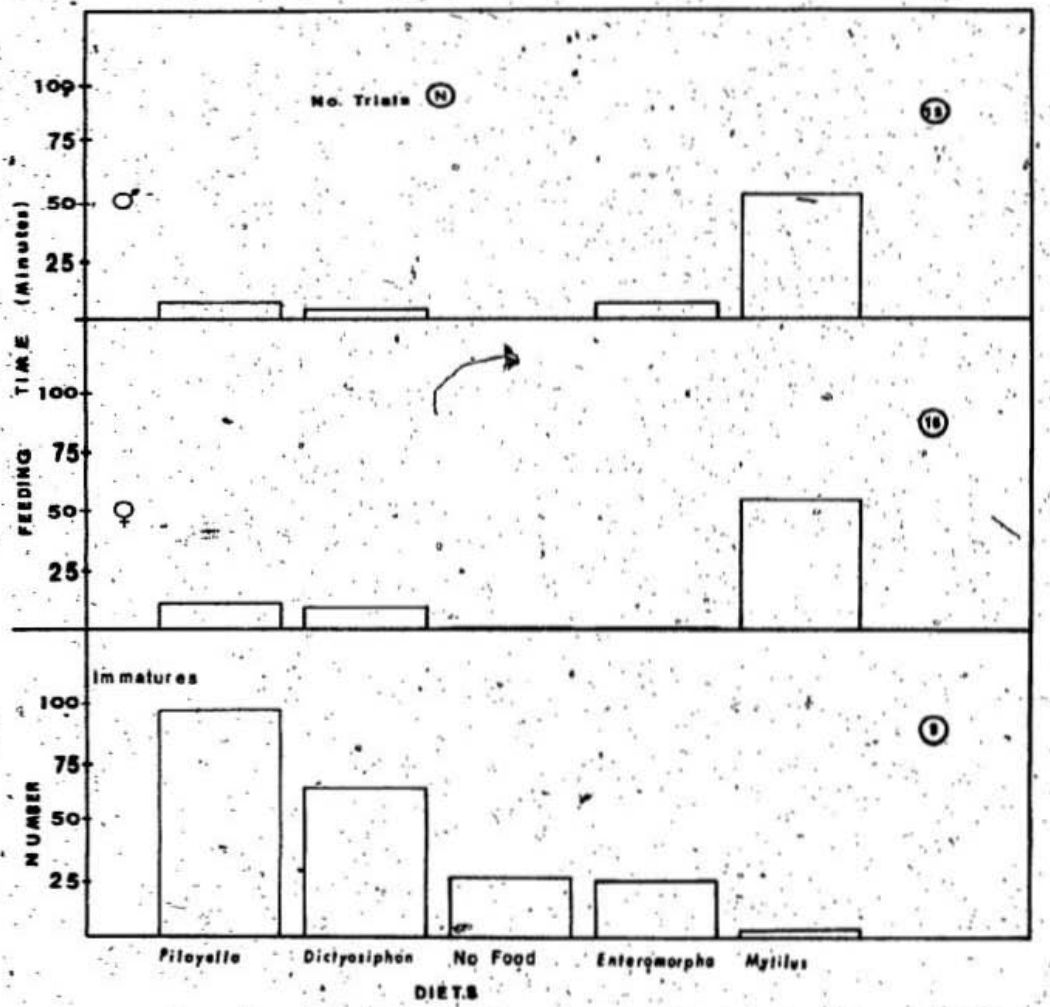

Mytilus
Dictyosiphon
log V = 0.918 log L3 - 2.585
logV = 1.104 log L3 - 3.179
VOLUME OF BROOD - mm3
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
100
200
400
600
800
1000
LENGTH3 - mm3

Figure 14. The selection of various food items by Gammarus lawrencianus.


No. Trials (N)
11
♂
10
♀
Immatures
8
FEEDING TIME (Minutes)
NUMBER
100
75
50
25
Pilayella
Dictyosiphon
No Food
Enteromorpha
Mytilus
DIETS

immature selectivity experiment, food preference could not be proven because the small size and secretive habits of the young precluded direct observation of food selectivity. Instead their preference for association with the various food items was investigated. By comparing the preference for various food items with that for no food, the selectivity of young G. lawrencianus could be determined. Young (Length 1-2 mm) prefer fine algae, especially Pilayella (Figure 14). Pilayella and Dictyosiphon together accounted for 74% of the selections. They appeared to show no preference for Enteromorpha since the number of selections was very similar to that for no food. They selected Mytilus far fewer times than no food.

iv) Food analysis

Energy content

The energy content per gram dry weight and per gram ash free dry weight, of Gammarus lawrencianus and various foods are presented in Figure 15 and Table 10. In comparison to G. lawrencianus, Mytilus and TetraMin had a higher, and the algae a lower energy content as presented in Table 10.

The energy content of G. lawrencianus (16,612.2 J/g dry weight and 21,305.8 J/g ash free dry weight) was similar to that found by Rodgers and Qadri (1977) for the freshwater amphipod G. fasciatus. The energy content of G. fasciatus varied seasonally from 16,497.5 to 17,815.5 J/g dry weight and 21,242.2 to 22,823.7 J/g ash free dry weight. Brawn et al. (1968) found that the amphipods collected in St. Margaret's Bay, Nova Scotia had a dry weight energy content of 15,736.0 J/g. Not all amphipods

Figure 15. The energy content of Gammarus lawrencianus and various food items.

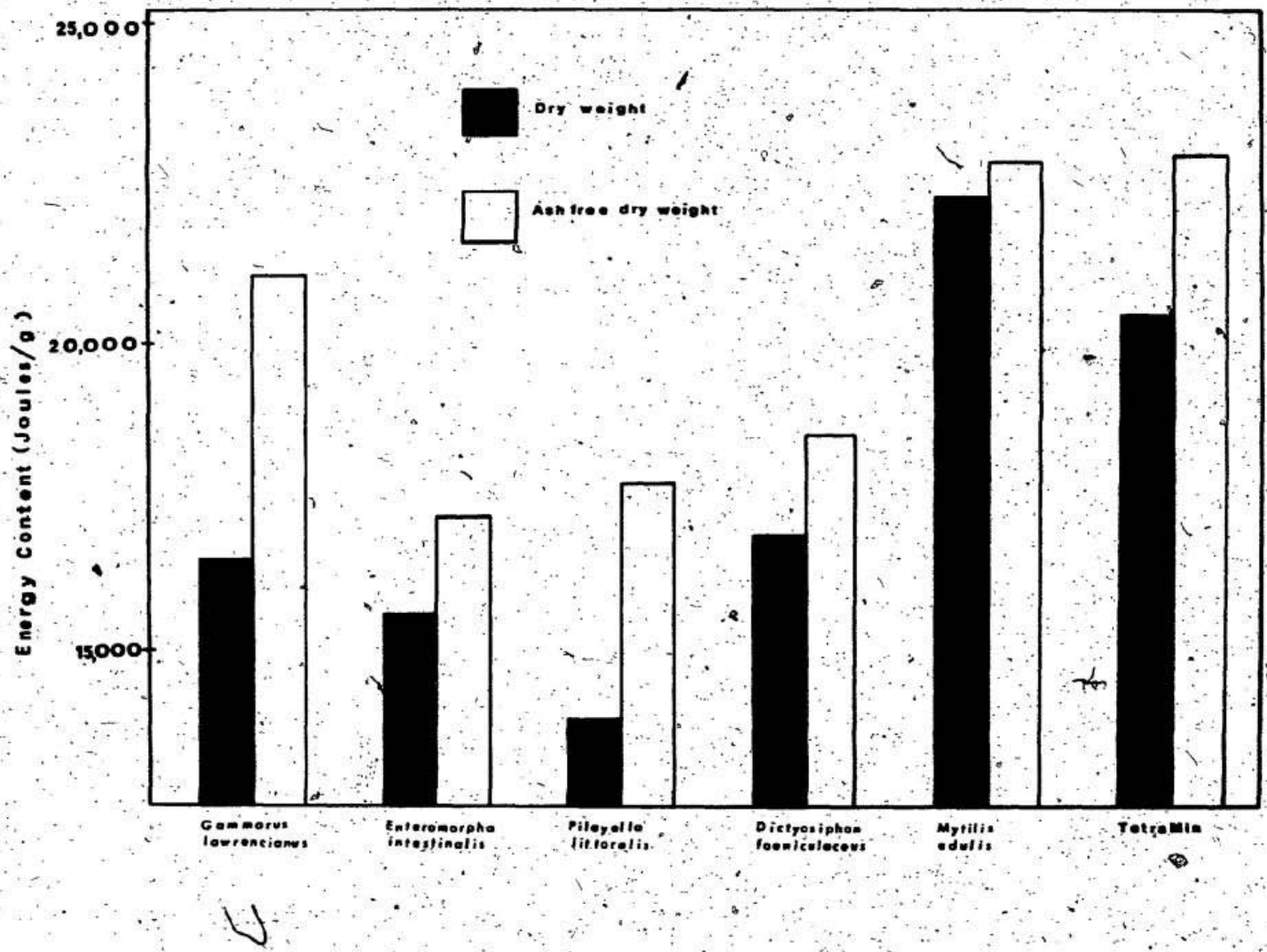

25,000
20,000
15,000
Energy Content (Joules/g)
Dry weight
Ash free dry weight
Gammarus lawrencianus
Enteromorpha intestinalis
Pilayella littoralis
Dictyosiphon foeniculaceus
Mytilis edulis
Tetramin

Table 10. The energy content of Gammarus lawrencianus and various food.

	ENERGY CONTENT (J/g)	
	DRY WEIGHT	ASH FREE DRY WEIGHT
Gammarus lawrencianus	16,612.2	21,305.8
Mytilus	22,516.2	23,019.5
TetraMin	20,503.7	23,123.3
Pilayella	14,192.1	17,740.2
Dictyosiphon	17,027.2	18,629.7
Enteromorpha	15,765.7	17,262.8

fall within the range of these readings. Tyler (1973) found that the dry weight energy content of the gammarid amphipod Leptocheirus pinguis varied seasonally from 9702.7 to 14,008.0 J/g.

Amino acids

The amino acid composition of the amphipod G. lawrencianus and various food items is presented in Table 11. The mean total quantity of each amino acid per mg of residue and the per cent composition of each amino acid of the total amount of amino acids in the residue was calculated and the number of amino acids in the foods that were within the range of those of the amphipod determined as Deshimaru and Shigeno (1972) did for the shrimp Panaeus japonicus (Table 12).

In both the mean and per cent comparisons TetraMin had the smallest number of amino acids within the range of the amphipod. Enteromorpha had the largest number with Mytilus a close second. The fine algae Pilayella and Dictyosiphon had few amino acids whose mean came within the range of the amphipod, but they did much better in the percentage comparison, with close to twice as many similar amino acids as were found in TetraMin.

Hadjistephanou (1978) performed a similar amino acid analysis on a number of food items including TetraMin and Mytilus. He found that Mytilus contained 3767.1 nanomoles of amino acid per mg of residue. This study found 3371.3 nanomoles of amino acid per mg of residue. The per cent composition of the various amino acids was also similar. For the TetraMin analysis he found 2356.4 nanomoles per mg of residue, this study 1521.9, a difference of over 35%. This may mirror variations in the quality of TetraMin. Despite large differences in total amount of amino acid, the per cent composition was similar.

Table 11. The amino acid composition of Gammarus lawrencianus and various foods. (* – mean and range from triplicate samples; ** – % composition of each amino acid to total of amino acids in residue part; T= trace).

AMINO ACIDS	Gammarus			Mytilus			TETRAMIN		
	MEAN* Nanomoles/mg	RANGE*	%**	MEAN* Nanomoles/mg	RANGE*	%**	MEAN* Nanomoles/mg	RANGE*	%**
CYSTEIC ACID	0	0	0	4.1	T-11	0.2	4.3	2-8	0.3
METHIONINE SULFONE	0	0	0	1/3T	0-T	T	T	T	T
HYDROXYPROLINE	0	0	0	3.6	2-5	0.1	22.3	21-24	1.4
ASPARTIC ACID	370.5	322-396	11.5	347.0	334-360	10.3	101.9	99-106	6.6
THREONINE	159.6	134-174	5.0	197.6	195-202	5.9	63.6	63-66	4.1
SERINE	176.6	155-190	5.5	192.9	179-202	5.7	80.4	75-83	5.2
PROLINE	138.0	117-149	4.3	137.0	132-141	4.1	125.8	123-131	8.1
GLUTAMIC ACID	357.5	306-388	11.1	412.0	406-424	12.2	225.4	213-237	14.5
GLYCINE	240.9	207-260	7.5	222.2	219-227	6.6	162.1	156-172	10.4
ALANINE	263.9	228-284	8.2	238.8	235-244	7.1	90.9	88-95	5.8
HALF CYSTINE	44.8	37-50	1.4	25.7	15-33	0.8	5.5	4-6	0.4
VALINE	169.1	125-196	5.2	161.7	143-178	4.8	66.2	64-70	4.3
METHIONINE	70.1	60-76	2.2	93.7	85-101	2.8	13.0	8-17	0.8
TAURINE	0	0	0	6.5	5-8	0.2	3.3	3-4	0.2
ISOLEUCINE	112.6	82-131	3.5	151.4	133-169	4.5	47.2	44-51	3.0
LEUCINE	231.9	196-252	7.2	233.5	225-238	6.9	89.3	86-94	5.7
TYROSINE	90.4	78-97	2.8	93.8	89-100	2.8	24.7	22-27	1.6
PHENYLALANINE	120.3	101-130	3.7	99.8	96-103	3.0	42.8	41-45	2.8
AMMONIA	278.3	231-306	8.6	292.3	283-306	8.7	217.8	198-240	14.0
LYSINE	189.8	160-207	5.9	236.8	230-242	7.0	60.5	59-64	3.9
HISTIDINE	70.1	58-77	2.2	54.6	52-56	1.6	22.2	21-24	1.4
ARGININE	137.4	117-149	4.3	162.7	160-167	4.8	52.7	51-55	3.4
3 ME HIS	0	0	0	3.6	3-4	0.1	0	0	0

	Enteromorpha			Pilayella			Dictyosiphon		
CYSTEIC ACID	12.3	11-13	0.5	2.6	2-3	0.3	2.7	2-3	0.3
METHIONINE SULFONE	T	T	T	0	0	0	0	0	0
HYDROXYPROLINE	10.3	7-12	0.4	0	0	0	0	0	0
ASPARTIC ACID	264.5	263-267	10.2	91.0	69-106	10.3	100.2	63-134	9.6
THREONINE	140.9	140-142	5.4	50.4	38-59	5.7	55.1	36-76	5.3
SERINE	136.8	132-143	5.3	51.2	37-58	5.8	59.6	39-79	5.8
PROLINE	126.1	124-127	4.9	35.2	25-43	4.0	44.1	28-61	4.2
GLUTAMIC ACID	210.0	208-213	8.1	78.2	59-91	8.8	91.4	56-123	8.8
GLYCINE	245.7	241-248	9.5	79.5	60-94	9.0	99.4	61-133	9.5
ALANINE	256.6	254-259	9.9	77.5	56-91	8.7	99.5	61-132	9.6
HALF CYSTINE	22.1	19-25	0.9	3.9	2-7	0.5	6.0	4-8	0.6
VALINE	150.1	132-161	5.8	54.4	44-65	6.2	61.9	33-89	5.8
METHIONINE	52.3	48-54	2.0	8.4	4-15	0.9	21.3	15-28	2.1
TAURINE	0	0	0	0	0	0	0	0	0
ISOLEUCINE	95.3	80-104	3.7	33.6	28-43	3.8	35.4	20-52	3.3
LEUCINE	199.4	191-205	7.7	58.6	45-70	6.6	71.0	44-100	6.8
TYROSINE	60.8	60-62	2.4	13.8	10-16	1.6	21.7	15-32	2.1
PHENYLALANINE	107.9	101-112	4.2	29.1	22-34	3.3	34.1	21-49	3.3
AMMONIA	241.1	203-284	9.3	134.9	112-176	15.4	133.9	66-169	12.6
LYSINE	111.8	110-113	4.3	40.3	31-48	4.6	50.0	30-69	4.8
HISTIDINE	37.1	35-38	1.4	10.8	8-13	1.2	15.8	11-22	1.5
ARGININE	103.3	102-104	4.0	28.6	24-34	3.3	41.9	26-59	4.0
3 ME HIS	0	0	0	0	0	0	0	0	0

Table 12. Similarity of the amino acid composition pattern of various foods to that of Gammarus lawrencianus.

AMINO ACIDS	DIETS									
	Mytilus		TetraMin		Enteromorpha		Pilayella		Dictyosiphon	
	MEAN	%	MEAN	%	MEAN	%	MEAN	%	MEAN	%
Cysteic acid	+	*	+	*	+	*	+	*	*	*
Methionine sulfone	*	*	+	*	+	*	*	*	*	*
Hydroxyproline	+	*	+	+	+	*	*	*	*	*
Aspartic acid	*	-	-	-	-	-	-	-	-	-
Threonine	+	+	-	-	*	*	-	+	-	*
Serine	*	*	-	*	-	*	-	*	-	*
Proline	*	*	*	+	*	+	-	*	-	*
Glutamic acid	+	+	-	+	-	-	-	-	-	-
Glycine	*	-	-	+	*	+	-	+	-	+
Alanine	*	-	-	-	*	+	-	*	-	+
Half cystine	-	-	-	-	-	*	-	-	-	-
Valine	*	*	-	-	*	+	-	+	-	+
Methionine	+	+	-	-	-	*	-	-	-	*
Taurine	+	*	+	*	*	*	*	*	*	*
Isoleucine	+	+	-	*	*	*	-	*	-	*
Leucine	*	*	-	-	*	*	-	-	-	*
Tyrosine	*	*	-	-	-	*	-	-	-	-
Phenylalanine	*	-	-	-	*	*	-	*	-	*
Ammonia	*	*	*	+	*	+	-	+	-	+
Lysine	-	+	-	-	-	-	-	-	-	-
Histidine	-	-	-	-	-	-	-	-	-	-
Arginine	+	*	-	-	-	*	-	-	-	*
3 Me His	+	*	*	*	*	*	*	*	*	*
NUMBER WITHIN RANGE	11	12	3	6	11	14	4	10	4	13

*- The amino acid composition-rate within the range of ± 0.5% for percentage comparison and within range (Table 11) for mean comparison, from that of G.lawrencianus

\+ Over the range

\- Below the range

DISCUSSION

i) Life cycle and female reproductive cycle in the field

The life history of Gammarus lawrencianus consists of overwintering adults which release their broods in the spring. By the time the first brood matures, the overwintering adults disappear from the population. This dual life history of large overwintering adults and a faster maturing summer cohort of smaller individuals is found in a number of other gammarids, including G. pulex (Hobrough 1973) and G. palustris Bousfield (Van Dolah 1978).

The life cycle and female reproductive cycle were similar to those found by Steele and Steele (1970), and did not vary appreciably between the two sampling locations (Figure 4). A number of factors that affect the life and reproductive cycle such as the duration of embryonic development (Steele and Steele 1973) are significantly influenced by temperature. The temperatures at the two sites were markedly different (Figure 3). Possibly the animals in North Arm Holyrood spent an appreciable amount of time in the warmer surface water and/or the sampling program was not sensitive enough to pick up the differences in the female reproductive cycle that existed.

ii) Distribution and abundance

North Arm Holyrood has a more "marine" environment than Witless Bay Pond. Fresh water coming down the North Arm River flows over the denser seawater with little mixing (Appendix 1b). Mixing is almost complete in Witless Bay Pond at low water. Saline water flows into the pond through a shallow channel above the lighter brackish water already in the pond, and as the denser seawater sinks, it mixes with the brackish pond water.

Invertebrates in North Arm Holyrood, if stressed by high temperature or low salinity surface water can escape to the more saline, lower temperature water below. In Witless Bay Pond no such escape is possible at low water and any animal living there must be able to tolerate larger changes in temperature and salinity than those at North Arm Holyrood.

G. oceanicus has a more northerly distribution than G. lawrencianus (Steele and Steele 1974) and does not appear to thrive in temperatures over 15° C (Steele and Steele 1972). G. lawrencianus can grow and reproduce at temperatures over 20° C (Steele and Steele 1973). Witless Bay Pond is a better habitat for G. lawrencianus than G. oceanicus. G. lawrencianus was the only amphipod collected in Witless Bay Pond.

In North Arm Holyrood only site 4 contained considerable numbers of G. lawrencianus. G. oceanicus and G. lawrencianus are both euryhaline and eurythermic (Bousfield 1973). Physiologically there appears to be no reason for their absence from any of the sampling sites in North Arm Holyrood. The lack of spatial overlap in gammarid amphipods has been observed previously. Vassallo (1975) found that of the 4 species of Gammarus collected in Bridgeport Basin, Nova Scotia, 90% of the individuals per sample consisted of only 1 species. Discrete distributions of closely associated species is the rule rather than the exception in marine invertebrates (Meadows and Campbell 1972). Rygg (1972) studied the distribution of G. duebeni Lillj. and concluded that specific behaviour patterns were probably responsible for its restricted habitat. Bettison and Davenport (1976) demonstrated the high degree of salinity preference of a number of gammarids. They hypothesized that animals stay well within their physiological limits, but if they are forced

outside their normal distribution they can still survive. Other stresses can also be handled more easily if the animals are at optimum salinity. These theories may explain why the two species were not found in large numbers together, but not why there was an apparent replacement of G. lawrencianus by G. oceanicus at site 4 in North Arm Holyrood as summer progressed (Figure 6). This may be due to a summer migration of G. lawrencianus from highly saline, low temperature habitats to brackish, warmer water. This habitat was not sampled in North Arm Holyrood due to the swiftness of the North Arm River. In Witless Bay Pond there was a general shift in the abundance of G. lawrencianus from the outflow of the pond to the inflow (Figure 5). Steele and Steele (1970) also note a summer increase in the number of individuals in fresher, rapidly flowing water and suggested that these were animals dispersing from the population's center of abundance in more saline waters. Van Dolah (1978) studied a similar but more southerly species, G. palustris and found that it migrates into subtidal regions during the winter and moves back into intertidal habitats during the spring. Sears and Wilce (1975) found that ectocarpoids, of which Pilayella is one, have a seasonal distribution. They are more obvious in the summer when their center of distribution is in intertidal and shallow water areas. In winter they are abundant in deeper water. Possibly G. lawrencianus has developed a seasonal migration which corresponds to the distribution of this important food item. If G. lawrencianus migrates this would explain the population distributions observed at both Witless Bay Pond and North Arm Holyrood. Migration has not been conclusively demonstrated in G. lawrencianus and more research is necessary before any conclusions can be drawn.

Young were collected in Pilayella samples and not in benthic samples at Witless Bay Pond. This may be due to behavioral preferences of the adults and young. Young are quite sedentary, tending to attach themselves to filamentous algae (MacKay and Vassallo 1977). They are poor swimmers and as they are released from the brood pouch they would probably be carried out of the estuary if they did not hold on to something. Adults are much more active. They feed on algae by breaking a branch off and ingesting it while swimming (personal observations).

G. lawrencianus is quite cannibalistic (MacKay and Vassallo 1977) and females will even consume young as they are released from the brood pouch (Personal observations). The behaviour of the young may protect them from the voracious adults. Adults are strong swimmers. They can move up stream against a moderate current with no difficulty (personal observations). They are generally found in fast flowing brackish water during the summer (Steele and Steele 1970). Pilayella, the dominant filamentous alga in the estuaries studied, appears to grow in small pools and slowly moving water and not in stream beds. The adults release their young in lotic waters and they are probably quickly carried away from the adults and towards the algae. In this way the adults and young are effectively separated.

iii) Size composition

If the two sampling techniques accurately sampled the North Arm Holyrood and Witless Bay Pond populations of G. lawrencianus, a number of differences exist within and between the two populations. At both locations, males were larger than females (Table 3). This is common to most gammarid populations and is probably the result of a faster growth

rate in the males. After maturation females must expend a great deal of energy producing eggs and therefore grow at a slower rate than males.

The mean size of the North Arm Holyrood population was smaller than the one at Witless Bay Pond (Table 3). A variety of factors affect growth including temperature and food. The latter probably differed at the two locations. Unfortunately not enough animals were collected at North Arm Holyrood during July and August to determine the size at maturation. This may have provided further insights into the controlling factors of maturation size (Wenner et al. 1974).

iv) Sex ratio

There was a general predominance of females throughout the year, except in the fall when the earlier maturing males outnumbered the females (Table 4). The relative number of males in the overwintering cohort decreased as the season progressed. The maturation of the summer cohort brought the ratio close to 1. This was similar to that found in a population of G. palustris by Van Dolah (1978), but unlike the population at Witless Bay Pond, the ratio stayed close to 1 until September. The unbiassed sex ratio in the newly matured summer cohort suggests that there is no direct genetic adjustment but an indirect cause such as differential mortality. Wenner (1972), after reviewing the literature, concluded that in Crustacea, an unbiassed sex ratio among mature animals is the exception rather than the rule. A number of factors controlling sex ratio have been identified including microsporidean infections, photoperiod, genetic background (Bulnheim 1978) environmental conditions (Wildish 1971; Myers 1978) and differential growth (Wenner 1972). Wenner (1972) found that the sex ratio for most Crustacea was a function of

size. At maturation most sex ratios are close to 1. As one sex outgrows the other, ratios tend to be biassed. This appears to be the case in this study. Males are consistently larger than females (Table 4) and the size difference increased as the sex ratio decreased.

The adaptive significance of a biassed sex ratio was discussed by Wildish (1971). He stressed the impact biassed sex ratios could have on the reproductive potential (R) of a population and developed an equation to mathematically describe it. He determined that

$$R = x\,(bnp)$$ where

x= absolute number of females

b= mean brood number

n= estimated number of broods in a season

p= per cent females in the population

He stated that if b and n are constants, an unequal sex ratio would increase or decrease the reproductive potential of a population, provided each female could mate successfully. Therefore the reproductive potential of G. lawrencianus populations studied was enhanced by the predominance of females. Wildish (1971) studied a number of populations of the genus Orchestia. He found that those exposed to stringent estuarine conditions tended to have a high percentage of females. He hypothesized that their reproductive strategy was to maximize R. G. lawrencianus is also found at sites where dramatic changes in temperature and salinity occur. The biassed sex ratio in G. lawrencianus populations could also be part of the reproductive strategy of the species.

v) Effects of diet and temperature

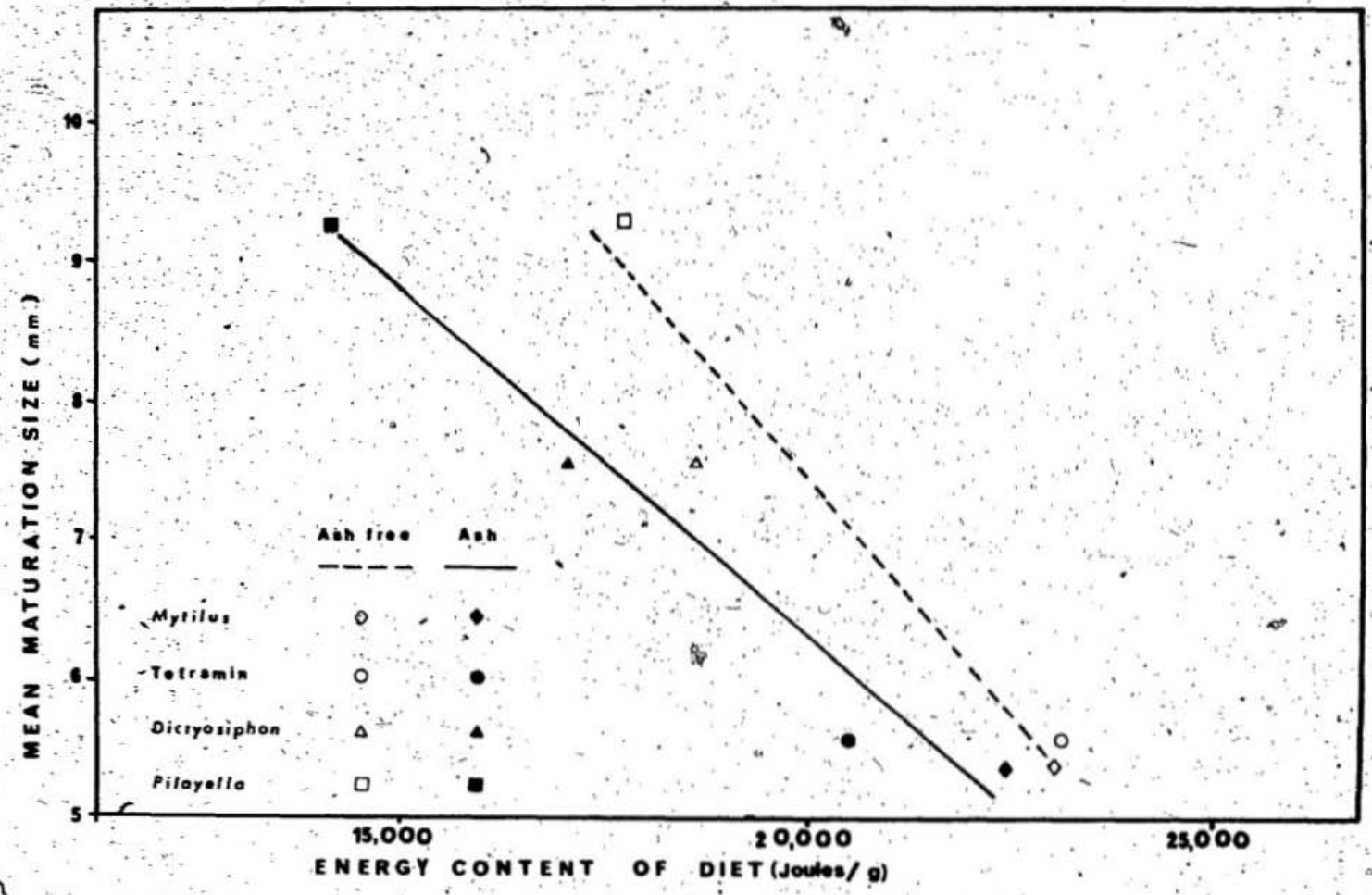
The results of this study show that food quality as well as temperature are important factors in the biology of gammarid amphipods. Diet had a significant effect on survival (Figure 8), growth (Figure 10), size and age at maturation (Figure 10) and fecundity (Figure 12). Survival was maximized on a diet of fine algae. Steele and Steele (1975) found that the timing of the release of the young was correlated to the spring bloom of ephemeral algae and hypothesized that fine algae allow for the greatest survival of the young. This hypothesis was supported by this study, but Mytilus rather than fine algae was the optimum diet for maximum growth and fecundity. Animal material would appear necessary for rapid growth and early maturation.

No obvious correlation was found between the quantity of amino acids in the foods and the growth, survival and fecundity of G. lawrencianus. Mytilus most closely approximated the amino acid makeup of the amphipod (Table 11) and had the best growth and fecundity, but TetraMin which was deficient in many amino acids also had very good growth and fecundity, closely approximating that of Mytilus. TetraMin had a poor survival rate (Figure 8) and this could be due to the lack of essential amino acids.

The energy content of the diet appears to influence the growth and maturation of G. lawrencianus. The total energy content of the foods was compared to the resulting maturation size and the results are presented in Figure 16. There was a high correlation coefficient, 0.98 for dry weight energy content and 0.96 for ash free dry weight energy content.

However other factors evidently influence the effect certain diets have on growth and maturation since Enteromorpha had a dry weight energy

Figure 16. Mean maturation size of Gammarus lawrencianus in relation to the energy content of the diet.


MEAN MATURATION SIZE (mm.)
10
9
8
7
6
5
Ash free
Ash
Mytilus
Tetramin
Dictyosiphon
Pilayella
15,000
20,000
25,000
ENERGY CONTENT OF DIET (Joules/g)

content well above that of the other algae tested but no animals fed Enteromorpha matured during the course of the experiment. The amount of energy an animal actually assimilates is determined by such factors as absorption efficiency, feeding rate, etc. Vadas (1977) found that for the sea urchins Strongylocentrotus droebachiensis and S. franciscanus there was an inverse correlation between growth and absolute energy value of the algae consumed, but a positive correlation with energy uptake.

Vadas (1977) suggested that algae have developed various mechanisms to reduce predation. Some have reduced their availability by becoming ephemeral. Other algae have developed various structural and chemical defense mechanisms to inhibit grazing activity (Vadas 1977). Jansson and Matthieson (1971) found that Idotea chelipes (Pallas) could not consume coarser textured Cladophora glomerata (Kutzing) filaments.

The quantity of cellulose in the cell wall may be important in the digestability of a cell. Cronshaw et al. (1958) determined the cellulose content of a wide variety of algae. They found that the cell wall of green algae generally had a higher cellulose content than brown algae. For example the brown alga Fucus serratus (L.) had a cellulose content of 13.5% whereas the green alga Enteromorpha sp. had 21%. Cellulose generally makes up a small percentage of the cell wall of algae (Dodge 1973) and is present in the form of microfibrils. These microfibrils are embedded in an amorphous matrix. The make up of the amorphous matrix could also effect the texture of the cell wall. The arrangement of the cellulose microfibrils may influence the strength of the cell wall. Enteromorpha sp. cellulose fibrils are randomly arranged whereas Ectocarpus, an ectocarpoid brown alga similar to Pilayella, has a predominately transverse orientation (Dodge 1973). This would make Ectocarpus cell

walls easier to break. In this study animals fed Enteromorpha had a much lower growth and survival rate than diets of Pilayella or Dictyosiphon.

Cellulase activity has been found in the gut of a number of crustaceans including G. oceanicus (Halcrow 1971), G. pulex (Monk 1977), Orchestia gammarella (Pallas) (Agrawal 1964) and Mysis stenolepsis (Smith) (Foulds and Mann 1978). The cellulase enzymes do not appear to digest cell walls. Agrawal (1964) found that O. gammarella was able to digest filter paper but not the cell walls of algae. Monk (1977) suggested that other enzymes not present in the gut of amphipods must first work on cell walls before cellulase is effective.

Non- cellulose cell coverings also inhibit digestion. Moore (1975) found that when (G. pulex)was fed the diatom Cymbella affinis Kz., the most abundant alga in the gut of G. pulex in the field, 66% of the cells possessed intact chloroplasts after passing through the gut. Virtually, all the intact cells were able to survive and reproduce. Moore (1977) reported that the relative number of intact cells increased with a decrease in temperature. Abolmasova (1975) found that G. olivii M.-Edw. had an assimilation efficiency of 65% when fed the diatom Cystoseira barbata (Goodet Wood) Ag. and that temperature had no appreciable effect. The literature appears contradictory but this may be due to the specific properties of the amphipod species and/or algae tested or methods used.

A number of studies on gammarid amphipods have found that texture was a primary factor in food preference. Lubyanova and Zubchenko (1970) found that when G. balcanicus (R.) was offered various plant foods, its preference appeared to be dependent on the mechanical toughness of the material. Ravanko (1969) reported that G. oceanicus preferred soft and

fragile algae. Martin (1966) found that G. pulex also selected soft membranous and filamentous algae. The potential nutritional value of the algae appeared to be unimportant. Moore (1977) suggested that what was influencing preference was the relative strength of the cell walls. He stated that any cell walls not broken during mechanical mastication would not be digested by the animal.

Obviously food texture is important in the feeding biology of gammarid amphipods, especially young who have smaller mouth parts. Young G. lawrencianus preferred fine algae, especially Pilayella and showed no preference for the coarse green alga Enteromorpha (Figure 14) which had a higher energy content (Figure 15) and an amino acid composition closer to that of the amphipod than was Pilayella (Table 11). They avoided Mytilus even though in lab cultures it produced optimum growth and reproduction. In the field young tended to stay in the Pilayella and were not collected to any great extent in benthic samples (Appendix 2). Young are not very active swimmers and at least under laboratory conditions tended to cling to filamentous algae if it was available (MacKay and Vassallo 1977). This would suggest that protection is more important than optimum growth and early maturation. Feeding on animal material could increase competition with the cannibalistic adults, place them in anoxic conditions or increase the danger of the young being washed out of the estuary due to lack of proper substrate.

Adult G. lawrencianus had a marked preference for animal material (Figure 14). This is not uncommon in amphipods. Anderson and Raasveldt (1974) found that G. lacustris lacustris G.O. Sars rejected plant material if live animal prey was available. Lubyanov and Zubchenko (1970)

reported similar results for G. balcanicus. G. lawrencianus has been observed in the field, feeding on dead squid and flatfish, old bones and live insect larvae (personal observations). Adults also show predatory behaviour patterns. They actively attack food items. If the animals were completely herbivorous or detritivorous, such behaviour would not occur. Animal material could provide a high energy (Table 9), high quality (Table 10) diet. The density of G. lawrencianus in the field (Appendix 2) would suggest that animal material does not normally make up the bulk of its diet but could act as an important supplement even in small quantities. This could be especially important in summer when increased metabolic and reproductive activity place extra stress on the population.

The lower growth rate and increased maturation size of G. lawrencianus fed Pilayella and Dictyosiphon could be due to the texture of the algae. In the field the maturation size was much smaller than that found for the animals fed algae, but comparable to those fed Mytilus and TetraMin if 1 mm is added to the maturation size of the field populations to allow for growth in the female when the oogonia are released into the brood pouch as suggested by Steele and Steele (1970). Immature G. lawrencianus could be feeding on animal material in the field. Such activity has been observed in adults from field populations of G. lacustris lacustris (Anderson and Raasveldt 1974), G. pulex (Hobrough 1973), Pontoporeia affinis Lindstrom (Segerstrale 1978) and G. lawrencianus (personal observations).

In the field the young may be feeding on epiphytic diatoms which were washed from the algae before it was fed to the lab cultures. The water used to wash the Pilayella often turned brown with epiphytic diatoms. Jansson (1967) found that newly hatched Idotea baltica, a

marine isopod, required diatoms for survival but G. oceanicus did not. G. pulex and the freshwater isopod, Asellus aquaticus (L.) both prefer diatoms to other types of algae (Moore 1975). Moore suggested that this was due to the relative weakness of the diatom's cell wall. This is further evidence for the relative importance of mechanical mastication to break down cell walls rather than digestion by cellulase. The silica frustule of diatoms is indigestable but brittle. Diatoms also have a higher energy content than other types of algae. Paine and Vadas (1969) found that Nitzschia paradoxa, a common benthic diatom, had an ash free dry weight energy content of 22,886.5 J/g. This is equivalent to TetraMin or Mytilus. The relative abundance of diatoms throughout the season could account for the reduction in size at maturation as the season progressed (Table 3). Although Pilayella blooms in the spring it does not become covered with epiphytic diatoms until well into summer (MacFarlane and Bell 1933). Changes in algal quality may also occur seasonally, thus changing the energy uptake of the animals.

Wenner et al. (1974) suggested that the comparative size at the onset of sexual maturation in Crustacea could serve to compare growth rates of animals in different populations. They suspected that food supply was a primary factor in the growth rate and/or egg production in natural populations. They included temperature in their model. This study found that temperature did affect growth rate and fecundity but not size at maturation. What appeared to be the primary factor affecting size at maturation and egg production in this study was food quality. In lab cultures, diets producing high growth rates had a small size at maturation and vice versa (Figure 10). This could explain differences in

size at maturation in field populations. The smaller maturation size of field populations in Witless Bay Pond during late summer could be due to a diatom bloom as mentioned previously. Steele and Steele (1970) found that populations of G. lawrencianus at St. Andrew's, New Brunswick matured at 4.4 mm as compared to 5.2 mm at Holyrood, Newfoundland. The above model would suggest that a higher quality food was present at St. Andrew's. Ectocarpus sp. is abundant in warmer water estuaries and this appears to be a better food than either Pilayella or Dictyosiphon (MacKay and Vassallo 1977). Wenner et al. also hypothesized that food supply would affect egg production. The animals fed Dictyosiphon produced a smaller number of larger eggs than those fed Mytilus. Steele and Steele (1970) found that populations of G. lawrencianus at St. Andrew's produced a larger number of eggs than Holyrood populations. The quality of the diet does affect maturation and fecundity in lab populations but further research is necessary to actually demonstrate this in the field. Vadas (1977) found that sea urchins had higher growth rates and earlier and higher reproduction when fed their preferred algae. This would suggest that Wenner et al.'s hypothesis may have wider applications than just crustaceans.

It is possible that another mechanism may be affecting maturation size in field populations. De March (1978) found that temperatures during ova production in the ovary and early embryonic development produced the same seasonal changes in size at maturation in Hyalella azteca (Saussure) as was determined in field populations of G. lawrencianus. Low temperatures produced a relatively large size at maturation and high temperatures a smaller size. Further research is necessary to

determine if this mechanism is operative in gammarids. It was not a factor in comparison of animals fed Dictyosiphon and Mytilus since the young used in these two cultures were collected together and randomly mixed before the experiment began.

Temperature plays an important part in the biology of all poikilothermic organisms and its effect on the growth and survival of gammarid amphipods have been documented (Kinne 1959; Nilsson 1977). In this study growth was found to be directly related to temperature (Figure 9). There appeared to be less growth at 10° C than at 12° and 15° C. Similarly there was no difference detectable in the age at maturity at 12° and 15° C while there was a large difference between 10° and 12° C. This could be due to the lack of acclimation to temperature as described by Steele and Steele (1973) for the duration of embryonic development in gammarids. At the upper end of the temperature scale, temperature differences have relatively little effect on temperature dependent processes, while at low temperatures, small changes can have large effects. The coldroom which held the 10° C cultures had less fluctuation in temperature than the Hot Pack Incubators where the 12° and 15° C cultures were kept and this could have had some effect on the results. Also the Hot Pack Incubators were often above the desired temperature because of high temperatures in the room where the incubators were kept.

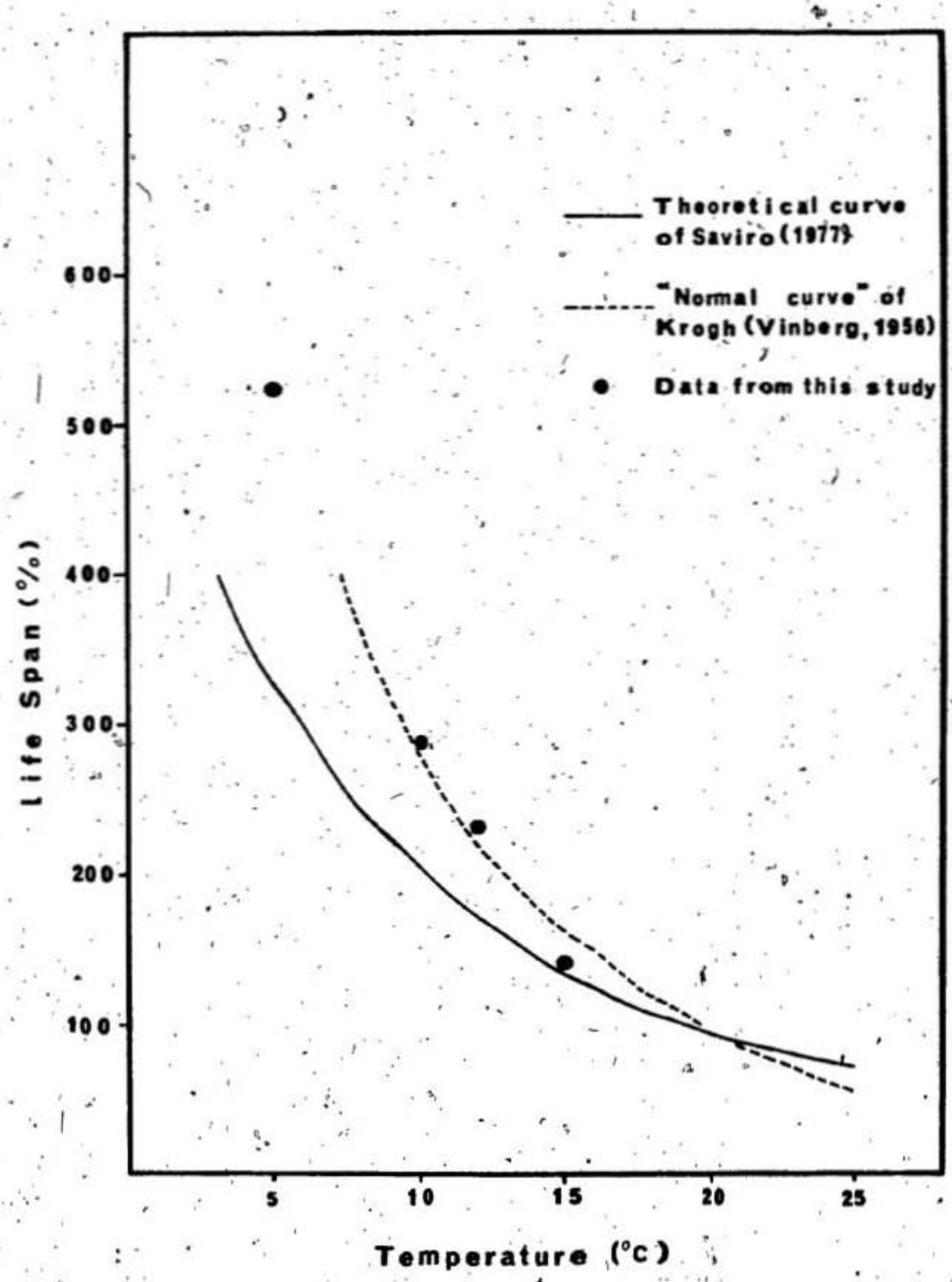
Survival was inversely related to temperature (Figure 7). Sarviro (1977) summarized some of the literature on the metabolic rate in Crustacea and related it to life span. He developed a curve relating life span to temperature by setting the life span at 20° C as 100% and comparing the life span at various temperatures above and below this set point.

After determining curves for various species of Crustacea, he produced a hypothetical curve for the temperature dependence of life span. He also modified the "normal curve of Krogh" (Vinberg 1956) to fit the graph. Sarviro's theoretical curve, the modified "normal curve of Krogh" and comparable points extracted from this data are presented in Figure 17. Sarviro's line was slightly below the one from this study but Krogh's curve was a good fit. Temperature did not significantly influence size at maturation (Table 8)in the range of the temperatures tested. Temperature did appear to have a significant effect on fecundity (Figure 11) but the level of significance was not high. Moore (1975) found that the digestive efficiency of Gammarus varied with temperature. The animals at higher temperatures could be assimilating a larger amount of energy from the same food and increasing their fecundity.

Seasonality has selected for amphipods which maximize reproduction when conditions are optimum. Different mechanisms have evolved to accomplish this in various genera. For example in Gammarus (Steele 1967; Steele et al. 1977) and Hyalella (DeMarch 1977) the timing of the release of the young in the spring is aided by a resting stage. In Ampelisca the same result is produced by postponing the hatching of the fully developed embryos for approximately two months (Kanneworff 1965). Different mechanisms could also be controlling size at maturation of Gammarus and Hyalella. Another possibility is that both mechanisms are influencing the reproductive biology of the animals.

The possible changes in the adaptive strategies of field populations of G. lawrencianus to variations in the food quality in the habitat may be interpreted in terms of r- & k-selection as expounded by MacArthur

Figure 17. Temperature dependence of life span of certain poikilothermic animals after Sarviro (1977), with comparable points extracted from this study.


Theoretical curve of Saviro (1977)
"Normal curve" of Krogh (Vinberg, 1956)
Data from this study
600
500
400
300
200
100
life Span (%)
5
10
15
20
25
Temperature (°C)

and Wilson (1967). When food quality is low, survival is increased at the expense of growth and reproduction. The population becomes k-selected and delays reproduction until the animals reach a larger size when fecundity would be higher. More energy is channelled into each young. When food quality improves the population becomes more r-selected with shorter individual life span, earlier maturation and increased reproductive capacity, investing less energy into each young. G. lawrencianus appeared to shift strategies with different diets. Those fed Mytilus were more r-selected. They reproduced at a smaller size, had a shorter life expectancy and higher fecundity. Those fed Dictyosiphon were more k-selected. They reproduced at a larger size, had a longer life expectancy and lower fecundity but produced larger eggs than did the animals fed Mytilus.

SUMMARY

Gammarus lawrencianus populations of Witless Bay Pond and North Arm Holyrood had a dual life history consisting of a winter cohort of large adults and a smaller, faster maturing summer cohort. A third, fall cohort may be present but could not be conclusively identified because of continuous recruitment. At both sampling areas adult males were found to be on the average larger than females, probably because of differential growth and mortality. The mean size of the North Arm Holyrood populations of *G. lawrencianus* were smaller than at Witless Bay Pond. Females predominated in both populations but as the summer cohort matured the sex ratio moved close to 1, suggesting that factors other than genetic ones are responsible.

In Witless Bay Pond numbers increased throughout the summer reaching a peak in September. The distribution did not appear to be random but clumped with its center shifting from more saline to brackish water during the summer, suggesting a migration . In North Arm Holyrood the population appeared to decline, being replaced by *G. oceanicus*. In Witless Bay Pond young were not found in benthic samples but tended to stay in *Pilayella* until maturation. The 50% maturation size at Witless Bay Pond varied from 5.2mm on August 2 to 4.4mm on August 31. The decrease in maturation size is probably due to a change in the quality of the diet.

In lab cultures survival and age at maturation were inversely related and growth directly related to temperature. Temperature had no significant effect on maturation size in the range of the temperatures tested.

Diet had a statistically significant effect on all the parameters tested. Survival was best on a diet of the fine algae *Dictyosiphon* and

Pilayella, intermediate on Mytilus, Enteromorpha and TetraMin and lowest without food. Growth however, was fastest on Mytilus or TetraMin when compared to an algal diet. Similarly size at maturity was least and within the range of field observations when fed Mytilus or TetraMin. Algal diets produced a much larger maturation size. This would suggest that fine textured algae improves the survival of newly released G. lawrencianus but animal material is necessary for normal growth and development.

Temperature had an influence on fecundity but the significance was low. Diet had a highly significant effect on fecundity. Animals fed Dictyosiphon produced a smaller number of larger eggs than Mytilus. The brood volumes produced by these two diets were somewhat similar despite the large differences in egg number and size. Possibly this mirrors reproductive strategies which the animals may follow depending on the quality of the diet.

Adult G. lawrencianus preferred Mytilus in selectivity experiments. The food preferences of immature animals could not be tested but they were found to prefer being in association with fine algae as opposed to coarse algae or animal material. This could act as an isolation factor separating the highly cannibalistic adults from the young.

A high correlation was found between the energy content of the diet and the resulting maturation size of G. lawrencianus. Although the total energy content of the diet is important other variables such as texture of the food probably influence the energy content that is actually available to the animal.

No correlation was found between the amino acid content of the diet and the survival, growth and fecundity of G. lawrencianus, except for

TetraMin . The highly deficient amino acid content of TetraMin probably reduced survival but had no effect on growth and fecundity.

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APPENDICES

Appendix 1a. Temperatures and salinities at Witless Bay Pond. S - surface; SD - sampling depth; * - no sample collected.

TEMPERATURE (°C)

DATE	SITE 1		SITE 2		SITE 3		AVERAGE	
	S	SD	S	SD	S	SD	S	SD
JUNE 18	17.0	17.0	16.5	14.0	16.0	13.5	16.5	14.8
JUNE 27	11.5	11.0	11.3	11.0	11.0	10.5	11.3	10.8
JULY 4	11.8	9.5	10.3	9.5	10.0	9.5	10.7	9.5
JULY 9	13.3	13.3	13.0	12.5	*	*	13.2	12.9
JULY 14	19.0	18.8	18.0	17.5	17.0	14.0	18.0	16.8
JULY 19	18.5	18.5	16.0	15.5	14.5	14.0	16.3	16.0
AUGUST 2	21.2	21.2	21.1	21.1	21.2	21.2	21.2	21.2
AUGUST 12	14.8	13.0	13.8	12.5	13.6	12.6	14.1	12.7
AUGUST 31	19.8	19.8	19.1	17.0	19.0	18.0	19.3	18.3
SEPTEMBER 25	12.9	12.9	12.8	12.5	12.5	11.8	12.7	12.4
NOVEMBER 1	7.5	7.5	7.8	7.8	7.9	7.8	7.7	7.7
AVERAGE	15.2	14.8	14.5	13.7	14.3	13.3	14.6	13.9

Appendix 1a continued

DATE	SALINITY (‰)							
	SITE 1		SITE 2		SITE 3		AVERAGE	
	S	SD	S	SD	S	SD	S	SD
JUNE 18	*	*	5.1	9.4	15.0	10.1	10.1	9.8
JUNE 27	10.8	17.2	20.4	19.2	14.6	18.9	15.3	18.4
JULY 4	17.9	21.8	21.0	25.3	24.8	24.7	21.2	23.9
JULY 9	1.4	0.0	2.8	4.9	*	*	2.1	2.4
JULY 14	2.0	4.9	4.5	9.5	10.7	27.0	5.7	13.8
JULY 19	*	*	*	*	*	*	*	*
AUGUST 2	*	*	*	*	*	*	*	*
AUGUST 12	2.2	15.7	5.0	16.1	8.5	16.0	5.2	15.9
AUGUST 31	0.3	0.5	7.2	16.1	6.0	9.5	4.5	8.7
SEPTEMBER 25	*	*	*	*	*	*	*	*
NOVEMBER 1	1.7	7.3	1.8	7.5	2.1	7.6	1.9	7.5
AVERAGE	5.2	9.6	8.5	13.5	11.7	16.3	8.2	12.6

Appendix 1b. Temperatures and salinities at North Arm Holyrood. S - surface; SD - sampling depth; * - no sample collected.

	TEMPERATURE (°C)									
DATE	SITE 1		SITE 2		SITE 3		SITE 4		AVERAGE	
	S	SD	S	SD	S	SD	S	SD	S	SD
APRIL 1	*	*	5.1	*	*	*	4.0	0.5	4.6	0.5
APRIL 15	5.0	*	*	*	*	*	5.8	*	5.4	*
APRIL 24	9.9	*	*	*	*	*	8.0	*	9.0	*
MAY 12	*	4.0	8.0	*	*	4.0	*	*	8.0	4.0
MAY 21	12.5	*	12.0	*	9.0	*	11.4	*	11.2	*
MAY 31	*	10.0	18.5	*	14.5	6.0	15.0	7.0	16.0	7.7
JUNE 9	8.9	7.5	13.0	12.7	10.0	7.0	9.5	7.0	10.4	8.6
JUNE 19	14.7	11.0	17.0	14.0	13.2	10.1	14.7	10.0	14.9	11.3
JUNE 25	15.5	11.0	14.8	13.0	13.5	10.8	12.1	10.5	14.0	11.3
JULY 2	12.8	*	17.0	12.0	14.5	8.5	*	*	14.8	10.2
JULY 23	13.8	10.5	15.5	11.0	11.0	10.5	11.0	10.9	12.8	10.7
JULY 30	15.0	15.0	21.0	17.0	13.5	13.0	9.8	9.5	14.8	13.6
AUGUST 5	16.0	10.2	21.0	14.0	14.5	10.0	16.0	10.0	16.9	11.1
AUGUST 14	16.0	12.8	24.2	21.0	15.0	14.5	13.5	12.0	17.2	15.1
AUGUST 19	16.8	11.5	20.8	20.0	15.5	12.5	18.0	12.0	17.8	14.0
AUGUST 28	14.8	13.0	17.8	17.8	15.0	13.0	13.5	12.0	15.3	14.0

Appendix 1b continued.

DATE	SITE 1		SITE 2		SITE 3		SITE 4		AVERAGE	
	S	SD	S	SD	S	SD	S	SD	S	SD
SEPTEMBER 2	15.5	11.0	19.5	17.0	12.5	12.0	15.0	11.0	15.6	12.8
SEPTEMBER 18	13.9	13.0	14.8	14.8	13.5	13.0	14.3	13.5	14.1	13.6
SEPTEMBER 24	10.2	10.2	10.2	10.1	9.8	9.3	9.3	8.8	9.9	9.6
AVERAGE	13.2	10.8	15.9	15.0	13.0	10.3	11.8	9.6	12.8	10.6
					SALINITY (‰)					
APRIL 1	*	*	0.2	*	*	*	7.0	22.5	3.6	22.5
APRIL 15	3.9	*	*	*	*	*	*	*	3.9	*
APRIL 24	5.5	*	*	*	*	*	19.9	*	12.7	*
MAY 12	*	25.2	7.0	*	*	28.9	*	*	7.0	27.1
MAY 21	3.3	*	5.8	*	7.8	*	3.3	*	5.1	*
MAY 31	*	33.0	0.0	*	*	32.4	*	31.2	0.0	32.2
JUNE 9	21.9	31.0	1.0	*	16.4	30.0	20.9	29.4	15.1	30.1
JUNE 19	12.8	27.5	6.0	17.3	16.2	27.9	18.0	27.3	13.2	25.0
JUNE 25	13.5	29.9	10.6	28.6	21.6	28.8	14.7	30.0	15.1	29.3
JULY 2	24.1	*	8.9	28.0	14.7	31.0	*	*	15.9	29.5
JULY 23	*	*	*	*	*	30.0	21.7	32.7	21.7	31.4
JULY 30	*	*	*	*	*	*	*	*	*	*
AUGUST 5	*	*	*	*	*	*	*	*	*	*
AUGUST 14	20.8	28.9	1.2	11.5	27.1	27.7	23.8	28.3	18.2	24.1

Appendix 1b continued.

DATE	SITE 1		SITE 2		SITE 3		SITE 4		AVERAGE	
	S	SD	S	SD	S	SD	S	SD	S	SD
AUGUST 19	10.7	29.8	0.5	2.5	18.5	29.6	9.5	30.2	9.8	23.0
AUGUST 28	*	*	2.3	20.8	*	*	*	*	2.3	20.8
SEPTEMBER 2	11.8	28.9	*	*	26.1	25.3	15.7	28.3	17.9	27.5
SEPTEMBER 18	*	*	*	*	*	*	*	*	*	*
SEPTEMBER 24	0.8	0.8	0.1	0.1	2.7	2.4	1.8	1.8	1.4	1.3
AVERAGE	11.7	26.1	3.6	15.5	16.8	26.7	14.2	26.2	10.6	24.9

Appendix 2a. Total number of Gammarus lawrencianus collected per month in various length classes at Witless Bay Pond. 1 - in air-lift samples; 2 - in Pilayella samples. (t - includes 2 samples from site 3; * - 5576 of total collected at site 4).

BODY	1						2		
LENGTH (mm)	JUNE 18	JULY 9	AUG. 2	AUG. 31	SEPT. 9	NOV. 1	JUNE 18-23	JULY 9-19	AUG. 2
1.0-1.9							813	1085	830
2.0-2.9			186	29	41	52	3	112	173
3.0-3.9			240	72	52	103		51	31
4.0-4.9			518	191	76	158		3	10
5.0-5.9	1	2	373	91	169	110			
6.0-6.9	20	7	160	44	89	17			
7.0-7.9	104	66	49	108	33	7			
8.0-8.9	95	96	4	20	28				
9.0-9.9	41	35	2						
10.0-10.9	46	38	19						
11.0-11.9	15	8	23						
12.0-12.9	4	1	2						
TOTAL SEXED	326	253	1576	555	488	447	816	1251	1044
TOTAL COLLECTED	326	253	3633	916	5631*	447	11,348	18,406	5352
TOTAL/m^2	10,860	10,120	121,100	36640	281560	12780			
TOTAL/mg dry weight of Pilayella							14.2	13.9	9.6
NUMBER OF SAMPLES	6	5	6	5	4	7[t]	8	12	6

Appendix 2b. Gammarus lawrencianus: number of males in various length classes at Witless Bay Pond.

BODY LENGTH (mm)	JUNE 18	JULY 9	AUG. 2	AUG 31	SEPT. 25	NOV. 1
3.0-3.0			55	2	1	
4.0-4.9			171	4	10	108
5.0-5.9		2	139	17	27	87
6.0-6.9		1	122	31	20	11
7.0-7.9	1	0	49	93	28	3
8.0-8.9	12	3	4	16	24	
9.0-9.9	28	16	2			
10.0-10.9	46	38	19			
11.0-11.9	15	8	23			
12.0-12.9	4	1	2			
TOTAL SEXED	106	69	586	163	110	209
TOTAL/m^2	5300	2760	45,120	10,760	13,480	5980

Appendix 2c. Gammarus lawrencianus: number of females without setae on oostegites in various length classes at Witless Bay Pond.

BODY LENGTH (mm)	JUNE 18	JULY 9	AUG. 2	AUG. 31	SEPT. 25	NOV. 1
3.0-3.9			90	5	2	
4.0-4.9			260	16	8	9
5.0-5.9			75	7	37	19
6.0-6.9			3		10	5
7.0-7.9						4
8.0-8.9						
TOTAL SEXED	0	0	428	28	57	37
TOTAL/m^2	0	0	32,960	1840	32,880	1060

Appendix 2d. Gammarus lawrencianus: number of females with setae on oostegites in various length classes at Witless Bay Pond.

BODY LENGTH (mm)	JUNE 18	JULY 9	AUG. 2	AUG. 31	SEPT. 25	NOV. 1
3.0-3.9				58		
4.0-4.9			75	163	18	
5.0-5.9	1		159	67	95	
6.0-6.9	20	6	35	13	59	1
7.0-7.9	103	66		15	5	
8.0-8.9	83	93		4	4	
9.0-9.9	13	19				
TOTAL SEXED	220	184	269	320	181	1
TOTAL/m^2	1100	7360	20,720	21,120	104,440	20

Appendix 2e. *Gammarus lawrencianus*: number of unsexables in various length classes at Witless Bay Pond. 1 - in air-lift samples; 2 - in *Pilayella* samples.

BODY LENGTH (mm)	JUNE 18	JULY 9	AUG. 2	AUG. 31	SEPT. 25	NOV. 1	JUNE 18-23	JULY 9-19	AUG. 2
1.0-1.9							813	1085	830
2.0-2.9			186	29	41	52	3	112	173
3.0-3.9			95	7	49	103		51	31
4.0-4.9			12	8	40	41		3	10
5.0-5.9					10	4			
TOTAL SEXED	0	0	293	44	140	200	816	1251	1044
NUMBER/m^2			22,460	2900	80,780	5720			
NUMBER/mg dry weight *Pilayella*							14.2	13.9	9.6

Appendix 3a. Total number of Gammarus lawrencianus collected per month in various length classes at North Arm Holyrood. (* - only site 4 sampled; t - all sites sampled).

BODY LENGTH (mm)	MARCH 18-29	APRIL 1-27	MAY 7-21	JUNE 25	JULY 23	AUG. 19	SEPT. 24
2.0-2.9					1		1
3.0-3.9	1	4			6		6
4.0-4.9	12	43	2		2	6	21
5.0-5.9	25	98	39	1	6	2	7
6.0-6.9	30	65	106	10	34	10	
7.0-7.9	14	39	80	9	32	6	
8.0-8.9	4	24	61	10	6	0	
9.0-9.9		2	34	5	11	1	
TOTAL COLLECTED	86	275	322	35	98	25	35
NUMBER/SAMPLE	28.7	55.0	20.1	3.9	10.9	2.8	3.9
NUMBER OF SAMPLES	3*	5*	16t	9t	9t	9t	9t

Appendix 3b. Gammarus lawrencianus: number of males in various length classes at North Arm Holyrood. (* - only site 4 sampled; t - all sites sampled).

BODY LENGTH (mm)	MARCH 18-29	APRIL 1-27	MAY 7-21	JUNE 25	JULY 23	AUG. 19	SEPT. 24
4.0-4.9	2	1				1	3
5.0-5.9	3	4	2		1	1	6
6.0-6.9	12	17	6			1	
7.0-7.9	14	28	17	2		0	
8.0-8.9	4	24	80	10	4	0	
9.0-9.9		2	34	5	11	1	
TOTAL COLLECTED	35	76	119	17	16	4	9
NUMBER/SAMPLE	11.7^{*}	15.2^{*}	7.4^{t}	1.9^{t}	1.8^{t}	0.4^{t}	1.0^{t}

Appendix 3c. Gammarus lawrencianus: number of females in various length classes at North Arm Holyrood. 1 - with setae on oostegites; 2 - without setae on oostegites. (* - only site 4 sampled; t - all sites sampled).

BODY LENGTH (mm)	1 MARCH 18-29	APRIL 1-27	MAY 7-21	JUNE 25	JULY 23	AUG. 19	SEPT. 24	2 JULY 23	AUG. 19
3.0-3.9	1	4						4	
4.0-4.9	10	42	2				4	2	1
5.0-5.9	22	94	37	1	5	1			
6.0-6.9	18	48	100	10	34	8			1
7.0-7.9		11	63	7	32	6			
8.0-8.9			1		2				
TOTAL COLLECTED	51	199	203	18	73	15	4	6	2
NUMBER/SAMPLE	17.0*	39.8*	12.7t	2.0t	8.1t	1.7t	0.4t	1.2t	0.1t

Appendix 3d. Gammarus lawrencianus: number of unsexables in various length classes at North Arm Holyrood.

BODY LENGTH (mm)	JULY 23	AUG. 19	SEPT. 24
2.0-2.9	1		1
3.0-3.9	2		6
4.0-4.9		4	14
5.0-5.9			1
TOTAL COLLECTED	3	4	22
NUMBER/SAMPLE	0.3	0.4	2.4

Appendix 4a. Number of *Gammarus lawrencianus* collected in air-lift samples at the various sampling sites at Witless Bay Pond. (* - no samples collected).

		JUNE 18	JULY 9	AUG. 2	AUG. 31	SEPT. 25	NOV. 1
SITE 1	TOTAL NUMBER	188	160	2816	161	*	4
	NUMBER OF SAMPLES	2	2	3	2	*	1
	NUMBER/SAMPLE	69.0	80.0	938.7	80.5	*	4.0
SITE 2	TOTAL NUMBER	183	4	817	49	55	252
	NUMBER OF SAMPLES	2	1	3	2	2	2
	NUMBER/SAMPLE	91.5	4.0	272.3	24.5	27.5	126.0
SITE 4	TOTAL NUMBER	5	89	*	706	5576	3
	NUMBER OF SAMPLES	2	2	*	1	2	2
	NUMBER/SAMPLE	2.5	44.5	*	706.0	2788.0	1.5
TOTAL	TOTAL NUMBER	326	253	3633	916	5631	259
	NUMBER OF SAMPLES	6	5	6	5	4	5
	NUMBER/SAMPLE	54.3	50.6	605.5	183.2	1407.8	51.8

Appendix 4b. Number of gammarid amphipods (mostly Gammarus oceanicus) collected in cage samplers at the various sampling sites at North Arm Holyrood. Site 2 is not included because of problems with the sampling procedure. (* – no samples collected).

SITE 1		MARCH 18-29	APRIL 1-27	MAY 7-21	JUNE 25	JULY 23	AUG. 19	SEPT. 24
	TOTAL NUMBER	*	*	570	1440	2108	3211	646
	NUMBER OF SAMPLES	*	*	4	3	3	3	3
	NUMBER/SAMPLE	*	*	142.5	480.0	702.7	1070.3	215.3
SITE 3								
	TOTAL NUMBER	*	*	726	1709	1285	998	1131
	NUMBER OF SAMPLES	*	*	4	3	3	3	3
	NUMBER/SAMPLE	*	*	181.5	569.7	428.3	332.7	377.0
SITE 4								
	TOTAL NUMBER	166	436	1369	1599	978	513	130
	NUMBER OF SAMPLES	3	5	6	3	3	3	2
	NUMBER/SAMPLE	55.3	87.2	228.2	533.0	326.0	171.0	65.0
TOTAL								
	TOTAL NUMBER	166	436	2665	4748	4371	4722	1907
	NUMBER OF SAMPLES	3	5	14	9	9	9	8
	NUMBER/SAMPLE	55.3	87.2	190.4	527.6	485.7	524.7	238.4

Appendix 5. Number of Gammarus lawrencianus and G. oceanicus collected at sampling site 4, North Arm Holyrood.

MONTH	G. oceanicus/SAMPLE	G. lawrencianus/SAMPLE
MAY	142.0	86.2
JUNE	527.0	6.0
JULY	318.0	8.0
AUGUST	167.0	4.0
SEPTEMBER	45.5	19.5

Appendix 6a. Survival of newly released Gammarus lawrencianus at 5° C. TetraMin was used as food.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	210	17	91.9	88.5
20	195	25	87.2	86.9
30	180	32	82.2	84.8
40	165	33	80.0	82.9
50	150	32	78.7	80.8
60	135	31	77.0	78.2
70	105	25	76.2	75.8
80	90	20	77.8	73.2
90	75	18	76.0	70.6
100	60	20	66.7	67.4
110	45	16	64.4	64.4

Appendix 6b. Survival of newly released Gammarus lawrencianus at 10° C. TetraMin was used as food.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	225	20	91.1	87.1
20	210	33	84.3	83.6
30	195	52	73.3	79.7
40	165	47	71.5	75.2
50	135	37	72.6	70.2
60	120	39	67.5	64.8
70	105	39	62.9	58.7
80	90	46	48.9	53.2
90	75	40	46.7	46.8
100	75	46	38.7	40.9
110	75	49	34.7	35.2
120	75	54	28.0	29.8
130	75	57	24.0	24.8
140	75	61	18.7	20.3
150	75	62	17.3	16.4
160	75	62	17.3	12.7

Appendix 6c. Survival of newly released Gammarus lawrencianus at 12° C. TetraMin was used as food.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	210	16	92.4	94.7
20	195	15	92.3	91.0
30	180	19	89.4	85.6
40	165	30	81.8	78.5
50	135	46	65.9	69.5
60	105	42	60.0	59.1
70	90	51	43.3	48.0
80	90	58	35.6	37.1
90	90	70	22.2	27.4
100	90	74	17.8	19.0
110	90	75	16.7	12.3

Appendix 6d. Survival of newly released Gammarus lawrencianus at 15° C. TetraMin was used as food.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	150	28	81.3	84.6
20	135	35	74.1	75.8
30	120	38	68.3	64.4
40	105	44	58.1	52.0
50	90	53	41.1	39.4
60	90	67	25.6	27.4
70	90	78	13.3	17.9

Appendix 7a. Survival of newly released Gammarus lawrencianus fed TetraMin. Temperature was maintained at 15° C.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	150	28	81.3	84.6
20	135	35	74.1	75.8
30	120	38	68.3	64.4
40	105	44	58.1	52.0
50	90	53	41.1	39.4
60	90	67	25.6	27.4
70	90	78	13.3	17.9

Appendix 7b. Survival of newly released Gammarus lawrencianus fed no food. Temperature was maintained at 15° C.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	150	107	28.7	28.1
20	135	122	9.6	10.4
30	120	116	3.3	2.6
40	105	105	0.0	0.5

Appendix 7c. Survival of newly released Gammarus lawrencianus fed Mytilus edulis. Temperature was maintained at 15° C.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	150	12	92.0	85.1
20	135	17	87.4	79.1
30	120	42	65.0	71.9
40	105	46	56.2	63.7
50	75	41	45.3	54.8
60	75	47	37.3	45.2
70	75	53	29.3	36.3
80	75	57	24.0	28.1
90	75	58	22.7	20.9
100	75	62	17.3	14.9
110	75	63	16.0	10.2
120	75	66	12.0	6.7

Appendix 7d. Survival of newly released Gammarus lawrencianus fed Dictyosiphon foeniculaceus. Temperature was maintained at 15° C.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	150	11	92.7	91.2
20	135	11	91.9	89.0
30	120	16	86.7	86.6
40	105	17	83.8	83.9
50	90	18	80.0	80.8
60	75	21	72.0	77.3
70	60	19	68.3	73.6
80	60	21	65.0	69.5
90	60	24	60.0	65.2
100	60	24	60.0	60.6
110	60	27	55.0	56.0
120	60	30	50.0	51.2
130	60	31	48.3	46.4
140	60	33	45.0	41.7
150	60	35	41.7	37.1
160	60	38	36.7	32.6

Appendix 7e. Survival of newly released Gammarus lawrencianus fed Pilayella littoralis. Temperature was maintained at 15° C.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	150	10	93.3	92.9
20	135	13	90.4	90.0
30	120	15	87.5	86.4
40	105	20	81.0	81.8
50	90	21	76.7	76.4
60	75	33	56.0	70.2
70	75	37	50.7	63.3
80	75	39	48.0	56.4
90	75	40	46.7	48.8
100	75	42	44.0	41.3
110	75	43	42.7	34.1
120	75	50	33.3	27.4
130	75	57	24.0	21.8

Appendix 7f. Survival of newly released Gammarus lawrencianus fed Enteromorpha intestinalis. Temperature was maintained at 15° C.

DAYS	NUMBER	NUMBER DEAD	EXPERIMENTAL % SURVIVAL	THEORETICAL % SURVIVAL
10	150	12	92.0	81.6
20	135	31	77.0	76.4
30	120	52	56.7	70.2
40	105	57	45.7	63.3
50	90	52	42.2	56.4
60	90	57	36.7	48.8
70	90	58	35.6	41.3
80	90	60	33.3	34.1
90	90	62	31.1	27.8
100	90	64	28.9	21.8
110	90	68	24.4	16.6
120	90	73	18.9	12.5

Appendix 8. Growth of newly released Gammarus lawrencianus at various temperatures. TetraMin was used as food. I - immature or unclassified.

AGE (DAYS)	MEAN LENGTH (MM) FEMALES	I	MALES	NUMBER FEMALES	I	MALES	95% CONFIDENCE LIMITS FEMALES	I	MALES
5° C									
0		1.2			30			0.03	
10		1.2			13			0.06	
20		1.3			13			0.06	
30		1.4			14			0.07	
40		1.4			10			0.07	
50		1.6			11			0.15	
60		2.1			11			0.13	
70		2.4			10			0.15	
10° C									
0		1.2			12			0.03	
10		1.4			12			0.05	
20		1.5			13			0.07	
30		1.7			9			0.13	
40		2.0			8			0.21	
50		2.5			14			0.20	
60		3.1			10			0.31	
70		4.4			11			0.64	
80		4.4			7			0.58	
90	5.5		7.5	4		5	0.19		0.48
100	6.1		8.5	4		6	0.58		0.72

Appendix 8 continued.

AGE (DAYS)	MEAN LENGTH (mm) FEMALES	I	MALES	NUMBER FEMALES	I	MALES	95% CONFIDENCE LIMITS FEMALES	I	MALES
110	6.5		8.7	5		6	0.28		0.53
120	6.6		9.2	4		6	0.50		0.54
130	6.9		9.9	4		5	0.20		1.15
140			10.4			5			1.06
				12° C					
0	1.2			12			0.03		
10	1.5			11			0.06		
20	2.6			12			0.12		
30	3.2			13			0.14		
40	4.5			15			0.23		
50	5.5			6			0.74		
60	6.2			7			0.94		
70	7.4			30			0.51		
80	8.3			24			0.61		
90	8.9			16			0.80		
100	9.1			15			0.70		
				15° C					
0	1.2			30			0.02		
10	1.6			12			0.06		
20	2.7			12			0.23		
30	4.6			8			0.32		
40	5.1			15			0.50		
50		6.7			25				0.42

Appendix 8 continued

AGE (DAYS)	MEAN LENGTH (mm)		NUMBER		95% CONFIDENCE LIMITS	
	FEMALES	MALES	FEMALES	MALES	FEMALES	MALES
60		7.6		21		0.75
70		8.8		10		1.60

Appendix 9. Growth of newly released Gammarus lawrencianus fed various diets. Temperature was maintained at 15° C. I - immature or unclassified.

AGE (DAYS)	MEAN LENGTH (mm) FEMALES	I	MALES	NUMBER FEMALES	I	MALES	95% CONFIDENCE LIMITS FEMALES	I	MALES
TETRAMIN									
0	1.2			30			0.02		
10	1.6			12			0.06		
20	2.7			12			0.23		
30	4.6			8			0.32		
40	5.1			15			0.50		
50			6.7			25			0.42
60			7.6			21			0.75
70			8.8			10			1.60
Mytilus									
0	1.2			14			0.06		
10	2.0			14			0.12		
20	3.4			11			0.26		
30	4.7			11			0.31		
40	5.3		6.3	11		9	0.16		0.24
50	5.6		7.0	10		10	0.25		0.33
60	6.4		7.7	8		20	0.29		0.59
70	7.0		8.7	6		15	0.39		0.56
80	7.1		9.3	5		13	0.40		0.70
90	7.3		9.3	5		12	0.57		0.77
100	7.4		9.8	4		9	0.74		0.60
110	7.9		10.3	4		10	0.89		0.84

Appendix 9 continued.

AGE (DAYS)	MEAN LENGTH (mm) FEMALES	I MALES	NUMBER FEMALES	I MALES	95% CONFIDENCE LIMITS FEMALES	I MALES
			Dictyosiphon			
0	1.2		15		0.04	
10	1.6		12		0.10	
20	2.3		15		0.24	
30	3.0		13		0.34	
40	4.1		13		0.45	
50	4.8		12		0.46	
60	5.3		11		0.32	
70	5.3		41		0.30	
80	5.8		36		0.30	
90	6.3		35		0.35	
100	7.0		35		0.34	
110	7.6		35		0.35	
120	8.1		31		0.41	
130	8.4		29		0.43	
140	8.9		27		0.51	
150	9.5		26		0.58	
160	9.5		18		0.77	
			Pilayella			
0	1.2		14		0.04	
10	1.7		14		0.07	
20	2.1		14		0.08	
30	2.4		14		0.11	

Appendix 9 continued.

AGE (DAYS)	MEAN LENGTH (mm) FEMALES	I	MALES	NUMBER FEMALES	I	MALES	95% CONFIDENCE LIMITS FEMALES	I	MALES
40		3.1			14			0.17	
50		3.7			13			0.17	
60		3.8			43			0.21	
70		4.8			38			0.27	
80		5.8			35			0.32	
90		6.6			35			0.34	
100		7.8			33			0.44	
110		8.9			25			0.50	
120	9.2	10.2	11.7	9	25	9	0.32	0.66	0.43
130	9.7		12.0	7		9	0.27		0.50
				Enteromorpha					
0		1.2			14			0.03	
10		1.5			15			0.07	
20		1.6			12			0.20	
30		3.1			8			0.39	
40		3.5			9			0.70	
50		4.6			38			0.27	
60		5.6			33			0.32	
70		6.1			32			0.34	
80		6.4			29			0.33	
90		6.5			28			0.38	
100		6.5			26			0.36	

Appendix 9 continued.

AGE (DAYS)	MEAN LENGTH (mm) FEMALES	I	MALES	NUMBER FEMALES	I	MALES	95% CONFIDENCE LIMITS FEMALES	I	MALES
110	6.8			23			0.45		
120	6.9			17			0.57		

Appendix 10. Fecundity of female Gammarus lawrencianus at various temperatures and diets.

TETRAMIN 10° C			TETRAMIN 15° C		
LENGTH (mm)	EGG NUMBER	FREQUENCY	LENGTH (mm)	EGG NUMBER	FREQUENCY
5.4	10	2	4.8	12	1
6.0	17	1	4.9	11	1
6.3	17	1	5.1	10	1
6.3	21	1	5.2	12	1
6.4	18	1	5.3	9	1
6.6	27	1	5.3	17	1
6.8	17	1	5.6	17	1
6.9	17	1	5.7	17	1
7.4	28	1	5.9	12	1
7.5	27	1	6.0	20	1
7.6	26	1	6.0	28	1
7.6	35	1	6.1	17	1
8.3	36	1	6.1	26	1
8.3	43	1	6.3	20	1
			6.6	20	1
			7.2	28	1
Mytilus 15° C			Dictyosiphon 15° C		
5.2	10	1	7.1	20	1
5.2	12	1	7.1	10	1
5.3	10	1	7.8	14	1
5.3	13	1	8.1	21	1
5.4	10	3	8.1	23	1

Appendix 10 continued.

LENGTH (mm)	EGG NUMBER	FREQUENCY	LENGTH (mm)	EGG NUMBER	FREQUENCY
5.6	16	1	8.3	30	1
5.7	13	1	8.6	20	1
5.7	17	1	8.7	31	1
5.7	18	1	8.8	25	1
6.1	20	1	9.0	39	1
6.2	23	1	9.0	44	1
6.3	13	1	9.0	28	1
6.4	15	1	9.2	40	1
6.4	17	1	9.6	25	1
6.5	22	1			
6.6	23	1			
6.7	19	1			
6.7	20	1			
6.7	21	1			
6.7	22	1			
6.7	26	1			
6.8	24	1			
6.8	29	1			
7.0	24	1			
7.0	27	1			
7.1	33	1			
7.4	28	1			
7.5	28	1			

Appendix 10 continued.

LENGTH (mm)	EGG NUMBER	FREQUENCY
7.5	31	1
7.6	36	1
7.7	27	1
8.5	34	1

Appendix 11. Volume of brood per volume of female *Gammarus lawrencianus* fed *Mytilus* and *Dictyosiphon*.

FEMALES		EGGS		NUMBER
MEAN LENGTH (mm)	MEAN VOLUME L^3 (mm^3)	MEAN NUMBER	MEAN VOLUME (mm^3)	
		Mytilus		
5.3	149.7	10.7	0.2359	8
5.7	181.3	16.0	0.3525	5
6.3	252.4	18.3	0.4038	6
6.8	310.3	23.5	0.5177	10
7.4	401.9	30.0	0.6609	4
7.6	447.7	31.5	0.6939	2
8.5	614.1	34.0	0.7490	1
		Dictyosiphon		
7.1	357.9	15.0	0.4688	2
7.8	474.6	14.0	0.4375	1
8.2	551.4	24.7	0.7719	3
8.7	658.5	25.3	0.7906	3
9.1	741.2	37.8	1.1797	4
9.6	884.7	25.0	0.7813	1

Appendix 12. The food selectivity of mature male Gammarus lawrencianus. The letters designate the order of preference and the numbers, the seconds spent feeding at each station.

TRIAL #	DICTYO. 1	DICTYO. 2	TISSUE 1	TISSUE 2	MUSSEL 1	MUSSEL 2	PIL. 1	PIL. 2	ENTERO. 1	ENTERO. 2
1	B-5	A-50			C-245					
2					C-170		B-35			A-95
3									A-300	
4						B-180			A-120	
5					A-300					
6						A-300				
7	C-15	A-15			D-250					B-20
8						A-300				
9						A-300				
10						A-300				
11	A-95	B-70				C-135				
12						B-110		A-190		
13					A-300					
14							A-300			
15						A-300				
TOTAL T	115	135	0	0	1265	1925	335	190	420	115
TOTAL N	3	3	0	0	5	8	2	1	2	2

Appendix 13. The food selectivity of mature female Gammarus lawrencianus. The letters designate the order of preference and the numbers, the seconds spent feeding at each station.

TRIAL #	DICTYO. 1	DICTYO. 2	TISSUE 1	TISSUE 2	MUSSEL 1	MUSSEL 2	PIL. 1	PIL. 2	ENTERO. 1	ENTERO. 2
1						B-290			A-10	
2	A-25					B-275				
3		A-5			B-295					
4					A-300					
5					A-300					
6	A-5				C-205		B-90			
7						A-20 B-280				
8					A-300					
9							A-300			
10					D-240	B-10	C-25	A-25		
11	A-300									
12	B-45				D-210		C-25	A-20		
13						A-300				
14						C-40	A-250	B-10		
15						A-300				
16	B-275		A-25							
TOTAL T	650	5	25	0	1850	1515	690	55	10	0
N	5	1	1	0	7	8	5	3	1	0

Appendix 14. The food selectivity of young Gammarus lawrencianus. The numbers represent the young found in each food item.

FOOD	TRIAL #								Total
	1	2	3	4	5	6	7	8	
Dictyosiphon 1	0	1	4	8	1	8	3	0	25
Dictyosiphon 2	1	0	1	7	6	20	0	2	37
NOTHING 1	0	7	0	0	3	0	8	0	18
NOTHING 2	0	2	0	0	5	0	3	5	15
MUSSEL 1	0	2	0	0	0	0	0	2	4
MUSSEL 1	1	3	0	0	0	0	0	0	3
Pilayella 1	2	4	0	18	1	9	1	7	42
Pilayella 2	0	0	0	15	24	3	2	6	50
Enteromorpha 1	1	1	5	1	0	0	2	3	13
Enteromorpha 2	2	0	7	0	1	0	0	1	11
NON SELECTING	14	32	2	0	9	6	30	73	